Harvard Papers in Botany

Volume 28, Number 2 December 2023

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

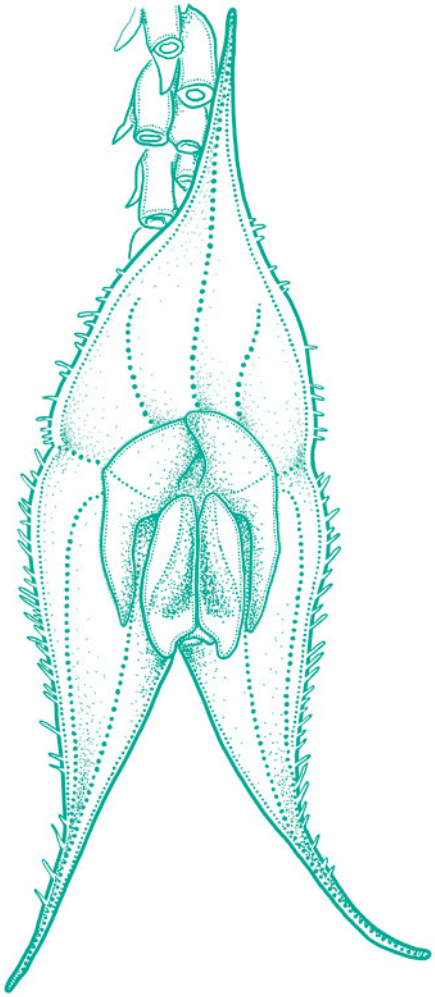
Arnold Arboretum

Botanical Museum

Farlow Herbarium

Gray Herbarium

Oakes Ames Orchid Herbarium



ISSN: 1938-2944

Harvard Papers in Botany

Initiated in 1989

Harvard Papers in Botany is a refereed journal that welcomes longer monographic and floristic accounts of plants and fungi, as well as papers concerning economic botany, systematic botany, molecular phylogenetics, the history of botany, relevant and significant bibliographies, and book reviews. Harvard Papers in Botany is open to all who wish to contribute.

Instructions for Authors

http://huh.harvard.edu/pages/manuscript-preparation

Manuscript Submission

Manuscripts, including tables and figures, should be submitted via email to papers@oeb.harvard.edu. The text should be in a major word-processing program for either Microsoft Windows or the Apple macOS, or in a compatible format. Authors should include a submission checklist available at http://huh.harvard.edu/files/herbaria/files/submission-checklist.pdf

Availability of Current and Back Issues

Harvard Papers in Botany publishes two numbers per year, in June and December. The two numbers of volume 18, 2013, made up the last issue distributed in printed form. Starting with volume 19, 2014, Harvard Papers in Botany became an electronic serial. It is available by subscription from volume 10, 2005, to the present via BioOne (http://www.bioone.org/). The content of the current issue is freely available at the Harvard University Herbaria & Libraries website (http://huh.harvard.edu/pdf-downloads). The content of back issues is also available from JSTOR (http://www.jstor.org/) volume 1, 1989 through volume 12, 2007, with a five-year moving wall.

Publication Exchange Agreements

Please send inquiries to botserials@oeb.harvard.edu or to the Serials Acquisition Manager at Serials Acquisitions & Exchanges, Harvard Botany Libraries, 22 Divinity Avenue, Cambridge, MA 02138, U.S.A.

To meet our publication exchange agreements, we are currently developing a mechanism to supply an electronic copy of each issue to the institutions with which we maintain an exchange program.

For all other questions and/or to order back issues, please email papers@oeb.harvard.edu.

Harvard Papers in Botany **Volume 28, Number 1, was published online June 30, 2023.**

Lepanthes laurarestrepoana J.S. Moreno, Gal.-Tar., & Sierra-Ariza (page 676, Figure 11B).
Drawn by J. S. Moreno.

Harvard Papers in Botany

Volume 28, Number 2 December 2023

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

SYSTEMATICS AND TAXONOMY OF *NOLANA* (NOLANEAE: SOLANACEAE)

MICHAEL O. DILLON[1]

Abstract. *Nolana* L.f. (Nolaneae-Solanaceae) is an easily recognized genus comprising 92 species confined to Peru and Chile, and one endemic in the Galapagos Islands, Ecuador. It is among the five or six largest genera in the family and has its greatest species diversity in coastal southern Peru and northern Chile. These regions are dominated by vegetation termed *lomas* formations that exist as virtual islands of highly endemic communities, all utilizing available moisture from fog (*camanchaca* or *garua*). While most species have their distributions in near-shore habitats, no fewer than five species can be found in habitats far removed from the ocean's influence and at elevations over 1000 m. *Nolana* stands out as the most wide-ranging and conspicuous floristic element of these formations. In many modern classifications, members of *Nolana* have been recognized at the familial (Nolanaceae) or subfamilial (Nolanoideae) rank due to their unusual carpel morphology, but data from molecular studies have provided unequivocal evidence that *Nolana* is nested within the Solanaceae. A phylogeny has been constructed for *Nolana* using a wide variety of markers, and this hypothesis of relationships provides a framework for establishing a classification, testing character evolution, and biogeographic reconstructions. *Nolana* is consistently monophyletic, and, of the many genera proposed within *Nolana, Alona* Lindl. and *Sorema* Lindl., specifically, are also monophyletic. Molecular and morphological studies have led to the recognition of 92 total species: 42 species from Peru, 46 species from Chile, three species have modern distributions in both Peru and Chile, and one species in the Galapagos Islands, Ecuador. Beginning in 1983, collecting and field observations were conducted throughout the range of *Nolana*. Results from Data-Interpolating Variational Analysis (DIVA) suggest Chile as the origin for *Nolana*. Evolution of diversity within this group must be viewed in the context of the climatic and geological changes within the deserts of coastal South America, including glacial cycles and sea level changes, continental uplift, global climate change, and the historical development of *El Niño* weather patterns. A key to species, descriptions, synonymies, designation of lectotypes or neotypes, illustrations, and distribution maps are provided for 92 species. An Index to Numbered Collections (Appendix I), with nearly 3000 accessions, and an Index to Scientific Names (Appendix II) are provided.

Keywords: Chile, Ecuador, Peru, *lomas* formations, *Nolana*, Solanaceae

Resumen. *Nolana* L. ex L.f. (Nolaneae-Solanaceae) es un género fácilmente reconocible compuesto por 92 especies limitadas a Perú y Chile, y una endémica de las Islas Galápagos en Ecuador. Se encuentra entre los cinco o seis géneros más grandes de la familia y tiene su mayor diversidad de especies en la costa sur de Perú y el norte de Chile. Estas regiones están dominadas por la vegetación conocida como formaciones de lomas, que se desarrollan en forma de islas virtuales de comunidades altamente endémicas, y utilizan la humedad disponible de la niebla (camanchaca o garúa). Si bien, la mayoría de las especies tienen su distribución en hábitats cercanos a la costa, algunas especies se distribuyen en hábitats muy alejados de la influencia del océano y a elevaciones superiores a 1000 m. *Nolana* se destaca como el elemento florístico más amplio y conspicuo de estas formaciones. En muchas clasificaciones modernas, los integrantes de *Nolana* han sido reconocidos en el rango de familia (Nolanaceae) o de subfamilia (Nolanoideae), debido a su inusual morfología del carpelo; pero los datos de estudios moleculares, han proporcionado evidencia inequívoca, que *Nolana* está incluida en la familia Solanaceae. La filogenia de *Nolana* ha sido construida utilizando una amplia variedad de marcadores y esta hipótesis de relaciones, proporciona un marco de referencia para su clasificación, prueba la evolución de caracteres y las reconstrucciones biogeográficas. *Nolana* es un género consistentemente monofilético y de muchos géneros propuestos dentro de *Nolana*, específicamente *Alona* Lindl. y *Sorema* Lindl. que también son monofiléticos. Los estudios moleculares y morfológicos han llevado al reconocimiento de un total de 92 especies, 42 especies de Perú, 46 especies de Chile, tres especies tienen distribuciones tanto en Perú como en Chile, y una especie en las Islas Galápagos en Ecuador. A partir de 1983, se realizaron recolecciones y observaciones de campo en toda el área de distribución de *Nolana*. Los resultados del análisis de Data-Interpolating Variational Analysis (DIVA) sugieren a Chile como el origen de *Nolana*. La evolución de la diversidad en este grupo debe ser visto en el contexto de los cambios climáticos y geológicos en los desiertos de la costa de América del Sur, incluyendo los ciclos glaciares y los cambios en el nivel del mar, el levantamiento continental y el cambio climático global, y el desarrollo histórico de los patrones climáticos de El Niño. Se proporcionan claves, descripciones, sinonimias, designación de lectotipos o neotipos, ilustraciones, mapas de distribución y para 92 especies. Se proporciona un índice de colecciones numeradas (Apéndice I) con ca. 3000 accesiones y un índice de nombres científicos (Apéndice II).

Palabras clave: Chile, Ecuador, Perú, formaciones de lomas, *Nolana*, Solanaceae

Nolana (Nolaneae-Solanaceae) is a ubiquitous group within the vegetation of coastal Peru and Chile, with one endemic shrub on the Galápagos Islands, Ecuador (Fig. 1). With 92 species, it is among the largest genera in the Solanaceae after *Solanum* L. (1000 spp.), *Lycianthes* (Dunal) Hassl. (200 spp.), *Cestrum* L. (175 spp.), *Physalis* L. (~90 spp.), and *Lycium* L. (~91 spp.) (Barboza et al., 2016). It contains annuals, facultative perennials, and long-lived shrubby species, and they are often dominant members within their respective environments. *Nolana* species (Table 1) exist from the Galápagos Islands (0˚00'S) and continental South America from ca. 6˚S latitude in Peru, south to Isla Chiloé, Chile at 42˚30'S latitude, but centers of the greatest diversity occur in Peru, between 15˚–18˚S latitude and in Chile, between 22˚–30˚S latitude. There are 46 species from Chile, 42 species from Peru, three species recorded from Chile and Peru, and one from Ecuador. While conducting field studies along coastal Peru during the 1982–1983 El Niño event, the striking diversity of *Nolana* species encountered was impressive in environments that were more normally

I acknowledge the contributions by the late Ivan Murray Johnston (†), the Harvard botanist who completed the first synthetic treatment for *Nolana*. His collections and observations provided a foundation for this work. Contributions by Ramón Ferreyra (†) and a monograph by Aldo Mesa-M. provided a wealth of information. I thank the curators and collection managers at the many institutions who have loaned collections, provided image scans, and hosted visits during this study, including A, B, BLK, BM, C, CDS, CGE, CONC, CUZ, E, F, FI, G, GH, H, HAL, HAO, HBG, HSP, HUH, HUSA, HUT, K, MA, MAK, MO, NY, P, SGO, U, UC, ULS, UNSA, US, and USM. I want to thank the staff at the Museo National de Historia National in Santiago (SGO),

Footnotes continued on page 142

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 141–646.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n1, Published online: 31 December 2023

Continued from page 141

including Mélica Muñoz, Sergio Moreira, Andres Moreira, Inez Meza, Vanezza Morales, Jimena Arriagada, Victor Hugo Ardiles, María E. Ramírez, and Gloria Rojas. Clodomiro Marticorena (†), Max Quezada (†), Alicia Marticorena, Marcelo Baeza, Rosa Montero and Sonia Maldonado provided unlimited access to the herbarium at the Universidad de Concepción (CONC). Curators and staff at the Herbarium Universitatis Florentinae of the Botanical Section of the Museo di Storia Naturale dell'Università in Florence, Italy (FI), provided access to the P. B. Webb Herbarium and Gaudichaud collections. I thank Renee Prakash at the Natural History Museum (BM), London, United Kingdom, and Nicolas Hind at Kew Gardens (K), Richmond, United Kingdom, for facilitating visits. I acknowledge Martin Gardner and Sabina Knees at The Royal Botanic Garden (E) in Edinburgh, United Kingdom, for collaboration. I thank David Boufford (HUH) and an anonymous reviewer for comments that greatly improved the manuscript.

Field studies were supported, in part, by grants from the National Geographic Society and the National Science Foundation (BSR-8513205, DEB-0415573). Studies were supported, in part, by a grant to Victor Quipuscoa Silvestre from UNSA-INVESTIGA (No 37-2016-UNSA) and the Department of Biology, UNSA, for the permits granted to carry out field studies in Peru. Members of IMOD (Instituto Michael Owen Dillon) participated in field studies: Daniel Montesinos, Felipe Sinca, Károl Durand, Daniel Ramos, Rafael Pérez, Italo Treviño, Margarita Balvín, Susan Huamaní, Geraldine Rosado, Maricruz Bedoya, Cristian Tejada, Raquel Medina, Wendy Ancalla, Claudia Sanz, and Martín Flores.

Many people have participated in field excursions, including Ulf Molau, Penny Matekaitis, Marucha Benavides de Tschudi, Rosanna Freyre, Mario Zapata, Magda Chanco, Elida Carrillo, Camilo Díaz, Blanca León, Pedro Lezama, Eduardo and Tina Martell, Eloy López, Eric Rodríguez, Monica Mancini and Osvaldo Quiroga, Manuel Ossa and Gabriela Zazzali, Miguel and Erika Finger, Guido Albiño, Jorge Guerra, Oswaldo Ibicache, Cecily and Héctor Luis García, Gloria Montenegro, Beatriz Palma, Philip Rundel, Roberto Perucci (†), Roberto Perucci Jr., Jorge Macaya, Tomas Vega-Zuniga, Bernardo Tay, Rudolf Schulz, Abundio Sagástegui (†), Nicolás García, and Federico Luebert. Oliver Whaley is thanked for contact with Alberto Benavides Ganoza and access to the Lomas of Amará in 2007. Alfredo Tupayachi (CUZ) is acknowledged for accompanying me in the field to Urubamba, Peru in 2000 and for his efforts at acquiring photographs and DNA material. Ms. Barbara Knapton of Putre, Chile is given a special thanks for making collections and photographing *Nolana* in northern Chile. Darío Canto Yañez, Director of CONAF in Copiapo-Chañaral is acknowledged for permits to collect within Parque Nacional de Pan de Azúcar. Field studies in Chile were aided by several field assistants, including Sebastián Teillier, Carmen Trujillo, Adolfo (Coyo) Casareggio, Victor Ascencio (†), and Verónica Poblete (†). I was very fortunate to have made the acquaintance of Maximino Nicolas (Nino) Villarroel who acted as my guide, assistant, and teacher exploring the quebradas in the Taltal region.

Field studies in Ecuador's Galapagos Islands were aided by people at the Charles Darwin Foundation, including Alan Tye, Cecilia Solís, and the staff in Quito, Ecuador. Herbarium study in Berlin was supported by Federico Luebert and the staff at the Berlin-Dahlem Museum. Urs Eggli and Sylvia Arroyo Leuenberger are thanked for sharing information garnered from collecting in Chile. Joanna Alfaro Shigueto, ProDelphinus Director, Lima, Peru is thanked for photographs of *Nolana insularis* from Isla San Gallán, Peru. Miyuki Nakazawa is acknowledged as the first person to broadly investigate *Nolana* with modern molecular techniques leading to her PhD with Mikio Ono (†); she participated in Peruvian field studies in 1997. Jun Wen (US) is acknowledged for directing the laboratory portion of molecular studies by Tieyao Tu, Lei Xie, and Hang Sun. I thank María Teresa Eyzaguirre Philippi of the R. A. Philippi Institute for sharing observations and photographs of various Chilean species. Adriana Hoffmann (†) shared her *Nolana* paintings, and especially the image of *Nolana reichei* executed by Chilean artist, Andrés Jullián. I thank Mauricio Gonzales for the images of *Nolana clivicola* and the *Corporación Ecológica Cultural Caminantes Del Desierto*, Antofagasta, Chile. I acknowledge the efforts of Dra. Nina Rønsted and Per Olof Ryding of the Natural History Museum of Denmark (C) for help in finding isotype material of *Nolana willeana*. Curatorial staff at Cambridge University, specifically Gina Murrell and Christine Bartram, are thanked for providing digital photographs of John Lindley type material (CGE). The photograph of Ivan M. Johnston was provided courtesy of the Archives of the Gray Herbarium, Harvard University Libraries, and Danielle Castronovo (HUH) and Lisa Pearson (A). Digital photographs were kindly provided by Marcelo Rosas, Eric Tepe, Claudio Latorrie, Paulina G. Ossa-Zazzali, and Gloria Barboza. Dra. Josefina Hepp is acknowledged for her collaboration with publishing *Nolana patachensis* and sharing images and information on *Nolana jaffuelii*. Digital photographs and identifications of bees were provided by Laurence Packer, and identifications of butterflies were provided by Alfredo Ugarte Peña. I thank Karina Araya, Paola Milla, Ana Sandoval, the Regional Government of Antofagasta, the Ministry of the Environment (MMA), and the Institute of Agricultural Research (INIA) for supporting a visit to Chile in late 2021. Victor Pariapaza is acknowledged for his observations of *Nolana* in the Department of Piura, Peru. The staff at Real Jardín Botánico, Madrid, are thanked, especially Esther García, Eva García, and Alberto Herrero.

Many people have given me encouragement; none more to thank than the late Jiří R. Haager (†) and Hana Šedivváat at The Botanical Garden of Teplice, Teplice, Czech Republic. Sebastián Teillier is thanked for critically reading an early version; his suggestions greatly improved the monograph. Christine Niezgoda, Collection Manager at F is thanked for many curatorial aspects and for providing French/English translation of Aldo Mesa's Flora Neotropica monograph (1981). Images were sent for identification by Maxim S. Nuraliev, Lomonosov Moscow State University, Moscow, Russia; with his permission, some were incorporated into this treatment. Images were gathered from the PhytoImages and used with the consent of P. B. Pelser internet: D. L. Nickrent, M. Costea, J. F. Barcelona, P. B. Pelser, & K. Nixon (2006) http://www.phytoimages.siu.edu.

Staff at the Field Museum provided mounted specimens, including Freddie Robinson, Darlene Dowdy, and Birthel Atkinson (†). Anna Balla handled all loans and exchange of material. Daniel Le is acknowledged for help with digital images. Original illustrations for *Nolana* species were completed by Nancy Klaud, Segundo Leiva, and Edgardo Ortiz; I thank Margarita Balvin Aguilar at IMOD for rendering distribution maps. Victor Quipuscoa and members of DIBIOS (*Grupo de Investigación de la Diversidad Biológica del Sur*) and later members of IMOD (Instituto Michael Owen Dillon) are thanked for work in the herbarium and in the field, including Marcelina Laura, Yeselia Cano, Claudia Sanz, Wendy Ancalla, Mary Bedoya, Laura Cáceres, Edgardo Ortiz, Massiel Corrales, Gina Castillo, Marco Cueva, Natalie Castro, Cristian Tejada, Margarita Balvin, Daissy Rodríguez, and Susan Huamani. Since my retirement in 2008, Susan Hamnik has volunteered for me in the herbarium and helped in so many ways; I will not attempt to list them. Without her help and encouragement this treatment might never have seen the light of day.

This monograph is dedicated to my late major professor, Billie Lee Turner (b. 1925–d. 2020), at the University of Texas at Austin; he always stressed the importance of monographic treatments and their contribution to botanical knowledge.

[1] Herbario Sur Peruano, Av. Jorge Chávez 610–Cercado, Arequipa, Perú; dillon@sacha.org

very dry desert. From that time onward, special attention has been given to *Nolana*, and I have attempted to view all species in their natural environments over the past 40 years.

The current treatment is the third monograph for *Nolana,* after those of Ivan M. Johnston (1936) and Aldo Mesa-M. (1981), and it incorporates extensive field observations, collections, and comparative studies (Dillon et al., 2007a, b). Furthermore, it is the first detailed study to benefit from molecular analyses (Tago, 1999; Dillon et al., 2007c, 2009; Tu et al., 2008), that have provided insights into internal classification. Type collections have been consulted from loans, herbarium visits, and images examined via internet sources. The field collections and the advantage of examining fresh material have been pivotal in the study of comparative morphology. In the process of preparing herbarium sheets, the pressing and drying process tends to obscure many diagnostic characteristics. The presentation of the taxonomy has been divided into seven putative clades as suggested by phylogenetic investigations and comparative morphology.

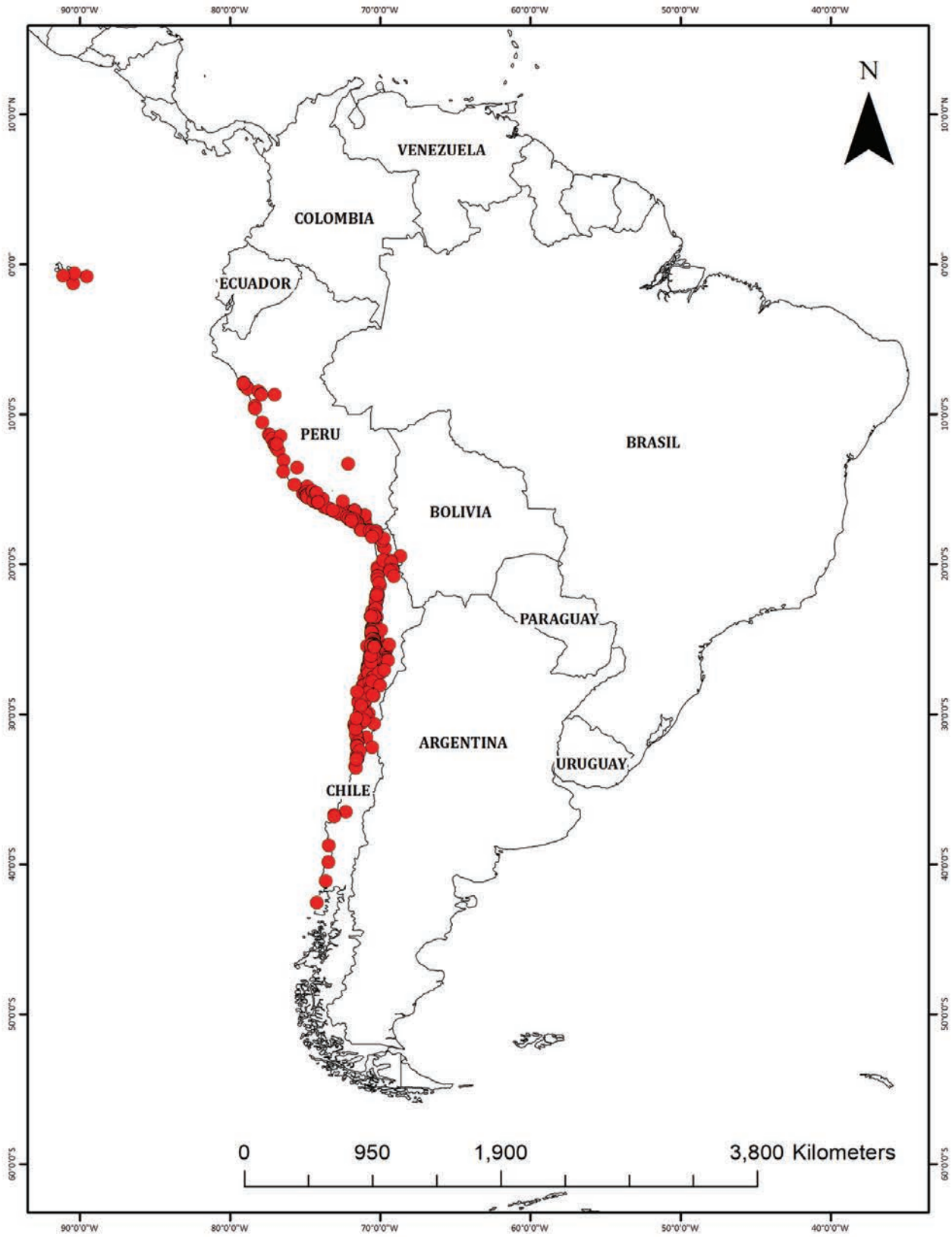


FIGURE 1. Distribution of *Nolana* L.f. in Ecuador, Peru, and Chile.

TABLE 1. Alphabetical list of accepted names and authors, distribution, and phylogenetic position as suggested by inclusion in clades of *Nolana* in South America (adapted from Dillon et al., 2009).

	SPECIES	DISTRIBUTION	CLADE
1	*N. acuminata* (Miers) Miers ex Dunal	Chile	B
2	*N. adansonii* (Roem & Schult.) I.M. Johnst.	Chile–Peru	F
3	*N. aenigma* M.O. Dillon & Quip.	Peru	F
4	*N. albescens* (Phil.) I.M. Johnst.	Chile	G
5	*N. aplocaryoides* (Gaudich.) I.M. Johnst.	Chile	G
6	*N. arenicola* I.M. Johnst.	Peru	D
7	*N. arequipensis* M.O. Dillon & Quip.	Peru	F
8	*N. aticoana* Ferreyra	Peru	F
9	*N. baccata* (Lindl.) Dunal	Chile	B
10	*N. balsamiflua* (Gaudich.) Mesa	Chile	C
11	*N. bombonensis* Quip. & M.O. Dillon	Peru	F
12	*N. callae* Quip. & M.O. Dillon	Peru	F
13	*N. carnosa* (Lindl.) Miers ex Dunal	Chile	C
14	*N. cerrateana* Ferreyra	Peru	F
15	*N. chancoana* M.O. Dillon & Quip.	Peru	D
16	*N. chapiensis* M.O. Dillon & Quip.	Peru	D
17	*N. clivicola* (I.M. Johnst.) I.M. Johnst.	Chile	E
18	*N. coelestis* (Lindl.) Miers ex Dunal	Chile	C
19	*N. confinis* I.M. Johnst.	Peru	F
20	*N. coronata* Ruiz & Pav.	Peru	F
21	*N. crassulifolia* Poepp.	Chile	G
22	*N. dianae* M.O. Dillon	Chile	G
23	*N. diffusa* I.M. Johnst.	Chile	G
24	*N. divaricata* (Lindl.) I.M. Johnst.	Chile	G
25	*N. elegans* (Phil.) Reiche	Chile	B
26	*N. filifolia* (Hook. & Arn.) I.M. Johnst.	Chile	C
27	*N. foliosa* (Phil.) I.M. Johnst.	Chile	E
28	*N. galapagensis* (Christoph.) I.M. Johnst.	Ecuador	D
29	*N. gayana* (Gaudich.) Koch	Peru	F
30	*N. glauca* (I.M. Johnst.) I.M. Johnst.	Chile	G
31	*N. gracillima* (I.M. Johnst.) I.M. Johnst.	Chile–Peru	E
32	*N. hoxeyi* M.O. Dillon & Quip.	Peru	D
33	*N. humifusa* (Gouan) I.M. Johnst.	Peru	F
34	*N. incana* (Phil.) I.M. Johnst.	Chile	G

TABLE 1 CONT. Alphabetical list of accepted names and authors, distribution, and phylogenetic position as suggested by inclusion in clades of *Nolana* in South America (adapted from Dillon et al., 2009).

	SPECIES	DISTRIBUTION	CLADE
35	*N. inconspicua* (I.M. Johnst.) I.M. Johnst.	Chile	G
36	*N. inflata* Ruiz & Pav.	Peru	D
37	*N. insularis* (I.M. Johnst.) I.M. Johnst.	Peru	D
38	*N. intonsa* I.M. Johnst.	Chile	F
39	*N. jaffuelii* I.M. Johnst.	Chile	B
40	*N. johnstonii* Ferreyra	Peru	F
41	*N. lachimbensis* M.O. Dillon & Luebert	Chile	G
42	*N. latipes* I.M. Johnst.	Peru	D
43	*N. laxa* (Miers) I.M. Johnst.	Peru	D
44	*N. leptophylla* (Miers) I.M. Johnst.	Chile	G
45	*N. lezamae* M.O. Dillon, S. Leiva & Quip.	Peru	F
46	*N. linearifolia* Phil.	Chile	G
47	*N. lycioides* I.M. Johnst.	Chile–Peru	D
48	*N. mariarosae* Ferreyra	Peru	F
49	*N. minor* Ferreyra	Peru	F
50	*N. mollis* (Phil.) I.M. Johnst.	Chile	G
51	*N. onoana* M.O. Dillon & Nakazawa	Chile	G
52	*N. pallida* I.M. Johnst.	Peru	F
53	*N. pallidula* I.M. Johnst.	Peru	D
54	*N. paradoxa* Lindl.	Chile	B
55	*N. parviflora* (Phil.) Phil.	Chile	B
56	*N. patachensis* J. Hepp & M.O. Dillon	Chile	G
57	*N. patula* (Phil.) Mesa ex M.O. Dillon	Chile	G
58	*N. pearcei* I.M. Johnst.	Peru	F
59	*N. peruviana* (Gaudich.) I.M. Johnst.	Chile	G
60	*N. philippiana* M.O. Dillon & Luebert	Chile	G
61	*N. pilosa* I.M. Johnst.	Peru	F
62	*N. platyphylla* (I.M. Johnst.) I.M. Johnst.	Peru	D
63	*N. plicata* I M. Johnst.	Peru	D
64	*N. pterocarpa* Phil. ex Wettst.	Chile	B
65	*N. quicachaensis* Quip. & M.O. Dillon	Peru	F
66	*N. ramosissima* I.M. Johnst.	Chile	G
67	*N. reichei* M.O. Dillon & Arancio	Chile	B
68	*N. rhombifolia* Marti. & Quez.	Chile	D

TABLE 1 CONT. Alphabetical list of accepted names and authors, distribution, and phylogenetic position as suggested by inclusion in clades of *Nolana* in South America (adapted from Dillon et al., 2009).

	SPECIES	DISTRIBUTION	CLADE
69	*N. rostrata* (Lindl.) Miers ex Dunal	Chile	C
70	*N. rupicola* Gaudich.	Chile	B
71	*N. salsoloides* (Lindl.) I.M. Johnst.	Chile	G
72	*N. samaensis* M.O. Dillon & Quip.	Peru	D
73	*N. scaposa* Ferreyra	Peru	D
74	*N. sedifolia* Poepp.	Chile	G
75	*N. sessiliflora* Phil.	Chile	A
76	*N. spathulata* Ruiz & Pav.	Peru	D
77	*N. spergularioides* Ferreyra	Peru	E
78	*N. sphaerophylla* (Phil.) Mesa ex M.O. Dillon	Chile	G
79	*N. stenophylla* I.M. Johnst.	Chile	C
80	*N. tarapacana* (Phil.) I.M. Johnst.	Chile	E
81	*N. thinophila* I.M. Johnst.	Peru	F
82	*N. tocopillensis* (I.M. Johnst.) I.M. Johnst.	Chile	G
83	*N. tomentella* Ferreyra	Peru	F
84	*N. tovariana* Ferreyra	Peru	F
85	*N. tricotiflora* Quip. & M.O. Dillon	Peru	F
86	*N. urubambae* Vargas	Peru	F
87	*N. villosa* (Phil.) I.M. Johnst.	Chile	G
88	*N. volcanica* Ferreyra	Peru	F
89	*N. weberbaueri* I.M. Johnst.	Peru	D
90	*N. weissiana* Ferreyra	Peru	D
91	*N. werdermannii* I.M. Johnst.	Chile	G
92	*N. willeana* Ferreyra	Peru	D

Taxonomic History

Ivan Murray Johnston's monograph was the first to examine the various nomenclatorial problems posed by *Nolana* (Johnston, 1936). As he pointed out (Johnston, 1936: 10), there are a few important names and dates in the history of this group. To establish the priority of *Nolana*, the dates of valid publication of other proposed genera were examined. Table 2 lists the synonymous genera that were established for species identified as members of *Nolana*. In addition to validly published generic names, several monomial names were proposed. When Michel Adanson (b. 1727–d. 1806) published *Familles des Plantes* (1763), his Solanaceae treatment included the monomial *Neudorfia* based upon "*Belladona peruviana HRP*", implying the plant from Peru and attributed to Hipólito Ruiz López and José Antonio Pavón Jiménez (= *Nolana humifusa*). The plant was described from Parisian garden material where it was called "*Belladona Peruviana, repens flora caerulea*". Adanson (1763) associated his *Neudorfia* with genera such as *Solanum*, *Capsicum* L., *Atropha* L. (as *Belladona*), and *Lycium* and called attention to 5-merous fruits in both *Neudorfia* (= *Nolana*) and *Nicandra* Adans.

In 1763, Adanson added the generic name *Tula*, for a plant collected by Louis Éconches Feuillée (b. 1660–d. 1732) in 1710 from southern Peru that was originally published under a phrase name (Feuillée, 1725). This is the first description for any taxon now considered *Nolana*, and it consisted of a polynomial or phrase name, *Soldanella facie, flore infundibuli forma*, for a plant now known as *Nolana adansonii* (1725). During Feuillée's

TABLE 2. Proposed genera, including monomial (*), authors and year of publication, and type species.

GENUS	AUTHOR	DATE	*NOLANA* SPECIES
Alibrexia	Miers	1845	*N. crassulifolia* (as *Alibrexia rupicola*)
Alona	Lindl.	1844	*N. coelestis*
Aplocarya	Lindl.	1844	*N. divaricata*
Bargemontia	Gaudich.	1841	*N. peruviana*
Dolia	Lindl.	1844	*N. sedifolia* (as *Dolia vermiculata*)
Gubleria	Gaudich.	1851–1852	*N. baccata*
Leloutrea	Gaudich.	1851–1852	*N. aplocaryoides*
*Neudorfia**	Adan.	1763	*N. humifusa* (as *Neudorfia peruviana*)
Nolana	L. fil.	1762	*N. humifusa* (as *N. prostrata*)
Osteocarpus	Phil.	1884	*N. rostrata*
Pachysolen	Phil.	1895	*N. incana* (as *Dolia eremobia*)
Periloba	Raf.	1838	*N. paradoxa*
Rayera	Gaudich.	1851–1852	*N. rostrata* (as *Rayera teretifolia*)
Sorema	Lindl.	1844	*N. paradoxa*
*Teganium**	Schmidel	1766	*N. humifusa*
Tula	Adans.	1763	*N. adansonii*
Velpeaulia	Gaudich.	1851–1852	*N. leptophylla* (as *Velpeaulia alibrexioides*)
*Walkeria**	Miller ex Ehret	1773	*N. humifusa*
Zwingera	Hofer	1763–1764	*N. humifusa*

South American voyage, he visited the Peruvian coastal cities Lima, Pisco, Ilo, and Arica, eventually making port at Coquimbo (Chile). He collected his material from near the port city of Ilo, Peru on 29 August 1710 and prepared a sketch. It was collected again in 1833 when another French botanist, Alcide d'Orbigny (b. 1802–d. 1857), encountered the plant near Islay, a port city north of Ilo (*d'Orbigny s.n.*, G, F neg. 23239).

George Dionyfius Ehret (b. 1708–d. 1770) established *Walkeria* (1763: 131) for a plant originally proposed by Philip Miller from Chelsea Gardens (London); this material was originally acquired from a Parisian botanical garden under the phrase name "*Belladona peruviana minor*" (tab. 10: 130). In 1766, Casimir Christoph Schmidel (b. 1718–d. 1792) established the monomial *Teganium* Schmid. based upon garden material and described *Teganium procumbens* (= *Nolana humifusa*) (Dandy, 1967).

Nolana was proposed as a genus by Carolinus Linnaeus (b. 1707–d. 1778), who listed the generic name and the specific epithet "*prostrata*", but the publication lacked other elements necessary for valid publication (*nomen*) (Linnaeus, 1762: 202). He formed the generic name from the Latin, *nola*, or small bell, referring to the corollas of plants in cultivation, and credited the Dutch physician, Adriaan von Royen (b. 1704–d. 1779), with the origin of the annual plant. He indicated that a figure and description would follow in his son's work of the same year, as the younger Carl Linnaeus (b. 1741–d. 1783) described several species from the botanical garden in Uppsala. In his description, Linnaeus fil. (1762) acknowledged the contribution of Adriaan von Royen and attributed to him the Latin phrase name, "*Belladona humifusa, flore violaceo, hispanicae*". In addition to the detailed description, an illustration in Tabula II of *N. prostrata* L. was likely based on plants grown at Uppsala from von Royen, who had the plant in cultivation in the Leiden Botanic Garden. Linnaeus indicated that the material treated was undoubtedly from Peruvian collections which had reached European gardens perhaps as early as 1755, and certainly by 1761. Also, in 1762, Antoine Gouan (b. 1733–d. 1821) published *Atropa humifusa* in his catalog of the botanical garden, *Hortus regius monspeliensis*, and type material is preserved in the herbarium of Université de Montpellier (see *Nolana humifusa*). This work was noteworthy, since it represented the first French botanical work that followed the binomial nomenclature of Linnaeus.

In their seminal work, *Flora Peruviana et Chilensis*, Hipólito Ruiz-López (b. 1754–d. 1816) and José Antonio Pavón (b. 1745–d. 1840) provided a full generic description

for *Nolana* and presented several species, including *Nolana prostrata* L. (=*N. humifusa*), *N. coronata*, *N. inflata*, *N. spathulata*, and *N. revoluta* (Ruiz-López and Pavón, 1799). The latter four species were described and illustrated by Juan José Tafalla, a Spanish pharmacist, who joined the Expedition of Ruiz and Pavón in 1785 after Joseph Dombey (b. 1742–d. 1794) had returned to France (Steele, 1964; Tepe, 2018). Type material for the first three species has been seen; however, no specimens referable to *N. revoluta* have yet to be encountered in Madrid or elsewhere. Due to the absence of a type collection, Johnston chose to describe *N. pallida*, in essence, as a replacement name for *N. revoluta* (Johnston, 1936: 69).

Constantine Samuel Rafinesque-Schmaltz (b. 1783–d. 1840) placed his mark upon *Nolana* beginning with his publication of a compilation of all life on Earth in his *Analyse de la nature,* or *Tableau de l'univers et des corps organisés* (Rafinesque, 1815). Rafinesque has been described as a "polymath", or a person whose expertise encompasses different subject areas. He was a strict disciple of Linnaeus' methodology and set about classifying all organisms on Earth in his system. He established his family Nolanidia (1815) within his Order Lobogynia. This "family" also initially contained *Siphonanthus* L. (Verbenaceae). He later published a multivolume work entitled *Flora Telluriana*, 1836–1838, where he re-listed "1062 Nolanidia Raf." (1838: 87). He moved *Siphonanthus* L. to another family and recognized a single genus, *Nolana*, with *N. prostrata* (= *N. humifusa*), *N. coronata*, *N. spathulata*, *N. inflata*, and *N. revoluta* (= *N. pallida*). He mentioned that these species would include several subgenera: *Nolana* subgenus *Iohypa* Raf. (type: *N. prostrata* = *N. humifusa*), *N.* subgenus *Periesta* Raf. (type: *N. coronata*), *N.* subgenus *Spatulina* Raf. (type: *N. spathulata*), and *N.* subgenus *Gastrina* Raf. (types: *N. inflata* and *N. revoluta*). Furthermore, Rafinesque published *Periloba* Raf. (p 87, 1063) based upon Lindley's *Nolana paradoxa* (1824). Johnston (1936) considered *Periloba* as synonymous with *Sorema*.

Charles Gaudichaud-Beaupré (b. 1789–d. 1854), a French botanist, collected various *Nolana* species along the coasts of Chile and Peru, first in 1831 during his travels on the frigate *l'Herminie* (under Captain Villenueve de Bargemont), and, subsequently, in 1836 and 1837 on the corvette *La Bonite* (under Captain Durand). He never published an actual treatment for these plants, but he published 16 folio plates representing five genera and nine species: *Bargemontia* Gaudich., *Gubleria* Gaudich., *Leloutrea* Gaudich., *Rayera* Gaudich., and *Velpeaulia* Gaudich. (Gaudichaud, 1849–1857). These species have been associated with collections that were made by Gaudichaud and others, which he likely had access to when making the illustrations (Table 3). Johnston stated that, under the rules of nomenclature, these plates represent legitimately published taxa (Johnston, 1936: 12). Given the inaccessibility of these beautiful illustrations, they are reproduced here in association with the various species they represent.

TABLE 3. Gaudichaud plates, accepted names, dates of publication, and herbarium specimens (*no specimen located).

PLATE	GAUDICHAUD NAME	ACCEPTED NAME	YEAR PUBLISHED	SPECIMEN
8	*Bargemontia peruviana*	*Nolana peruviana*	1841	*Gaudichaud 8* (F, FI, G, P)
28	*Nolana rupicola*	*Nolana rupicola*	1841	*Gaudichaud 67* (P)
33	*Nolana chastenayana*	*Nolana filifolia*	1842	*
101	*Nolana polymorpha*	*Nolana humifusa*	1851–1852	*Gaudichaud s.n.*
102	*Sorema lanceolata*	*Nolana rupicola*	1851–1852	[*non* Miers, 1845]
103	*Sorema longifolia*	*Nolana acuminata*	1851–1852	[*non* Miers, 1845]
104	*Gubleria baccata*	*Nolana baccata*	1851–1852	*
105	*Alibrexia gayana*	*Nolana gayana*	1851–1852	*
106	*Alona coelestis*	*Nolana coelestis*	1851–1852	*Gaudichaud 66* (CONC, FI, P), *Gaudichaud 72* (F, P)
107	*Alona balsamiflua*	*Nolana balsamiflua*	1851–1852	*Gaudichaud 7* (FI, P)
108	*Rayera teretifolia*	*Nolana rostrata*	1851–1852	*
109	*Velpeaulia alibrexioides*	*Nolana leptophylla*	1851–1852	*Gaudichaud 6* (FI, P)
110	*Leloutrea aplocaryoides*	*Nolana aplocaryoides*	1851–1852	*Gaudichaud 1* (P)
111	*Dolia clavata*	*Nolana divaricata*	1851–1852	*[*non* Miers, 1845]
112	*Dolia vermiculata*	*Nolana sedifolia*	1851–1852	*Gay 3* (P)
113	*Dolia salsoloides*	*Nolana clivicola*	1851–1852	*Gaudichaud 4* (F, P)

As part of Gaudichaud's planned treatment, he prepared the series of 16 folio plates, issued over a decade, in the botanical atlas of the reports of the voyage of *La Bonite* (tab. 8, 28, 33, 101–113). No descriptive text nor any designation of types was ever published by him for the five new genera and nine new species illustrated. These beautifully illustrated plates are legitimately published according to the rules of nomenclature and are accepted. The date of publication to be assigned to these plates is precise (Table 3; Johnston, 1944).

The *Nolana* illustrated by Gaudichaud are based in part upon the collections he made while serving as botanist during the voyage of *La Bonite* in 1836 and 1837. During that voyage, the ship visited only three ports within the range of the genus; Valparaíso (11–24 June 1836), Cobija (1–3 July 1836), and Callao (11–21 July 1836). Of the 16 plates in the botanical atlas of the reports of the Voyage of the Bonite, plates 33, 102, 103, 104, 106, 108, 111 and 112 represent species either known or expected to be found at the ports mentioned. Some of the illustrations were doubtless based upon the material collected by Gaudichaud during 1831, when he was attached to the frigate *l'Herminie*, under Capt. Villenueve de Bargemont, and visited Valparaíso, Coquimbo, and Callao. Others are no doubt based upon collections by Thomas Bridges and possibly by Claudio Gay.

The location of some of Gaudichaud's specimens, from which his plates were drawn, remains uncertain. There are duplicates of some of the collections made during the *La Bonite* voyage (1835–1837) at Paris, Geneva, Berlin, and Chicago; and other duplicates at Paris and Geneva are of collections made by Gaudichaud during the voyage of the frigate *l'Herminie* (1831). Johnston (1936) speculated that the missing types might be at the Webb Herbarium in Florence. In September 1997, I visited the Webb Herbarium and encountered selected Gaudichaud collections (e.g., *Gaudichaud 6* and *7*) but no material of any of the missing Gaudichaud types.

John Lindley (b. 1799–d. 1865) published *Nolana paradoxa* in August 1823 with a colored illustration rendered from plants grown at the Chiswick Garden (Lindley, 1824). He compared the difference in basic mericarp number between it and that of *N. humifusa* (as *N. prostrata*). Subsequently, Lindley (1828) published a species of known hybrid origin, *Nolana tenella* Lindl., and later (1844) published a more detailed study where he described *Alona* Lindl., *Dolia* Lindl., *Aplocarya* Lindl., and *Sorema* Lindl. His 1844 work included 19 species derived from the literature and his own studies (Table 4). He placed the group in or near the Convolvulaceae.

John Miers (b. 1789–d. 1878), an English botanist, arrived in Santiago, Chile in 1819 and lived in Concón, a coastal town north of Valparaíso, where he stayed until 1825 when he returned to England. His firsthand experience with *Nolana* that grew in the dunes (*Nolana paradoxa*) undoubtedly stimulated his interest in the group. Miers (1845, 1850) provided an extensive discussion of the group totaling 27 species, including *Alibrexia* and previously described species: *Eunolana* (5 spp), *Sorema* (7 spp), *Alona* (8 spp), *Dolia* (4 spp), and *Alibrexia* (3 spp).

Michel Félix Dunal (b. 1789–d. 1856), a French botanist, treated the Solanaceae in De Candolle's *Prodromus* (1852) and included *Nolana* in one of two tribes, Nolaneae and Solaneae Dunal (1852). He borrowed considerably from Miers' works and recognized 33 species in five genera: *Nolana*, *Dolia*, *Alibrexia*, *Aplocarya*, and *Bargemontia*. Within a year of Dunal's treatment, Miers (1853) published an outspoken critique arguing that it was regrettable that Dunal

TABLE 4. Listing of taxa proposed by Lindley (1844).

GENUS	SPECIES	CURRENT CLASSIFICATION
Nolana L.f.	*N. prostrata*	*N. humifusa*
	N. tenella	*N. humifusa x N. paradoxa*
	N. spathulata	*N. spathulata*
	N. inflata	*N. inflata*
	N. coronata	*N. coronata*
Alona Lindl.	*A. coelestis*	*N. coelestis*
	A. rostrata	*N. rostrata*
	A. obtusa	*N. rostrata*
	A. glandulosa	*N. filifolia*
	A. carnosa	*N. carnosa*
	A. tomentosa	*N. crassulifolia*
	A. revoluta	*N. gayana*
	A. baccata	*N. baccata*
	A. longifolia	*N. rupicola*
Dolia Lindl.	*D. vermiculata*	*N. sedifolia*
	D. salsoloides	*N. salsoloides*
Sorema Lindl.	*S. paradoxa*	*N. paradoxa*
	S. atriplicifolia	*N. paradoxa*
Aplocarya Lindl.	*A. divaricata*	*N. divaricata*

had associated Nolaneae and Solaneae as tribes in the same family. He maintained that they differed in the structure of the pistil and fruit and insisted that Nolanaceae was best viewed as an isolated family positioned after Boraginaceae and before Convolvulaceae. Miers did recognize the close relationship between *Nolana s.l* and *Grabowskia* Schlect. and placed the latter within a tribe in Nolanaceae. George Bentham (b. 1800–d. 1884) and Joseph Dalton Hooker (b. 1817–d. 1911) treated the group as tribe Nolaneae within Convolvulaceae (Bentham and Hooker, 1873); they recognized 27 species in four genera, *Alona*, *Nolana*, *Dolia*, and *Bargemontia*. The account of the families Nolanaceae, Solanaceae, and Scrophulariaceae for *Die Natürlichen Pflanzenfamilien* (Engler and Prantl, 1895) was contributed by Richard (Ritter von) Wettstein (b. 1863–d. 1931), (Wettstein, 1891); he recognized 50 species in three genera, *Alona* (14 spp.), *Dolia* (16 spp.), and *Nolana* (20 spp.).

Rodulfo Amando Philippi (b. 1808–d. 1904) described fourteen species in four genera from the material he encountered during his epic trip into the most northern areas in the Chilean Atacama Desert (Castro et al., 2006; Philippi, 1860). He added two new species in *Sorema* and *Alibrexia* (Philippi, 1864) and proposed two new Chilean genera, *Osteocarpus* (Philippi, 1884) and *Pachysolen* (Philippi, 1895). His 1895 work was his final treatment for Chile, where he proposed a total of 35 new species. In totality, R. A. Philippi described 48 new species in various *Nolana* segregate genera within the group, and in this monograph, 13 of Philippi's species are recognized.

Karl (Carlos) Friedrich Reiche (b. 1860–d. 1929), a German botanist who worked in Chile for over a decade, presented a classification for Nolanaceae (Reiche, 1910a) and reprinted a portion of it as a treatment for the Flora of Chile (Reiche, 1910b). He listed 40 species in three genera: 24 species in *Nolana*, three in *Alona*, and 13 *Dolia*.

Ivan Murray Johnston (b. 1898–d. 1960) traveled to Peru and Chile in 1925 (Fig. 2), a year recorded as having a strong El Niño event (Dillon and Rundel, 1990) with unusual moisture for the Atacama Desert. From these collections, he described 28 new species from Chile and Peru (Johnston, 1929, 1931) and, subsequently, provided the first modern monograph (Johnston, 1936). In that work, Johnston treated 63 species in two genera, *Alona* and *Nolana*, and provided a detailed discussion concerning the timing of publications and legitimacy of the genera and species proposed for *Nolana*. As mentioned above, Johnston had the good fortune to be in southern Peru and northern Chile during the extraordinary El Niño year of 1925. He was able to collect many novelties, allowing him to describe species from living material, a great advantage when working with succulents. Johnston (1929) initially accepted three genera, *Nolana*, *Alona*, and *Bargemontia*, but in his 1936 monograph he tentatively accepted *Alona*, with 6 species, but decided *Bargemontia* could not be maintained as distinct, and it was subsumed into *Nolana*. Johnston's monograph was very thorough; he consulted European type material and worked out many of the more difficult nomenclatorial issues. Johnston (1936: 11) was quite critical of Reiche's treatment for the Nolanaceae of Chile and characterized it as a "half-digested compilation". As for the familial placement, Johnston (1936: 5) published his monograph under Nolanaceae but stated that the relationships were so close that the Nolanaceae might even be treated as a well-marked group subordinate to the Solanaceae. The recent translation of Johnston's 1929 work into Spanish is a testament to its importance in the history of Chilean botany (Muñoz-S. and Moreira-M., 2022).

Ramón A. Ferreyra Huerta (b. 1910–d. 2005) began collecting in the 1940's throughout the *lomas* formations of coastal Peru and, in a series of publications, ultimately described thirteen new *Nolana* species (Ferreyra 1953, 1955, 1961, 1974). Julio César Vargas Calderón (b. 1903–d. 2002) described two species from the interior of Peru (Vargas, 1954). Clodomiro Marticorena Pairoa (b. 1929–d. 2013) and Max Quezada M. (b. 1936–d. 2019) described an additional Chilean species (Marticorena and Quezada, 1974), and those authors largely followed Johnston's monograph, accepting two genera, *Alona* and *Nolana*, and 46 species for Chile (Marticorena and Quezada, 1985).

Aldo Mesa-M. (1981, 1986), author of the most recent monograph, interpreted the group narrowly and accepted only 18 species in a single genus, *Nolana*. His concept of the genus includes two sections, *Nolana* section *Alona* (Lindl.) Miers with five species and *Nolana* section *Nolana* with two subsections, *Nolana* sect. *Nolana* subsect. *Bargemontia* (Gaudich.) Mesa with seven species, and *Nolana* sect. *Nolana* subsect. *Nolana* with six species. Most of the named species were reduced to synonymy. Later, Mesa-M. (1997; Mesa-M. et al., 1998) expanded his species concept to accept 70 species.

Dillon et al. (2007a, 2007b) published ten new species from Chile and Peru. In 2018, Quipuscoa and Dillon published another four new species from the Department of Arequipa in southern Peru. Hepp and Dillon (2018) published a new species from Alto Punta Patache in Province Iquique in northern Chile. Most recently, Dillon and Quipuscoa (2023) published two new species from Department Tacna in southern Peru.

In the current monograph, a total of 92 species are treated in a single genus, *Nolana* (Table 1). While there is some support for recognizing subgenera, such as *Alona* and *Sorema*, other groups have not been formally recognized and these categories continue to be evaluated. *Nolana* species form a well-defined and monophyletic group diagnosed by its DNA and unique morphology and anatomy (Dillon, 2017).

Materials and Methods

Over 2750 herbarium collections were examined in this study (Appendix I). Specimens were seen and examined during visits to the herbaria or via loans, including A, B, BLK, BM, C, CDS, CGE, CONC, CUZ, E, F, FI, G, GH, H, HAL, HAO, HBG, HSP, HUSA, HUT, K, MA, MAK, MO, NY, P, SGO, U, UC, ULS, UNSA, US, and USM (abbreviations from Index Herbariorum, http://sciweb.nybg.org/science2/IndexHerbariorum.asp). Field work has encompassed the entire geographic range of the genus, and over 400 accessions have been collected from Ecuador, Peru,

FIGURE 2. Photograph of Ivan Murray Johnston taken in the Plaza de Armas, Taltal, Chile, 27 November 1929.

and Chile. Over the duration of this study, I have collected and photographed 82 of the 92 species (~88%) treated here; all species have been examined from herbarium material. Unless indicated otherwise, photographs were taken by the author. Sequences derived from accessions are reported in GenBank (https://www.ncbi.nlm.nih.gov/nuccore). Many images of herbarium collections are accessible via the Field Museum's Searchable Database for the *Lomas Formations*, including 1283 scanned *Nolana* herbarium sheets; regrettably, the Field Museum's collections cannot be easily accessed.

Unless explicitly stated to the contrary, it can be assumed all types cited have been examined for this study, including the scanned sheets from internet sources, such as JSTOR (http://www.jstor.org). When images of types are available via the internet, links are cited under each species at the heading "Digital image." When no digital image is available via the internet, images of the types are included as figures. Other internet resources included Biodiversity Heritage Library for access to journals and other literature (http://www.biodiversitylibrary.org), Herbarium Berolinense, Botanic Garden and Botanical Museum, B, Berlin (http://ww2.bgbm.org/herbarium/), Geneva Herbaria Conservatoire et Jardín botaniques de la Ville de Genève, G, Geneva (http://www.ville-ge.ch/musinfo/bd/cjb/chg/?lang=en), Muséum National d'Histoire Naturelle, P, Paris (http://www.science.mnhn.fr), Naturhistorisches Museum Wien, W, Vienna (http://www.nhm-wien.ac.at/en/research/botany), Natural History Museum, BM, London (http://www.nhm.ac.uk), Royal Botanical Garden, Kew, K (http://www.plantsoftheworldonline.org), and the Swedish Museum of Natural History, S, Stockholm (http://www.nrm.se/krypto-s). Citation of literature follows BPH-2 (Bridson, 2004), Harvard University Index of Botanical Publications, GH, Cambridge (http://kiki.huh.harvard.edu/databases/publication_index.html). Unless stated otherwise (i.e., not seen), it can be assumed that all types were consulted. Many lectotype designations were established by Mesa-M. (1981), others were established by Dillon and Quipuscoa (2023), and others have been established here. For "ex" attributions, both the proposing and publishing author are cited to provide information. Author names are abbreviated according to IPNI (International Plant Names Index, http://www.ipni.org). Herbarium accession numbers follow the acronym (e.g., F 552696); barcodes are identified as such with no space between the herbarium acronym and the number (e.g., SGO000004387). J. Francis Macbride, a Field Museum curator, photographed many type specimens in European herbaria prior to WWII, including those at B that were destroyed. These photographs are cited here with an F negative number (F neg. #). A searchable database with images is contained within the Field Museum's database; however, the search engine does not allow for accessing these resources. References to published illustrations, especially those pre-1900, are provided and included within the monograph where appropriate. Given the importance of his monograph and associated papers, Johnston's (1929, 1930, 1931, and 1936) comments are quoted where appropriate, or paraphrased, within the discussions of various species that he observed in the field and/or subsequently described.

Results

Morphology

Habit. The habit and life forms within *Nolana* vary considerably, from large to minute annuals, such as *Nolana sessiliflora* (Fig. 3A), large populations of annuals as represented by *N. acuminata* (Fig. 3B), a recently germinated *N. adansonii* (Fig. 3C), a robust normally prostrate *N. thinophila* (Fig. 3D), and the long-lived, but annual, Peruvian taxa, *N. humifusa* (Fig. 3E) and *N. aticoana* (Fig. 3F). The annual species have large taproots of varying sizes. The amount of available moisture determines the ultimate size of the root, as in *Nolana sessiliflora* (Fig. 4A), or in *N. paradoxa* (Fig. 4C), which has a slightly enlarged root. In some annuals, the root is very thin, not thickened, as in *N. acuminata* (Fig. 4B) and *N. baccata* (Fig. 4D). The amount of available moisture is one of the primary factors determining the size and branching aspects of annual species; flowering may occur early in the developmental phase and after the plant has reached only a few centimeters. Species such as *Nolana baccata*, are short-lived and flower and fruit when they are less than 10 cm tall (Fig. 4D); they germinate whenever there is sufficient moisture, irrespective of the time of year.

Other members of the genus are long-lived shrubs that are considerably woody. With sufficient moisture, a few Chilean species (e.g., *Nolana villosa*) form much-branched mats that can reach over ten meters in diameter (Fig. 5A). Individuals of *N. crassulifolia* are always found near the ocean or even living in the waves (Fig. 5D). The stems of *Nolana incana* (Fig. 5E) can reach several meters in length when water is not a limiting factor. Shrubby habits are well-developed in *Nolana galapagensis* (Fig. 5B) and *N. ramosissima* (Fig. 5C), both large shrubs to two meters tall with thick trunks. In southern Peru, *Nolana hoxeyi* is woody with persistent trunks (Fig. 5F).

Stems are typically unmodified, and solitary flowers are borne in the leaf axils. In some species from southern Peru, stems are modified into recognizable inflorescences, such as in *N. inflata* and *N. weissiana*. In *N. scaposa*, this condition is well-developed, and the inflorescence is a modified branch with subtending floral bracts. Others in Chile, such as *N. elegans* and *N. acuminata*, have lax stems and solitary flowers in the leaf axils. Many are facultative perennials; these will continue producing flower-bearing stems as long as moisture is available. Others are long-lived perennials, especially when quantities of available moisture persist. These can form very large individuals with stems reaching many meters in length. A few species are perhaps true phreatophytes with well-developed root systems capable of reaching water in springs (*aguadas*) or residual moisture from episodic rains associated with the El Niño phenomenon (Herrera et al., 2017).

Wood. Carlquist (1987) examined the wood anatomy (vouchers listed) of a range of species: three Peruvian species, *Nolana adansonii* (*Mexia 7773*), *N. humifusa* (*Ferreyra*

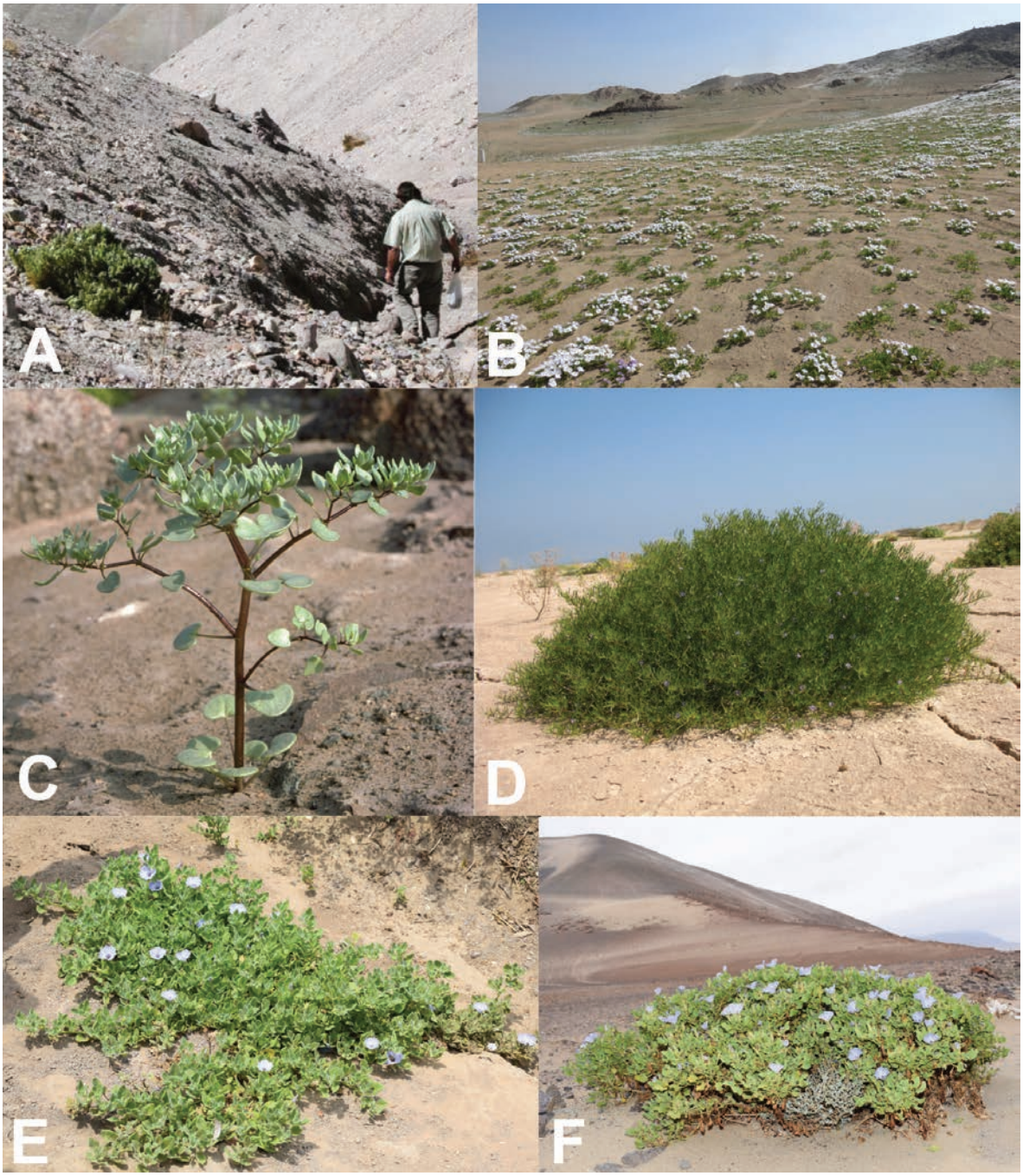


FIGURE 3. Annual habits in *Nolana*. **A**, *N. sessiliflora*; **B**, *N. acuminata*; **C**, *N. adansonii*; **D**, *N. thinophila*; **E**, *N. humifusa*; **F**, *N. aticoana*.

2560) and *N. lycioides* (*Hutchinson & Wright 1846*), and four Chilean species, *N. albescens* (*Johnston 5014*), *N. carnosa* (*Johnston 5047*), *N. crassulifolia* (*Carlquist 7325*), and *N. salsoloides* [as *N. divaricata* (*Werdermann 461*)]. He determined that all the wood anatomy features encountered in the study were also reported for the Solanaceae (Metcalf and Chalk, 1950), except in the terminal parenchyma. *Nolana* exhibited growth rings, vessels with simple perforation plates, lateral wall pitting of vessels composed of alternate circular pits with narrowly elliptical apertures, imperforate tracheary elements, either fiber tracheids with vestigial borders on pits or libriform fibers, vasicentric tracheids and axial parenchyma, tangential bands of axial parenchyma, ray cells that are predominantly erect and non-storied wood (Alfaro and Mesa-M., 1979, Carlquist, 1987). Carlquist (1987) suggested that the wood anatomy was indicative of paedomorphosis. Crystal sand has been observed in the wood of *Nolana* and other Solanaceae. He concluded that all *Nolana* could be considered essentially herbaceous with degrees of woodiness ranging from little

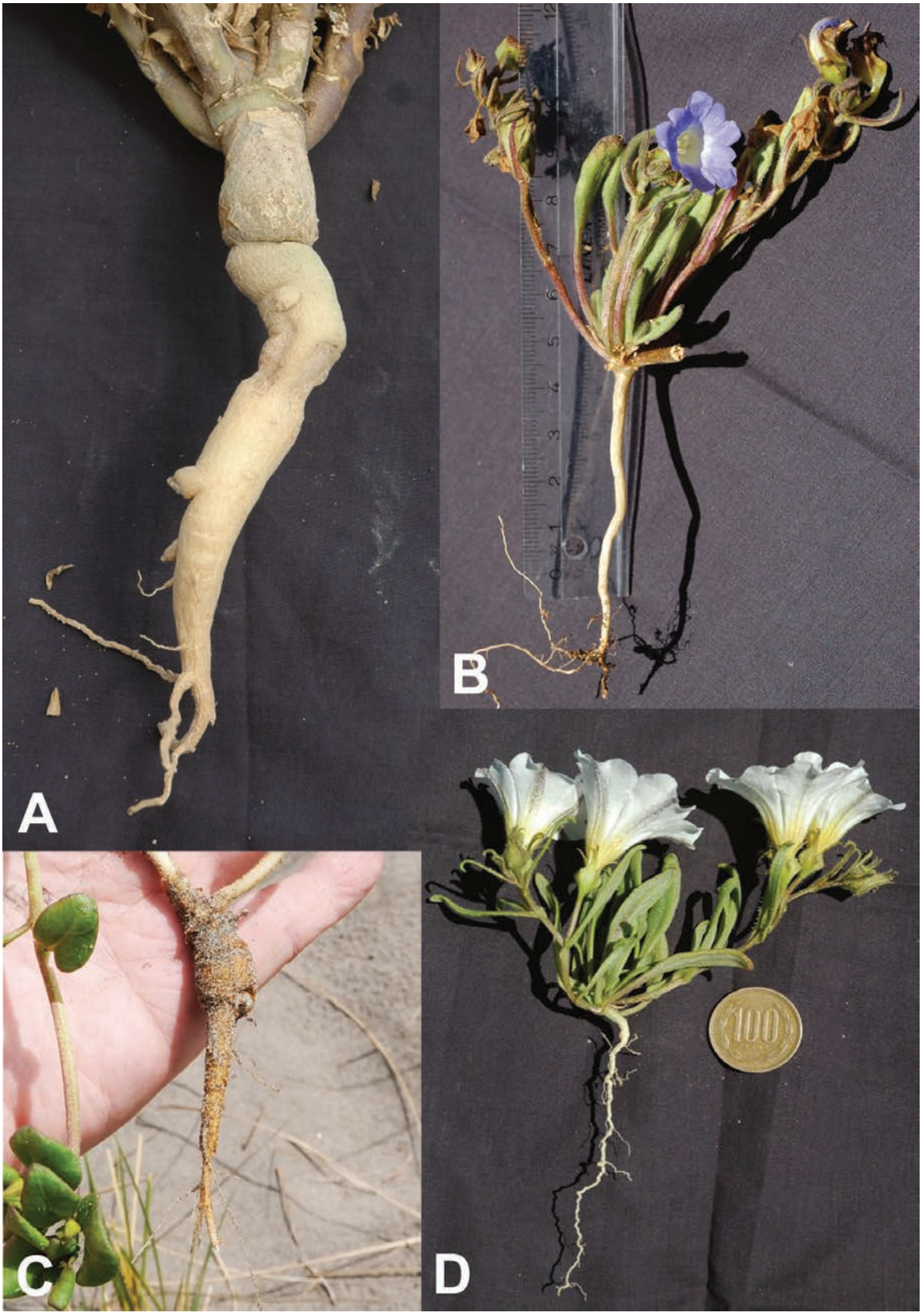


FIGURE 4. Annual roots in *Nolana*. **A**, *N. sessiliflora*; **B**, *N. acuminata*; **C**, *N. paradoxa*; **D**, *N. baccata*.

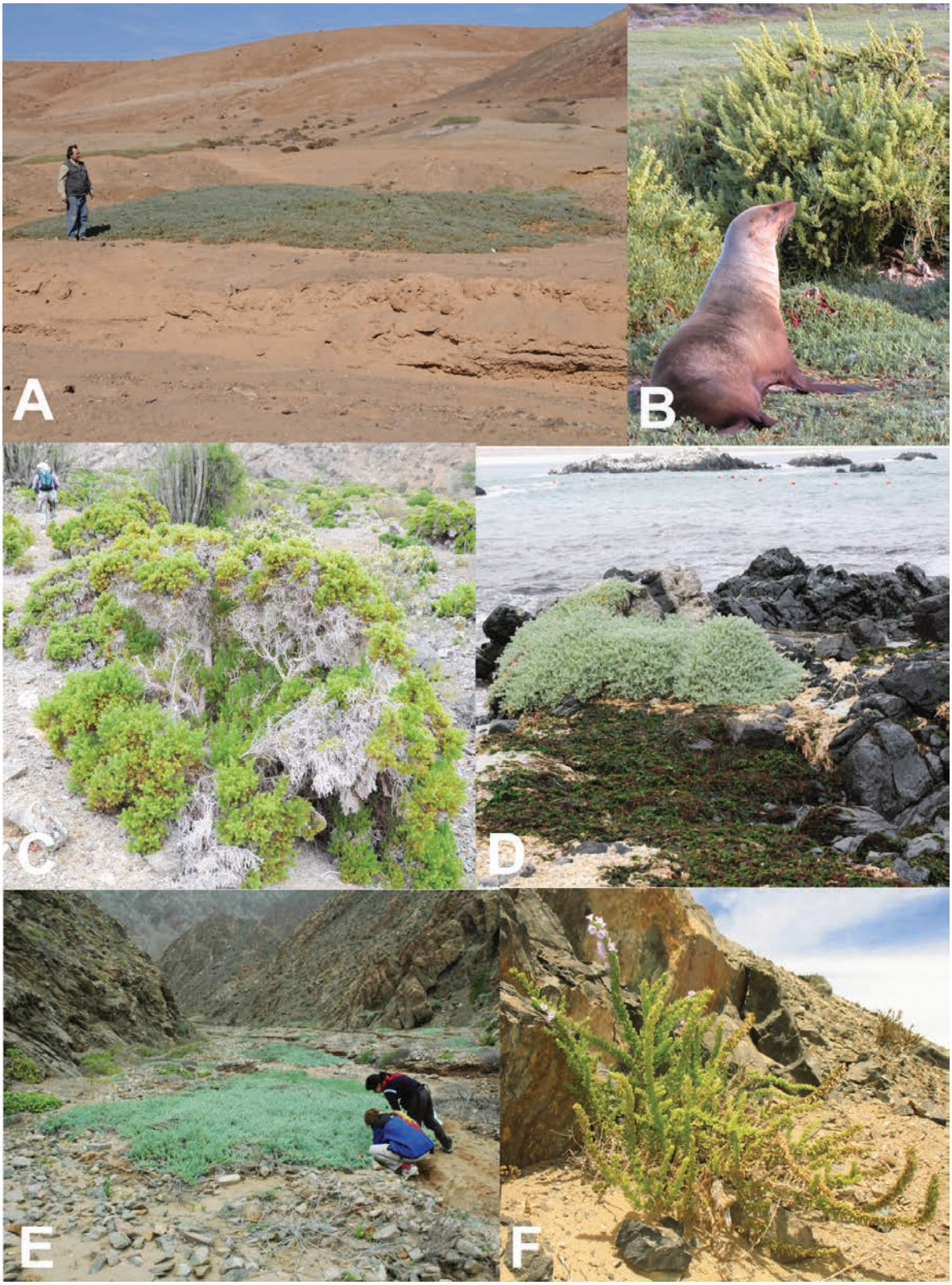


FIGURE 5. Perennial and shrubby habits in *Nolana*. **A**, *N. villosa*; **B**, *N. galapagensis*; **C**, *N. ramosissima*; **D**, *N. crassulifolia*; **E**, *N. incana*; **F**, *N. hoxeyi*.

in annuals to moderately woody shrubs. The greatest concentration of woody species is in northern Chile (ca. 20˚–26˚S latitude), and the most annuals and herbaceous perennials occur in southern Peru (12˚–18˚S latitude).

Stems. Branching is sympodial, sometimes little-branched, and zigzag. If allowed to mature with a continuing supply of water, some rosette-forming species (e.g., *N. rupicola*) will form a central stem that begins yet another rosette. *Nolana scaposa*, *N. inflata* and *N. weissiana* all have a basal rosette of leaves and scapose flowering branches.

Leaves. All *Nolana* species display some degree of leaf succulence. Perhaps nowhere in the genus is the condition more pronounced than in *N. thinophila*, a species that is found in proximity to the ocean. The leaf shape is highly variable, but the blades are often linear or, at times, nearly as wide as long, becoming spherical and terete. When the blades are laminar and with petioles, the blades are lanceolate to elliptic or ovate, but linear shapes dominate in the Chilean taxa. Leaf reduction to 1–5 mm long and ca. 1 mm wide is most pronounced in shrubby species in northern Chile. The largest leaves are basal leaves in rosette-forming *Nolana* species, such as *N. elegans* or *N. rupicola*. *Nolana rupicola* has basal leaves with ovate to lanceolate blades up to 15 cm long and 10 cm wide. Among the Peruvian taxa, *N. inflata*, *N. scaposa*, and *N. weissiana* all exhibit pronounced basal rosettes with long-petiolate leaves.

Cauline leaf morphology varies greatly, from laminar leaf blades with distinct petioles to highly modified succulent, terete or spherical forms. Leaf reduction is pronounced in some shrubby species, such as in *N. carnosa* and *N. tocopillensis*, where the leaves are reduced to ca. 5 mm long and ca. 1 mm wide. In *N. sedifolia*, the leaves are spherical and ca. 1 mm wide and long, marking the smallest leaves within the genus.

Pubescence. The amount of pubescence on both vegetative and floral parts is variable and ranges from entirely glabrous to densely pubescent with a range of trichome types, including both capitate-glandular and non-glandular. All trichomes are uniseriate, consistent with those reported previously in the Solanaceae (Adedeji et al., 2007; Barboza et al., 2016; Haegi, 1991; Johnson, 1975; Roe, 1971; Watts and Kariyat, 2021). The nomenclature of trichome types and their distribution largely follows that of Payne (1978). Non-glandular types include branched or dendritic trichomes easily observable and diagnostic in some groups. Other non-glandular, multicellular trichomes are long with collapsed cells here termed flagelliform trichomes (cf. *Nolana acuminata*, *N. baccata*, *N. elegans*). Some trichomes are longer and tangled and here termed curly trichomes (cf. *Nolana diffusa*, *N. tocopillensis*). Other non-glandular trichomes are defined by texture and trichome orientation; e.g., pilose, strigose, or villous, arachnoid or lanuginous, or tomentose. The capitate-glandular trichomes have stalks of variable lengths, and they can occur in combination with other types of trichomes on plant surfaces. Salt glands are found on the epidermis of several species (e.g., *N. adansonii*, *N. patula,* and *N. sphaerophylla*). They exude salt that is effective in condensing moisture from an unsaturated atmosphere. There are several distinct types of salt glands, and those in *Nolana* are in epidermal pits (see Dassanayake and Larkin, 2017). The moisture condensation on the leaves forms a highly saline solution that makes the leaves appear shiny, greasy. or slick to the touch. Recent hypotheses suggest that the occlusion of stomates by this solution retards transpiration (Thompson et al., 1998).

Inflorescences. Flowers are most commonly solitary in the leaf axils. Stems are typically unmodified, and flowers are borne along the branches, but, in a few species, modified branches arise from a basal rosette, and these form racemose inflorescences with reduced, subtending floral bracts. Some southern Peruvian species, which have modified flowering stems that are recognizable inflorescences with modified bracts subtending individual flowers, arise from a basal rosette of modified leaves (e.g., *N. inflata* and *N. weissiana*). In *N. scaposa*, the condition reaches it maximum development, where the inflorescence is a modified branch with subtending floral bracts. *Nolana hoxeyi* is a woody shrub with dense racemose inflorescences to 30 cm long or more. Most unusual is *N. tricotiflora*, where the inflorescence is a three-branched, scorpioid cyme with large flowers. Flowering may occur in the earliest developmental phase when the plant has reached only a few centimeters in height, as in *Nolana baccata*.

Pedicels. Flowers are borne singly on pedicels of varying length, sessile to over 2 cm long; however, *Nolana reichei* has pedicels to 6 cm long. The pedicels of sand-dwelling species elongate with maturity and curve downward. This action firmly places the ripening mericarps below the sand surface. This is most obvious in species growing on pure sand, such as *N. pallida* in Peru (Fig. 6A) and *N. paradoxa* in Chile (Fig. 6B).

Calyces. Pentamerous, synsepalous, actinomorphic, or sometimes bilabiate, zygomorphic or exceptionally asymmetric. Aestivation is valvate for the sepals, touching one another at the margin without overlapping. The calyx lobes or teeth are persistent, very frequently accrescent around the enlarging mericarps, at times slightly inflated or reflexed, exposing the mericarps. *Nicandra* and *Nolana* are unique in the family for having auriculate calyx segments, although it has previously been reported as a character unique to the former genus (Barboza et al., 2016). The lobes are equal to subequal in length and may be free apically or unequally fused. In *N. carnosa* and *N. rostrata*, the calyx is unequally divided, 1- to 2-cleft, and bilabiate. The unequal position or division of lobes is also present in *N. arenicola*, *N. latipes*, *N. mariarosae*, *N. spathulata* and *N. pallidula*.

Corollas. Corollas are actinomorphic or, more commonly, weakly zygomorphic, with the primary modifications in the size, shape, and coloration patterns. Aestivation is twisted or contorted, where one margin overlaps that of the adjacent. The unfolding corolla in *Nolana paradoxa* (Fig. 7A) and the post-flowering corollas are twisted (Fig. 7B). The most common colors are lavender to blue, with variation in the bands of colors or colored veins within the throats. Both pigmented and white forms are observed in most species, even if the frequency is not great. White corollas have been recorded in *N. acuminata*, *N. baccata*, *N. cerrateana*, *N. gayana*, *N. humifusa*, *N. pallida*, *N. rupicola*, and *N. scaposa*. White is the only corolla color recorded in *Nolana quicachaensis*, *N. johnstonii*, N. *parviflora*,

FIGURE 6. *Nolana* species with recurving pedicels forcing ripe mericarps into sand. **A**, *N. pallida*; **B**, *N. paradoxa*.

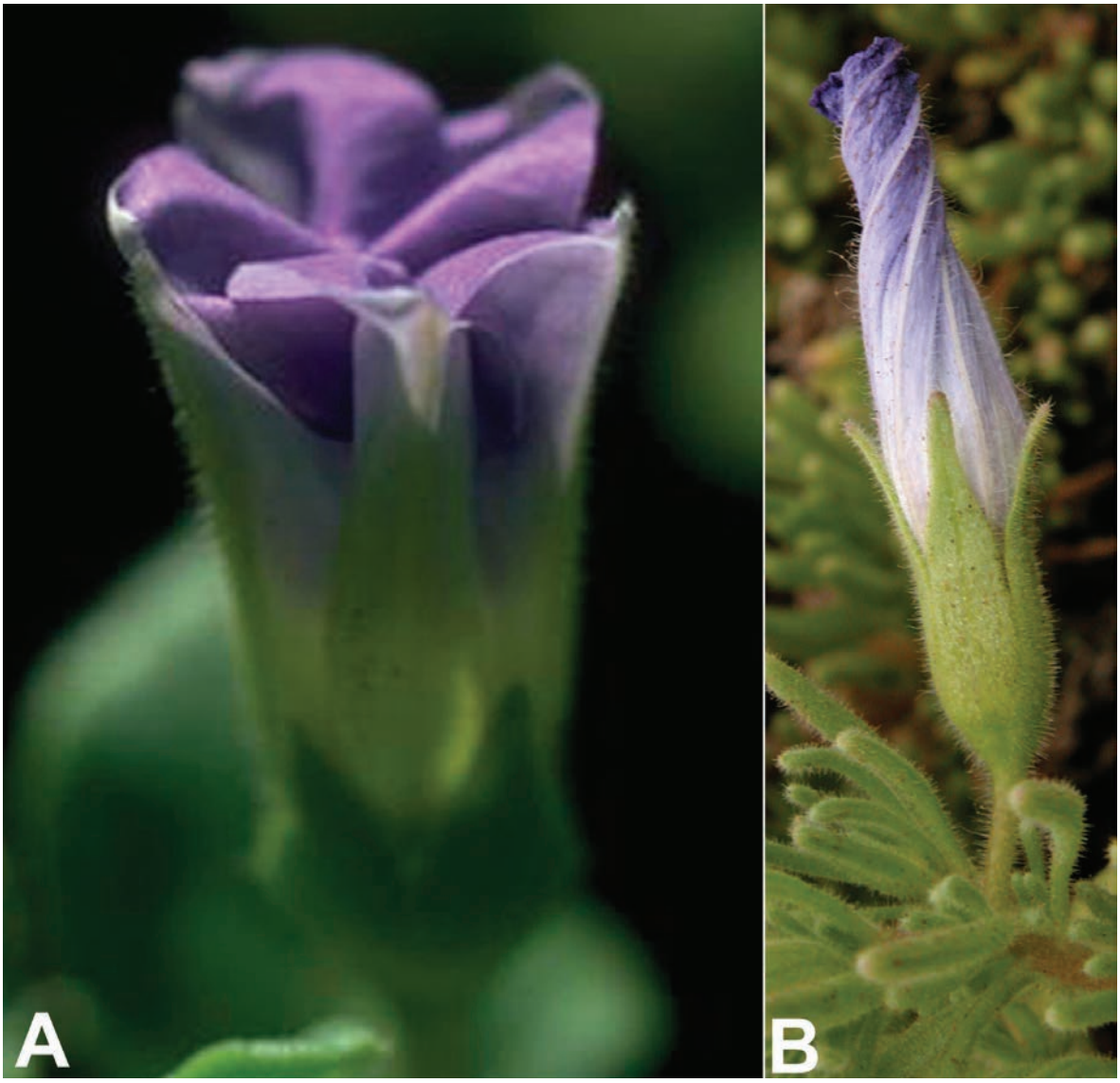


FIGURE 7. *Nolana* corollas opening and closing. **A**, Corolla opening in *N. paradoxa*; **B**, Corolla drying contorted-conduplicate in *N. stenophylla*.

N. albescens, *N. crassulifolia, N. glauca, N. incana*, *N. sessiliflora*, *N. sedifolia* and *N. villosa*, and creamy-yellow in *N. peruviana*.

Floral coloration has been studied in detail in only one species, *Nolana paradoxa* (Stavenga and van der Kooi, 2016). The results presented corolla surface architecture, or 3-D structure, and internal morphology combined with coloration patterns. The authors argued that the visual signal of flowers depends not only upon spectral properties and concentration of the expressed pigments, but also on the functional causes for attracting pollinators. The purplish pigment occurred only in the upper epidermis, causing a different coloration of adaxial and abaxial surfaces. More taxa will need to be examined before any hypotheses can be tested or conclusions made about floral patterns and pollination specificity.

Anthers. The androecium consists of five fertile stamens with unequal filaments, and anther length is dimorphic, with either two short and three long, or three short and two long filaments. Charles Darwin (1877, cf. *Reproductive System*) observed this, but he did not believe it was necessarily illustrative of true heterostyly. The base of the filaments are adnate to varying degrees to the base of the corolla (i.e., epipetalous). The proximal portion of the filaments are often pubescent with villous, obviously retrorse or flagelliform trichomes. It might be inferred that these trichomes inhibit access of smaller insects, such as arachnids or beetles, to the cavity containing the ovaries on top of the nectary and, ultimately, to the maturing mericarps. It is unlikely that these trichomes inhibit nectar gathering insects (cf. *Pollination*).

Pollen morphology. Pollen is tricolporate, blue or white, and comparable to that found in the Solanaceae (Di Fulvio, 1969; Mesa-M., 1981) and, specifically, the Solaneae (Solaninae fide Murry and Eshbaugh, 1971). Shapes range from subprolate or prolate spheroidal to oblate spheroidal; the exine is tectate; the ektexine is thicker than the endexine,

striate to striate-reticulate. Campin (1924) conducted a detailed cytological study of pollen development in *Nolana paradoxa* (as *N. atriplicifolia*) and *N. humifusa* (as *N. prostrata*) and confirmed a haploid chromosome number of 12. Finot et al. (2018) examined pollen grain morphology in *Nolana* and related genera of southern South American Solanaceae.

Gynoecium. The gynoecium in Solanaceae is predominantly 2-carpelled, but it is noteworthy that *Nicandra physalodes* (L.) Gaertner also exhibits an obviously 5-carpelled gynoecium (Huber, 1980; Dillon, 2017). The gynoecium in *Nolana* sits upon a well-developed nectary disk, either orange or green in color. It has 5 carpels, with a single style, either apical, as in taxa attributed to *Alona* (cf. Clade C), or gynobasic, as in all other recognized *Nolana*, and a capitate, wet-type stigma.

The development of the carpels is unique in the subdivision of the loculi into locelli (Bondeson, 1986). In the group historically called *Alona* (cf. Clade C), three to six, multi-seeded mericarps and a high degree of fusion serve to distinguish this group. The mericarps are broadly affixed to the receptacle, embedded within the receptacle tissue, and fused laterally. *Nolana carnosa*, *N. filifolia*, and *N. rostrata* have well-developed receptacles with tissue that completely engulfs the ovules, and the styles are apical. In nearly all other species, the mericarps separate individually and attachment to the receptacle is lateral or basal, and the styles are gynobasic. In a few Peruvian taxa, the mericarps can be weakly connate laterally, but not coherent as a unit. Stigmas were found to be receptive during a wide range of floral developmental stages, and pollen remained viable throughout the open flower period and into senescence (Douglas and Freyre, 2010).

Fruit and seed. The fruit type in the entire genus is technically a schizocarp, defined as a fruit that breaks apart without releasing seeds, each part termed a mericarp which contains one to many (>8) seeds and is indehiscent (Knapp, 2002). Mericarp number varies greatly, but based upon the pentamerous ovary, there are typically five mericarps. The number of mericarps is greatest in the group historically grouped under *Sorema* (cf. Clade B), where the total number can reach 35 in *N. paradoxa*. The mericarp number is reduced to only one or two in *N. arequipensis*, *N. minor*, *N. spergularioides, N. foliosa* and *N. tarapacana*, and one to three in *N. aplocaryoides*, or strictly three large mericarps in *N. stenophylla*. Mericarps are multiseeded and can have as many as eight seeds within a single segment. The germination is epigeal (phanerocotylar), and rarely has it been observed where more than one seed germinates from an individual mericarp. The degree of cohesion between mericarps also varies, with the fusion of carpel walls nearly complete in traditional *Alona* (cf. Clade C). In *Nolana plicata* the mericarps are slightly coherent, but in all others, they are unfused and separate individually. In the northern Chilean species (Clade G), the mericarps are neither fused nor coherent, but are attached to the receptacle basally. Mericarp shape is highly variable, from polygons to spheres with smooth to rugulose external sculpturing. In a few species, the carpel wall is drawn out into a thin wing; e.g., *N. baccata* and *N. pterocarpan*. The seeds have copious oily endosperm, and the ovules are anacampylotropous, unitegmic and tenuinucellate.

The surface of individual mericarps is variable, and the type of superficial sculpturing, or lack thereof, is sometimes diagnostic at the species level. The great majority of species have smooth, shiny, or polished surfaces. Some mericarps have undulating or convoluted surfaces appearing like raisins, as in *Nolana latipes* and *N. reichei*. *Nolana scaposa* mericarps have surfaces that are verrucose and are unique in the genus. A few have a superficial material that may be involved in interactions with ants (cf. *Dispersal*).

Floral anatomy. Floral anatomy and development have been studied in only a few species (Saunders, 1936; Di Fulvio, 1969; Huber, 1980; Armstrong, 1986; Bondeson, 1986; Bruno, 1994).

Embryology. Two species have been investigated (Datta, 1933; Di Fulvo, 1969). Embryo sac development was characterized as the *Polygonum* type, and endosperm formation is cellular, with haustoria absent, like that in other Solanaceae.

Pollination

Pollinator-dependency for reproduction is of great importance for plants. We evaluated the breeding system of *Nolana balsamiflua*, a threatened endemic shrub of the Atacama Desert, and performed four pollination trials. No flower produced seeds by agamospermy, autogamy and geitonogamy. However, xenogamy accounted for 51.4% of fruiting, indicating its full dependency on exogenous pollen and pollinators for reproduction (Humaña et al., 2019). *Nolana* species have many different corolla types and coloration patterns.

Field observations suggest most species are generalists and are visited by bees, beetles, butterflies, moths, flies, ants, and wasps. One Coleopteran, *Pseudomeloe sanguinolentus* (Meloinae), has been recorded feeding on various *Nolana* corollas in Peru and Chile; it is only assumed that they may complete pollination. Both females (Fig. 8A) and males (Fig. 8B) are seen on various *Nolana* species. *Nolana villosa* is visited by flower flies (Syrphidae) (Fig. 9A, photograph by Hanna Sediva). The common hawkmoth, *Hyles annei* (Sphingidae), has been observed visiting *Nolana intonsa* (Fig. 9B, photograph Josefina Hepp). Butterflies were often observed visiting *Nolana* flowers; no effort was made to collect pollinators. *Nolana patachensis* was visited by *Pyrgus bocchoris trisignatus* (Fig. 10A), and *Nolana latipes* was visited by *Pyrgus bocchoris bocchoris* (Lepidoptera: Hespercidae) (Fig. 10B).

The presence of abundant Thripidae in the corollas of several species suggests that they may be reservoirs or alternative hosts for agricultural pests. Severe infestations of corollas by red spider mites were observed; for example, *Tetranychus cinnabarinus* (Acari: Phytoseiidae, Tetranychidae) is common in *Nolana baccata* (Fig. 11A–B) and *Nolana rostrata* (Fig. 11C) (Tello, et al., 2009).

On at least one occasion, *Rhodopis vesper* (Oasis Hummingbird, a northern Chilean bird) was observed visiting *Nolana villosa*, and it may be reasonably assumed to affect pollination in its quest for nectar (Fig. 12A–C). These are mid-sized hummingbirds with long, decurved

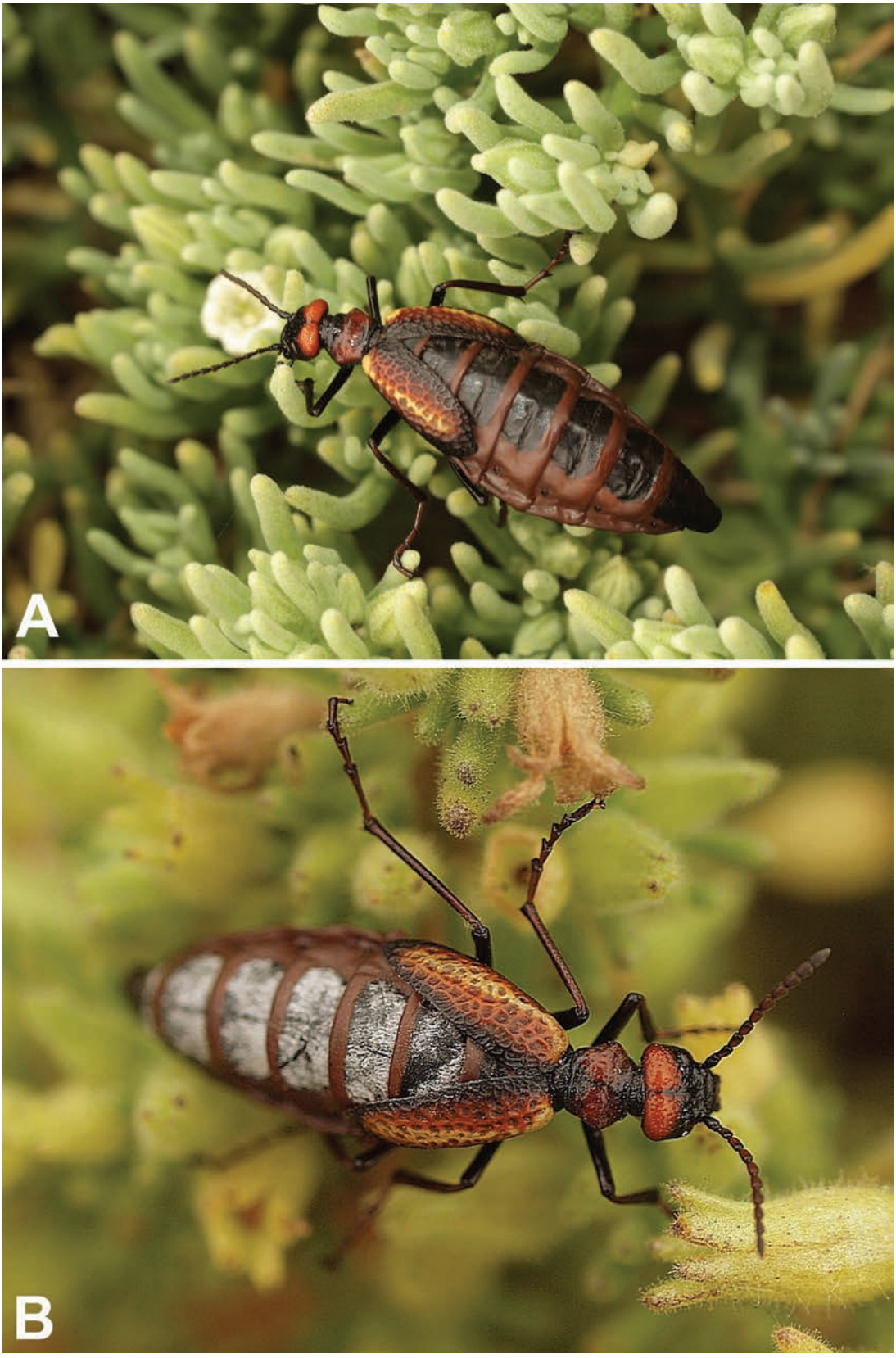


FIGURE 8. *Pseudomeloe sanguinolentus* (Coleoptera, Meloidae) as potential pollinators collected on *Nolana* species. **A**, Female; **B**, Male. (Source: internet, unattributable).

FIGURE 9. Visitors to *Nolana* flowers as potential pollinators. **A**, *N. villosa* visited by a hoverfly (Syrphidae); **B**, *N. intonsa* visited by a common hawkmoth, *Hyles annei* (Sphingidae).

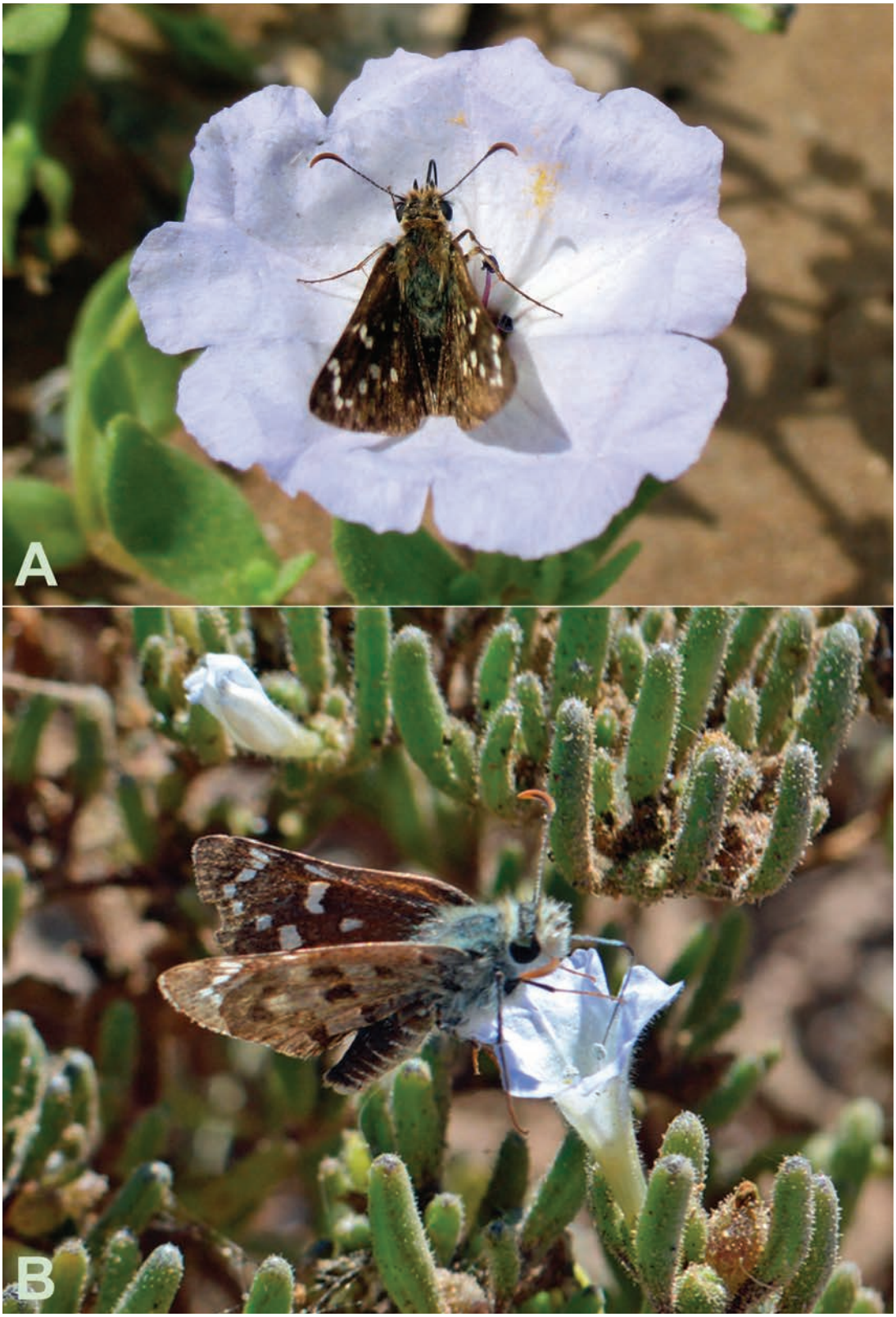


FIGURE 10. Butterflies visiting *Nolana* corollas. **A**, *Nolana patachensis* visited by *Pyrgus bocchoris trisignatus* (Lepidoptera: Hespercidae); **B**, *Nolana latipes* visited by *Pyrgus bocchoris bocchoris*.

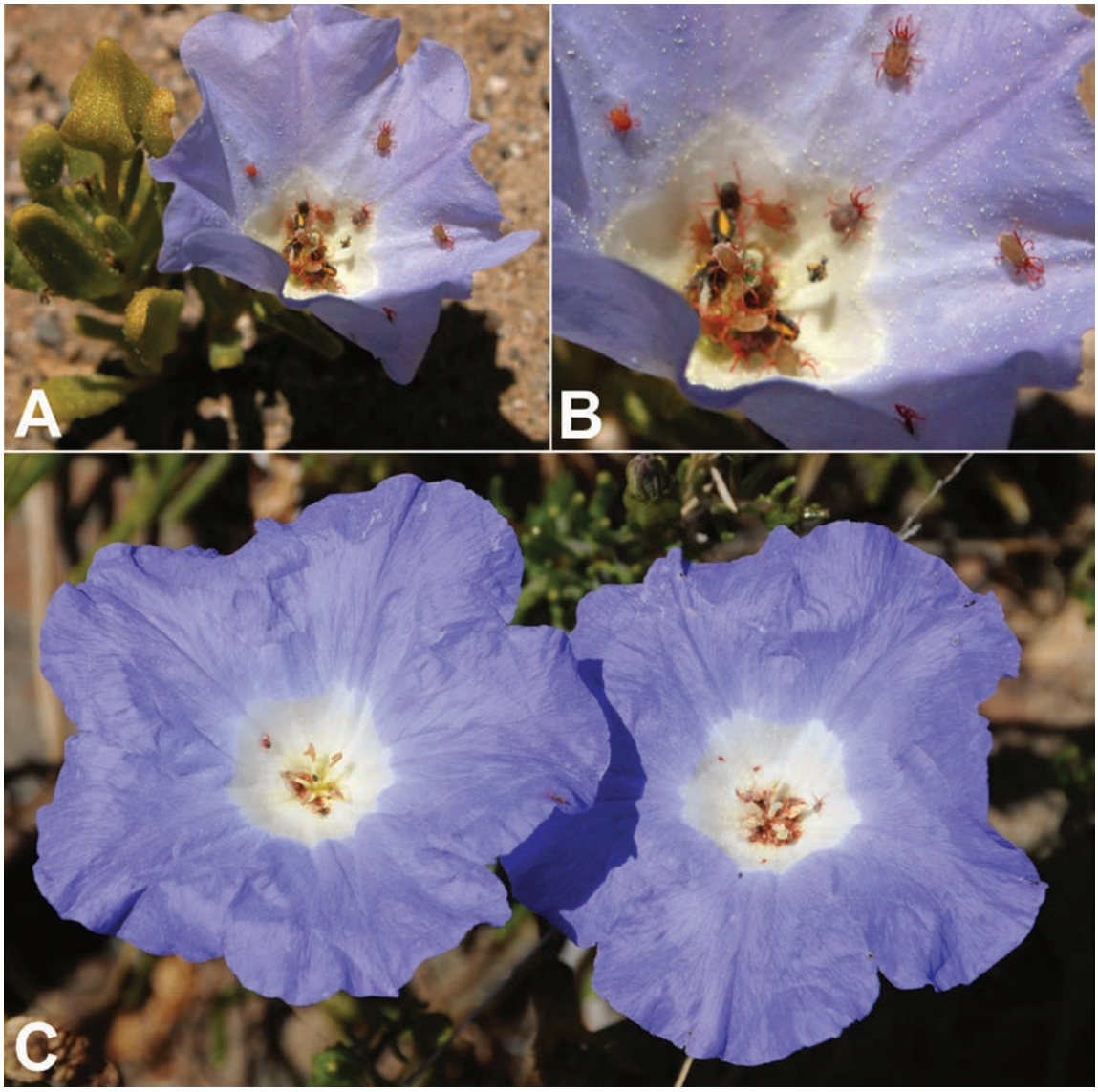


FIGURE 11. *Nolana* corollas infested with red spider mites, such as *Tetranychus cinnabarinus* (Acari: Phytoseiidae, Tetranychidae).

bills. It occurs in vegetated habitats in the extremely dry coastal desert in both Peru and northern Chile.

Various types of bees that appear to be *Nolana*-specific have been studied in northern Chile. *Nolanomelissa toroi* has been observed collecting pollen and nectar from *Nolana rostrata* (Rozen 2003, Fig. 13A). Laurence Packer has studied various genera implicated in pollination of *Nolana* species, including *Penapis* (Packer, 2012), *Neofidelia* (Dumesh and Packer, 2013), *Xeromelissa roseni* (Miklasevskaja and Packer, 2015; Rozen and Wyman, 2015, Fig. 13B), and *Liphanthus jenamro* Mir Sharifi and Packer (Mir Sharifi et al., 2019). While the crown age in the *Nolana* group has been estimated to be between ~ 4.01 and 12.4 mya, paradoxically, some of the bees now closely associated with *Nolana* have much older dates in their phylogenies; for example, *Nolanomelissa* at >45 mya, *Neofidelia* at >7 mya, *Xeromelissa* group1 at > 8 mya, and the youngest, *Xeromelissa* group2, at > 3 mya (Laurence Packer, pers. comm.).

In a study of pollination patterns and breeding systems in the Isla Galápagos, *Xylocopa darwini* (Hymenoptera, Apidae) was reported as a pollinator for *Nolana galapagensis* (Chamorro et al., 2012). This group of bees is generally called "Carpenter bees" and are large, up to 20 mm, but it is unclear what their visits to the small flowers of *N. galapagensis* would accomplish (Vargas et al., 2015).

Dispersal

Mericarp dispersal is essentially passive, with the persistent accrescent calyx containing the detached mericarps; however, transport by birds or small mammals cannot be ruled out. Mericarps have been found in underground rodent middens in northern Chile (Betancourt et al., 2000) and in waste dumps for ants, suggesting myrmecophily (see below). The rounded mericarps in some species may be dispersed by wind or water. In a few species, the mericarps are flattened with the edges narrowed into wings that may play a role in dispersal.

FIGURE 12. *Nolana villosa* flowers visited by Oasis Hummingbird, *Rhodopis vesper*. **A**, Hovering above the flowers; **B**, Inserting tongue into corolla; **C**, View of feeding.

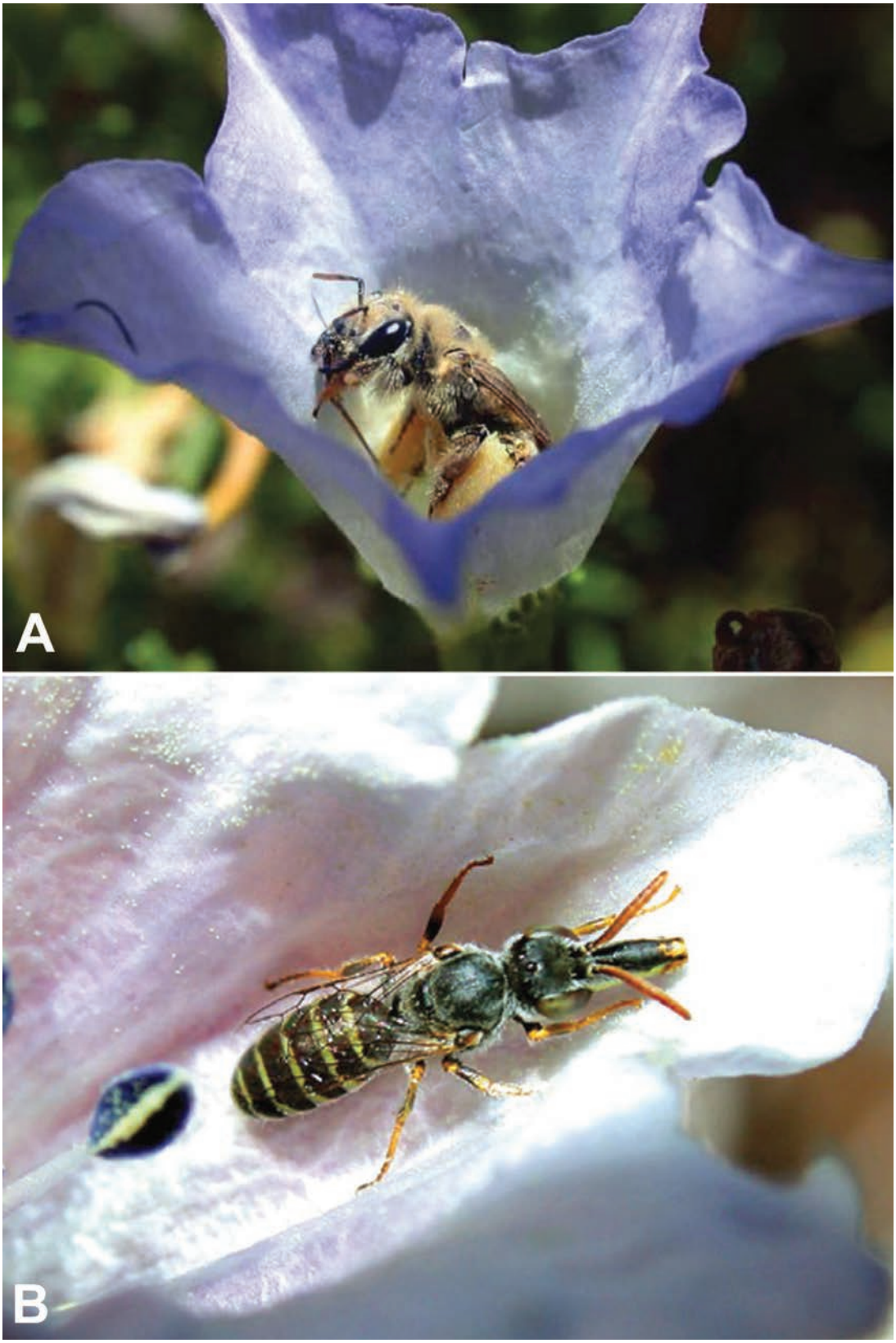


FIGURE 13. Endemic bees visiting *Nolana* corollas. **A**, *Nolanomelissa toroi* collecting pollen and nectar from *N. rostrata*; **B**, *Xeromelissa roseni* collected on *N. patula*.

In species from dune habitats, like *Nolana pallidula*, the branches bend inward during senescence, curling into a sphere with the characteristics of a tumbleweed, uprooting and rolling over the dunes (Fig. 14). This may be a putative adaptation for seed dispersal. *Nolana pallida* and *N. paradoxa*, among others, have pedicels that bend downward, thrusting the maturing and fragmenting mericarps directly into the fine sand (Fig. 6A-B).

Seed dispersal by oceanic currents, or thalassochory, was investigated in *Nolana galapagensis* by Fuster-Calvo et al. (2021) as part of their search for mechanisms of the colonization of oceanic islands. In that study, they examined the seeds of littoral species that were thought to have either physiological or morphological adaptations to saltwater dispersal. In 2001, an earthquake occurred in southern Peru and caused a tsunami that inundated the beachfront of the Camaná. It would have been easy for mericarps to be transported by the currents, either north or south. Similar phenomena may have been responsible for the extended distribution of *Nolana paradoxa* in near-shore habitats from central to southern Chile.

Myrmecochory, or "ant-dispersal," is the collection and dispersal of mericarps (seeds) by ants. In the only recorded case, mericarps were deposited as "trash" on the outside of ant nests in northern Chile (Fig. 15A–B). The ants likely remove the elaiosome once the seed has been transported to the nest. *Nolana albescens, N. incana* and *N. mollis* have mericarps with a thin, unorganized elaiosome or a colored substance on the surface of the mericarp (Fig. 15 C–E). While nothing is known about the composition of these elaiosomes, they generally have been reported to be high in lipids and fatty acids (Lengyel et al., 2010).

Reproductive System

Darwin (1877: 261) commented on the individual variability of pistils in *Nolana* and suggested that the condition was a step towards heterostyly. Darwin wrote, "It is probable that the first step towards a species becoming heterostyled is great variability in the length of the pistil and stamens, or of the pistil alone. Such variations are not very rare: with *Amsinckia spectabilis* and *Nolana prostrate* [=*N. humifusa*] these organs differ so much in length in different individuals that, until experimenting on them, I thought both species heterostyled." Heterostyly was reported in *Nolana* by Mesa-M. (1981), and many species exhibit some degree of style-stamen polymorphism accompanied by polymorphisms in the color and size of pollen. Detailed studies are needed to confirm the existence of heterostyly or simply variability of pistils in relation to anther length demonstrated in *Nolana*.

Reproductive isolation was investigated by Jewell et al. (2012), who reported reproductive barriers at four post-mating stages among eleven species from diverse species in *Nolana*. They reported that at least one stage was positively correlated with both genetic and geographic distance between species. Post-zygotic isolation was generally stronger and faster evolving than post-mating prezygotic isolation. Additionally, there was no evidence for mechanical isolation or for reproductive character displacement in floral traits that can influence pollinator isolation. In general, among the potential isolating stages examined, post-zygotic barriers appear more effective contributors to reducing gene flow, including between sympatric species.

Humaña et al. (2019) investigated the breeding system in *Nolana balsamiflua* with four pollination trials. No seeds were produced by agamospermy, autogamy or geitonogamy. Xenogamy accounted for 51.4% of fruiting, which they interpreted as full dependency on exogenous pollen and pollinator for reproduction.

Hybridization

Both artificial and natural hybridization has been recorded in *Nolana*: spontaneous hybrids in English gardens (Lindley, 1830; Johnston, 1936: 81), artificial hybridizations (Saunders, 1934; Freyre et al., 2005), and evidence for naturally occurring hybridization in sympatric species (Victor Quipuscoa, pers. comm.). There appear to be few barriers to artificial crossing (Freyre et al., 2005), and it remains a paradox that so many *Nolana* species can occur in complete sympatry, and yet hybrids appear to be rare.

Artificial hybridization. John Lindley (1824) published *Nolana paradoxa*, and subsequently described *Nolana tenella* (Lindley, 1830) based upon cultivated material from Chiswick, 1824, presented by *Robert Barclay s.n.*, (Holotype: CGE [05022]; Isotypes: G [GDC014138], K [000532266]), Fig. 16.

Ivan M. Johnston's (1936) discussion of *Nolana tenella* is concise and interesting, and, for that reason, it is presented here in its entirety (1936: 81–82):

"This species is of garden origin and apparently a chance hybrid of *N. humifusa* of Peru and *N. paradoxa* of Chile. It was originally described by Lindley from material 'Presented to the [London Horticultural] Society, in 1824, by Robert Barclay, Esq. by whom it was raised from Chilean seeds.' It is said to have flowered in the garden of the Society at Chiswick in August 1825. Lindley's paper concerning it was read in September 1827 and published the following year. Of *N. tenella* I have studied material in the Bentham collections at Kew labelled, '*Nolana tenella*, Hort. Barclay 15–7–30' and quite similar collections at Geneva labeled "*Nolana tenella* du Peru, Jardin de M. Barclay, Juill. 1830, M. Alphonse DC." These two collections agree closely with the original description and are, I believe, authentic representatives of the species. They are evidently hairy, especially on the stems, petioles and pedicels where the slimy spreading hairs are at least one millimeter long. Other material that I am content to refer to *N. tenella* is practically glabrous. This is the condition in the specimens at Washington distributed from a St. Petersburg garden as this species, and in the material at the Gray Herbarium which was grown in the Harvard gardens in 1865 (as *N. prostrata*).

When he described *N. tenella*, Lindley remarked, "This very pretty species has been confounded in the Botanical Magazine, tab. 2604 with my *Nolana paradoxa*, an extremely curious and widely different plant." This ambiguous remark

FIGURE 14. *Nolana pallidula*. Plant drying into a round tumbleweed held by Dra. Miyuki Nakazawa in Lomas of Sama Grande, Tacna, Peru (February 1998).

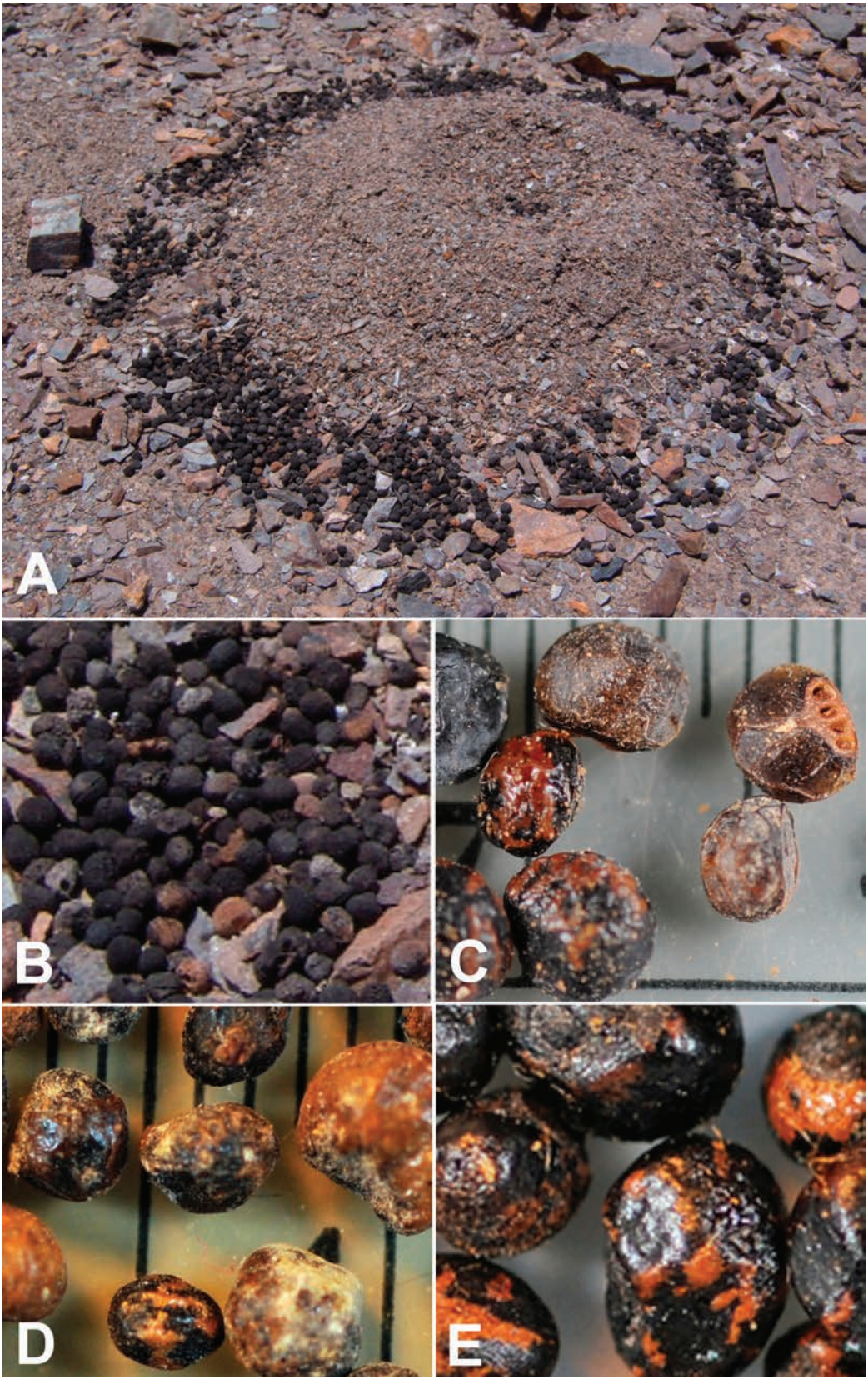


FIGURE 15. Myrmecochory or "ant-dispersal" of mericarps. **A**, Ant nest, desert in northern Chile; **B**, Mericarps with elaiosome removed and discarded outside the nest; **C**, Unorganized orange elaiosomes on *Nolana albescens* mericarps; **D**, Unorganized orange elaiosomes on *N. incana* mericarps; **E**, Unorganized orange elaiosomes on *N. mollis* mericarps.

FIGURE 16. *Nolana tenella*. Holotype from Cambridge University Herbarium, Cambridge, UK (CGE).

by Lindley has resulted in much confusion. The plant illustrated on plate 2604 (as I have fully discussed under *N. paradoxa*) is characteristic *Nolana paradoxa* of Chile and not representative of *N. tenella* as so many authors have supposed. Only the observations in the text accompanying this plate apply to *N. tenella*!

"Very significant is the following final paragraph in the Botanical Magazine, 'Our drawings were taken at the collection of the late John Walker, Esq. in May 1823, where it was raised from seeds imported from Chili, by Mr. Francis Place [who had also imported the seeds from which the type of *N. paradoxa* was grown]. But we had no opportunity of examining the plant particularly, and comparing it with *prostrata*, till we received specimens of both species from Bury Hill in August [1824] last.' It is to be noted that Bury Hill was the estate of Robert Barclay and the place from which the Chiswick plants described by Lindley as *N. tenella* were also obtained. What is more, the material studied by Lindley and by the editor of the Botanical Magazine seems to be part of the same distribution, for both authors mention August 1824 as the date upon which their material from Barclay's garden was described as *N. tenella* by Lindley. That received by the editor of the Botanical Magazine was misidentified with *N. paradoxa*, associated with the plate of that species, and discussed at length in the text where it was compared with *N. prostrata* of Peru.

"The status of *N. tenella* has recently been well established through breeding experiments conducted by Saunders (1934). She demonstrated that it is 'not a species but the F_1 hybrid between *prostrata* ♀ and *atriplicifolia* ♂' and has given some excellent colored plates showing the parents as well as the hybrid. Her *N. atriplicifolia* I consider to be a form of *N. paradoxa* Lindl. *Nolana prostrata* is a synonym of *N. humifusa*. Miss Saunders believes *N. tenella* to be a natural hybrid. As I have discussed under *N. paradoxa*, however, the distribution of the two parents is such that a wild hybrid is out of the question. *Nolana tenella* must have had a garden origin."

As Johnston politely pointed out, the likelihood of natural hybrids between a northern Peruvian species, *Nolana humifusa*, and a central Chilean species, *N. paradoxa*, was an impossibility; however, Miss Saunders was quite correct in her characterization of the origins of the parental species. The colored illustration of the hybrid she produced corresponds to what has been the named hybrid, *N. tenella* Lindl. (Fig. 17).

Nolana Patents. Two *Nolana* hybrids have been registered with the United States Plant Patent Office. The first is called "Nolgold" (US PP14141-P2) and was the product of a hybrid cross between a cultivated accession of *Nolana paradoxa* (♀) and *N. humifusa* (♂). This is essentially the same product as the plant described by Lindley (1828) as *Nolana tenella* (see above). The hybrid *Nolana* in Dijon, France originated from a cross-pollination made in May 1995 of *N. paradoxa*, as the female, or seed parent, with an unidentified selection of *Nolana humifusa*, as the male, or pollen parent. The new *Nolana* was selected as a single flowering plant from the resulting progeny from the cross-pollination.

The second patented *Nolana* was called "*Loma Blanca*" (US PP19450-P3) and was the product of a hybrid cross between a cultivated accession of *Nolana paradoxa* (♀) and wildtype *N. aplocaryoides* (♂). The registration of "*Loma Blanca*" was an outcome of Freyre and Douglas breeding experiments with *Nolana* species at the University of New Hampshire Research Greenhouses, including crosses involving *N. acuminata, N. aplocaryoides, N. elegans, N. patula* (as *N. flaccida), N. humifusa*, *N. paradoxa* and *N. rupicola*. Between July and September 2001, 324 interspecific pollinations were performed in all possible combinations. A total of 61 interspecific hybrids were obtained, combining *N. paradoxa* x *N. aplocaryoides*, *N. paradoxa* x *N. elegans*, *N. paradoxa* x *N. rupicola*, *N. elegans* x *N. paradoxa* and *N. rupicola* x *N. paradoxa*. These results were published (Freyre et al., 2005), and two subsequent publications documented the floral development and sexual compatibility (Douglas and Freyre, 2010; Douglas, 2016).

In the patent statement, "*Loma Blanca*" was described as follows, "A new and distinct cultivar of *Nolana* plant named 'Loma Blanca', characterized by numerous single flowers that are white in color with a dark purple veined center; dark purple anthers and pollen grains, freely branching growth habit, no fruit set from self-pollination, and good performance in the garden and as a hanging basket."

Putative natural hybridization. After studying *Nolana* populations over many years, it has always been of interest how so many *Nolana* species could grow sympatrically in disturbed habitats, but with few clear visual evidence of hybrids. In northern Peru, *N. humifusa* and *N. gayana* are sympatric over much of their range, and Ferreyra (1961: 15) suggested that they may hybridize at some localities. No putative hybrids were recognized or encountered between these two in this study. Another, example is in coastal southern Peru, where *N. pilosa* (Fig. 18A, D) occurs sympatrically with *N. thinophila* (Fig. 18C, F). Individuals with intermediate morphology may represent hybridization or introgression (Fig. 18B, E). Further studies will be necessary to confirm these initial observations.

Chromosome Numbers

The five chromosome counts reported for *Nolana* suggest the base chromosome number to be x=12 with $2n$=24 reported from the following species: *N. galapagensis* (Eliasson, 1970), *N. humifusa* (Datta, 1933, as *N. prostrata*), *N. paradoxa* (Di Fulvio, 1969), *N. carnosa* (Di Fulvio, 1984, as *N. rostrata* var. *carnosa*), and *N. crassulifolia* (Chiarini et al., 2010). This base number recorded in chromosome counts within potentially related genera, include *Sclerophylax* Miers (2n=24), *Lycium* (2n=24, 36, 48) [*sub. nom. Grabowskia* (2n=24, Chiang, 1983)]. Chiarini et al. (2010) reported the first karyotype for *Nolana* with a mitotic count of 2n=24 for *N. crassulifolia*. They further stated that the karyotype for *Nolana* was close to that of *Lycium* and *Grabowskia*. Lujea and Chiarini (2017) investigated the differentiation of *Nolana* and *Sclerophylax* by looking at heterochromatin and rDNA patterns. They concluded that while they were morphologically distinct, the chromosome number and karyotype features were consistent with their position within the "x=12 clade."

FIGURE 17. *Nolana tenella*. Illustration of the artificial hybrid, Plate 34, Saunders (1934).

Distribution

Nolana species are recorded from three countries: Ecuador, with one species confined to the Galapagos Islands, Peru, with 42 endemics, Chile, with 46 endemics, and three species (*N. adansonii*, *N. gracillima*, *N. lycioides*) with modern distributions in Peru and Chile (Fig. 1). Species occur in a full range of environments at elevations ranging from sea level to 4100 m.a.s.l.; however, the great majority of species are in near-ocean habitats between 50–600 m.a.s.l. and within a unique coastal environment termed the *lomas* formations (Dillon, 1997; Dillon and Hoffmann, 1997).

A few species are widely distributed or occur over wide altitudinal ranges. It is often overlooked that the southern distribution of *N. paradoxa* ranges to well below 42˚S latitude. Others, such as *N. acuminata* and *N. sedifolia* in Chile, and *N. humifusa*, *N. gayana*, and *N. spathulata* in Peru, have wide distributions, occurring within several *lomas*

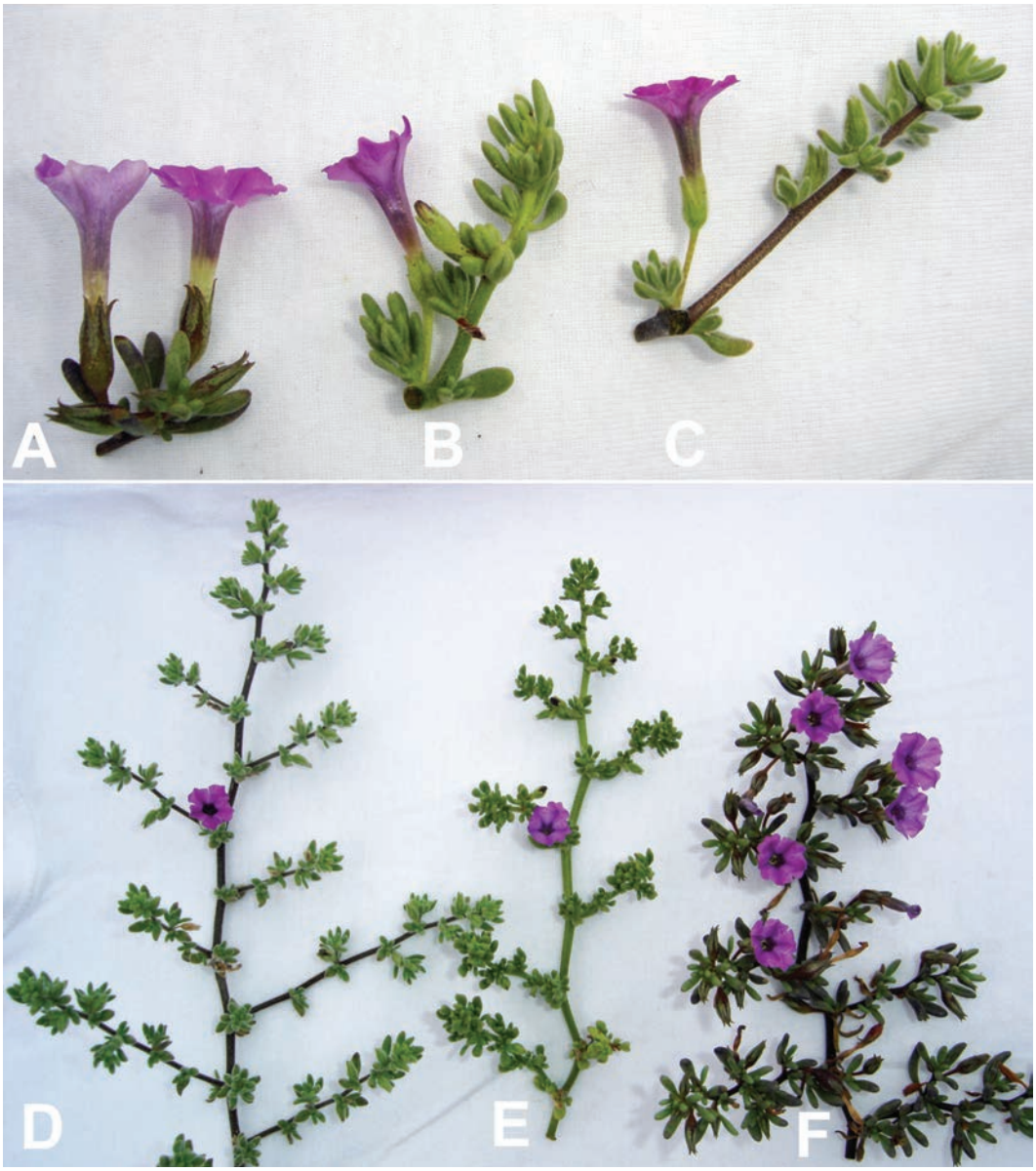


FIGURE 18. Putative natural hybrids between *Nolana pilosa* and *N. thinophila* from coastal southern Peru. **A** & **D**, *N. pilosa*; **C** & **F**, *N. thinophila*; **B** & **E**, Putative hybrids.

formations. Still other species are distributed over wide elevational ranges. *Nolana linearifolia* can be found from near sea level near Taltal, Chile to the upper reaches of the Quebrada Paposo (1000 m.a.s.l.), and there are a few records from over 3000 m.a.s.l. Likewise, *N. leptophylla* was found from near sea level at Quebrada Bandurrias to over 1000 m.a.s.l. above El Cobre, with at least one record from 4200 m.a.s.l. One potential source of range extension may be the transport of *Nolana* mericarps downslope during episodic flooding events, where large quantities of water run from high elevation localities to lower sites, and sometimes even reaching the coast (Houston, 2006a).

Disjunctions. *Nolana galapagensis* occurs 1500 km from the continental Peruvian coast. The evidence is far from conclusive, but it appears it is more closely aligned with coastal Peruvian taxa. Three species are essentially Peruvian taxa, *N. adansonii*, *N. gracillima*, and *N. lycioides*, that have disjunct populations south of 18˚S latitude. A single collection of *N. arenicola* from 1880 cites Arica as the origin; it appears that this species is confined to extreme southern Peru, and no modern collections have been examined from Chile. The Chilean species, *N. jaffuelii,* has one collection cited from Tacna, Peru in September 1864; however, no modern collections confirm this distribution. No fewer than five Peruvian species, including *Nolana chapiensis*, *N. lezamae*, *N. laxa*, *N. urubambae*, and *N. weberbaueri*, are at elevations over 1000 m.a.s.l., and more than 50 km from the coast. In Chile, *N. rhombifolia* is notable for being related to inland, southern Peruvian species.

Sympatric species. The geographic distribution of some *Nolana* species overlaps within the same geographic range. At times the phenomenon can be explained by species

occupying different ecological niches; however, in some locations, sympatry of *Nolana* species is immediate and extensive. For example, in the region of Las Lomitas in Parque Nacional Pan de Azúcar (northern Chile), as many as ten well-marked *Nolana* species were recorded growing in proximity (Fig. 19A–G). The collections in Figure 19 were made in an area no more than 500 m^2 on 30 September 1988 and include *Nolana mollis* (Fig. 19A), *N. linearifolia* (Fig. 19B), *N. patula* (Fig. 19C), *N. leptophylla* (Fig. 19D), *N. elegans* (Fig. 19E), *N. aplocaryoides* (Fig. 19F), and *N. glauca* (Fig. 19G).

Rundel et al. (1996), in a list for the flora of Pan de Azúcar National Park, reported several *Nolana* species from personal observations and incorporated observations made by other botanists. The following species were listed as occurring in the park; however, since that time, voucher data do *not* support the occurrence of the following species from that area; *Nolana crassulifolia*, *N. paradoxa*, *N. peruviana*, *N. rostrata*, and *N. stenophylla*. All of these species have distributions restricted to areas much farther north or much farther south than Pan de Azúcar National Park. The list of recorded *Nolana* is currently amended to include 13 species: *N. acuminata*, *N. aplocaryoides*, *N. divaricata*, *N. elegans*, *N. glauca*, *N. incana*, *N. leptophylla*, *N. linearifolia*, *N. mollis*, *N. patula*, *N. salsoloides*, *N. rupicola*, and *N. villosa*.

At the type locality for *Nolana reichei*, five species are recorded in an area ca. 25 m^2; these include *N. crassulifolia*, *N. werdermannii*, *N. rupicola*, and *N. sedifolia* (Fig. 20A–E). Nothing obvious in the immediate area separates them, and no instances of intermediate or "hybrid-looking" individuals were encountered. At the type locality for *Nolana dianae* in a quebrada above Playa de los Hornos, three other *Nolana* species are present, including *N. balsamiflua*, *N. linearifolia*, and *N. peruviana*. Storms can create excessive runoff that often culminates in pooling that brings mericarps from upslope into proximity. As the water evaporates, the accumulated mericarps germinate and result in congregations of several species.

There are many species in Peru that have overlapping distributions and that co-occur in the *lomas* formations. In the Lomas of Jahuay, for example, *N. spathulata* and *N. tomentella* grow sympatrically, and farther south, *N. arequipensis* and *N. plicata* co-occur over large areas. In a narrow, near-ocean habitat near Punta Bombón,

FIGURE 19. *Nolana* species occurring sympatrically at Pan de Azúcar, northern Chile, 30 September 1988. **A**, *N. mollis*; **B**, *N. linearifolia*; **C**, *N. patula*; **D**, *N. leptophylla*; **E**, *N. elegans*; **F**, *N. aplocaryoides*; **G**, *N. glauca*.

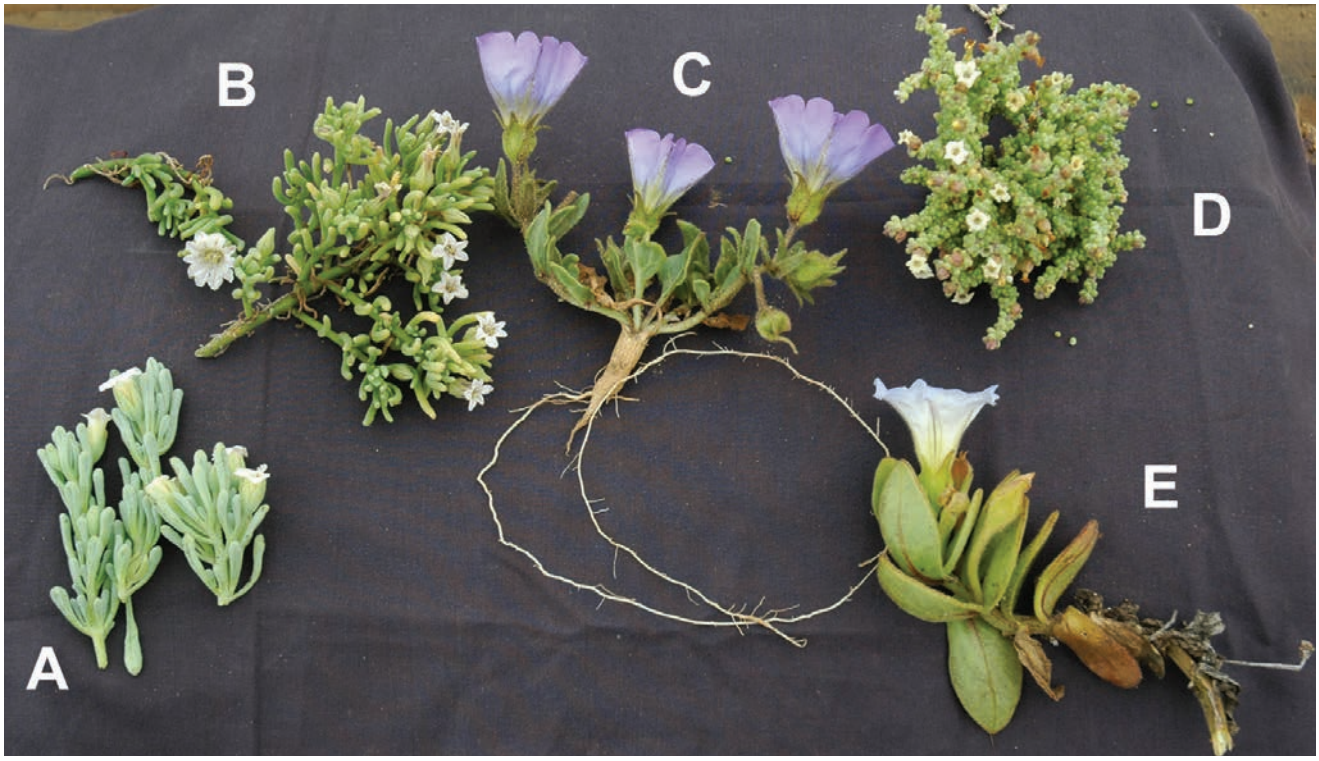


FIGURE 20. *Nolana* species occurring sympatrically at Caleta El Toro, northcentral Chile, 11 December 2004. **A**, *N. crassulifolia*; **B**, *N. werdermannii*; **C**, *N. reichei*; **D**, *N. sedifolia*; **E**, *N. rupicola*.

several species are growing sympatrically, including *N. bombonensis*, *N. adansonii*, *N. pilosa*, *N. spathulata*, and *N. thinophila*.

Ecology

Within the entirety of *Nolana* in continental South America, most *Nolana* species (>70) are restricted to *lomas* formations (Dillon, 1997; Dillon and Hoffmann, 1997; Rundel et al., 1991) and are strongly influenced by coastal fog formations. Furthermore, within the *lomas* formations, *Nolana* is one of the flora's more conspicuous or dominant elements (Dillon, 2005). The ecological preferences of *Nolana* are essentially arid and semi-arid habitats throughout the Atacama and Peruvian deserts (Rundel et al., 1991).

The ecological differences between coastal Peru (6°–18°S latitude) and Chile (18°–42°S latitude) are immense and are likely responsible for the high degree of geographic fidelity recorded in *Nolana*. Most species have very narrow distributions with small, restricted geographic ranges and specific ecological requirements. The greatest concentration of species is in near-ocean localities within a few kilometers of the shoreline. The two primary differences that distinguish Chile and Peru are in their respective physiographic characters. In Chile, in areas of the greatest concentration of species, the coast is cut by only a few large river valleys that carry water, including Río Lluta, Río Camarones, Río Loa, Río Copiapó, and Río Elqui. In northern Chile, there are "aguadas", or springs, that provide a source of underground water. An exact number is difficult to calculate, but perhaps over 70 localities with these springs exist. In Peru, the coastal plain is dissected by no fewer than 28 river valleys, some carrying water, while others are only seasonally active. No sites recognized as "aguadas" are recorded in Peru.

Species common to shoreline and beach dunes include *Nolana aplocaryoides, N. bombonensis, N. crassulifolia*, *N. carnosa*, *N. divaricata*, *N. peruviana*, *N. paradoxa*, *N. adansonii*, *N. minor*, *N. stenophylla*, and *N. thinophila*. Other species are common to inland and/or upland habitats far from the coast, including, but not restricted to, *Nolana foliosa*, *N. gracillima*, *N. rhombifolia*, *N. leptophylla*, *N. onoana*, *N. patula*, *N. chapiensis*, *N. confinis*. *N. laxa*, *N. lezamae*, *N. sessiliflora*, *N. sphaerophylla*, *N. tarapacana*, *N. urubambae*, and *N. weberbaueri*. Some Chilean species are growing in *aguadas*, as mentioned above. These areas are fed by underground springs in an otherwise dry *quebrada* with typically highly saline or alkaline water. Among the species to be encountered near *aguadas* are *Nolana divaricata*, *N. incana*, *N. mollis, N. peruviana*, and *N. villosa*. When available moisture is not limiting, individuals can attain very large sizes; single plants of the prostrate shrubs *N. incana* or *N. villosa* can grow to of several meters in diameter. *Nolana galapagensis* is the northernmost species and is restricted to sandy dunes near the ocean on several islands within the Galápagos Island chain on the Equator (Wiggins and Porter, 1971).

Nolana species are often important within their respective communities and often are dominant members, occurring with great frequency. During the El Niño years of 1982–1983, 1987–1988, and 1997–1998, various *Nolana* species were seen to produce enormous populations (Dillon et al., 2003).

For example, in 1998, the near-shore mountains at various localities in northern Peru (e.g., Cerro Cabezón, Cerro Campana, and Virú) had a 100% ground cover of *Nolana humifusa* for perhaps 50–100 hectares. Seed production in annuals is impressive under El Niño conditions and allows the replenishment of the seedbanks for the annuals of the *lomas* formations (Ohga, 1991, 1992). In southern Peru in 1998, the vegetative ground cover was less than 50%, but the dominant species, as measured by individuals and those of greatest size, were *Nolana spathulata*, *N. plicata*, *N. aticoana*, *N. thinophila*. In some localities, *Nolana* species are the only species present; for example, *Nolana pallida* is the only flowering plant species growing on bare sand dunes north of Chala in southern Peru. Likewise, *Nolana thinophila* is one of a few plants to grow on pure sand and in proximity of the ocean near Mejia, coastal Arequipa.

Ecophysiology

Nolana species are, to varying degrees, leaf and stem succulents with most occupying saline and/or hyper-arid habitats. With infrequent precipitation in the form of rainfall, it has been suggested that *Nolana* species have developed the ability to utilize water gained from more frequent fog in coastal environments. One mechanism is simply the physical condensation on pubescent leaf surfaces covered with dendritic or branched trichomes or other types of multicellular trichomes.

Plant adaptation or tolerance to salinity stress has been studied, and it apparently involves complex physiological traits, metabolic pathways, and molecular or gene networks (Gupta and Huang, 2014; McCue and Hanson, 1990). While several representatives of genera in the Solanaceae have been analyzed (De la Torre-González et al., 2018; Escalante-Magaña et al., 2019; Palchetti et al., 2021), no *Nolana* species have been investigated, although several species are halophytes that can withstand high salinity. *Nolana adansonii*, *N. thinophila*, *N. carnosa*, *N. crassulifolia*, *N. divaricata*, and *N. paradoxa* all occur near the ocean, often within the spray from waves (Fig. 5D). In a few *Nolana* species (Gibson, 1996; Thompson et al., 1998; Dassanayake and Larkin, 2017), salt glands on leaf surfaces exude salt, and that salt becomes hydrated during diurnal fog periods (hygroscopic effect). Mooney et al. (1980) hypothesized that in *Nolana mollis*, the "salty dew" condenses on the leaf surfaces and drips to the soil surface below to be taken up by the roots, or it might be taken up directly through the leaf surfaces during the day. Thompson et al. (1998) suggested an alternative hypothesis for *Nolana patula* (as *N. flaccida*); i.e., the salty water coating the leaves acts as a surrogate for inhibiting transpiration. The salty layer prevents excessive transpiration during the day by both increasing the relative humidity of the boundary layer and by decreasing leaf temperature.

The high concentrations of mineral salt and calcium oxalates within the plant body can be seen when plants die and their leaves and stems degrade, leaving a characteristic halo of mineral ashes. Several species display this phenomenon, such as *Nolana mollis* (Fig. 21) and *N. villosa* (Fig. 22). The foliar content of the mineral ash has been calculated to be 20–40% of total weight (Rundel et al., 1980). Rundel (pers. comm.) radiocarbon dated two samples of ash haloes of *Nolana villosa* lacking any woody remains; one sample was dated to be ca. 300 years old and the other as ca. 2000 years old.

The photosynthetic strategies of desert plants have been studied extensively (Gibson and Rundel, 2012), and the presence of various patterns has been documented, including C3, C4 and CAM. The photosynthetic apparatus in several *Nolana* species has been investigated (Ehleringer et al., 1998; Tago, 1999). In theory, CAM and C_4 plants can be detected by their relative proportions of $^{13}C/^{12}C$ isotopes, expressed as ^{13}C values to estimate carbon isotope discrimination values (Farquhar et al., 1989). Tago (1999) reported values of greater than -24‰ for various Chilean species, including *N. elegans*, *N. acuminata*, *N. stenophylla, N. glauca*, *N. albescens*, *N. crassulifolia*, *N. mollis*, *N. patula*, *N. leptophylla*, *N. peruviana, N. divaricata*, *N. carnosa*, and *N. rostrata*. These results are not evidence of CAM, and Ehleringer et al. (1998) considered values of -19.8‰ to be consistent with C_3 photosynthesis. The *Nolana* species analyzed suggest high water use efficiency values (WUE), but not actually CAM. Neither C_4 nor CAM plants have been reported for the Solanaceae (Smith and Winter, 1996).

While no experimental data has been presented, *Nolana* taxa have been included in lists of Chilean species that could potentially be useful in phyto-stabilization, a process where native species are capable of spontaneously colonizing abandoned mining tailing storage facilities in north-central Chile (Orchard et al., 2009). The use of *Nolana* species may well be effective in colonizing environments high in salts and/or mine wastes, thus adding to their potential economic importance.

Phytochemistry

Bate-Smith (1962) reported the occurrence of hydroxyflavonols, quercetin and kaempferol in *Nolana*, compounds also previously reported from within the Solanaceae. Chamy et al. (1997), Chamy et al. (2002), and Garbarino et al. (1986, 1988) reported the occurrence of diterpenoids, and Garbarino et al. (1993) reported the occurrence of sesquiterpenoids. No evidence of cyanogenic compounds, iridoids, ellagic acid or proanthocyanidins is found in the literature. Simirgiotis et al. (2015) conducted a large-scale analysis of phenolic compounds in *Nolana aplocaryoides*, *N. leptophylla*, and *N. ramosissima*, three northern Chilean species, utilizing high pressure liquid chromatography with a subsequent characterization of extracts. The 30 compounds identified were primarily flavones, flavanones, phenolic acids, fatty acids, some glycoside flavonoid conjugates and their derivatives. Cifuentes et al. (2020) isolated 61 compounds from *Nolana ramosissima*, mainly glycosylated flavonoids, flavanones and several oxylipins, and these were tested for smooth muscle relaxation in rat aorta. Vio-Michaelis et al. (2012) examined the antifungal effect of complete methanolic extracts from native Chilean plants, including *Nolana sedifolia*. *Nolana sedifolia* extracts included

FIGURE 21. *Nolana mollis* undergoing auto-combustion resulting in an ash halo.

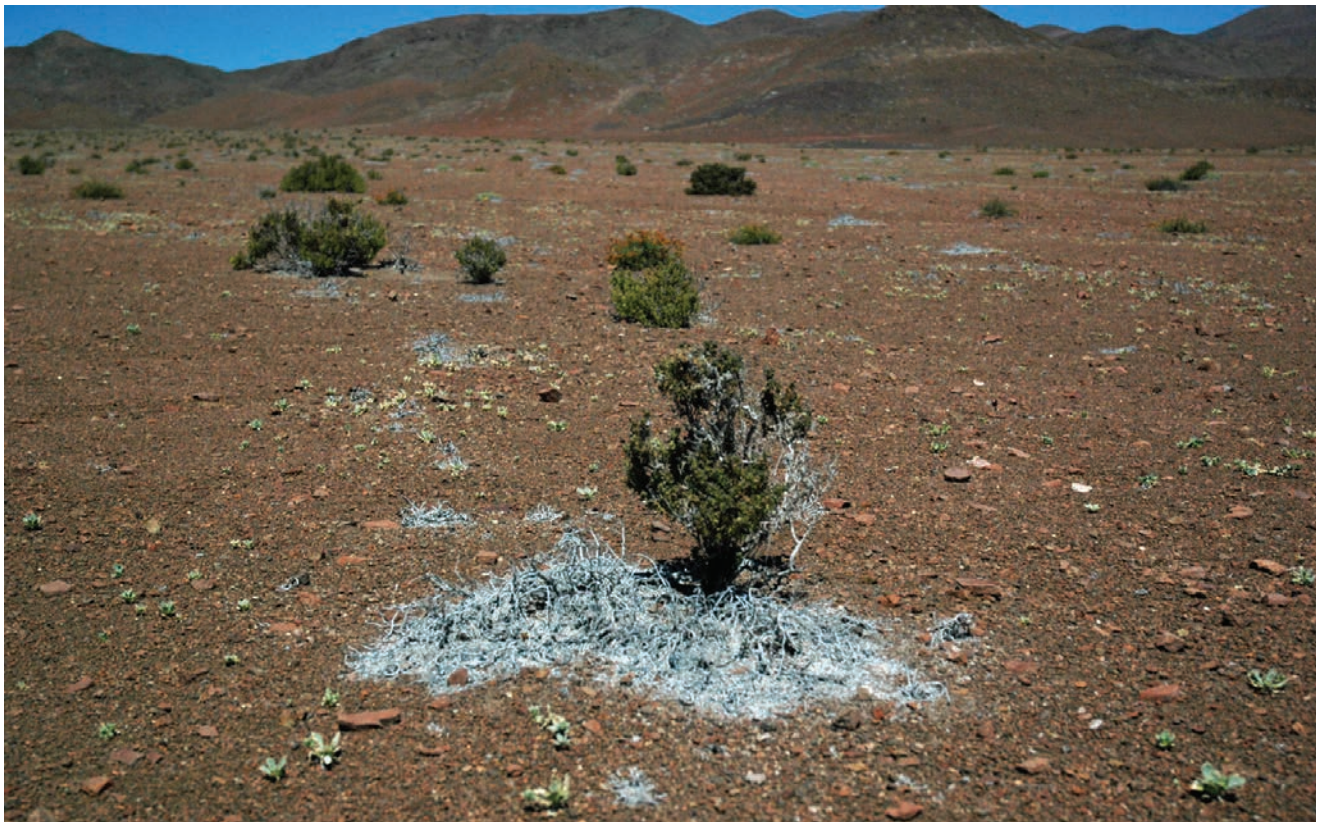


FIGURE 22. *Nolana villosa* undergoing auto-combustion resulting in an ash halo.

various phenolic acids (e.g., chlorogenic acid, cinnamic acid, p-coumaric acid, ferulic acid, vanillin, vanillic acid, caffeic acid, 3, 4-hydroxybenzoic acid, procatechuic acid, and rutoside) that showed an inhibitory effect on *Botrytis cinerea* Pers. mycelial growth.

Biogeography and Evolution

The Solanaceae are found on all continents except Antarctica, and recent analysis suggests that South America is the center of diversity and its ancestral range (Dupin et al., 2017). While *Nolana* was not mentioned specifically, the analysis confirmed that early evolution took place in South America. The geographic distribution in *Nolana* has been shaped by the age and extent of the prevailingly arid habitats they occupy (Dillon et al., 2009). Short-term climatic fluctuations, such as El Niño events (5- to 50-year cycles), and longer-term climatic change associated with glacial cycles (13,000- to 200,000-year cycles) have been influential in changes in the floras associated with the Andean Cordillera. Glacial cycles have had global effects before and throughout the Pleistocene, with the formation of glaciers on mountaintops resulting in dramatic sea level fluctuations. Estimates of the extent of lowering of sea level range from between 120–230 m.a.s.l., a drop that would have significantly changed the position of the seashore relative to the present-day boundary and exposed the northern Peruvian continental shelf from 5° to 15°S latitude (Dillon et al., 2003). Three primary floristic segments within the coastal deserts reflect independent histories: the northern Peruvian unit from 7°55'S to 12°S latitude, the southern Peru unit from 12°S to 18°S latitude, and a northern Chilean unit from 20°S to 28°S latitude (Dillon et al., 2003). The greatest number of *Nolana* endemics are in southern Peru, and a separate group of endemics occurs in northern Chile. This pattern is reflected in the overall flora, with three distinctive units, in addition to a central Chilean unit from 28° to >40°S latitude. Only three species have distributions that span the 18°S latitude segment. The first of these, *N. adansonii*, clusters with southern Peruvian species and potentially originated in Peru. The second, *N. gracillima*, is recorded from several upland localities (>2500 m.a.s.l.) in Peru and northern Chile, a pattern displayed by other taxa (Pinto and Luebert, 2009). Its origins remain equivocal, and it has been recovered in a group with both southern Peruvian and northern Chilean species (cf. Clade E). The origins of *N. lycioides* display conflicting marker data suggesting either southern Peru or northern Chile, so its origin remains equivocal. While there are reports of *N. jaffuelii* from extreme northern Chile, there are no modern collections of this taxon from Peru. It would cluster with other Chilean species based upon its morphology and is considered a Chilean species with putative extension into southern Peru historically. *Nolana arenicola* is a Peruvian species that has one collection recorded from Arica, Chile in 1880, the second year of the War of the Pacific (1879–1883); prior to the war, Arica was a Peruvian city. Based upon both shared morphology and molecular data (Dillon et al., 2009), *N. arenicola* is considered a Peruvian species with a putative historical extension into northern Chile. There are no modern collections of *Nolana arenicola* from Chile.

Regardless of the gene sequences analyzed, the first appearance of *Nolana* is calculated to be in the lower Tertiary (Miocene, 10.6–11.6 mya) or older. Divergence data from ITS suggests *N. galapagensis* reached the island chain sometime between 4–8 mya. Furthermore, due to character evolution in the continental members of *Nolana*, *N. galapagensis* was pre-adapted to beach habitats prior to its dispersal to the island chain. Based upon geography, Johnston (1936) suggested that the closest relatives of *N. galapagensis* were *N. humifusa* or *N. laxa*; however, results suggested that *N. lycioides* may be a more logical choice given preliminary molecular analysis (Dillon et al., 2009). In that analysis, the divergence time between *N. galapagensis* and *N. adansonii* was estimated to be 0.35 mya.

The distribution of various morphological characters in relation to hypotheses of phylogenetic relationships indicates that many of the characters used in previous classifications of *Nolana* are highly homoplasious. The distribution of life forms in *Nolana* suggests independent development of annuals, perennial herbs, and shrubs in both Peru and Chile, and the Galapagos Islands (Ecuador). The distribution of leaf shapes, either laminar or linear, also suggests independent development in both Peru and Chile. While several *Nolana* species are largely glabrous (e.g., *N. arenicola*, *N. coronata*, *N. glauca*, *N. gracillima*, *N. humifusa*, *N. pterocarpa*, and *N. thinophila*), others have various types of co-occurring trichomes. Some smaller groups can be circumscribed with pubescence, but only within certain parameters. Finally, the number of mericarps appears to be variable within both Peruvian and Chilean taxa and is not a reliable character to diagnose groups.

Molecular Systematics

Family and Generic Relationships. The family Nolanaceae was proposed by Berchtold and Presl in 1820, and their name has priority over that proposed by Barthélemy Charles Joseph Dumortier (b. 1797–d. 1878), a Belgian botanist who simply listed it as "Family 70" (Dumortier, 1829: 24). Until recently, most modern classifications treated *Nolana* at the familial level (Cronquist, 1981; Mesa-M., 1986) or at a subfamilial rank within the Solanaceae (Thorne, 1968, 1983; D'Arcy, 1979, 1991; Dahlgren, 1980; Takhtajan, 1980). William G. D'Arcy (b. 1931–d. 1999) treated it as a tribe, Nolaneae, in the Solanaceae, and included 22 species in two genera, *Alona* and *Nolana* (D'Arcy, 1991). Armando T. Hunziker (b. 1919–d. 2001) excluded all *Nolana* taxa from his monumental treatment of the family, *The Genera of Solanaceae* (Hunziker, 2001) and would not allow *Nolana* or *Sclerophylax* to be considered for the treatment of the Solanaceae in the series *Families and Genera of Vascular Plants* (FGVP). The familial status of *Nolana* was tested by Olmstead and Palmer (1992) using chloroplast DNA restriction site mapping and recognized a *Nolana* clade within the Solanaceae. Furthermore, their study suggested *Nolana* to be deeply nested within the subfamily Solanoideae (Solanaceae) and related it to *Lycium* and *Grabowskia* (Olmstead et al., 1999, 2008; Olmstead and Bohs, 2007).

Upon Armando Hunziker's death in 2001, the editors moved the treatment of the "Nolanaceae" to the FGVP treatment as a single genus, *Nolana*, within the Solanaceae (Dillon, 2016). In all discussions of relationships, authors have perhaps placed undue emphasis upon the characters of the ovary.

Olmstead and Bohs (2007), in their summary of molecular results for the Solanaceae, discussed a clade comprising *Lycium*, *Nolana*, and *Sclerophylax* as "Lyciina", an unranked informal name. Olmstead et al. (2008) recovered *Nolana* as the sister taxon to *Sclerophylax* within the Solanoideae (Chiarini et al., 2022), this within a moderately well-supported clade with Hyoscyameae, Lycieae (i.e., *Lycium*), *Grabowskia*, *Phrodus*, *Nolana*, *Jaborosa*, *Sclerophylax* and *Latua* that is sister to the remainder of the Solanoideae. Phylogenetic studies (Levin and Miller, 2005; Levin et al., 2007, 2011) suggested that the Chilean *Phrodus* and the exclusively American *Grabowskia* be included in *Lycium*. Martins and Barkman (2005) used the nuclear gene SAMT (salicylic acid methyltransferase) to estimate intergeneric relationships within the Solanaceae and reported a strong sister relationship between *Nolana* and *Lycium*.

Huang et al. (2023) provided additional molecular data and established their hypotheses of phylogenetic relationships based on transcriptomic and/or genomic datasets. In the resulting classification and arguments for paraphyly, they chose to establish the subtribe encompassing *Nolana* and its closest relatives in the Lycieae Lowe (1872). This does not conform with existing nomenclatural regulations, since Nolaneae Rchb. (1837) has priority at that level. Subtribal relationships are becoming clearer but are not fully resolved.

Species Relationships. Tago (1999) analyzed DNA sequence data (ITS and *mat*K) from 37 *Nolana* species, and her analysis supported the monophyly of the genus and only weak support for two subgenera, *Alona* and *Nolana*. Initial marker data suggested conflicting hypotheses of relationships within *Nolana*. Tago-Nakawaza and Dillon (1999) discussed some of the issues with the internal classification and suggested that further sampling would be necessary to resolve this. Beginning in 2007, a series of investigations with broader sampling within the genus, and utilizing additional DNA markers, further confirmed the monophyly of the genus and suggested seven groups. Each clade is discussed in the following section (Dillon et al., 2007c, 2009; Tu et al., 2008). Olmstead et al. (2008) and Olmstead and Bohs (2007) made a significant modification to Armando Hunziker's (2001) classification by moving *Nolana* and *Sclerophylax* into subfamily Solanoideae.

Species age and diversification

Calculation of age and species diversification using molecular sequence data is controversial. One issue is the absence of good fossil data with which to root any analysis. Dillon et al. (2009) presented an analysis using sequence data that suggested an estimated age point for the divergence of *Nolana* from its sister *Sclerophylax* to be 8.48 mya (Miocene) and the crown age of *Nolana* to be 4.02 mya. Divergence estimates of 8.48 mya is timed with the final uplift of the Frontal Cordillera and Precordillera in Chile (Hoke and Garzione, 2008). Should the timing be essentially correct, the crown group for *Nolana* is dated at 4.02 mya (Pliocene), a time when western South America was responding to increasing aridity. The divergence of *N. sessiliflora* and the entirety of *Nolana* is dated at 2.88 mya. The dating results presented by Dillon et al. (2009) have been challenged (Guerrero et al., 2013) in an analysis conducted with molecular sequence data culled from several original studies, including those published by Dillon et al. (2007c, 2009) and Tu et al. (2008). Those authors combined published sequences from three plant genera and one lizard and concluded that the calculations by Dillon et al. (2009) were incorrect. Särkinen et al. (2013) completed a supermatrix analysis, which suggested the *Nolana* clade is slightly older at 6.34 mya.

Tripp et al. (2017) suggested that deserts typically have low levels of plant diversity, particularly infrageneric diversity. They reported that *Peltidium* (Acanthaceae), with 37 species in the Namibian Desert, yielded a crown age for the African species of 1.5–4.8 mya and a diversification rate of 0.8–2.1 species per one million years, a rate they considered as on par with diverse genera in tropical, Mediterranean, and alpine environments. The development of no fewer than 92 species in *Nolana* in 4–6 million years from within what has been called the driest desert in the World (Hartley et al., 2005; Houston, 2006b) is noteworthy. Huang et al. (2023) calculated putative ages of 28.4 mya for the Lycieae and Nolaneae clade and 12.4 mya as the divergence date for *Nolana*. Calculations of putative ages of clades is controversial, and this topic is under active investigation in several laboratories.

Major Clades

Molecular studies completed to date have confirmed that all *Nolana* species (Table 1) recognized here are members of a monophyletic clade (Tago, 1999; Dillon et al., 2007c, 2009; Tu et al., 2008) within the Solanaceae (Olmstead et al., 2008). The primary morphological character for diagnosis of the genus is the mericarp, either fused or individual. Classifications have varied widely, with authors attempting to organize the genus according to cohesive morphological attributes such as plant form, leaf size and pubescence, corolla size, or mericarp number and fusion. The internal classification of *Nolana* was addressed by Johnston (1936), where he grappled with the recognition of genera and circumscribing groups of species. As discussed in the *Taxonomic History*, I. M. Johnston first accepted four genera, *Alona*, *Bargemontia*, *Periloba*, and *Nolana*. It seems that the more he observed, the more difficult it became to define these four genera, and he ultimately only accepted two weakly defined genera, *Alona* and *Nolana*. *Alona* was the easiest to recognize, but the large genus, *Nolana*, was clearly a complex mixture of taxa defined by applying emphasis to one character or another, making the diagnosis of additional genera impossible. Johnston went on to say, "Though these species are surprisingly diverse and well-marked, they do not fall into any groupings that are convincingly natural and monophyletic."

The clarification of relationships within *Nolana* has greatly benefited from detailed molecular studies, which provided insights into the internal classification of *Nolana*. These results recovered seven clades (Dillon et al., 2009) (Table 1).

Clade A (1 sp). *Nolana sessiliflora* is in the basal position and is sister taxon to the remainder of the genus with high support among all the various DNA markers utilized (Dillon et al., 2007c, 2009; Tu et al., 2008). *Nolana sessiliflora* is sister to Clade B, which in turn is sister to the remainder of *Nolana* (Clades C–G).

Clade B (9 spp). The recovered members of this clade have historically been recognized as a segregate genus, *Sorema,* a group with morphological fidelity and recovered by all DNA markers (Tago-Nakazawa and Dillon, 1999; Dillon et al., 2007c, 2009; Tu et al., 2008). The diagnostic characters, thickened taproot and petiolate basal leaves in a rosette are also recorded in three species from southern Peru as members of Clade D (i.e., *N. inflata*, *N. scaposa*, and *N. weissiana*). The corollas and mericarps are quite different between these three Peruvian species and the Chilean species with basal rosettes.

Clade C (6 spp). The recovered members of this clade have historically been recognized as a segregate genus, *Alona* Lindl., and it was accepted by Johnston (1936) at the generic level, and at sectional or subgeneric status by Miers (1845), Mesa-M. (1981), and Tago-Nakazawa and Dillon (1999). Strong support for this clade has not been universal within all markers, but its support is very high in analysis using the LEAFY second intron marker. and it exhibits a series of morphological characters and a restricted geographic distribution (Dillon et al., 2009). It contains six species, all of which were included in the molecular analysis: *N. balsamiflua*, *N. carnosa*, *N. coelestis*, *N. filifolia*, *N. rostrata*, and *N. stenophylla*. The data from the LEAFY second intron marker (Tu et al., 2008) showed robust support for all of the members of the clade. Furthermore, marker data suggest close relationships between the two most northern members of the clade, *Nolana balsamiflua* and *N. stenophylla*; however, they do not share close comparative overall morphology. The other species, *N. carnosa*, *N. coelestis*, *N. filifolia*, and *N. rostrata*, show close DNA relationships. The array of morphological characters presented by these four taxa is confusing and has led to many misidentifications. Various populations manifest combinations of characters, and, after assessing the habit, pubescence, leaf size, and flower coloration patterns, the only character to be reliable at this point has been the actinomorphic versus zygomorphic calyces, combined with other vegetative characters. These observed population variations are discussed under each species, where such variations have been encountered.

Clade D (21 spp). The recovered members of this clade represent one of two major clades present in Peru. It was recovered with sequence data from the LEAFY second intron marker (Dillon et al., 2009; Tu et al., 2008) of mostly Peruvian species ranging from central to southern Peru. In addition to the 14 species recovered in the DNA analysis, seven other species were added through comparative morphology and phytogeography.

Clade E (5 spp). This clade was recovered as a well-supported pair of species, *Nolana clivicola* and *N. gracillima* (Dillon et al., 2009). On purely morphological criteria, three other species are added here to Clade E, the southern Peruvian, *N. spergularioides*, and the northern Chilean species, *N. foliosa* and *N. tarapacana*. Overall morphology provides some indications of the relationships between these species and members of other clades. *Nolana clivicola* is an endemic from northern Chile (Tocopilla region) and is related to, and resembles, members of Clade G (Dillon et al., 2007c). Specifically, the floral morphology resembles *Nolana ramosissima* and *N. incana*. In addition to *N. gracillima*, three other potential members of Clade E are *N. tarapacana* (Chile), *N. spergularioides* (Peru) and *N. foliosa* (Chile). These species all have larger, purple corollas with a dark purple ring at the mouth of the limb. The position of all these taxa will hopefully be resolved with additional sampling and are maintained here tentatively for purposes of discussion.

Clade F (25 spp). This clade has strong support in the analysis using the LEAFY second intron marker (Dillon et al., 2009) and comprises primarily Peruvian species. Two predominately Peruvian species have disjunct populations in northern Chile; *N. adansonii* and *N. lycioides* populations likely reached Chile via some mode of long-distance dispersal.

Clade G (25 spp). This clade has strong support in the analysis using the LEAFY second intron marker (Dillon et al., 2009) and is a strictly Chilean clade. *Nolana aplocaryoides* is the sister taxon to the remainder of Clade G. Dillon et al. (2007c, 2009), and Tu et al. (2008) recovered 18 members of Clade G, and comparative morphology was utilized to add an additional seven species to the clade, bringing the total to 25 species from northern to central Chile, but not extending south of 33˚20'S latitude. In most aspects, the Chilean members of Clade E suggest relationships with members of Clade G; e.g., *N. clivicola* and *N. foliosa*.

Species concept

An important task for a monographer is to empirically state how circumscription of species was accomplished and to, hopefully, provide the reader with an idea of the principles used in this difficult process. Knapp (2013) articulated the approach viewing species as "assemblages of individuals" sharing morphological features correlated with discontinuities. In *Nolana*, an added degree of definition is associated with geographic distribution. No subspecies or varieties have been recognized in this treatment.

An attempt has been made to examine living populations, which allows for observations and data on phenology and distribution, often sympatric, during, or shortly after, El Nino events. When rendered flat in the drying process of making herbarium specimens, *Nolana* species typically lose many of the salient characters that are easily observed in the living state. Following several decades of examining populations and their ecological parameters, the species

accepted here have their basis in diagnostic morphological characters, supported by a geographic and genetic component suggested by molecular studies. Several "complexes" of clearly related taxa are discussed, and "lumping" has been done with caution until component taxa can be tested by modern molecular methods mentioned above.

Identification key details

Providing a useable key to species within a selected group is perhaps one of the most important contributions of a monograph. Identification of *Nolana* species is difficult due to a high degree of succulence in the leaves and calyces and the loss of diagnostic characters during the pressing and drying process. Add this to rampant homoplasy, and the difficulty of correct identifications is magnified. To circumvent the problems of construction of dichotomous keys, especially where characters are shared by species but not necessarily present in their common ancestor, the key to species begins with modern political geographic boundaries: Chile, Peru, and Ecuador. No species identified as having Chilean origins have distributions extending north of the current political boundary at 18˚S latitude; however, three species considered to have originated in Peru, have slightly extended ranges into northern Chile. The Ecuadorian species, *Nolana galapagensis*, has been aligned with species with geographic proximity and origins from within coastal Peruvian taxa (Dillon et al., 2009). Peruvian species, principally in Clades D and F, are difficult to differentiate in the dried state. Assignment of clades are represented by letters in parenthesis after the species names.

Key To *Nolana* Species

1a. Plants confined to continental South America south of 6˚S latitude (modern-day Peru and Chile) 2
1b. Plants confined to Ecuador, Galapagos Islands, ca. 0˚S latitude . . . . . *Nolana galapagensis* (D4)
2a. Plants confined to modern-day Chile, 18˚–42˚S latitude (exceptions noted: *N. adansonii*, *N. gracillima*, and *N. lycioides*) 3
2b. Plants confined to modern-day Peru, 6˚–18˚S latitude (exceptions noted: *N. adansonii*, *N. gracillima*, and *N. lycioides*) 4
3a. Annuals, basal leaves in a rosette; taproot swollen and "carrot-like"; flowering stems decumbent to prostrate, cauline leaves petiolate and laminar, or sessile, occasionally decurrent or auriculate on the stems; flowers 30–50 mm in diameter; stigma gynobasic; mericarps 20–30, 3- to 5-seriate, rarely 10–15, 2-seriate 5
3b. Small to large shrubs, perennials, or, more rarely, annuals, lacking swollen taproots and lacking a persistent rosette of basal leaves; corollas either large and showy (30–50 mm wide) or reduced (<10 mm wide); gynoecia with gynobasic or apical stigmas; mericarps fused or unfused 6
4a. Plants glabrous, leaves and calyces essentially lacking pubescence 51
4b. Plants with indumentum, trichomes variable from capitate-glandular to non-glandular, including strigose, sericeous, villous, dendritic, arachnoid, lanuginous, or tomentose 61
5a. Middle cauline leaves lacking distinct petioles, gradually expanded from attachments, leaf bases often auriculate or decurrent on stems; blades linear to spathulate or oblanceolate; mericarps not corky, sometimes quadrate to flattened; upland habitats from extreme northern to central Chile, more rarely in seashore habitats 7
5b. Middle cauline leaves with a definite petiole that is abruptly expanded above into a broad flat blade; mericarps 10–15, the pericarp becoming corky; seashore perennial with fleshy taproot; central to southern Chile . . . . . *N. paradoxa* (B5)
6a. Shrubs with large showy flowers, 30–50 cm wide; gynoecium (3–)5(–6) sulcate, broadly affixed to the receptacle, embedded within the receptacle tissue, and fused laterally with tissue that completely engulfs the ovules; styles apical 14
6b. Various habits, seldom single-stemmed annuals, more typically perennial herbs or shrubs; gynoecium 3–10 mericarps, free, style gynobasic 19
7a. Plants generally with few basal leaves; corollas scarcely surpassing the calyx, white; mericarps angular . . . . . *N. parviflora* (B6)
7b. Plants with basal leaves; corollas conspicuous, clearly surpassing calyces, 30–50 mm wide 8
8a. Leaf margins irregularly undulate; corollas multi-colored, with distal blue, black, and ultimately yellow at the base; mericarps ca. 15; narrow endemic, coastal, central Chile . . . . . *N. reichei* (B8)
8b. Leaf margins strictly entire, corollas blue to lavender distally, with white throats, or all, more rarely, white, but never multi-colored 9
9a. Plant developing a perennial caudex; abundantly pubescent with capitate-glandular trichomes in the inflorescence; cauline leaves elongate, firm, strap-shaped, with a subauriculate somewhat clasping sessile base; coastal Chile . . . . . *N. rupicola* (B9)
9b. Plant from a taproot, spreading, prostrate or decumbent, the leafy basal rosette persistent; corolla blue or white in some frequency; mericarps lacking wings 10
10a. Plants annual or, more commonly, perennials, with enlarged taproots; mericarps rounded and lacking wings 11
10b. Plants annual herbs with slender roots; mericarps polyhedrons, angulate, keeled or winged 12
11a. Plant hairy; corolla 30–50 mm long; mericarps 5 larger (–10 smaller), rounded, smooth, not angular, coastal Chile . . . . . *N. elegans* (B3)
11b. Plant sparsely glandular and, hence, greener, leaves broader and less firm, bases decurrent; plant an annual, never with a shrubby caudex . . . . . *N. acuminata* (B1)
12a. Mericarps compressed laterally and encircled by a broad evident vertical wing; leaf margins strongly revolute . . . . . *N. pterocarpa* (B7)
12b. Mericarps rounded or angulate, irregular polyhedrons, wingless or narrowly and horizontally winged around the apical end 13
13a. Plant an erect annual herb, ascending branched above the middle; mericarps with an apical wing; corollas blue or white . . . . . *N. baccata* (B2)
13b. Plant spreading prostrate or decumbent; branching from the base; mericarps apterous . . . . . *N. jaffuelii* (B4)
14a. Calyx with lobes only 1–3 mm long, split and becoming deeply 1- to 2-cleft by the expanding corolla, zygomorphic 15
14b. Calyx with well-developed lobes, 3–9 mm long, not split by the expanding corolla, actinomorphic 16
15a. Shrub, slender-stemmed and loosely branched; stems prostrate to ascending with glandular pubescence; leaves scattered, terete and slender; corolla bluish, 20–25 mm long; pedicels short to 5–8 mm long . . . . . *N. rostrata* (C5)

15b. Shrub, low and dense; stems glabrous; leaves crowded, short, triquetrous, divergent; corolla pinkish, 25–30 mm long; pedicels to 10–25 mm long . . . . . *N. carnosa* (C2)
16a. Stems, leaves, and calyx finely glandular and distinctly resinous, sticky, viscid; occasional populations with additional villous pubescence 17
16b. Stems, leaves, and calyx covered with fine, soft, spreading trichomes, glandular but not sticky 18
17a. Calyx lobes linear, separated by a very broad rounded, open sinus . . . . . *N. filifolia* (C4)
17b. Calyx lobes subulate, separated by a narrow, acute sinus . . . . . *N. balsamiflua* (C1)
18a. Shrub, erect, 3–10 dm tall; leaves 1.5–2.0 mm wide, very slender; calyx cut only down to middle . . . . . *N. coelestis* (C3)
18b. Shrub, spreading, 1.5–3.0 dm tall; leaves 1.0–2.5 mm wide; calyx cut to beyond the middle . . . . . *N. stenophylla* (C6)
19a. Annuals, sometimes robust when moisture is abundant; leaves, (1–)10–20(–40) mm long and (1–)2–5(–7) mm wide; corollas variously colored, some white or yellowish; leaf pubescence variable from glabrous to densely canescent with dendritic, arachnoid, or simple trichomes, and, rarely, with superficial salt glands 20
19b. Annuals, round, shrublike habit, to 50 cm tall, to 50 cm in diam., with elliptic to spathulate, laminar leaves, densely viscid, pubescent with capitate-glandular trichomes; corollas all white, ca. 2 cm long, ca. 1.5 cm wide, sessile; 6–10 rounded mericarps (Northern Chile; hyperarid inland localities 1250–2500 m.a.s.l.) . . . . . *N. sessiliflora* (A1)
20a. Leaves clearly petiolate, bases auriculate, occasionally connate, blades cordiform, rarely reniform or elliptic, appearing glabrous but with salt glands (Peru and northern Chile) . . . . . *N. adansonii* (F1)
20b. Leaves lacking distinct petioles, bases not auriculate, blades variously linear, oblong, spathulate, to elliptic; never cordiform or reniform; variously pubescent or, more rarely, glabrous 21
21a. Leaf pubescence of dendritic trichomes; corollas white to yellowish white 22
21b. Leaf pubescence various but never with abundant dendritic trichomes; corollas white, lavender, blue, or purple 27
22a. Leaves with loose, dendritic trichomes, appearing fuzzy . . . . . *N. villosa* (G24)
22b. Leaves with tightly appressed dendritic trichomes, appearing canescent 23
23a. Leaves broadly clavate to globular-obovate, 5–10 mm long; corollas suburceolate, white to yellowish . . . . . *N. peruviana* (G17)
23b. Leaves spathulate, gradually expanded upward toward the apex; corollas tubular, white 24
24a. Plant with erect or ascending stems, commonly a shrub one or more meters tall; mericarps 4 25
24b. Plant with weak, prostrate stems; mericarps 4 or 5 26
25a. Leaves 5–11 mm long; corollas twice the length of the calyx, 10–13 mm long . . . . . *N. albescens* (G1)
25b. Leaves 15–25 mm long; corollas only slightly surpassing the calyx, 7–8 mm long . . . . . *N. werdermannii* (G25)
26a. Leaves 12–32 mm long; corolla 11–13 mm long; mericarps five (plants of central Chile) . . . . . *N. crassulifolia* (G3)
26b. Leaves 6–18 mm long; corollas 6–10 mm long; mericarps four (plants of northern Chile) . . . . . *N. incana* (G8)
27a. Perennial herbs, subshrubs or shrubs; primary and secondary roots 28
27b. Robust annuals reaching 1 meter with adequate available moisture, long-lived but no secondary roots 43
28a. Leaves narrowly linear-spathulate, 20–30 mm long, 10–20 mm wide, conspicuously shaggy-villous; corollas with a dark purple band in the mouth of the limb, dark purple guides . . . . . *N. intonsa* (F12)
28b. Leaves variously shaped, <25 mm long, <10 mm wide, variously pubescent, arachnoid-tomentose, densely capitate-glandular trichomes, or, more rarely, glabrous, never shaggy-villous; corollas lacking pronounced dark purple band in the mouth of the limb 29
29a. Calyces at anthesis cylindrical, lobes only half the length of the tube 30
29b. Calyces at anthesis cupulate, lobes more than half the length of the tube 32
30a. Foliage and calyces with elongate trichomes, surfaces appearing pubescent . . . . . *N. mollis* (G13)
30b. Foliage and calyces with salt glands, surfaces appearing shiny 31
31a. Leaves clavate, 2–3 mm long, leaf base with 4–6 apiculate, uniseriate, multicellular trichomes at each side . . . . . *N. sphaerophylla* (G22)
31b. Leaves oblong, 5–11 mm long, strictly glabrous but with numerous salt glands . . . . . *N. patula* (G16)
32a. Stems and leaves glabrous to glabrescent 33
32b. Stem and leaf pubescence arachnoid, and/or capitate-glandular trichomes 34
33a. Dense shrubs, plants yellowish green to deep green; calyx lobes linear-oblanceolate, swollen, apically rounded; corollas variously colored from blue to, rarely, white . . . . . *N. divaricata* (G6)
33b. Small crooked shrubs, plants glabrous, gray; calyx lobes triangular, obtuse, not swollen or rounded; corollas white . . . . . *N. glauca* (G7)
34a. Stems and leaves with arachnoid-tomentose pubescence 35
34b. Stems and leaves principally pubescent with capitate-glandular trichomes 37
35a. Erect shrubs, 50–100 cm tall; leaves globular or, less often, clavate; corollas white . . . . . *N. sedifolia* (G21)
35b. Decumbent subshrubs, no greater than 30 cm tall; leaf blades oblong to oval; corollas pink to blue 36
36a. Leaves and calyces with arachnoid-tomentose pubescence, 2–4 mm long; corollas 12–18 mm long . . . . . *N. diffusa* (G5)
36b. Leaves and calyces inconspicuously pubescent with capitate-glandular trichomes, and villous with flaccid, elongate trichomes, (2–)4–6 mm long; corollas 15–16 mm long . . . . . *N. tocopillensis* (G23)
37a. Leaves 4–5 mm long 38
37b. Leaves 5–25 mm long 39
38a. Leaves linear-oblong; calyx lobes revolute, corollas 10–24 mm long . . . . . *N. leptophylla* (G11)
38b. Leaves oval to oblong-spherical, 3–4 mm long; calyx lobes plain, not revolute, corollas ca. 8 mm long . . . . . *N. lachimbensis* (G10)
39a. Leaves 10–25 mm long (plants of southern Peru and northern Chile) . . . . . *N. lycioides* (D10)
39b. Leaves 5–13 mm long 40

40a. Leaves 8–10 mm long; calyx ca. 6 mm long, lobes ca. 4 mm long, succulent, expanded; corollas ca. 6 mm long . . . . . *N. salsoloides* (G20)
40b. Leaves 5–13 mm long; calyx 10–12 mm long, lobes 6–8 mm long; corollas 10–14 mm long 41
41a. Large, robust shrubs to two meters tall; leaves 5–13 mm long; calyx 8–10 mm long, lobes 6–8 mm long . . . . . *N. ramosissima* (G19)
41b. Shrubs to 1 m; leaves 7–10 mm long; calyx lobes 10–12 mm long 42
42a. Leaves 8–10 mm long, 1.0–1.5 mm wide; calyces ca. 12 mm long, lobes ca. 5 mm; corollas 12–13 mm long . . . . . *N. inconspicua* (G9)
42b. Leaves 7–10 mm long, 1.0–1.5 mm wide; calyces 10–12 mm long, lobes ca. 8 mm long; corollas 12–14 mm long . . . . . *N. clivicola* (E1)
43a. Erect, single-stemmed annuals to 30 cm tall or less, dichotomously branched above the midpoint; leaves lance-ovate to rhomboid, mostly 15–20 mm long, 7–12 mm wide; confined to elevations 1800–1900 m.a.s.l. . . . . *N. rhombifolia* (D15)
43b. Basally branched, short- to long-lived annuals; stems generally greater than 30 cm long; leaves linear to oblong, 10–40 mm long, 1–4 mm wide 44
44a. Leaves linear, 10–40 mm long, 1–2 mm wide; calyces 12–18 mm long; corollas 12–30 mm long; lobes deeply notched as to appear 10-lobed . . . . . *N. linearifolia* (G12)
44b. Leaves linear-spathulate, 7–30 mm long, ca. 2 mm wide; calyces 8–12 mm long; corollas 7–40 mm long; lobes not deeply notched 45
45a. Corollas 7–12 mm long 46
45b. Corollas 18–40 mm long 48
46a. Corollas 7–8 mm long . . . . . *N. tarapacana* (E5)
46b. Corollas 10–12 mm long 47
47a. Leaves linear, 8–25 mm long, glabrous or, more rarely, sparsely or finely pubescent, mericarps pyriform, 1.5–2.0 mm long . . . . . *N. gracillima* (E3)
47b. Leaves linear, 10 mm long, 3–4 mm wide, pubescent with simple trichomes, mericarps 2(–3) . . . . . *N. foliosa* (E2)
48a. Leaves 20–30 mm long; corollas 35–40 mm long . . . . . *N. philippiana* (G18)
48b. Leaves 10–20 mm long, pubescent with capitate-glandular trichomes; corollas 18–24 mm long 49
49a. Mericarps oval to elliptic . . . . . *N. patachensis* (G15)
49b. Mericarps spherical 50
50a. Habit erect; leaves densely set, internodes not evident; corollas light lavender with 5 distinct dark guides or color patches in the throat . . . . . *N. onoana* (G14)
50b. Habit prostrate, spreading, leaves not crowded, internodes evident; corollas with pronounced star-shaped purple guide in the throat . . . . . *N. dianae* (G4)
51a. Calyces narrowly tubular, 1.5–3.0 mm in diam., bilobed, lobes unequal 52
51b. Calyces turbinate, campanulate, globose or suburceolate, >3 mm in diam., 5-lobed 54
52a. Plants erect, annuals, 2–5 cm tall; leaves linear to spathulate, rarely with bases amplexicaul; calyces 5.5–6.0 mm long; corollas blue; mericarps 2 . . . . . *N. minor* (F16)
52b. Plants spreading, long-lived perennials, forming decumbent mats, to 50 cm in diam.; mericarps 1 or 3–5 53
53a. Leaf blades obovate to oblanceolate, 2–4 mm wide; corollas mostly white, 7–10 mm long, 5.0–7.5 mm in diam.; mericarps 1 (inland habitats, above 100 m.a.s.l.) . . . . . *N. arequipensis* (F3)
53b. Leaf blades linear to spathulate, 2.5–7.0 mm wide; corollas violet to purple, 7–20(–25) mm long, 10–15 mm in diam.; mericarps 3–5 (near-ocean habitats, below 100 m.a.s.l.) . . . . . *N. thinophila* (F20)
54a. Calyces turbinate, bifid, lobes 6–10 mm long, cut to the base . . . . . *N. pallidula* (D11)
54b. Calyces campanulate, globose or suburceolate, lobes 5, evenly spaced, deltoid to lanceolate, cut to half the tube 55
55a. Leaf blades narrowly linear to linear oblanceolate, 0.8–4.0(–6.5) mm wide, bases cuneate; petioles lacking 56
55b. Leaf blades broadly lanceolate, oblong, cordate to reniform or ovate, 6–30 mm wide, bases various; petiolate 58
56a. Calyces globose to suburceolate, 10–15 mm in diam.; mericarps 10 . . . . . *N. chancoana* (D2)
56b. Calyces campanulate, 3.0–4.5 mm in diam.; mericarps 5 57
57a. Calyces narrowly campanulate, lobes lanceolate, acute; calyx 5.0–5.5(–6.0) mm long (plants of southern Peru and northern Chile) . . . . . *N. gracillima*
57b. Calyces campanulate 4.0–4.5 mm wide at anthesis (plants of interior northern Peru, Ancash; 2000–3000 m.a.s.l.) . . . . . *N. lezamae* (F14)
58a. Leaf blades oblong to oblanceolate, 5–12 mm long, 2.0–4.5 mm wide (plants of interior southern Peru, Dept. Cuzco; >2800 m.a.s.l.) . . . . . *N. urubambae* (F24)
58b. Leaf blades elliptic, lanceolate, cordate, or reniform, 10–40(–55) mm wide (plants of coastal or near-coastal habitats; <1200 m.a.s.l.) . . . 59
59a. Corollas small, obscure, ca. 12 mm wide, scarcely surpassing the calyx, lobes not elongated or prolonged into spurs, actinomorphic . . . . . *N. aenigma* (F2)
59b. Corollas large, showy, 15–30 mm wide, clearly exceeding the calyx, lobes slightly prolonged into projections or spurs 60
60a. Leaves elliptic to broadly lanceolate; calyces strongly bilabiate, lobes with pronounced projections or spurs (central to northern Peru; 100–600 m.a.s.l.) . . . . . *N. humifusa* (F11)
60b. Leaves lanceolate to ovate; calyces actinomorphic, lobes with slight projections but lacking spurs (coastal southern Peru; 260–1100 m.a.s.l.) . . . . . *N. coronata* (F9)
61a. Plants pubescent with dendritic or branched trichomes, loosely or densely pubescent 62
61b. Plants pubescent with various types of pubescence, branched and unbranched; capitate-glandular, or non-glandular trichomes, but never branched or dendritic 67
62a. Plants and leaves appearing green, sparsely pubescent with dendritic trichomes with stalked basal cells; calyces bilabiate 63
62b. Plants and leaves appearing canescent or gray, densely pubescent with dendritic trichomes and, occasionally, also with capitate-glandular trichomes; calyces actinomorphic to zygomorphic 64

63a. Leaves with dendritic and capitate-glandular trichomes; calyces cupulate, tube 2–3 mm long, 2.0–2.5 mm wide, lobes ca. 7 mm long (endemic to Peru, Dept. Moquegua; >2000 m.a.s.l.). . . . . *N. platyphylla* (D13)

63b. Leaves with dendritic trichomes without obvious capitate-glandular trichomes; calyces fusiform, tube 4.5–6.0 mm long, lobes 4.5–5.0 mm long; (endemic to Peru, Dept. Arequipa; <1000 m.a.s.l.) . . . . . *N. tovariana* (F22)

64a. Leaves ovate to obovate, 10–15 mm long, 6–8 mm wide, thick and fleshy, densely glandular-pubescent with capitate-glandular and dendritic trichomes (endemic to Isla San Gabon, Ica, Peru) . . . . . *N. insularis* (D7)

64b. Leaves lanceolate to oblong with all trichomes dendritic, lacking capitate-glandular trichomes (continental Peru) 65

65a. Leaf blades canescent, linear to lanceolate or oblanceolate, 5–40 mm long, 1.2–9.0 mm wide; corollas lavender-blue or, rarely, white (southern Peru) . . . . . *N. pallida* (F17)

65b. Leaf blades pale gray green, spathulate to oblong; corollas violet or white 66

66a. Calyces campanulate to hemispheric, actinomorphic, 4–10 mm long, 2.5–6.0 mm wide, lobes equal, corollas violet or, rarely, white (northern and central Peru) . . . . . *N. gayana* (F10)

66b. Calyces campanulate, zygomorphic, 10–14 mm long, 6–7 mm wide, lobes unequal; corollas white (endemic to Lomas de Jahuay, Arequipa, Peru) . . . . . *N. tomentella* (F21)

67a. Flowers in organized cymose inflorescences; with or without a basal rosette of long-petiolate leaves (30–50 cm long) 68

67b. Flowers solitary in leaf axils, terminal and axillary, no organized inflorescences; plants lacking basal rosette of long-petiolate leaves, rarely with ephemeral central rosette 72

68a. Plants with basal rosette of leaves 69

68b. Plants lacking rosettes of leaves 71

69a. Leaf blades with densely strigose pubescence; flowering shoots congested into dense cymose inflorescences, subtending bracts oval to ovate, sessile . . . . . *N. scaposa* (D17)

69b. Leaf blades with arachnoid or lanuginose pubescence; flowering shoots prostrate; calyces pubescent with arachnoid or lanuginous pubescence and capitate-glandular trichomes 70

70a. Cauline leaves ovate, hirsute with capitate-glandular trichomes; margins entire . . . . . *N. inflata* (D6)

70b. Cauline leaves lanceolate, densely arachnoid-tomentose; margins undulate . . . . . *N. weissiana* (D20)

71a. Inflorescences of 3 terminal, scorpioid cymes, 7–12 cm long, each with ca. 12 flowers . . . . . *N. tricotiflora* (F23)

71b. Inflorescences of solitary, dense spike-like racemes, 30–40 cm long, each with over 50 flowers . . . . . *N. hoxeyi* (D5)

72a. Leaf blades cordate or, more rarely, elliptic, petiole bases auriculate and occasionally connate, margins with strigose trichomes, adaxial leaf surfaces shiny, oily with concentrated salt solution (plants of southern Peru and disjunct in northernmost Chile) . . . . . *N. adansonii* (F1)

72b. Leaf blades linear, narrowly lanceolate, spathulate, elliptic, lanceolate, lanceolate-spathulate, or rhomboid, bases never auriculate, adaxial surfaces variously pubescent, no salt glands, adaxial surfaces not shiny or oily 73

73a. Plants pubescent with non-glandular trichomes of varying densities, including strigose, sericeous, flagelliform, lanuginous, or tomentose (more rarely in combination with capitate-glandular trichomes) 74

73b. Plants with capitate-glandular trichomes of various lengths, rarely in combination with non-glandular trichomes 80

74a. Leaf blades densely pubescent, canescent or gray and tomentose with elongate, intertangled trichomes 75

74b. Leaf blades sparsely pubescent giving the plant a green appearance 78

75a. Calyces globose, 7–9 mm wide, trilobed, lanuginose (endemic to Lomas Amará, Ica, Peru) . . . . . *N. willeana* (D19)

75b. Calyces campanulate, 5-lobed, equal 76

76a. Leaf blades linear, 10–20 mm long, 0.8–1.0 mm wide, lanuginose . . . . . *N. spergularioides* (E4)

76b. Leaf blades not linear, rather linear-lanceolate or linear-oblong to elliptic, greater than 1 mm wide 77

77a. Leaf blades oblong, 5–8(–11) mm long, 1.0–2.5 mm wide; corollas 15–20 mm wide, 15–22 mm long, lavender . . . . . *N. bombonensis* (F5)

77b. Leaf blades lanceolate to elliptic, (5–)7–10 mm long, 1.2–2.8 mm wide; corollas 8–10 mm wide, 9–13 mm long, pale blue with a dark purple band and nectar guides within the throat . . . . . *N. volcanica* (F25)

78a. Leaf blades spathulate, scarcely pubescent with elongate curly trichomes, 6–14 mm long, 1.6–1.8 mm wide . . . . . *N. confinis* (F8)

78b. Leaf blades elliptic to lanceolate, villous to sericeous 79

79a. Leaf blades lanceolate, 11–26 mm long, 2.0–5.5 mm wide, villous . . . . . *N. cerrateana* (F7)

79b. Leaf blades elliptic to lanceolate, 15–30(–40) mm long, 5–12(–15) mm wide, sericeous . . . . . *N. callae* (F6)

80a. Calyces campanulate to turbinate, strongly zygomorphic, 2–4(–5) connate lobes 81

80b. Calyces narrowly campanulate to cupulate, regular, actinomorphic with lobes equally spaced, equal to subequal. 86

81a. Calyces bilabiate, lobes cut to half the tube or less; leaves lanceolate to narrowly ovate 82

81b. Calyces zygomorphic, lobes cut to more than half the tube; leaves ovate 84

82a. Leaf blades lanceolate, 9–20 mm long, 4–12 mm wide; calyces campanulate, 18–30 mm long, 6–10 mm wide, interior and exterior pubescent, tube 8–10 mm long, all the lobes on one side, lobes 5, unequal, acuminate, pubescent, the longer 5–8 mm long, 1.0–1.5 mm wide . . . . . *N. mariarosae* (F15)

82b. Leaf blades lanceolate to narrowly ovate or ovate-elliptic 83

83a. Leaf blades lanceolate to narrowly ovate, strap-shaped upon drying, 10–65 mm long, ca. 13 mm wide. . . . . *N. plicata* (D14)

83b. Leaf blades lanceolate to ovate-elliptic, 40–70 mm long, 15–30 mm wide . . . . . *N. aticoana* (F4)

84a. Leaf blades oblanceolate to ovate-oblong, the base gradually attenuate, sessile; calyx lobes attenuate . . . . . *N. latipes* (D8)

84b. Leaf blades lanceolate-spathulate or ovate to elliptic, cordiform or spathulate-reniform, petioles 6–25 mm long; calyx apically expanded or spathulate 85

85a. Leaf blade lanceolate-spathulate, 18–45 mm long, 6–18 mm wide, basally cuneate to attenuate; petioles 7–16 mm long, densely pubescent with curly trichomes . . . . . *N. arenicola* (D1)

85b. Leaf blades ovate to elliptic, cordiform or spathulate-reniform, 10–60 mm long, 8–38 mm wide, basally truncate, cordate or reniform; petioles 6–25 mm long, villous to hirsute with capitate-glandular trichomes. . . . . *N. spathulata* (D18)
86a. Multi-stemmed perennials or shrubs, branches leafy with short internodes 87
86b. Single-stemmed annuals, 3- to much-branched above, villous with flagelliform trichomes to puberulent with capitate-glandular trichomes 91
87a. Corollas white, tubular-hypocrateriform, zygomorphic, 18–23 mm long, 10–12 mm wide at anthesis. . . . . *N. quicachaensis* (F19)
87b. Corollas blue to violet, hypocrateriformis to infundibularis, actinomorphic 88
88a. Leaf blades lanceolate, rarely spathulate, 10–18 mm long, 1.2–4.0 mm wide, densely pilose with long-stalked, moniliform, capitate-glandular trichomes (near-coastal distribution, 100–800 m.a.s.l.) . . . . . *N. pilosa* (F18)
88b. Leaves linear, elliptic, or oblanceolate to obovate 89
89a. Leaf blades linear, 5–25 mm long, <1 mm wide. . . . . *N. lycioides* (D10)
89b. Leaf blades elliptic to oblanceolate or obovate. 90
90a. Leaf blades oblanceolate or obovate, 4–7 mm long, 1.0–1.5 mm wide, pilose (near-coastal environment; ca. 500 m.a.s.l.) . . . . . *N. samaensis* (D16)
90b. Leaf blades elliptic, 8–15 mm long, 2.0–3.5 mm wide, puberulent with short-stalked, capitate-glandular trichomes (inland localities; 2200–2400 m.a.s.l.) . . . . . *N. chapiensis* (D3)
91a. Erect annuals, 3-branched above, branches villous with flagelliform trichomes; leaf blades elliptic or narrowly lanceolate, 10–20 mm long, 3–6 mm wide, villous with flagelliform trichomes; calyces 6–8 mm long (endemic to Peru, Dept. Tacna) . . . . . *N. pearcei* (D12)
91b. Erect annuals, multi-branched above, branches with stout, capitate-glandular trichomes 92
92a. Leaf blades ovate or deltoid-ovate to lanceolate, 7–15 mm long, 4–10 mm wide; petioles 5–20 mm long; calyces cupulate, 4–5 mm in diam.; mericarps 4–6. . . . . *N. weberbaueri* (D19)
92b. Leaf blades linear to lanceolate-spathulate, or rhomboid, 9–20 mm long, 2–5 mm wide, sessile; calyces campanulate, 2.5–4.0 mm in diam.; mericarps 3 . . . . . *N. laxa* (D9)

Taxonomic Treatment

Family: Solanaceae Juss., Gen. Pl.: 124. 1789, *nom. cons.*
Order: Nolanales Lindl., Nixus Pl.: 18. 1835.
Family: Nolanaceae Bercht. & J. Presl, Přir. Rostlin: 244. 1820, *nom. cons.*
Nolanles Lindl., Nixus Pl. 18. 1833.
Nolanidia Rafinesque, Analys. Nat. 186. 1815, Fl. Tellur. 4: 87. 1838 (subfamily)
Nolanidae Burnett, Outlines Bot. 2: 1106. 1835. (family)
Nolanoideae D'Arcy, Linnean Soc. Symp. 7: 3–47. 1979.
Nolaneae Rchb.f., Consp. Reg. Veg. 125. 1828 (excl. *Triguera*, sect. Solanaceae)
Nolaneae Rchb.f., Handb. Nat. Pfl.-Syst.: 200. 1–7 Oct 1837. Validated by a diagnosis in Latin. T: *Nolana* L.f. (1762).
Subfamily: Nolanoideae Kostel., Allg. Med.-Pharm. Fl. 3: 939. 1834, as "*Nolaneae*"
Tribe: Nolaneae Bercht. and J. Presl, Prir. Rostlin: 244. 1820 = Rchb.f., Handb. Nat. Pfl.-Syst.: 200. 1–7 October 1837, with Latin diagnosis
Subtribe: Nolaninae Miers, London J. Bot. 4: 514. 1845, as "*Nolaneae*"
Genus: *Nolana* L.f., Decas Pl. Rar. Upsal. 1: 3, t. 2. 1762.
Type species: *N. humifusa* (Gouan) I.M. Johnst. as *N. prostrata* L., Herb. Linn. No. 194.1 (LINN).
Generic synonymy:
Alibrexia Miers, London J. Bot. 4: 505. 1845. Type species: *A. rupicola* Miers
Alona Lindl., Edwards's Bot. Reg. 30: tab. 46. 1844. Type species: *A. coelestis* Lindl.
Nolana sect. *Alona* (Lindl.) Miers, London J. Bot. 4: 500. 1845.
Aplocarya Lindl., Bot. Reg. 30: tab. 46. 1844. Type species: *A. divaricata* Lindl.
Bargemontia Gaudich., Bot. Voyage Bonite, Atlas tab. 8. 1841. Type species: *B. peruviana* Gaud.
Dolia Lindl., Bot. Reg. 30: tab. 46. 1844. Type species: *D. vermiculata* Lindl.
Gubleria Gaudich., Bot. Voyage Bonite, Atlas tab. 104. 1851–1852. Type species: *G. baccata* (Lindl.) Gaudich.
Leloutrea Gaudich., Bot. Voyage Bonite, Atlas tab. 100. 1851–1852. Type species: *L. aplocaryoides* Gaudich.
Osteocarpus Phil., Gartenflora 33: 39 and 356, tab. 1175. 1884. Type species: *Alona rostrata* Lindl.
Pachysolen Phil., Anal. Univ. Chile 91: 45. 1895. Type species: *Dolia eremobia* Phil.
Periloba Raf., Flora Tell. 4:87. 1838. Type species: *P. paradoxa* (Lindl.) Raf.
Rayera Gaudich., Voy. Bonite pl. 108. 1851–1852. Type species: *R. teretifolia* Gaudich.
Sorema Lindl., Bot. Reg. 30: tab. 46. 1844. Type species: *S. paradoxa* (Lindl.) Lindl.
Tula Adans., Fam. Pl. (Adanson) 2: 500. 1763, monomial. Type: *T. adansonii* Roemer and Schultes
Velpeaulia Gaudich., Bot. Voyage Bonite, tab. 109. 1851–1852. Type species: *V. alibrexioides* Gaudich. (= *N. leptophylla*).
Walkeria Ehret, Philos. Trans. 53: 130. 1764. Type species: *Atropa humifusa* Gouan
Zwingera Hofer, Acta Helv. 5: 267, tab. 1. 1763–64. Type species: *Atropa humifusa* Gouan

Annual to perennial, tap-rooted *herbs*, or *subshrubs* to *shrubs*; stems erect to ascending, prostrate or procumbent, growth rings present, glabrous to pubescent. *Leaves* rosulate and/or cauline, alternate or subopposite to fasciculate, simple; petiolate or sessile, exstipulate; blades entire, succulent, terete to laminar, dorsiventral, ovate to linear or spathulate, occasionally the bases obliquely decurrent on stems, or greatly reduced, laminar to terete, densely pubescent with simple to branched trichomes, sometimes with apical capitate glands, occasionally with abundant salt

glands. *Inflorescences* solitary in leaf axils or, more rarely, racemose or cymose on modified ascending branches with subtending floral bracts. *Flowers* 5-merous, hermaphrodite, actinomorphic to zygomorphic, floral asymmetry involving perianth and the androecium or only the androecium; sepals 5, 1-whorled; calyces fused, equal to unequal, actinomorphic to sub-bilabiate, or zygomorphic, rarely reduced to an unlobed truncate tube, persistent, enclosing the ovaries; imbricate or valvate; petals 5, corollas gamopetalous, plicate between lobes; infundibuliform, less frequently hypocrateriformis, campanulate or tubular, more rarely suburceolate; regular or zygomorphic; blue, purple, lavender or white, limb basally dark purple or white, with or without pale yellow, white or green bands; stamens 5, filaments adnate basally, often pubescent, unequal (3 long, 2 short), antisepalous, anthers dehiscing via longitudinal slits, introrse; pollen shed as single grains, 3-colporate; hypogynous nectary disc patelliform to crateriform, margins plain, crenate or lobulate, nectar secreting; gynoecium fundamentally 5-carpellate; carpels are united to form a superior, (3–)5(–6) locular ovary with a terminal style and basal-axial placentation which develops into a dry fruit with (1–)3–5(–6) seeds per mericarp; or the carpels are strongly lobed with each lobe normally containing one ovule; stigma capitate or peltate, wet, style gynobasic and the ovary develops into a dry fruits. *Mericarps* (1–)3–5(–35), 1–5(–7)-seeded, shape highly variable, polygons to spheres, surface sculpturing smooth to rugulose, or, rarely, muricate. Seeds with copious oily endosperm; cotyledons 2. Embryo curved or coiled. Chromosome number: x=12 (2n=24).

Taxonomy

Clade A

A1. ***Nolana sessiliflora*** Phil., Anal. Univ. Chile 91: 32. 1895. TYPE: CHILE. Antofagasta: Sierra Esmeralda, 1884–1885, *F. J. San Román s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55132], SGO000004387). Fig. 23–25.

Digital image: Lectotype of *Nolana sessiliflora* from Museo National de Historia Natural, Santiago [SGO 55132]. https://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004387

Robust, annual to perennial *herbs* to 30 cm tall, stems erect to decumbent, branched from the base, viscid, pubescent with minute, capitate-glandular trichomes. *Leaves* alternate, blades elliptic to ovate, ca. 30 mm long, ca. 15 mm wide, fasciculate, succulent, viscid with minute, capitate-glandular trichomes, margins plain, apically acute, basally cuneate. *Inflorescence* pseudoaxillary; pedicels 2–3 mm long. *Flowers* 5-merous; calyces ovate-tubular, lobes unequal, 11–16 mm long, lanceolate to elliptic, apically rounded, pubescent with capitate-glandular trichomes; corollas infundibularis, zygomorphic, ca. 20 mm long, ca. 15 mm wide at mouth, white, limb white; lobes retuse; stamens unequal; filaments not widened at the base, pubescent; nectary disc patelliform; style gynobasic; stigma capitate. *Mericarps* 6–10, oblong-oval, 3.0–3.5 mm long, unequal, shiny; seeds, 1 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *sessil-*, sessile, and *-iflorus*, flowers, and refers to sessile flowers due to short pedicels at the base of the calyces.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; (1250–) 2500–3050 m.a.s.l. It is recorded from interior, hyperarid environments far distant from the influence of coastal fog (Fig. 23); Matorral Desértico Tropical Interior (Luebert and Pliscoff, 2006).

Nolana sessiliflora is a shrubby, facultative annual that will continue to grow if moisture is available (Fig. 24A–C). The root is thick (Fig. 24D), and it is clearly an annual species. Its leaves are succulent, elliptic to ovate and quite sticky with viscid capitate-glandular trichomes. Flowers are sessile, subtended by fleshy, foliaceous bracts, and the mericarps are black, shiny and attached basally (Fig. 24E, 25B–C). The corollas are strictly white (Fig. 24F, 25A) and do not resemble any other species in size or form.

When the site near Mina Potrerillos, at ca. 2400 m.a.s.l., was visited in November 2004, it was very dry and had sparse vegetation (Fig. 24A–B). Only two additional species were encountered, *Phrodus microphyllus* (Miers) Miers and *Nolana leptophylla*. The lower elevation records, 1250–1400 m.a.s.l., were made from *pozos*, or ponds formed from rain runoff from upland sites (Fig. 24C); as the water evaporates, the mericarps germinate.

In the analysis by Dillon et al. (2009), *N. sessiliflora* was recovered as the sister taxon to the remainder of the genus, a position also suggested by previous analysis (Dillon et al., 2007c; Tu et al., 2008). Genetically, this species is clearly a member of the genus, but its morphology is unique.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, 5 km S of fundición Alto Norte at La Negra, 24°23'44"S, 69°55'45"W, 1250 m.a.s.l., 31 October 2007, *M. O. Dillon & M. Finger C. 9052* (F 2292847, SGO 158732); Quebrada Chaco Norte, 25°22'S, 69°23'W, 3050 m.a.s.l., *C. Latorre, C. Villagrán, & A. Maldonado 182* (CONC 150997); Trayecto Agua Verde–Chañaral, 25°30'S, 70°00'W, 1300 m.a.s.l., 26 February 2001, *C. Latorre, C. Villagrán, & A. Maldonado 249* (CONC 150968); Prov. El Loa, Camino de Augusta Victoria a La Escondida, 2520 m.a.s.l., *R. Rodríguez & E. Ruiz 3547* (CONC 137792). **Atacama**: Prov. Chañaral, 4 km NNW of Mina Potrerillos, 120 km from coast, 26°24'37"S, 69°30'35"W, 2460 m.a.s.l., 4 November 2004, *M. O. Dillon & M. Finger C. 8644* (CONC 179089, F 2292833, SGO 158709); Quebrada San Juan, 26°18'S, 69°30'W, 2700 m.a.s.l., 1 October 1995, *M. F. Gardner & S. G. Knees 5881* (E00014472); Quebrada Doña Inés Chica, 26°00'05"S, 69°59'25"W, 1080 m.a.s.l., 19 September 2005, *F. Luebert & N. García 2513/907* (F 2290708); 5 km bajando desde Potrerillos, en quebrada con escasa vegetación, 26°26'S, 69°27'W, 2470 m.a.s.l., 30 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2762* (SGO 126123). Prov. Copiapó, N Llanos de Llampos, Km 54, 27°14'S, 70°05'W, 1400 m.a.s.l., *M. Muñoz S., S. Teillier, & I. Meza P. 2732* (SGO 126124); El Salvador, camino a Potrerillos, cuesta Los Patos, 26°25'59"S, 69°30'28"W, 2672 m.a.s.l., 11 December 2011, O. *Toro & T. Fernández 81* (CONC 184725).

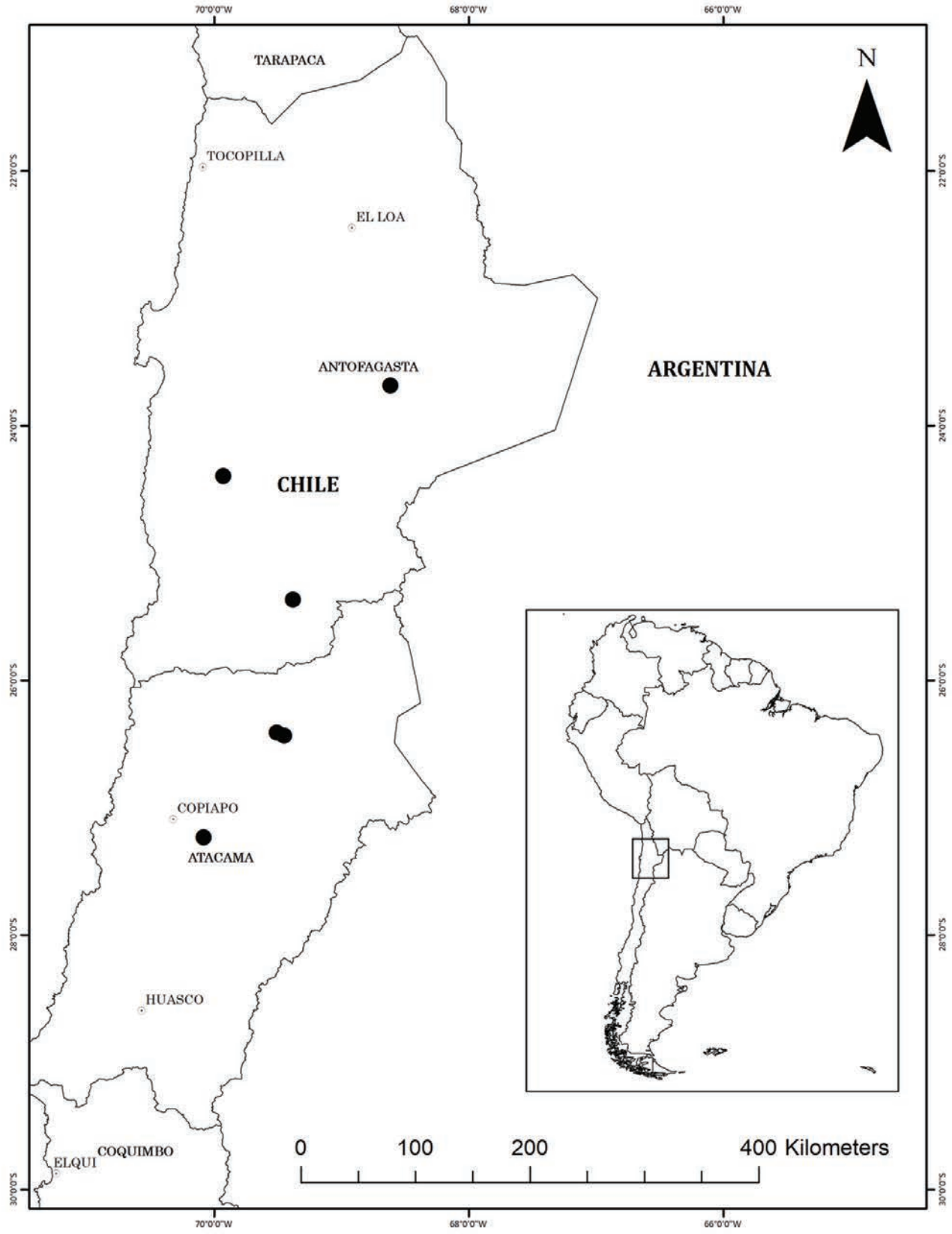


FIGURE 23. Distribution of *Nolana sessiliflora* Phil.

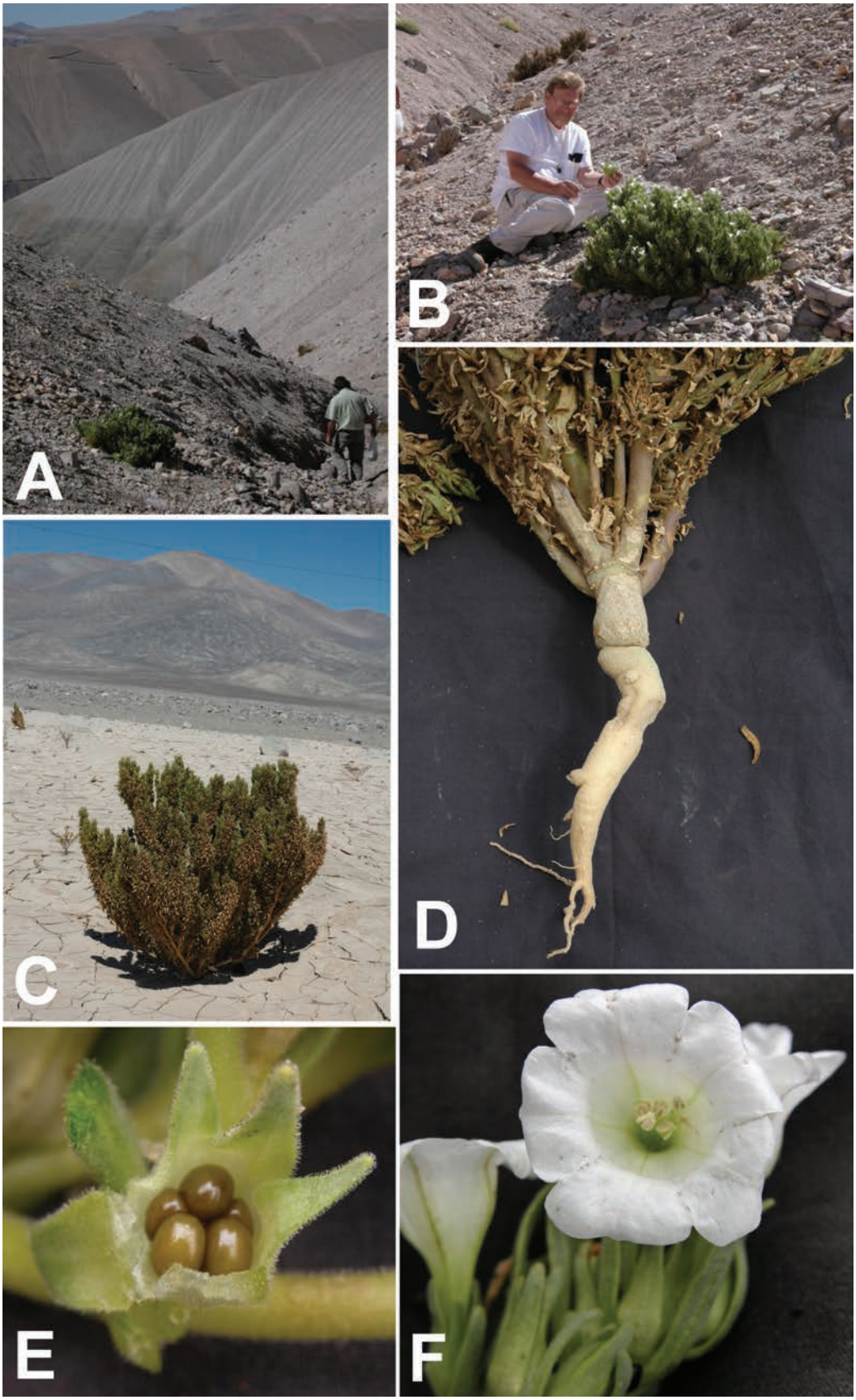


FIGURE 24. *Nolana sessiliflora*. **A**, Upland hyper-arid habitat near Mina Potrerillos, ca. 2400 m.a.s.l., Chile; **B**, Individual in high elevation habitat; **C**, Individual in low elevation habitat 5 km S of fundición Alto Norte at La Negra, ca. 1250 m.a.s.l., Chile; **D**, Annual root; **E**, Unripe mericarps; **F**, Corolla with pale green throat and white anther thecae.

FIGURE 25. *Nolana sessiliflora*. **A**, Longitudinal section exposing anther filaments and thecae; **B**, Flower bud and mericarps; **D**, Ripe, shiny mericarps.

Clade B

B1. ***Nolana acuminata*** (Miers) Miers ex Dunal, Prodr. 13: 12. 1852. Fig. 26–33.

Basionym: *Sorema acuminata* Miers, London Jour. Bot. 4: 370. 1845. TYPE: CHILE. Coquimbo: ["Concepcioneum"], *T. Bridges 1322* [notebook–*1325*] (Lectotype designated by Mesa-M., 1981: K [000532195]).

Digital image: Lectotype image of *Sorema acuminata* from Royal Botanic Gardens, Kew [K000532195]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.k000532195

Heterotypic synonyms: *Sorema lanceolata* Miers, London Jour. Bot. 4: 498. 1845. TYPE: CHILE. Coquimbo: Coquimbo, *H. Cuming 856* (Lectotype designated by Mesa-M., 1981: E [E00130951]; Isolectotypes, BM [000941283], CGE [CGE05021], E [E00130946], K [K0005321190], [K000532191]); *Sorema longifolia* Miers, *sensu* Gaudichaud, *non* Miers, 1845; *Nolana angustifolia* Phil., Linnaea 29: 26. 1857–1858. TYPE: CHILE. Coquimbo: "in maritimis cerca de Coquimbo", October 1836, *C. Gay 1207* (Lectotype designated by Mesa-M., 1981: SGO [55144]); *Nolana leucantha* Phil., Anal. Univ. Chile 91: 34. 1895. TYPE: CHILE. Atacama: Copiapó, Caldera, October 1886, *G. Geisse s.n.* (Lectotype designated by Mesa-M., 1981: SGO [72457], SGO000004373). **Paratype**: CHILE. Atacama: Copiapó, Quebrada del Leónes, Caldera, November 1886, *G. Geisse s.n.* (SGO [072447], SGO000004374); *Nolana navarri* Phil., Anal. Univ. Chile 91: 30. 1895. TYPE: CHILE. Coquimbo: Coquimbo, Puerto de Tongoy ["Tongoi"], January 1880, *L. Navarro s.n.* (Lectotype designated by Mesa-M., 1981: SGO [055143], SGO000004378). **Paratypes**: CHILE. Atacama:] Huasco, Carrizal, 1885, *T. King s.n.* (SGO [55142], SGO000004379); *Nolana grandiflora* Herzog, Meded. Rijks-Herb. 29: 21. 1916. TYPE: CHILE. Antofagasta: "*Plantae in itinere secundo per Boliviam lectae, In der Felswüste des Küstengebirges von Antofagasta*", ca. 300 m.a.s.l., September 1911, *C. T. J. Herzog 2457* (Holotype: L, not seen; Isotypes: S [04-2772], W [1922-0001577], F neg. 33148 ex W). – non *Nolana grandiflora* Lehm. ex G.Don (1837).

Annual *herbs* from a fleshy tap root, rarely perennating; flowering branches flexulose, prostrate, (10–)30–40 cm long, reddish streaks, densely pubescent with flagelliform trichomes, occasionally with shorter strigose trichomes. Basal rosette of *leaves*, blades lanceolate to spathulate, 10–12 cm long, 2–4 cm wide, erect; petioles slender, 4–8 cm long; cauline leaves on flowering stems, alternate to geminate distally, blades lanceolate, 4–6 cm long, 2–4 cm wide, bases obliquely decurrent, abaxial midvein prominent, reddish-purple, apex acute, margins subrevolute, pubescent with flagelliform trichomes. *Inflorescences* of solitary flowers, terminal and axillary. *Flowers* 5-merous; calyces ca. 25 mm long, villous with flagelliform trichomes, basally ovate with lobes projecting into shoulders, base ca. 8 mm wide, tapering abruptly to lanceolate-attenuate apex, 12–15 mm long; corollas infundibularis, weakly zygomorphic, 30–40 mm long, limb 40–50 mm wide, distal 2/5 corolla dark blue, proximal 2/5 white inner throat, rarely corollas all white, each lobe with 3 prominent, yellowish, nectar guides lines, lobes truncate, terminally cuspidate; stamen filaments white, ca. 8 mm long, pubescent at base; anther thecae white; styles ca. 7 mm long, stigma green. *Mericarps* 5 large, 3–6 mm long, 5–10 small, 1–2 mm long, polyhedrons to rounded, black; seeds 1–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *acuminatus*, tapering gradually or abruptly from inwardly curved sides into a narrow point. The leaves, especially the more apical leaves subtending the flowers, are this shape, as are the calyx lobes.

Distribution and Ecology: Chile, Regions of Antofagasta, Atacama, and Coquimbo; extending over 800 km; 10–780(–1500) m. It is recorded from a wide variety of environments with sandy soils; near-coast habitats or, more rarely, to higher, inland elevations (Fig. 26); Matorral Desértico Tropical Costero, Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Illustrations: Fig. 27. Illustration of *Nolana acuminata* as *Sorema longifolia* Miers, Plate 103. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944). Fig. 28. Illustration of *Nolana acuminata* as *Nolana lanceolata* Dunal published in Curtis's Botanical Magazine 88, series 3, vol. 18, tab. 5327, 1862.

Nolana acuminata has showy flowers and, episodically, they produce dense, extensive blooming populations, especially during years with increased moisture availability, such as El Niño events or rare rainstorms. When conditions are appropriate, annuals spring up from seed banks lying dormant for extended periods of time (Fig. 29). The size of individuals largely depends upon how much available moisture is present at the time of germination and early development (Fig. 30–31). Within any population, and growing completely sympatrically, individuals with entirely white corollas can be observed in some frequency (Fig. 32A–B). The corolla color can vary in *N. acuminata* but is typically a light to deep blue distally and white proximally to yellowish (Fig. 33A). The lobes of the blue corolla morphs are rounded with shallow indentations (Fig. 33A), and the lobes of the white corolla morphs are more acute or prolonged (Fig. 33B).

The floral morphology of *Nolana acuminata* is close to that of *N. elegans* and *N. baccata*. The populations encompassing this taxon are polymorphic, with floral and leaf variation over its extensive distributional range; consequently, and several regional "forms" have been described, as reflected in the synonyms (see discussion below). The study of diversity in *N. acuminata* and its congeners has proven difficult to quantify. As facultative annuals, the individuals within a population that germinate under appropriate conditions will vary from year to year.

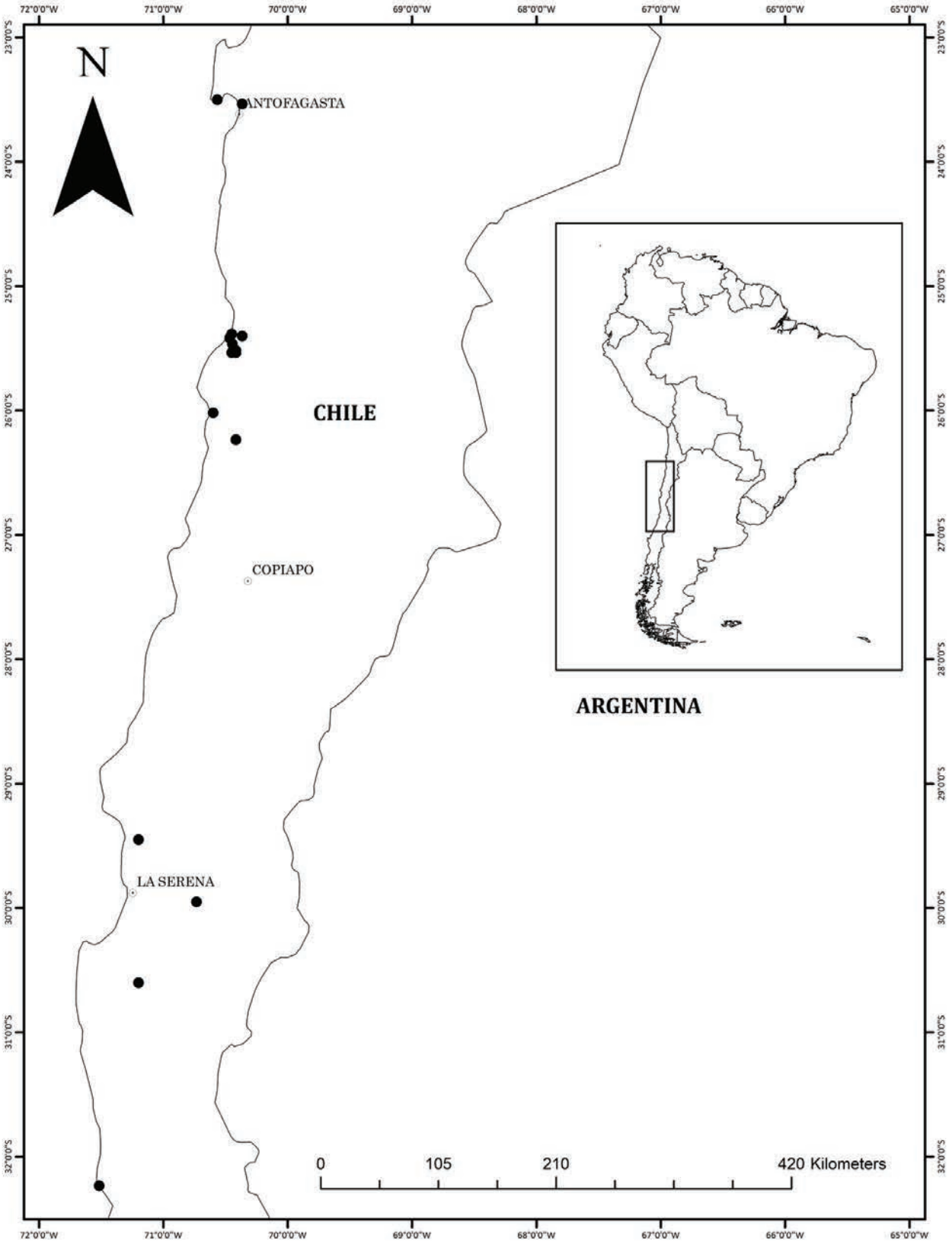


FIGURE 26. Distribution of *Nolana acuminata* (Miers) Miers ex Dunal.

FIGURE 27. Illustration of *Nolana acuminata* as *Sorema longifolia* Miers, Plate 103, *sensu* Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 28. Illustration of *Nolana acuminata* as *N. lanceolata* Dunal published in Curtis's Botanical Magazine, plate 5327 (1862).

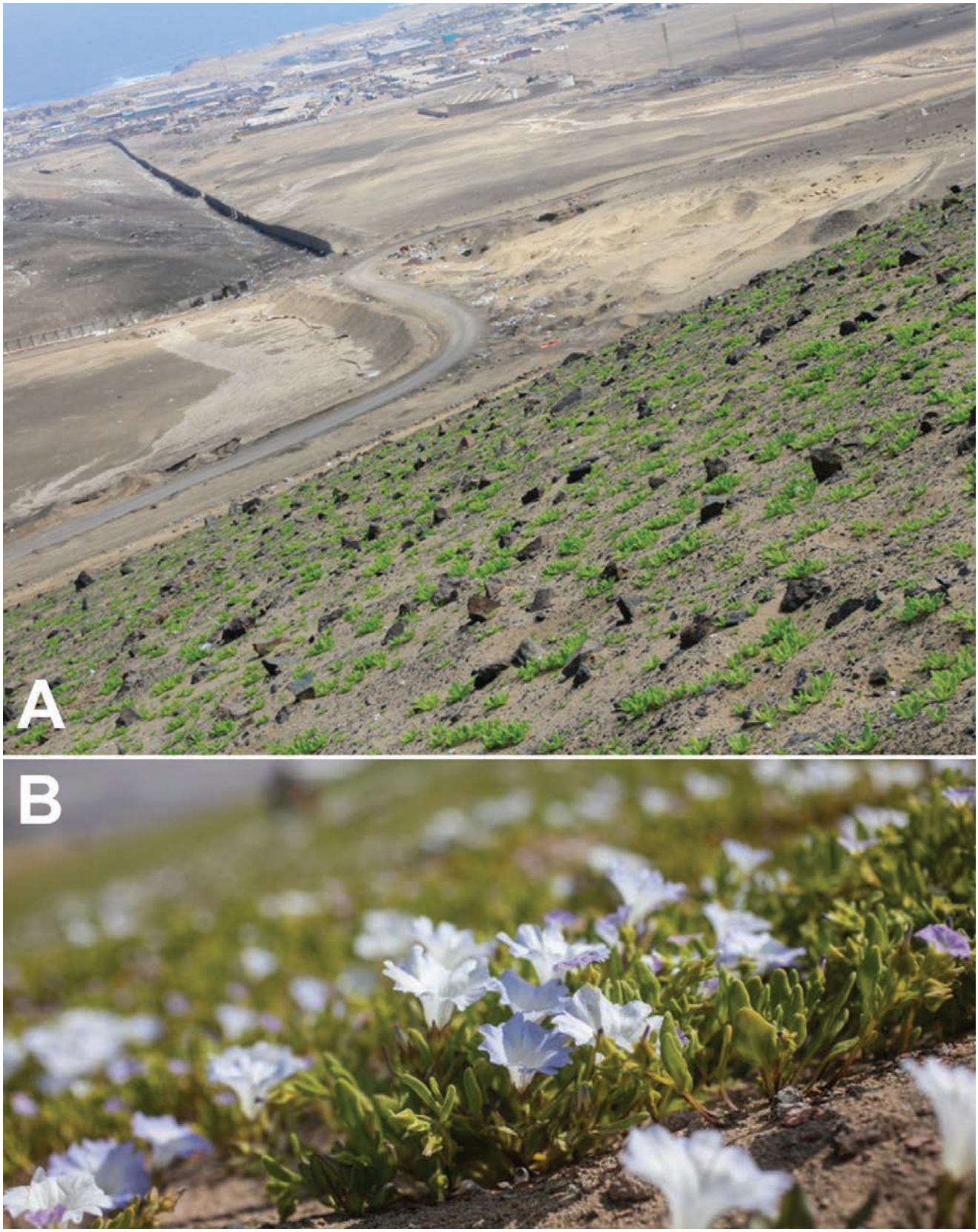


FIGURE 29. *Nolana acuminata*. **A**, Hillsides above Antofagasta, Chile after rare rainfall; **B**, Closeup of plants. Photographs by Laurence Packer.

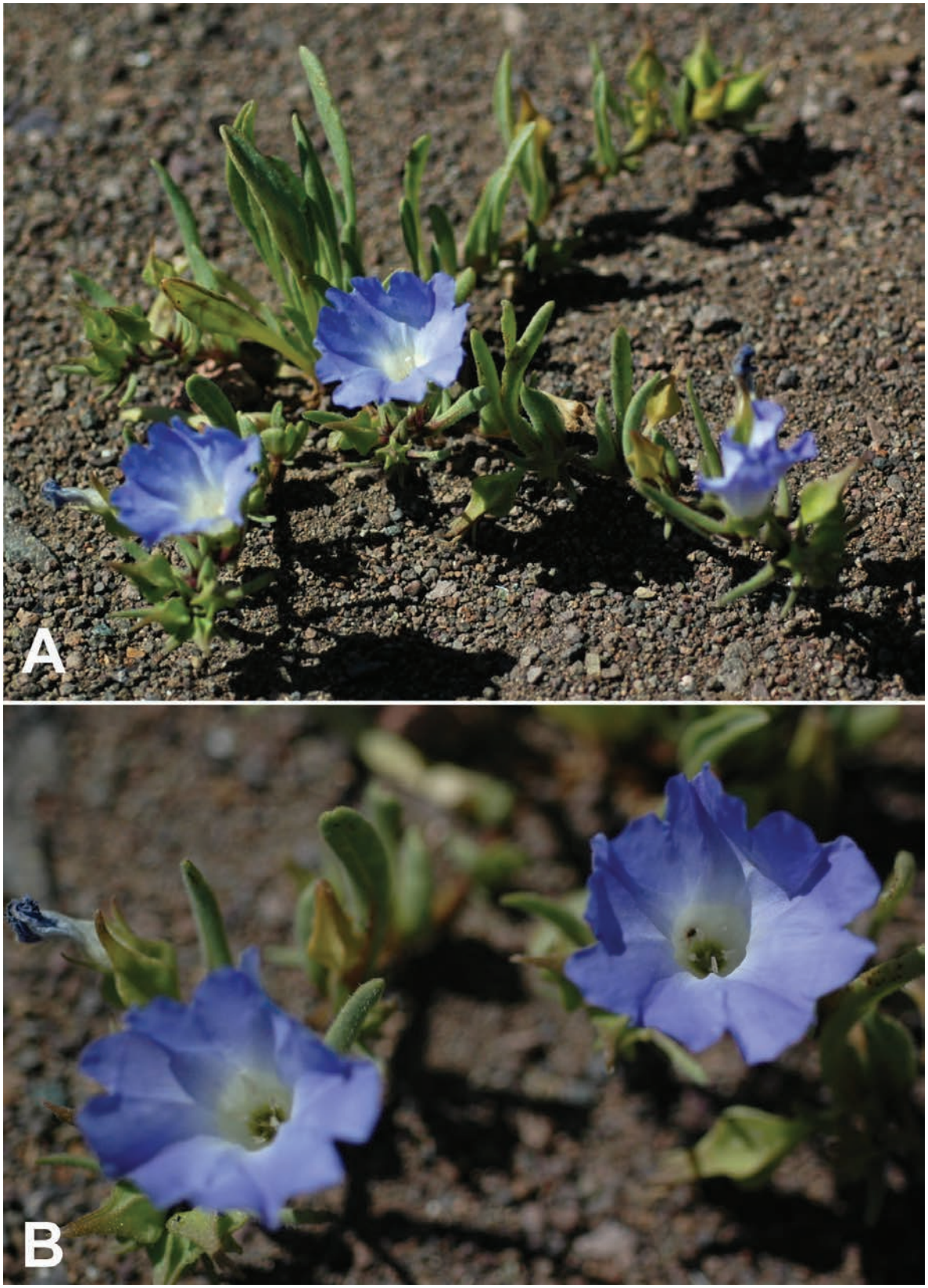


FIGURE 30. *Nolana acuminata*. **A**, Individual growing near Taltal, Chile; **B**, Closeup of flowers.

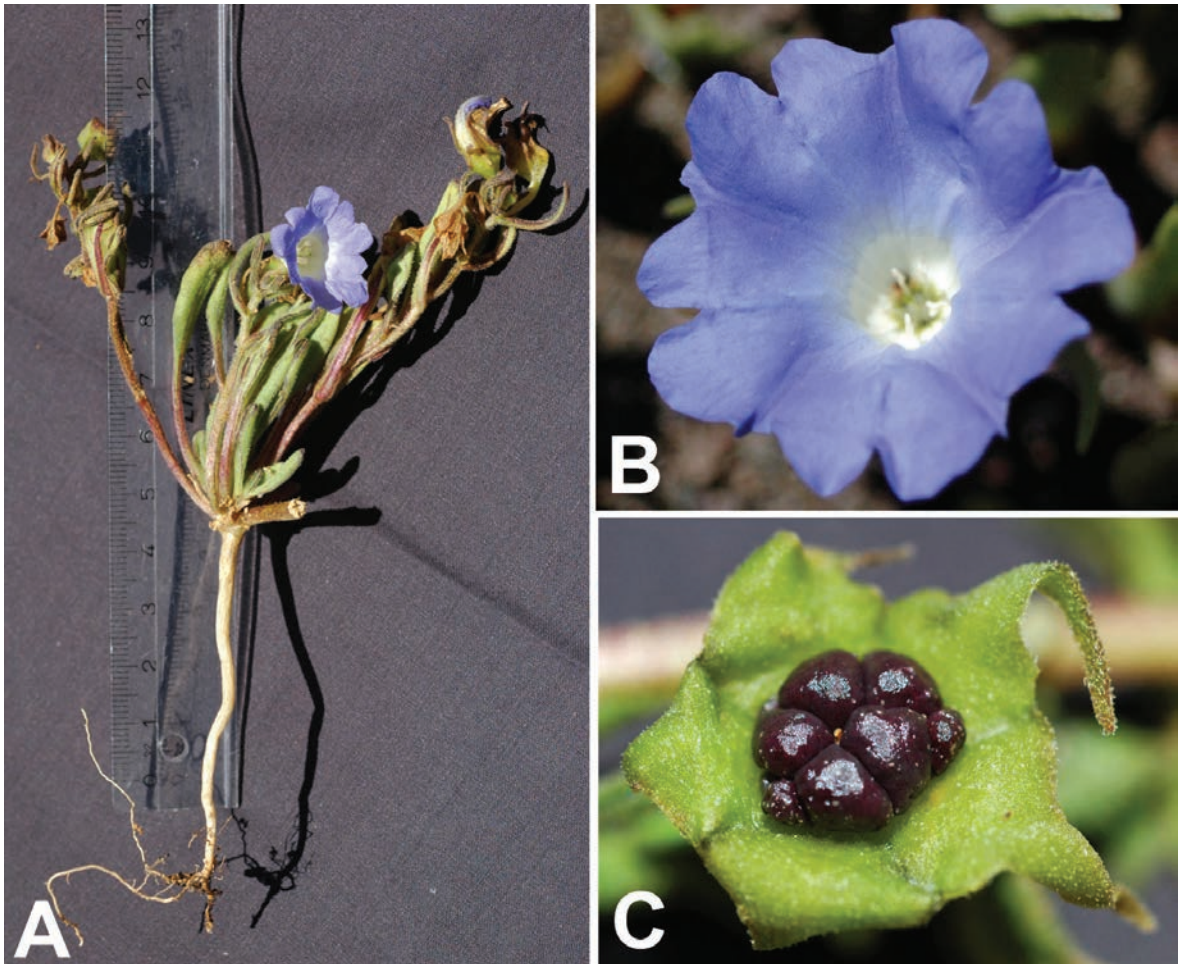


FIGURE 31. *Nolana acuminata*. **A**, Plant with exposed annual root; **B**, Closeup of corolla; **C**, Ovary with ripening mericarps.

The size of the basal leaves is variable, and, given enough moisture, the root can develop and thicken, but it never develops into a woody caudex as seen in *N. rupicola*.

The corollas of *Nolana acuminata* are similar in appearance to those of *N. elegans*. When pressed, herbarium material of these two species is separated with some difficulty; *N. acuminata* is distinguished by possessing smaller basal leaves and corollas that lack the deep purple spot in the proximal portion of the corolla (Fig. 31B, 32B, 33A–B). The similarity of *N. acuminata* and *N. elegans* in the dried state is evidenced by my determining duplicates of the same collection as different species. Duplicate collections of *E. Pisano V. & R. Bravo F. 580* from near Pan de Azúcar were determined as *N. acuminata* (CONC 144533) or *N. elegans* (SGO 138783). After examining material from within this region, the collections are here considered to fall within the variation of *N. acuminata*. Furthermore, collections by *G. Baumann 59* and *N. Schulz 2*, both from Cerro Moreno, were originally thought to represent *N. elegans*; however, they lack decurrent leaf bases that are diagnostic for that species and are treated as *N. acuminata* here. The collection by *Latorre et al. 241* represents the upper elevational limit for this taxon at 1500 m. Newly germinated forms of *N. acuminata* resemble *N. baccata*; however, the mericarps easily separate these two species (see discussion under *N. baccata*). Collections from near Taltal have been treated in the past as *N. jaffuelii*; however, these are here considered as *N. acuminata* (i.e., *Ch. von Bohlen V. 1298*; *Muñoz & Meza 2301*, *Teillier 452*, and *Teillier 481*). A collection from Limarí, Fray Jorge, *C. Jiles 672*, was thought to represent *N. acuminata*; however, it represents *Nolana reichei* and is cited under that taxon.

Although Johnston (1936: 37) placed *Nolana leucantha* in synonymy with *N. baccata*, it is here placed in synonymy with *N. acuminata* on a preponderance of characters. The sheet designated as a paratype, *Geisse s.n.* (SGO 72447), was collected at Quebrada El León, north of Caldera. It has long attenuate calyx lobes and narrow upper leaves that are decurrent on the stems and white corollas with yellow throats. *Nolana navarri* was also placed in synonymy with *N. baccata* by Johnston (1936: 38), but an examination of the lectotype shows it to possess warty mericarps and long calyx lobes, unlike those typical in *N. baccata*. The paratype sheet associated with *N. navarri* was collected much farther north, near Carrizal, and is more likely *N. acuminata*, and it is significantly different from the *N. navarri* lectotype.

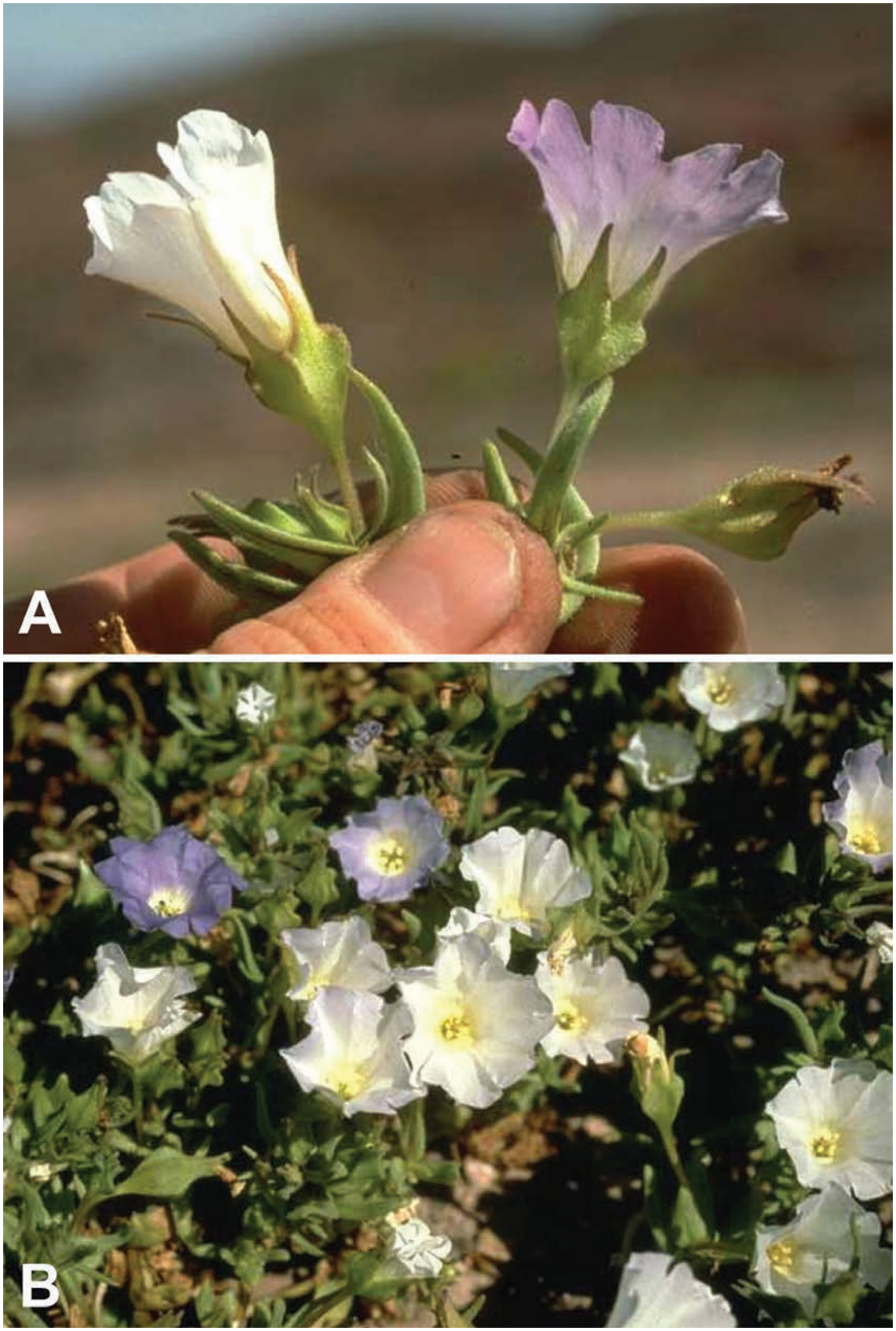


FIGURE 32. *Nolana acuminata*. **A**. Plants growing sympatrically with white and blue corolla forms; **B**, Blue and white forms growing intermixed.

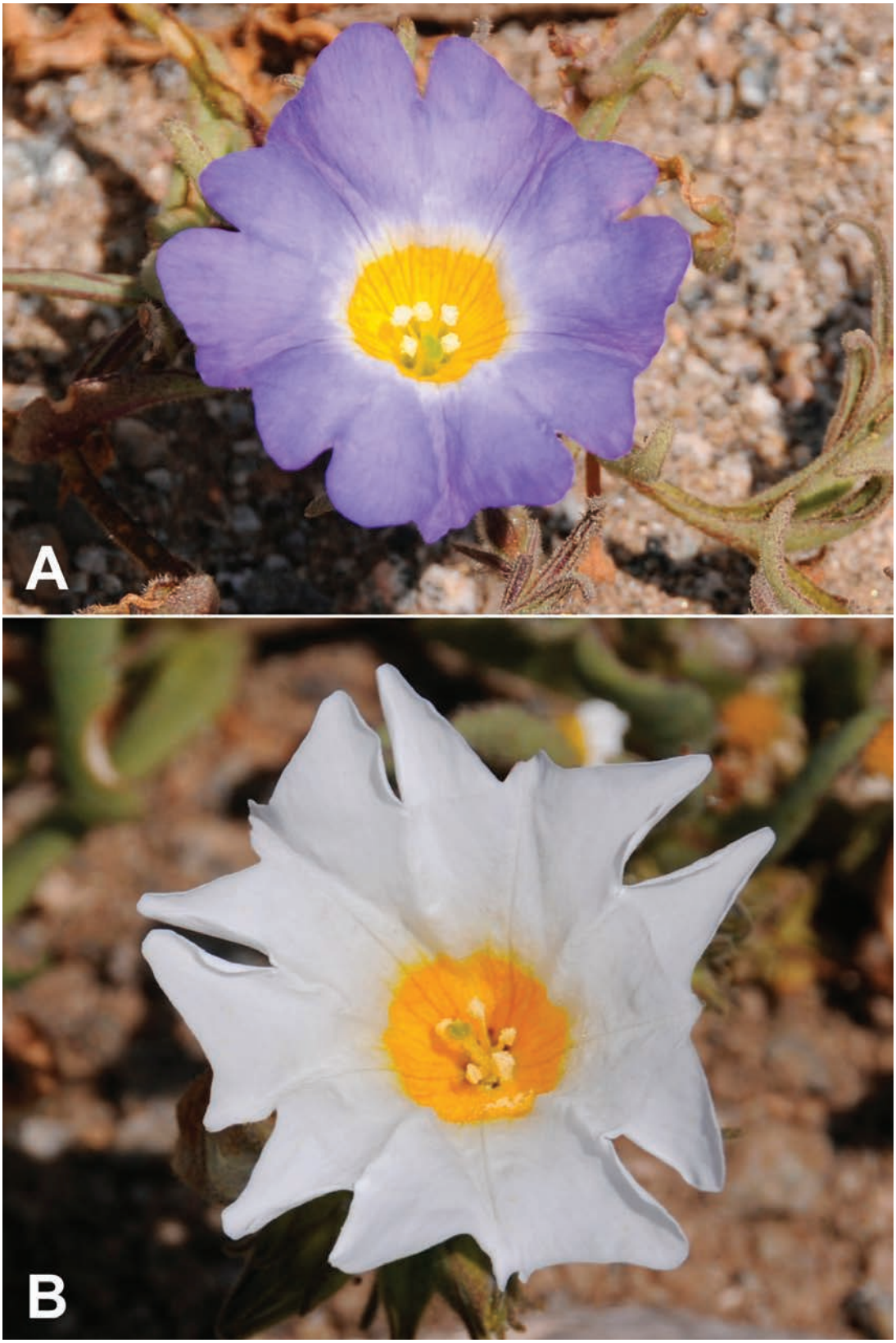


FIGURE 33. *Nolana acuminata*. **A**, Light to deep blue corolla with rounded, shallow indentations; **B**, White corolla with acute or prolonged indentations.

Type material of *N. grandiflora* was collected by Herzog near Antofagasta in 1916, and no additional collections conforming to the type had been seen until April–May 2015, when unusual rains stimulated local blooming on the slopes directly west of the city (Fig. 29A–B). These individuals corresponded with Herzog's description and type photographs from the type locality. It is not surprising that this isolated population perhaps diverged morphologically.

There is potential for confusion in discrepancies between Thomas Bridges' numerical list in his notebook and herbarium sheet numbers. The type designation cites the collection as *1325*; however, the sheet in Hooker's Herbarium is clearly labeled *1322*.

Additional specimens examined: CHILE. **Antofagasta**: Lomas de Taltal, from Taltal along the coast to the south ca. 7 km, 25°26'45"S, 70°30'57"W, 30 m.a.s.l., 25 October 2002, *M. Ackermann 486* (B, CONC 157527, SGO 150966); Lomas de Taltal, near road from Taltal to Panamericana, 25°27'50"S, 70°26'42"W, 360 m.a.s.l., 24 October 2002, *M. Ackermann 463* (B, CONC 157509, SGO 150947); Peninsula Moreno, cerros al lado Oeste de Juan López, 23°30'S, 70°34'W, 840 m.a.s.l., 18 October 1992, *G. Baumann 59* (CONC 122465, SGO 127862); Cerro Moreno, 700 m.a.s.l., 5 February 1968, *F. Behn s.n.* (CONC 36253); Quebrada al norte de Antofagasta, 23°39'S, 70°24'W, 150 m.a.s.l., 6 February 1968, *F. Behn 1* (CONC 144819); 10 km al Sur de Caleta Blanco Encalada, 200–800 m.a.s.l., 11 December 1949, blanco, *W. Biese 3179* (SGO 96783), azul, *3180* (SGO 96782); cercanías de Paposo, 25°00'34"S, 70°27'57"W, 20 June 2015, *K. Bull H. 674* (SGO 166635); Quebrada La Chimba, 27 September 1953, *A. Cabrera 11338* (CONC 24173, SGO 126660); Quebrada Taltal, ca. 18 km SE of Taltal near junction to Antofagasta, 25°32'S, 70°23'W, 740 m.a.s.l., 23 December 1987, *M. O. Dillon 5383* (CONC, E, F 2010978, GH, SGO); Quebrada Taltal, ca. 18 km SE of Taltal, 25°32'S, 70°23'W, 740 m.a.s.l., 23 December 1987, *M. O. Dillon 5385* (F 2010976); Quebrada Los Zanjones, 25°31'S, 70°25'W, 610–620 m.a.s.l., 25 September 1988, *M. O. Dillon, D. Dillon & V. Poblete 5497* (CONC, E, F 2011625, GH); Quebrada to Bahía Tórtolas, S side of Cerro San Pedro, ca. 22 (air) SW of Taltal; ca. 16 km SE of Taltal, 2–5 km NE of Estación Breas, 25°29'S, 70°22'W, 590–610 m.a.s.l., 29 October 1988, *M. O. Dillon & D. Dillon 5795* (E, F 2329923, G, GH); Quebrada de Taltal, ca. 1.5 km E of Taltal, 25°25'S, 70°28'W, 90 m.a.s.l., 26 November 1997, *M. O. Dillon 8100* (CONC 149962, F 2182966, GH, SGO 143698); road to Cifuncho, 25°31'41"S, 70°25'43"W, ca. 90 m.a.s.l., 7 October 2005, *M. O. Dillon & A. Casareggio M. 8700* (E, F 2294695, GH, SGO); Hueso Parado, 25°23'S, 70°27'W, 40 m.a.s.l., 13 November 1997, *M. O. Dillon & C. Trujillo C. 8022* (F 2183337, GH); Quebrada Los Zanjones on route to Cifuncho, 25°32'S, 70°27'W, 890 m.a.s.l., 17 November 1997, *M. O. Dillon & C. Trujillo C. 8053* (CONC 150024, F 2183326, SGO 143706); Quebrada Taltal, 25°29'04"S, 70°26'10"W, ca. 435 m.a.s.l., 27 September 2010, *M. O. Dillon 9127* (CONC, F 2331757, SGO); Taltal, 25°26'S, 70°35'W, 7 October 1983, *M. Elgueta 22* (SGO 145501); Taltal, 1 November 1930, *F. Jaffuel 974* (GH); La Chimba, 23°32'S, 70°22'W, 100 m.a.s.l., 16 November 1987, *A. Hoffmann & X. Rodríguez 3* (CONC 99181); La Chimba, 23°32'S, 70°22'W, 300 m.a.s.l., 16 November 1987, *A. Hoffmann & X. Rodríguez 51* (CONC 99244); Quebrada La Peineta, Km 1085, 25°33'S, 70°19'W, 900 m.a.s.l., 6 November 1969, *C. Jiles 5314* (CONC 103335); Quebrada Taltal, 25°19'S, 70°26'W, 450 m.a.s.l., 10 November 1969, *C. Jiles 5477* (CONC 103334); Antofagasta, base of hills just SE of La Chimba, *I. M. Johnston 3638* (GH); Trayecto Estación Agua Verde Ruta 5, 1500 m.a.s.l., *C. Latorre, C. Villagrán & A. Maldonado 241* (CONC 150971); Taltal, Valle de Changos, 16 October 1940, *R. López* (CONC 129585, *Herb. Gunckel 19154*); Taltal, *G. Montero O. 6317* (CONC 112955); Km 1055, camino a Taltal, 27 October 1987, *M. Muñoz S. & I. Meza P. 2270* (SGO 137718); Antofagasta, 100–300 m.a.s.l., 3 April 1926, *F. W. Pennell 13019* (F 557495, GH, US 1343021); La Chimba, 300 m.a.s.l., 30 September 1991, *M. Quezada & E. Ruiz 98* (CONC 121787); La Chimba, 1 October 1954, *M. Ricardi 3065* (CONC 18298); Taltal, Chépica, 17 September 1954, *M. Ricardi 3078* (CONC 18311); Cerro Moreno, 23°30'S, 70°34'W, 16 November 2006, *N. Schulz 2* (SGO 154764); Cerro Perales, 25°26'S, 70°35'W, 3 October 1987, *S. Teillier 620* (CONC 138418, SGO 141654); camino entre Paposo y Taltal, Quebrada Cascabeles, *Ch. von Bohlen V. 1298* (CONC 144822, SGO 131124); Quebrada La Chimba, 23°32'S, 70°25'W, 30 September 1987, *S. Teillier 452* (CONC 138416, SGO 141652); camino a Caleta El Cobre, 24°15'S, 70°33'W, 600 m.a.s.l., *S. Teillier 481* (CONC 138417, SGO 141653); Quebrada de Taltal, 25°26'S, 70°35'W, 330 m.a.s.l., 17 September 1992, *S. Teillier, P. Rundel, & P. Garcia 2824* (F 2114621, SGO 129372); ca. 10 km E of Taltal, Quebrada de Taltal, 50 m.a.s.l., 12 October 1936, *C. R. Worth & J. L. Morrison 15772* (F 1488345, GH, K); Taltal, *E. Werdermann 769* (B, BM000941329, CONC 22597, E00130960, F 564214, GH, K, SGO 59537, US 1474280, US 3310754). **Atacama**: Quebrada El León, 10 October 1965, *M. Andaur V. s.n.* (CONC 129686); Posada, 11 October 1987, *Ch. von Bohlen 472* (SGO 163966); Copiapó, Panamericana norte, entre Caldera y Obispito, 4 October 1991, *Ch. von Bohlen V. 1218* (SGO 131109); ca. 24 km SW of Chañaral, 26°31'53"S, 70°41'36"W, 16 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9089* (CONC, F 2293456, SGO); ca. 14 km SW of Chañaral, 26°39'53"S, 70°43'02"W, 18 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9092* (CONC, F 2293459, F 2293460, SGO); white morphs, *9092A* (F 2293461); 14 km SW of Chañaral, 26°39'53"S, 70°43'02"W, 18 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9093* (CONC, F 2293462, SGO); ca. 14 km SW of Chañaral, 26°40'36"S, 70°43'13"W, 28 October 2009, *M. O. Dillon & R. Concha 9094* (CONC, F 2293463, SGO); ca. 33 km NE of Chañaral, Km 1005 along Panamericana, 26°14'S, 70°29'W, ca. 650 m.a.s.l., 3 December 1987, *M. O. Dillon & S. Teillier 5056* (CONC, E, F 2010279, GH, K, SGO); Quebrada de León, ca. 17 km NNE of Caldera, 26°56'00"S, 70°44'30"W, ca. 326 m.a.s.l., 2 October 2010, *M. O. Dillon 9140* (SGO); Quebrada de León, ca. 17 km NNE of Caldera, 26°56'00"S, 70°44'30"W,

326 m.a.s.l., 2 October 2010, *M. O. Dillon 9141* (SGO), *9142* (SGO), *9143* (SGO), *9144* (SGO), *9145* (SGO), *9146* (CONC), *9147* (CONC), *9148* (CONC); vicinity of Puerto de Chañaral, hills back of El Barquito, *I. M. Johnston 4769* (GH); camino de Vallenar a Huasco, 17 September 1965, *E. M. L. Kausel 4962* (SGO 137155); Quebrada El León, 26°57'S, 70°44'W, 240 m.a.s.l., 16 October 2005, *F. Luebert & C. Becker 2847* (F 2290721; SGO 159442); carretera Panamericana, entre Chañaral y Caldera, Km 59, frente a Rada Blanca, 26°47'S, 70°46'W, 5 m.a.s.l., 9 February 1988, *C. Marticorena, T. Stuessy, & M. Baeza P. 9914* (CONC 136305, MA); Huasco, Llanos de Carrizalillo, a 4 km de Carrizalillo, hacia Vallenar, 140 m.a.s.l., 24 September 1941, *C. Muñoz P. & G. T. Johnson 1977* (SGO 112309); Prov. Chañaral, Parque Nacional Pan de Azúcar, *M. Muñoz S. & I. Meza P. 2301* (SGO 137719); Cerca Posada Donde mi Tía, 27 October1984, *M. Muñoz S. 2018* (SGO 108208); Camino Carrizal Bajo a Huasco, Tres Playitas, 12 October 1992, *M. Muñoz S. 3042* (SGO 131457); Playa Puerto Fino, Posada San Ramón, 26°30'59"S, 70°41'43"W, 22 m.a.s.l., 29 September 2005, *M. Muñoz S. 4580* (SGO 153607); Parque Nacional Pan de Azúcar, Quebrada de Coquimbo, 26°09'S, 70°45'W, 10 November 1987, *I. Páez s.n.* (SGO 141775); Quebrada Agua Grande, entre Pan de Azúcar y Caleta Esmeralda, 780 m.a.s.l., *E. Pisano V. & R. Bravo F. 580* (CONC 144533, SGO 138783); Chañaral–Caldera, *M. Ricardi 1093* (CONC 30064); entre Las Bombas y Chañaral, Km 27, 700 m.a.s.l., 23 October 1965, *M. Ricardi, C. Marticorena & O. Matthei 1426* (CONC 31169); Prov. Chañaral, bajando a la caleta Flamenco, 26°34'05"S, 70°32'21"W, 325 m.a.s.l., 28 September 2017, *S. Teillier, J. Delaunoy, A. Zapata, & J. Torres-Mura 8401* (CONC 186731); Caldera, 400 m.a.s.l., 16 September 1967, *O. Zöllner 1851* (CONC 129685, *Herb. Gunckel 47490*). **Coquimbo**: Prov. Elqui, Los Choros, 29°14'S, 71°27'W, 10 m.a.s.l., 12 November 2001, *C. Aedo 6865* (CONC 161220, MA); Coquimbo, 16 September 1952, *E. Barros V. s.n.* (CONC 14022); Prov. Elqui, entre Choros Bajos y La Higuera, 29°20'S, 71°14'W, 50 m.a.s.l., June 2010, *A. Cea 21* (CONC 172460); La Serena, 29°56'06"S, 71°16'54"W, 10 m.a.s.l., 22 October 1990, *O. F. Clark 4-05* (CONC 158486); La Serena, 29°55'S, 71°13'W, 28 January 1991, *M. DeVore 1549* (CONC 128705); Elqui. 2 km W of Choros Bajos, 29°18'32"S, 71°21'20"W, 20 m.a.s.l., 19 October 1997, *U. Eggli & B. E. Leuenberger 2961* (B, SGO 144077); Coquimbo, 200–300 ft, *C. Elliot 4* (E00130964); alrededores de La Serena, 50–100 m.a.s.l., 28 October 1948, *R. Ferreyra 4065* (US 1998595, USM); Ovalle, Cerrillos, 21 September 1952, *C. Hempel s.n.* (CONC 13254); Camarico, 300 m.a.s.l., 11 October 1949, *C. Jiles 1339* (CONC 36169); Estancia Talca, 19 September 1949, *C. Jiles 1421* (CONC 36168); Cruz Grande, 29°27'S, 71°15'W, 600 m.a.s.l., 27 October 1971, *C. Jiles 5833* (CONC 102995); Ovalle, Tongoy, 30°15'S, 71°30'W, 10 m.a.s.l., *C. Jiles 6358* (CONC 102351); Panamericana entre Trapiche e Incahuasi, 17 September 1996, *E. M. L. Kausel 5134* (SGO 137151); Tofo, 29°27'S, 71°12'W, *C. Marticorena & O. Matthei 201* (CONC 28354); La Herradura, 26 September 1934, 5 m.a.s.l., *G. Montero O. 1843* (CONC 112953); Los Vilos, 2 m.a.s.l., 8 October 1965, *G. Montero O. 7228* (CONC 112954); camino interior Guanaqueros a Tongoy, primer Km, 12 October 1989, *M. Muñoz S. 2416* (SGO 123032); Elqui, Caleta Hornos, 29°37'00"S, 71°17'11"W, September 2009, *P. G. Ossa 174* (SGO 162569); El Tofo, camino a Cruz Grande, 600 m.a.s.l., 10 October 1958, *M. Ricardi & C. Marticorena 4924/1309* (CONC 25719); Cerro Grande, vicinity of La Serena, 10 October 1914, *Mr. & Mrs. J. N. Rose 19282* (US 761826); Totoralillo, 30°04'S, 71°21'W, 50 m.a.s.l., 20 September 1961, *F. Schlegel 3915* (CONC 42579); Herradura, 27 September 1917, *C. J. F. Skottsberg & I. Skottsberg 1049* (F 737491); La Serena, Campania, 17 September 1947, *B. Sparre 2583* (SGO 98207); Huasco, Canto del Agua, 28°09'S, 70°58'W, 200 m.a.s.l., 19 March 1988, *F. Squeo 88-193* (CONC 99519); ca. 25 km from La Serena, road to El Tofo, *C. R. Worth & J. L. Morrison 16407* (GH, K, US 3634880); ca. 26 km from Ovalle, road to Cerillos, *C. R. Worth & J. L. Morrison 16411* (GH, K, US 3634883); Playa de Tongoy, 12 October 1967, *O. Zöllner 2474* (CONC 129687).

B2. ***Nolana baccata*** (Lindl.) Dunal, Prodr. 13: 14. 1852. Fig. 34–38.

Basionym: *Alona baccata* Lindl., Edwards's Bot. Reg. 30, tab. 46. 1844. TYPE: CHILE. Atacama: Copiapó, between Copiapó and Huasco, 1842, *T. Bridges 1322* [notebook–*1323*] (Lectotype designated by Mesa-M., 1981: CGE [CGE05009]; Isolectotypes: E [E00130952], FI-Webb [FI009588], K [K000532188]).

Digital image: Isolectotype of *Alona baccata* from Royal Botanic Gardens, Edinburgh [E00130952]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.e00130952

Homotypic synonyms: *Gubleria baccata* (Lindl.) Gaudich., Voy. Bonite, Bot., t. 104. 1851–1852 (Fig. 34); *Periloba baccata* (Lindl.) I.M. Johnst., Contrib. Gray Herb. 85: 105. 1929.

Heterotypic synonyms: *Sorema linearis* Miers, London J. Bot. 4: 499. 1845. TYPE: CHILE. Atacama: Copiapó, between Copiapó and Huasco ["Concepción"], 1842, *T. Bridges 1322* (Lectotype designated by Mesa-M., 1981: K [K000532188]). *Nolana linearis* (Miers) ex Dunal, Prodr. 13: 13. 1852; *Nolana alba* Phil., Ann. Univ. Chile 91: 32. 1895. TYPE: CHILE. Atacama: Copiapó, "Primum de Bandurrias prope Chañarcillo a Guillermo Geisse accepi, prope Caldera frequens", 1885, *G. Geisse s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 55136, SGO000004364]; Isolectotype: SGO [SGO 42668, SGO000004363]). **Paratypes**: CHILE. Atacama: Copiapó, Bandurrias, October 1886, *G. Geisse s.n.* (SGO [72451, SGO000004362]); Cerro Bandurrias, *G. Geisse s.n.* (SGO [71693, SGO000004361]); *Nolana carrera* Phil., Anal. Univ. Chile 91: 31. 1895. TYPE: CHILE. Atacama: Huasco, September 1885, *F. Philippi s.n.* (Lectotype designated by Mesa-M.,

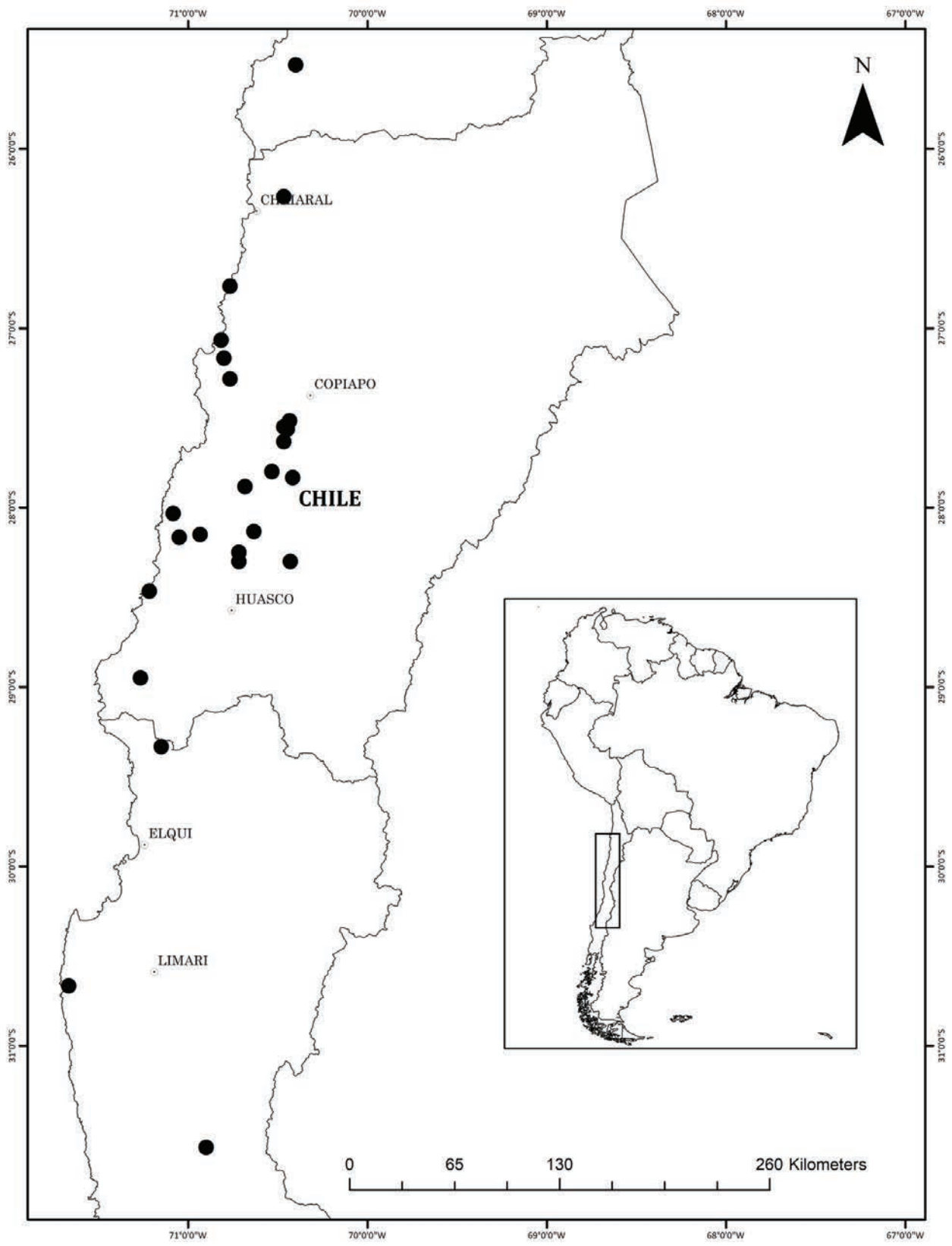


FIGURE 34. Distribution of *Nolana baccata* (Lindl.) Dunal.

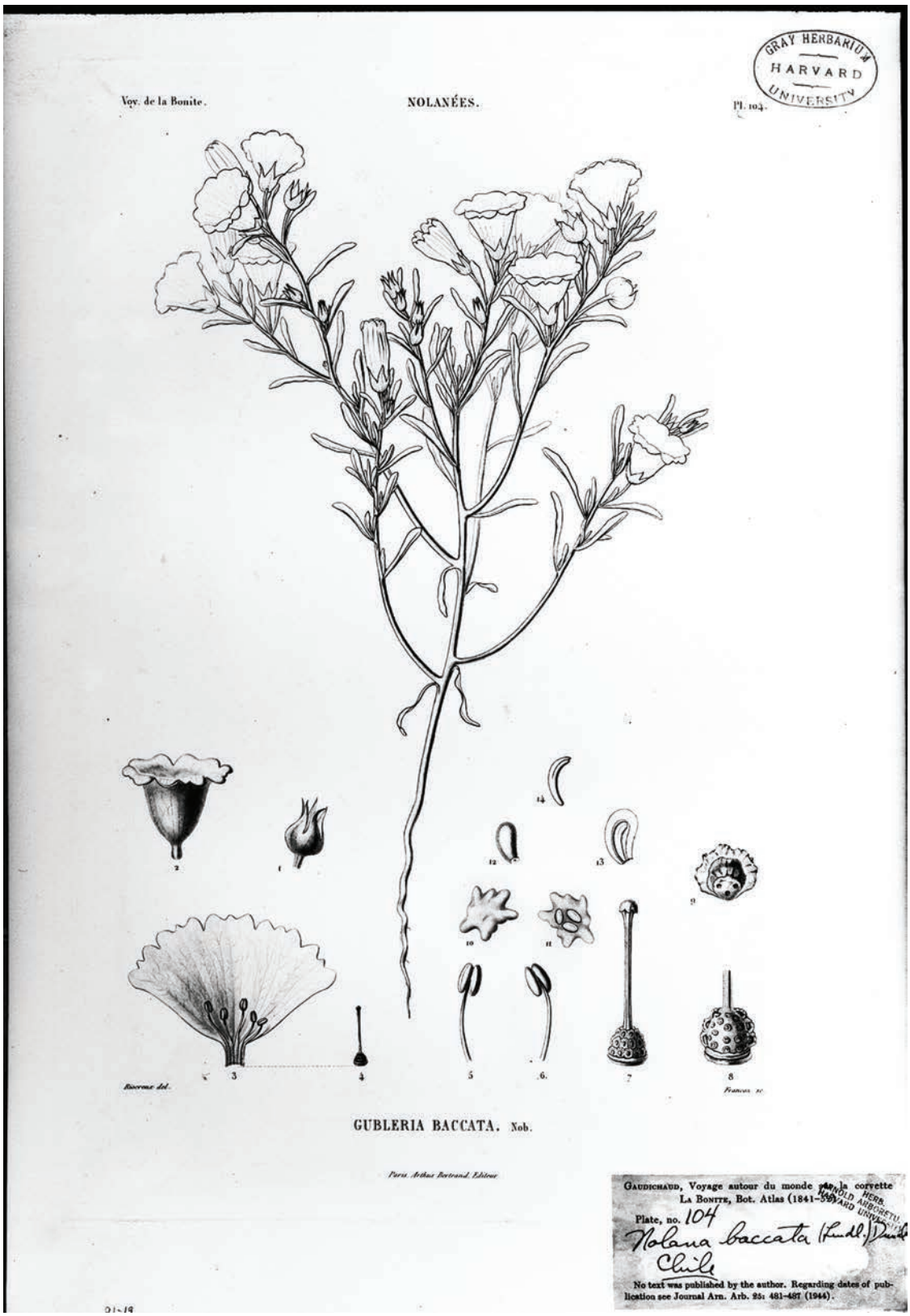


FIGURE 35. Illustration of *Nolana baccata* as *Gubleria baccata* (Lindl.) Gaudich., Plate 104, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 36. *Nolana baccata*. Fully developed flowering individual at only 8 cm tall.

1981: SGO [55089], SGO000004368; Isolectotypes: BM (BM000941302), K (K000532186)). **Paratypes**: CHILE. Atacama: Copiapó, 1881, *José [2°] Rivero s.n.* (SGO 55137); Copiapó, Pabellon, September 1885, *F. J. San Román s.n.* (SGO 55138)]; *Sorema glutinosa* Phil., Fl. Atac. 44. 1860. TYPE: CHILE. Atacama: Playas de Caldera, December 1853, *R. A. Philippi s.n.* (SGO [55149, SGO000004399]); *Nolana debilis* Phil., Anal. Univ. Chile 91: 29. 1895. TYPE: CHILE. Atacama: Piedra Colgada, entre Caldera y Copiapó, September 1885, *F. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 55145, SGO000004369]; Isolectotype: SGO [SGO 42649, SGO000004370]). **Paratype**: CHILE. Atacama: Piedra Colgada, entre Caldera y Copiapó, September 1885, *R. A. Philippi s.n.* (K [K000532193]); *Nolana pulchella* Reiche, Anal. Univ. Chile 125: 493. 1910. TYPE: CHILE. Atacama, [without locality], July 1900, *T. King s.n.* (Lectotype designated here: E (E00130953).

Annual *herbs* to 25 cm tall; stems erect to decumbent, unbranched or branched basally with 2–4 branches; root simple, delicate, not thickened, 10–15 cm long. Basal *leaves* rosulate, blades lanceolate, 3–4 cm long, ca. 1 cm

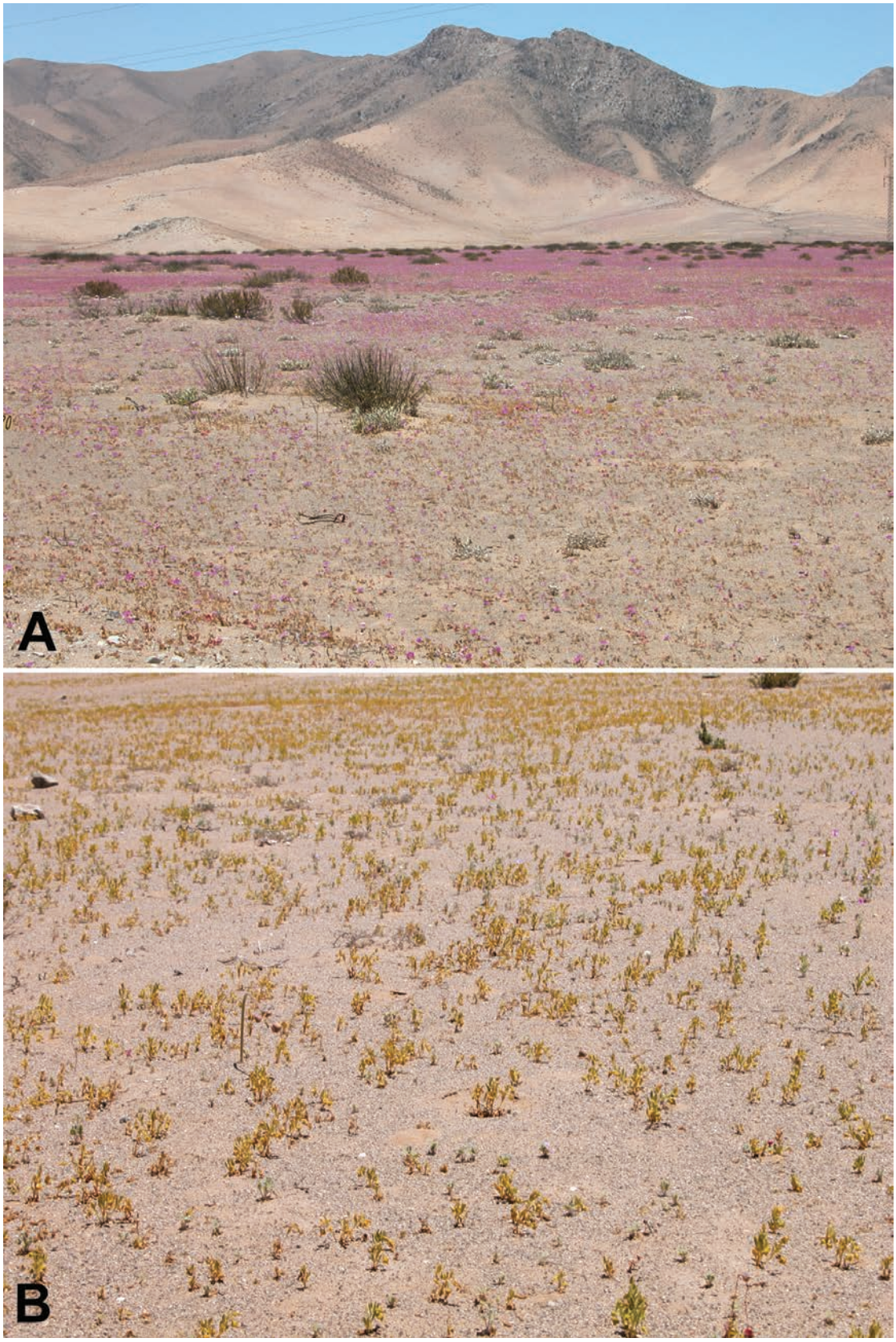


FIGURE 37. *Nolana baccata* population south of Copiapó, Chile. **A**, Landscape with flowering community following rains, including red-flowered *Cistanthe longiscapa*; **B**, *Nolana baccata* individuals past bloom and turning yellow.

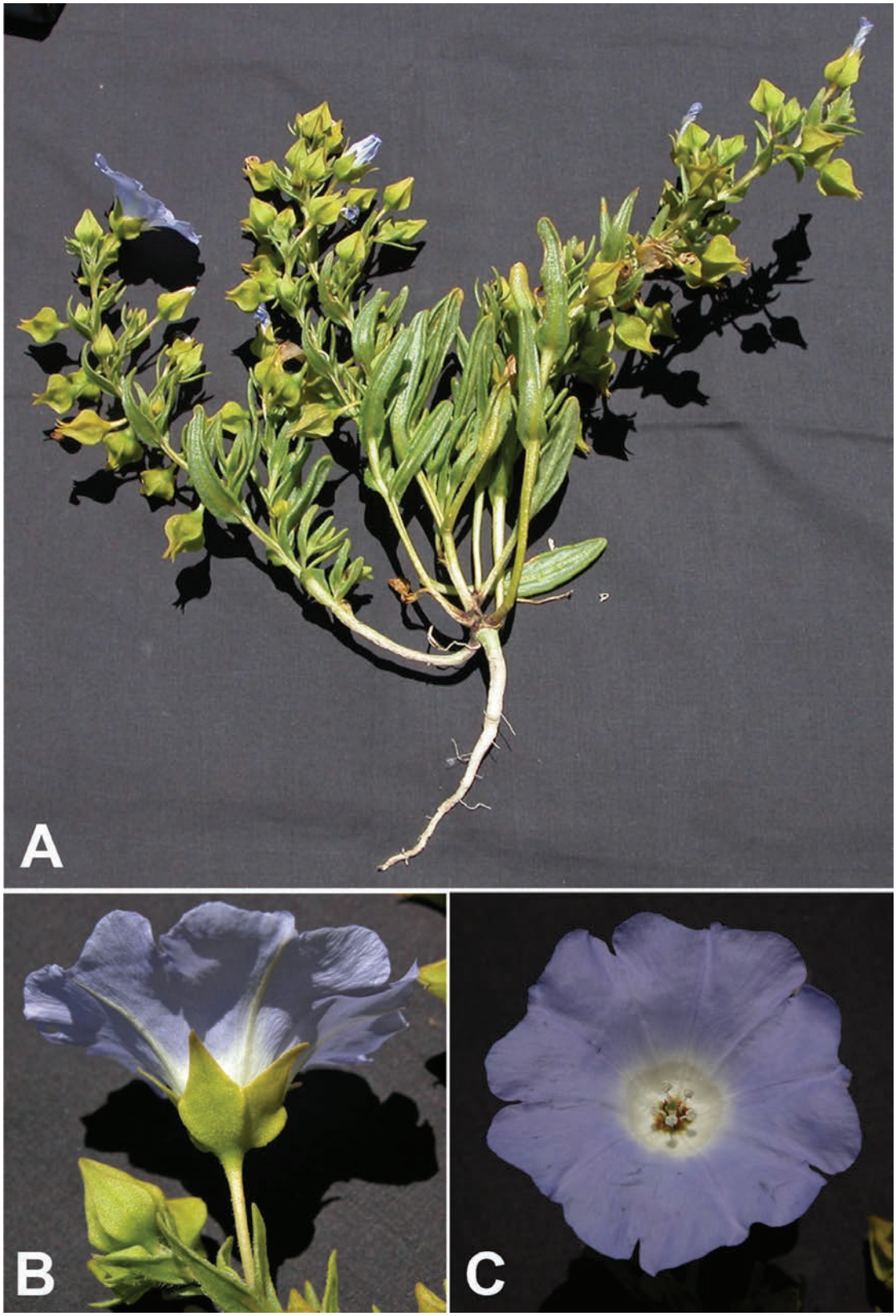


FIGURE 38. *Nolana baccata*. **A**, Individuals illustrating the annual root and flowering stems; **B**, Lateral view of the flower showing the triangular calyx lobes; **C**, Frontal view of the corolla with red mites.

wide, margins thickened, apically acute, basally cuneate; petiole 1–2 cm long; cauline leaves alternate, blades linear-spathulate, 1–3(–5) cm long, 3–8 mm wide, apically rounded, basally cuneate to rounded, pubescent with long, flagelliform trichomes, and short capitate-glandular trichomes. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 10–14 mm long. *Flowers* 5-merous; calyces campanulate, 10–13 mm long, lobes equal, 5–8 mm long, 2–3 mm wide at base, dentate to triangular, apically rounded, pubescent with capitate-glandular trichomes; corollas infundibularis, regular, 20–25 mm long, 20–30 mm wide at mouth, pale blue or white, drying yellowish, frequently with a dark proximal spot. *Mericarps* 18–35, the largest ca. 3 mm long, polyhedrons with an attenuate projection forming a wing or, more rarely, with angled or sharp, conic protrusions; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *bacca*, and alludes to the mericarps described by Lindley as "drupes quite pulpy in the dried state". Lindley had not seen fresh material of this species and thought they had dried out; all members of the genus have mericarps that dry throughout their development.

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 140–670 m.a.s.l. It is recorded from a wide variety of environments with sandy soils; near-coast habitats or, more typically, inland areas (Fig. 34). Matorral Desértico Mediterráneo Interior (Luebert and Pliscoff, 2006).

Illustration: Fig. 35. Illustration of *Nolana baccata* as *Gubleria baccata*, Plate 104. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Common name: *suspiro*

Nolana baccata is a small annual (Fig. 36), that forms large populations in open sandy plains (Fig. 37A–B). Mixed flowering communities develop following rains, including the distinctive reddish flowers of *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk. (Fig. 37A), in addition to the plantlets of *N. baccata* that are yellowish (Fig. 37B). The plants are 10–20 cm tall and flower almost immediately in response to increased moisture that is often associated with reoccurring El Niño events. Within populations, it is easy to observe variable individuals with many different sizes, corolla coloration, and mericarp numbers (Fig. 38A–C, 39A–D). This variation may be reflected in the number of described synonyms attributed to *N. baccata*. Future studies may support the recognition of some of the taxa currently in synonymy with this taxon. The annual forms of *Nolana acuminata* approach those of *N. baccata*; however, *N. baccata* has many more mericarps (18–35 vs. ca. 10–15) with more angular surfaces that are often deeply pock-marked, or the edges form wings or, more rarely, conic protrusions. The calyx lobes in *N. baccata* are more dentate or triangular and not lanceolate or attenuate as in *N. acuminata*. In general, the distribution for *N. baccata* is more southern than for *N. acuminata*; the two species potentially overlap but have not been observed growing sympatrically.

A collection of *Nolana acuminata* in the British Museum of Natural History attributed to *H. Cuming 856* (BM000941283) is labeled as being collected at "Coquimbo, 1832", and a collection of *N. baccata* by *Marticorena et al. 1647* from Choros Bajos, suggests overlap between Chañaral (26°20'40"S latitude) and Fray Jorge (30°42'32"S latitude). Collections from near Bahía Inglesa are small annuals with thin taproots; the corollas are invariably white, with a broad, sharply delineated yellow band in the throat, and the vascular traces appear as green veins. At the very base of the corollas, there is a dark band a few millimeters wide, not unlike that in *Nolana elegans*.

Johnston (1936: 38) first noted that the types of *Alona baccata* and *Sorema linearis* were duplicates of the same collection made by Thomas Bridges between Copiapó and Huasco in 1841. Miers designated a duplicate collection at Kew (*T. Bridges 1323*) as the type for *Sorema linearis*; however, that number is properly assigned to the holotype collection of *Alona ericifolia*, Huasco, *T. Bridges 1323* (K). The collection housed at Kew is surely mislabeled as from "Concepción", but is more likely from between Copiapó and Huasco, as is the type of *Alona baccata*.

An herbarium sheet housed at SGO (*Muñoz & Johnson 1978*) was collected at the same locality as their number *1977* and is here considered to be *Nolana acuminata*; the collectors mentioned both white and blue forms of that species. It is assumed the collection number was assigned to something different, and it is treated here as *N. baccata*. Collections made by Guillermo Geisse in 1885, 1886, and 1887 from the "Bandurrias" area include lectotypes and paratypes of *Nolana alba* (see above). Another collection by Geisse during October 1888, and housed at CONC (CONC 129690), is labeled as from Cerro Bandurrias. It was originally in Herbarium Gunckel 8333 and is perhaps best considered a topotype. Based upon overall morphology, a collection from Pajonales, 27°50'S, 70°25'W, October 1888, *G. Geisse s.n.* (CONC 129684; SGO 72459) is here treated as *Nolana baccata*.

Johnston annotated the K sheet (K000532193) as *N. pterocarpa*. The first sheet has an original R. A. Philippi label and was subsequently annotated by Carlos Muñoz (III-1946) as the type. This sheet also has the annotation by Aldo Mesa as *Nolana paradoxa* spp. *atriplicifolia* (1981). It should be treated as a paratype of *Nolana debilis*. Johnston (1936) placed *Nolana debilis* in synonymy with *N. pterocarpa*; however, it more closely resembles *N. baccata* in its stature, and the geographic locality is within its range. *Nolana pulchella* Reiche was listed in synonymy with *N. debilis*, and the lectotype sheet resembles *N. baccata*.

The second sheet has the herbarium label of Federico Philippi, "Piedra Colgada, prope Copiapó, IX 1885." It is annotated by C. Muñoz P. as "ined.," but there is also a note that designates it as the isotype; furthermore, this sheet was annotated by Aldo Mesa in 1978 as *Nolana baccata*. The plants on these two sheets have the same calyx and small stature as the material here placed under *Nolana baccata*, from just south of Copiapó. The Kew sheet "Chile, Com. R. A. Philippi, 2/1888, Caldera" is annotated by Johnston as

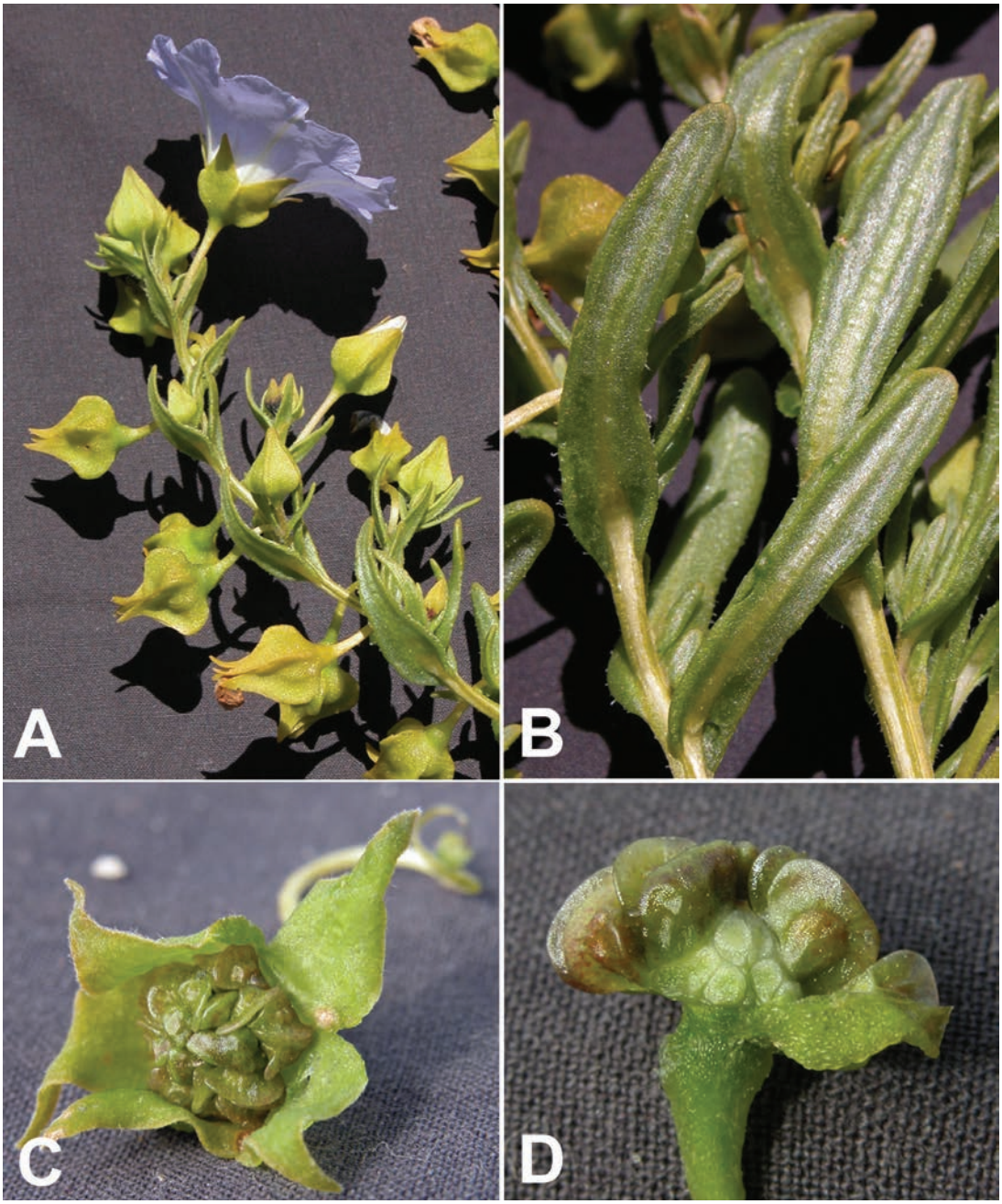


FIGURE 39. *Nolana baccata*. **A**, Closeup of flowering stem; **B**, Closeup of cauline leaf; **C**, Ovary with ripening mericarps; **D**, Lateral closeup with mericarps removed, exposing the receptacle scars.

N. pterocarpa Phil.; however, it seems that these plants are very small and have the same calyx as material referred to as *N. baccata*.

The type collection of *Nolana carrera* is a small annual, 15 to 20 cm tall, with a thin taproot. It is densely pubescent with long trichomes; the leaves are lanceolate to oblong-lanceolate, apically rounded, not obviously decurrent, the pedicels to 2 cm long, densely pubescent; the calyx lobes are long attenuate, corollas blue, campanulate, to 2.5 cm wide at the mouth. The SGO sheet has an original Philippi label and another one in pencil with the annotation "*Nolana pterocarpa* Phil." Aldo Mesa annotated the sheet as "*Nolana baccata*" in 1978 and then as "*Nolana carrera*" in 1979. Additional sheets are annotated by C. Muñoz as types of *N. carrera* and in pencil as a paratype. [Paratypes: Copiapó, 1881, *José [2°] Rivero s.n.* (SGO 55137); Copiapó, Pabellón [27°39'S, 70°14'W], September 1885, *F. J. San Román s.n.* (SGO 55138)].

Johnston placed *Sorema glutinosa* Phil., Fl. Atac. 44. 1860 (SGO 55149) in synonymy with *N. elegans*, but it has many characteristics of *N. baccata*, including the geographic locality where it was collected.

Additional specimens examined: CHILE. **Atacama**: between La Serena and Vallenar, 4 October 1971, *K. Beckett, M. Cheese, & J. Watson 4054* (SGO 110078); Vallenar, camino a Carrizal a 15 km, 600 m.a.s.l., 17 September 1949, *F. Behn s.n.* (CONC 8951); Estancia Castilla, 28 October 1965, *F. Behn s.n.* (CONC 30860); entre Vallenar y Copiapó, posada El Pimiento, 28 October 1965, *F. Behn s.n.* (CONC 30926); Freirina, Carrizal Bajo, 15 September 1965, *F. Behn s.n.* (CONC 36170); Copiapó, Quebrada Paipote, 12 October1949, *W. Biese 2662* (SGO 96581); Copiapó, Sierra Infante, 16 December 1949, *W. Biese 3376* (SGO 75178); 20 km N de Posada "La Frontera" entre Vallenar y Copiapó, 12 October 1987, *Ch. von Bohlen V. 443* (E00719015); Huasco, Camino entre Panamericana y Totoral, frente Estancia Castilla, 280 m.a.s.l., 8 September 1991, *Ch. von Bohlen V. 1389* (SGO 133298); 20 km S of Copiapó, 27°33'48"S, 70°26'48"W, 670 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8612* (CONC 179075, F 2292838, SGO 158943); Copiapó. S of Bahia Inglesa on route to Puerta Viejo, near Grotto Todo Santos, 27°08'57"S, 70°53'45"W, ca. 22 m.a.s.l., 18 September 2010, *M. O. Dillon 9112* (CONC, SGO); coastal road between Bahia Inglesa and Carrizal Bajo, 12 km S of Barranquilla, 27°51'41"S, 70°04'29"W, 222 m.a.s.l., 15 October 2011, *M. O. Dillon & J. Guerra 9203* (CONC 179095, SGO); coastal road between Bahia Inglesa and Carrizal Bajo, 10 km N of Bahia Salado, 27°34'45"S, 70°51'28"W, 204 m.a.s.l., 15 October 2011, *M. O. Dillon & J. Guerra 9205* (CONC 179093, SGO); ca. 12 km S of Caldera, ca. 6.5 km S of Bahia Inglesa en route to Puerto Viejo, 27°09'07"S, 70°53'16"W, ca. 20 m.a.s.l., 30 September 2010, *M. O. Dillon 9136* (CONC, SGO); Bahía Inglesa, 16 September 1991, *C. Fernández & H. Niemeyer F. 91-153* (SGO 127522); entre Vallenar y Copiapó, 27 October 1961, *A. Garaventa H. 4395* (CONC 68824); La Travesia, 27 October 1961, *A. Garaventa H. 7081* (CONC 92461); Pajonales, 27°50'S, 70°25'W, October 1888, *G. Geisse s.n.* (CONC 129684; SGO 72459), Cerro Bandurrias, *G. Geisse s.n.* (CONC 129690, SGO 42671), *G. Geisse s.n.* (SGO 55103); vicinity of Caldera, *E. E. Gigoux s.n.* (GH); Estancia Castilla, 17 September 1965, *G. Gleisner 66* (CONC 34548); entre Vallenar y Estancia Castilla, 18 September 1965, *G. Gleisner 67* (CONC 34550); Huasco, Cerca de Algarrobal, 19 September 1952, *C. Jiles 2177* (CONC 36166); Dept. Copiapó, Llanos de Travesía, 19 September 1952, *C. Jiles 2199* (CONC 36167); Llano de Caldera, 50 m.a.s.l., 10 September 1969, *C. Jiles 5483* (CONC 103297); Travesía, 27°33'S, 70°28'W, 520 m.a.s.l., 5 November 1969, *C. Jiles 5270* (CONC 102014); Domeyko a Vallenar, 9 October 1971, *E. M. L. Kausel 5468* (SGO 80561); Carrizal, *T. King 15* (E00130968); entre Vallenar y Copiapó, 14 September 1965, *A. Kohler 128* (CONC 33115, CONC 129691), *129* (CONC 33114, CONC 129693); Travesía, al norte de Vallenar, 5 October 1966, *A. Kohler 541* (CONC 33112); Camino de Copiapó a Bahía Salada, 27°24'37"S, 70°41'58"W, 190 m.a.s.l., 18 October 2005, *F. Luebert & C. Becker 2892* (F 2290696); camino a Bahía Salada, cerca del Cerro Chascón, 27°34'31"S, 70°47'48"W, 265 m.a.s.l., *F. Luebert & C. Becker 2893* (F 2290732); Freirina, Quebrada El Morado, 1 km S.O. de la junta del camino Carrizalillo–El Morado, 23 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1793* (CONC 43015); camino de Caldera a Copiapó, Km 12, 24 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1868* (CONC 70449); Panamericana norte, Copiapó–Caldera, 27°14'19"S, 70°46'35"W, 189 m, 26 September 2015, *P. Medina 3125* (CONC 186914); cercanías de Copiapó, 27°30'41"S, 70°25'10"W, 739 m.a.s.l., 21 September 2015, *P. Medina 3134* (CONC 186923); cercanías de Copiapó, 27°30'47"S, 70°25'13"W, 743 m, 26 September 2015, *P. Medina 3139* (CONC 168928); Quebrada de la Difunta, 27°35'06"S, 70°47'26"W, 20 October 2011, *G. Mieres s.n.* (CONC 179993); Freirina, Llanos de Carrizalillo, a 4 km de Carrizalillo, hacia Vallenar, 140 m.a.s.l., 24 September 1941, *C. Muñoz P. & G. T. Johnson 1978* (SGO 12310); entre Vallenar y Copiapó, 40 km sur de Copiapó, 11 October 1965, *C. Muñoz S. 34* (SGO 135292); 1 km antes desvío a Algarrobo viniendo desde Vallenar a Copiapó, 21 September 1977, flores azules, *M. Muñoz S., I. Meza P., & E. Barrera M. 1002* (SGO 108640), flores blancas, *M. Muñoz S., I. Meza P., & E. Barrera M. 1003* (SGO 108641); 1 km antes desvío a Algarrobo viniendo desde Vallenar a Copiapó, 21 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1004* (SGO 108642); Quebradita, Copiapó a Vallenar, 21 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1008* (SGO 108643); Posada Los Pajaritos, 400 m.a.s.l., 22 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1034* (SGO 108656); Quebrada Marguarita, between Punta de Vacas and Copiapó, 50 km N of Copiapó, 2 November 1991, *M. Ono & S. Oka s.n.* (MAK 274962); coastal desert near Totoral, NW of Vallenar, 14 November 1991, *M. Ono & T. Masuzawa s.n.* (MAK 274964); Caldera, September 1876, *P. Ortega s.n.* (SGO 42646), Caldera, September 1876, *P. Ortega s.n.* (SGO 55105); Caldera, September 1879, *R. A. Philippi s.n.* (SGO 42670, US 1336133); Travesía, s.d. (SGO 55085); Caldera, September 1879, *R. A. Philippi s.n.* (SGO 55086); 5 km al sur de Obispito, camino Caldera–Chañaral, 10 February 1968, *M. Ricardi 5490* (CONC 36175); Canto de Agua, 17 September 1957, *M. Ricardi & C. Marticorena 4418/803* (CONC 24966); Este de Estación Barros Lucco, hacia Estación Travesía, 27°40'56"S, 70°38'16"W, 253 m.a.s.l., *M. Rosas 9144* (INIA); Travesía, 18 September 1965, *J. Saá L. s.n.* (CONC 129692); Llano Travesía, 23°33'S, 70°28'W, 580 m.a.s.l., 19 September 1961, *F. Schlegel 3885* (B, CONC 42727); Llano Travesía, 27°33'S, 70°28'W, 580 m.a.s.l., 19 September 1961, *F. Schlegel 3891* (CONC 42728); Copiapó, Llanos de Churque, 27°38'S, 70°28'W, 7 October 1987, *S. Teillier 828* (CONC 143325; SGO 141774); Chañaral, ca. 1 km N of Caldera, 27°16'S, 70°46'W, 100 m.a.s.l., 26 October 2000, *S. Teillier & M. O. Dillon 4926* (F 2331768); Copiapó, Monte Amargo, 200 m.a.s.l., October 1924, *E. Werdermann 444* (BM000941313, CONC 109130, E00130959, F 565266, GH, K, US 1444747). **Coquimbo**: Ovalle, Fray Jorge, 30°40'S, 71°40'W, 280 m.a.s.l., September 1958, *J. Kummerow s.n.* (CONC 42636); La Serena, carretera Panamericana, entrada del camino a Choros Bajos, 21 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1647* (CONC 38444, F 1803468); camino de la Carretera Panamericana a Choros, Km 3, 200

m.a.s.l., 21 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1667* (CONC 36120); Cuesta de Las Palmas, entre Ovalle y Illapel, 11 October 1965, *V. Rojas s.n.* (CONC 129584). **Collector unknown**: CHILE. Caldera, September 1879, *s.d.* (SGO 55111); Caldera, September 1876, *s.d.* (SGO 55107); Caldera, September 1879, *s.d.* (SGO 42672); Caldera, September 1876, *s.d.* (SGO 55124). **No exact locality**: CHILE. 1888–1890, *T. Morong 1373* (E00130965, F 166496, GH, US 1417076); "*Nolana alba* Phil.", 1904, *F. Philippi s.n.* (BM000941324); "*Nolana carrerae* Ph." *F. Philippi s.n.* (BM000941284); "*Nolana debilis* Ph." *F. Philippi s.n.* [1904] (BM000941301); "*Nolana navarri* Ph." *F. Philippi s.n.* [1904] (BM000941307).

B3. ***Nolana elegans*** (Phil.) Reiche, Anal. Univ. Chile 125: 487. 1910. Fig. 40–45.

Basionym: *Sorema elegans* Phil., Fl. Atac. 43. 1860. TYPE: CHILE. Antofagasta: Paposo, December 1853, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 55147, SGO000004398], Isolectotype: W, not seen).

Digital image: Lectotype of *Sorema elegans* from Museo National de Historia Natural, Santiago [SGO 55147]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004398

Annual *herbs*, or, under certain conditions, perenating from a fleshy tap root; branches prostrate, to 1 m long. Basal rosette of *leaves*, blades lanceolate to spathulate, rarely ovate, 12–15 cm long, ca. 10 cm wide, glabrescent, bases unequal; petioles to 5 cm long, sparsely pubescent with flagelliform trichomes; cauline leaves on flowering stems, geminate, subopposite, blades oblong to oblanceolate, 25–40 mm long, 15–20 mm wide, sessile, basally unequal, conspicuously auriculate to decurrent, adaxial midvein prominent, deep red. *Inflorescences* of solitary flowers, terminal and axillary, subtending bracts ovate to lanceolate, bases strongly oblique. *Flowers* 5-merous; calyces ca. 25 mm long, ca. 15 mm wide, basally campanulate, lobes not projecting into shoulders, base ca. 8 mm wide, tapering abruptly to lanceolate-attenuate apex, 12–15 mm long; corollas infundibularis, weakly zygomorphic, ca. 50 mm long, limb 30–50 mm wide, dark blue with a white to yellowish central band, and a dark purple inner or proximal dark spot. *Mericarps* polyhedrons or angular, 2-seriate, 5 large, 4–5 mm long, 5–6 smaller, spherical to rounded, 3–4 mm long; seeds 2–8 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *elegans*, and refers to the handsome or attractive corollas in this species.

Distribution and Ecology: Chile, Regions of Antofagasta, Atacama, and Coquimbo; 5–780 m.a.s.l. It is recorded from a wide variety of environments with sandy soils; near-coast habitats over a range of 800 km (Fig. 40); Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Nolana elegans is a facultative annual with large, showy flowers to over 5 cm in diameter. The type was collected by R. A. Philippi on the slopes above Paposo, in an area called Paposo National Reserve. This population has been sampled extensively to understand the variation in vegetative and floral characters. When conditions are appropriate, *N. elegans* can become a dominate species within the landscape when blooming covers extensive areas, as witnessed, for example, at the Paposo Reserve on 17 October 2005 (Fig. 41A–B). It most closely resembles *N. acuminata* but can be separated in the living state with a combination of characters, including a dark central spot in the proximal portion of the corolla (Fig. 42A–B). This is determined with some difficulty in the dried state, and, for that reason, assigning determinations to herbarium material is often completed with difficulty. Basal leaves are very well- developed and are some of the largest in the genus (Fig. 43A–C). The character of the obliquely, unequally decurrent bases on the cauline leaves or bracts that subtend flowers on the stems (Fig. 44A) has been used to separate it from other closely related species, such as *N. acuminata*. Johnston (1936: 40) commented on the abundance and beauty of this species collected by R. A. Philippi from the fog-bathed slopes near Paposo, with corollas becoming 5 cm in diameter, and various colors ranging from blue to white are observed throughout (Fig. 44B). The comparison of living material illustrates the obvious characters that separate *Nolana elegans* and the related species, *N. rupicola* (Fig. 45A–B).

Some collections are difficult to determine with certainty. The collection by *C. R. Worth & J. L. Morrison 16141* (GH, K) has long decurrent leaf bases and white flowers that correspond to *Nolana elegans*; however, *N. acuminata* cannot be eliminated from consideration. Furthermore, *M. Muñoz S. 1890*, *M. Muñoz S. 1903*, and *Sparre 2530* were originally determined as *N. acuminata* by Mesa-M., but here are considered, provisionally, to be *N. elegans*. A collection by *N. Schulz 2* from Cerro Moreno and identified as *N. elegans* may be *N. acuminata*. Additionally, a collection by *G. Baumann 59* from Cerro Moreno was determined as *N. elegans* by Mesa-M. (1997), but it lacks the decurrent leaf bases and has much smaller flowers that are typical of *N. acuminata*. A robust, white-flowered form collected by *A. Moreira M. 704* at Punta Choros, 5 km from Carrizalillo, has the characteristic decurrent leaf bases.

Additional specimens examined: CHILE. **Antofagasta**: Antofagasta, vicinity of Miguel Díaz, directly N of Quebrada Iscuña, ca. 55 km N of Paposo and ca. 40 km S of El Cobre, 24°33'S, 70°33'W, 100–350 m.a.s.l., 15 December 1987, *M. O. Dillon & J. T. S. Teillier 5290* (CONC, E, F 2010897, GH, K, SGO); vicinity of Miguel Díaz, directly N of Quebrada Iscuña, ca. 55 km N of Paposo and ca. 40 km S of El Cobre, 24°33'S, 70°33'W, 100–150 m.a.s.l., 15 December 1987, *M. O. Dillon & J. T. S. Teillier 5310* (CONC, E, F 2010878, GH, K, SGO, US); near Quebrada Botija, ca. 11 km N of Miguel Díaz; ca. 60 km N of Paposo, 24°31'S, 70°33'W, 18 December 1987, *M. O. Dillon 5352* (F 2010906, GH); Chañaral: 21 km W of Pan-American Hwy 5, N route to Parque Nacional Pan de Azúcar; ca. 100 km S of Taltal, 85 m.a.s.l., 26°08'S, 70°37'W, 30 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5483* (E, F

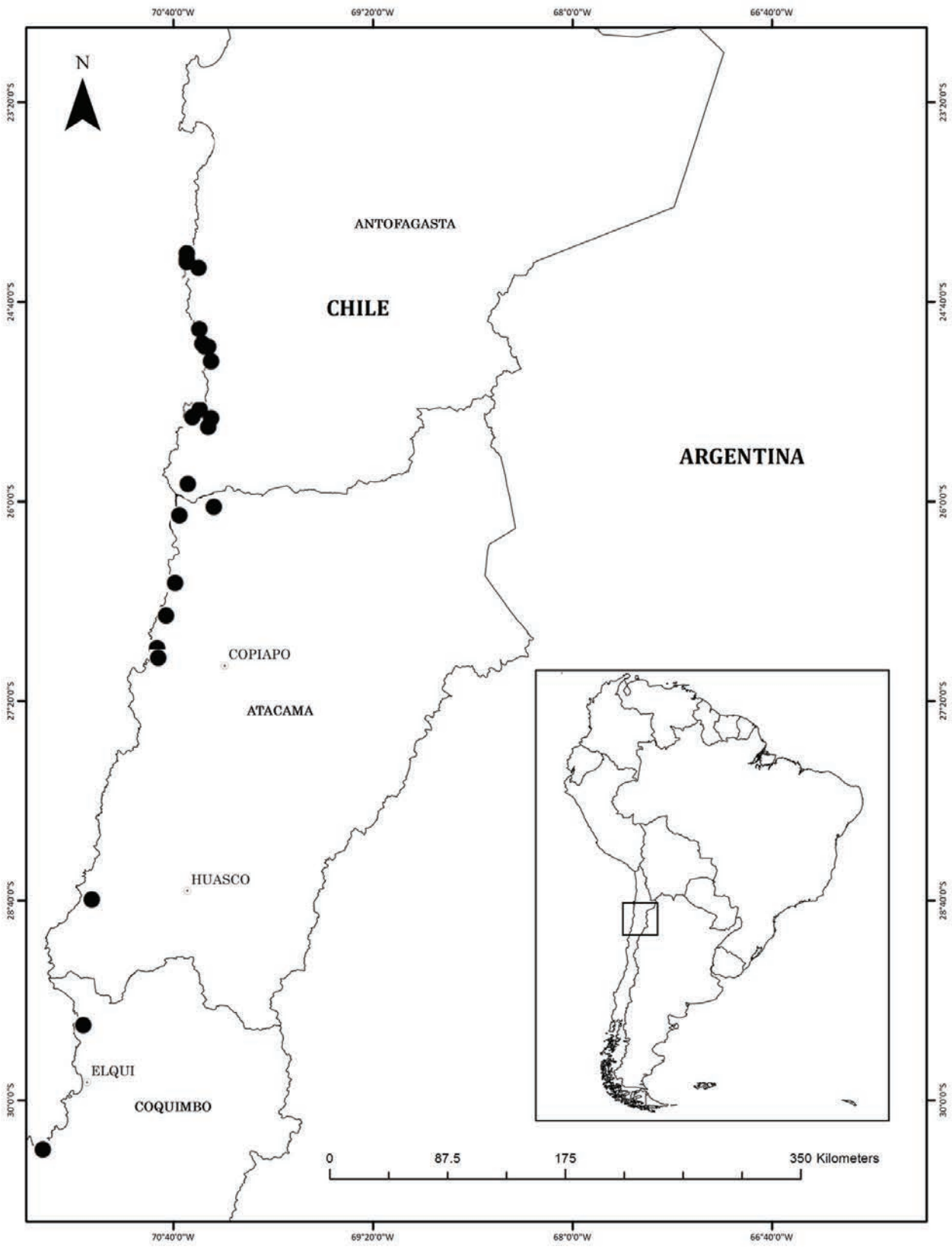


FIGURE 40. Distribution of *Nolana elegans* (Phil.) Reiche.

FIGURE 41. *Nolana elegans* population above Paposo, Chile, the type locality designated by Philippi on his 1853 collection. **A**, Extensive population ranging over a large area; **B**, Panorama facing south in an area dominated by *N. elegans*.

2011634, GH, US); Aguada directly W of Quebrada de Iscuña, ca. 46 km S of Caleta El Cobre, 24°34'S, 70°33'W, 20–30 m.a.s.l., 7 October 1988, *M. O. Dillon & D. Dillon 5661* (F 2014403); ridge E of Punta Dos Reyes, 24°36'S, 70°33'W, 500–950 m.a.s.l., 15 November 1988, *M. O. Dillon & D. Dillon 5933* (F 2144376); Quebrada Paposo E of Caleta Paposo, Quebrada Los Yales inside Reserva, 25°01'S, 70°27'W, 550 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8039* (CONC 149991, E, F 2183331, GH, K, SGO 143695, US); Quebrada La Rinconada, ca. 5 km N of Paposo, 24°56'S, 70°29'W, 410–500 m.a.s.l., 18 November 1997, *M. O. Dillon, C. Trujillo C. & M. Villarroel O. 8056* (E, F 2183324); Quebrada Bandurrias, 25°13'S, 70°26'W, 80 m.a.s.l., 19 November 1997, *M. O. Dillon & C. Trujillo C. 8071* (E, F 2183323, GH); Mirador ca. 2.4 km ESE above the ThermoElectric plant, 25°00'06"S, 70°26'48"W, 720 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8667* (F 2292819, SGO 158938); ca. 20 km N of the ThermoElectric plant N of Paposo, 24°50'40"S, 70°32'06"W, 100 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8678* (CONC 179104, F 2292800, SGO 158927); Cerro Perales, 25°25'41"S, 70°26'12"W, ca. 860 m.a.s.l., 9 October 2005, *M. O. Dillon, A. Casareggio M., & M. Finger C. 8707* (F 2294688, GH, SGO); La Brea, 25°29'56"S, 70°25'14"W, 10 October 2005, *M. O. Dillon & M. Finger C. 8710* (F 2294685, GH, SGO); Chile. Region II (Antofagasta): Reserva Nacional de Paposo. Ca. 43 km north of Taltal, 25°00'12"S, 70°26'40"W, ca. 681 m.a.s.l., 25 September 2010, *M. O. Dillon & A. Casareggio M. 9113* (CONC, F 2331755, SGO); Quebrada Taltal, 6.5 Taltal, 25°29'04"S, 70°26'10"W, ca. 435 m.a.s.l., 27 September 2010, *M. O. Dillon 9124* [A–J] (CONC, SGO); Paposo, 25°03'S, 70°30'W, 10 October 1983, *M. Elgueta 49* (SGO 145518); El Rincón near Paposo, succulent herb of the fertile belt, prostrate or clambering through bushes, corolla blue, December 1925, *I. M. Johnston 5511* (GH); grassy slopes in fertile belt above Aguada Miguel Diaz, decumbent rather succulent herb, December 1925, *I. M. Johnston*

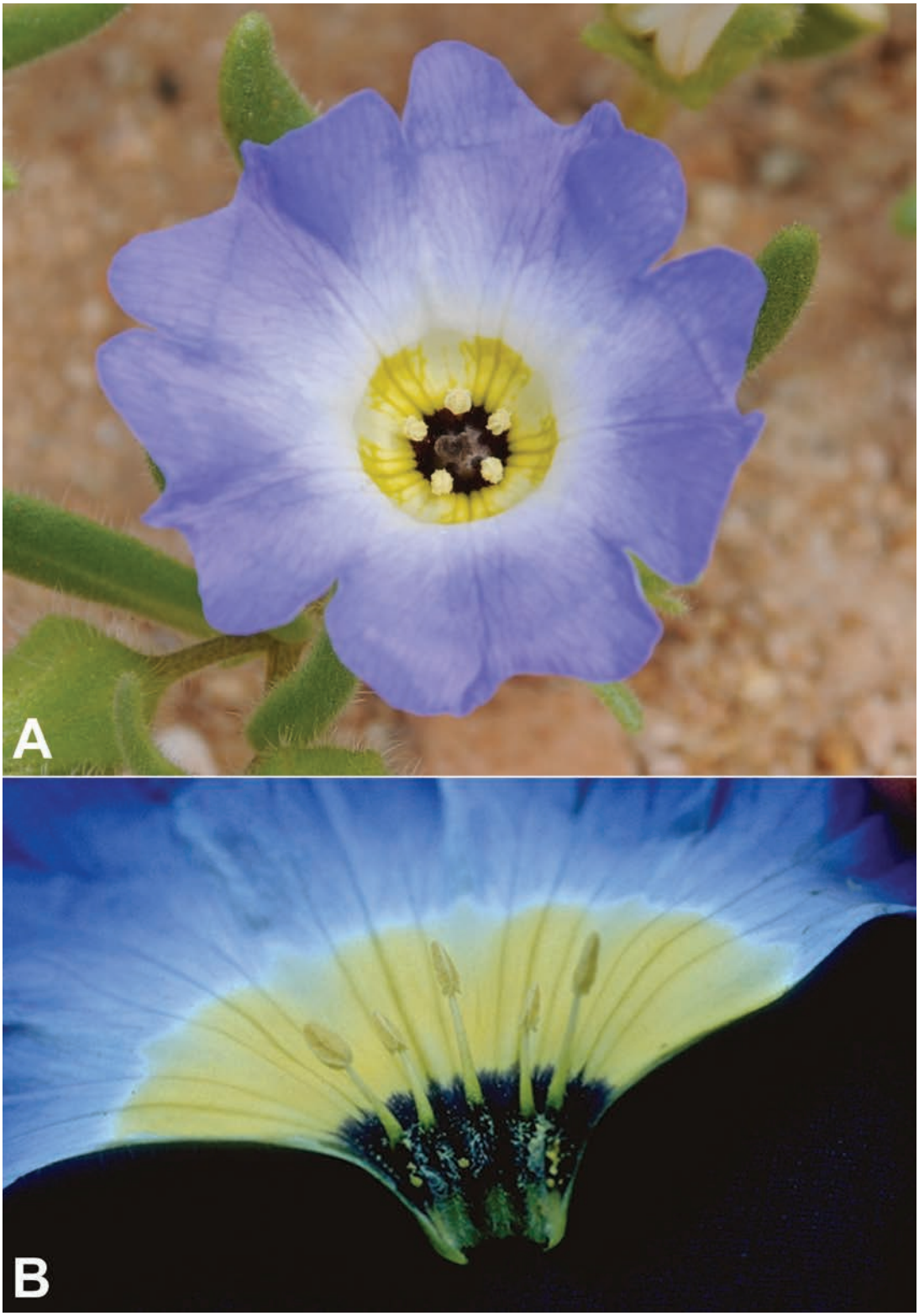


FIGURE 42. *Nolana elegans* corolla. **A**, Frontal view of corolla illustrating the yellow band in the throat and dark purple coloration at the base; **B**, Dissected corolla with dark purple base, including the proximal anther filaments.

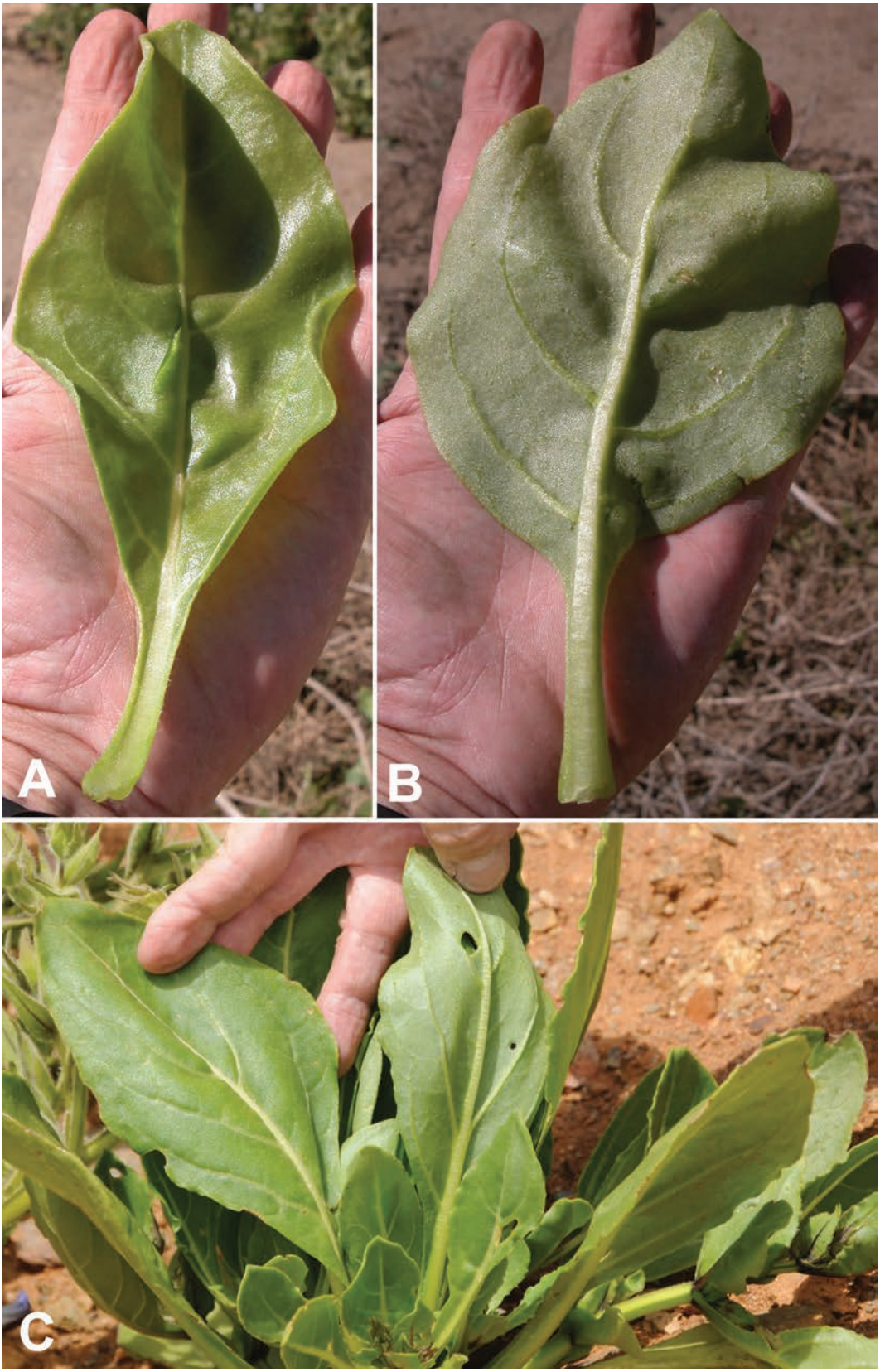


FIGURE 43. *Nolana elegans*. **A**, Adaxial view of basal leaf; **B**, Abaxial view of basal leaf; **C**, View of basal leaves *in situ*.

FIGURE 44. *Nolana elegans*. **A**, Flowering branches illustrating the obliquely, unequally decurrent bases on the cauline leaves or bracts subtending branchlets; **B**, Corollas displaying the range of colors, from blue with dark purple coloration at the base to pure white and lacking the dark spot.

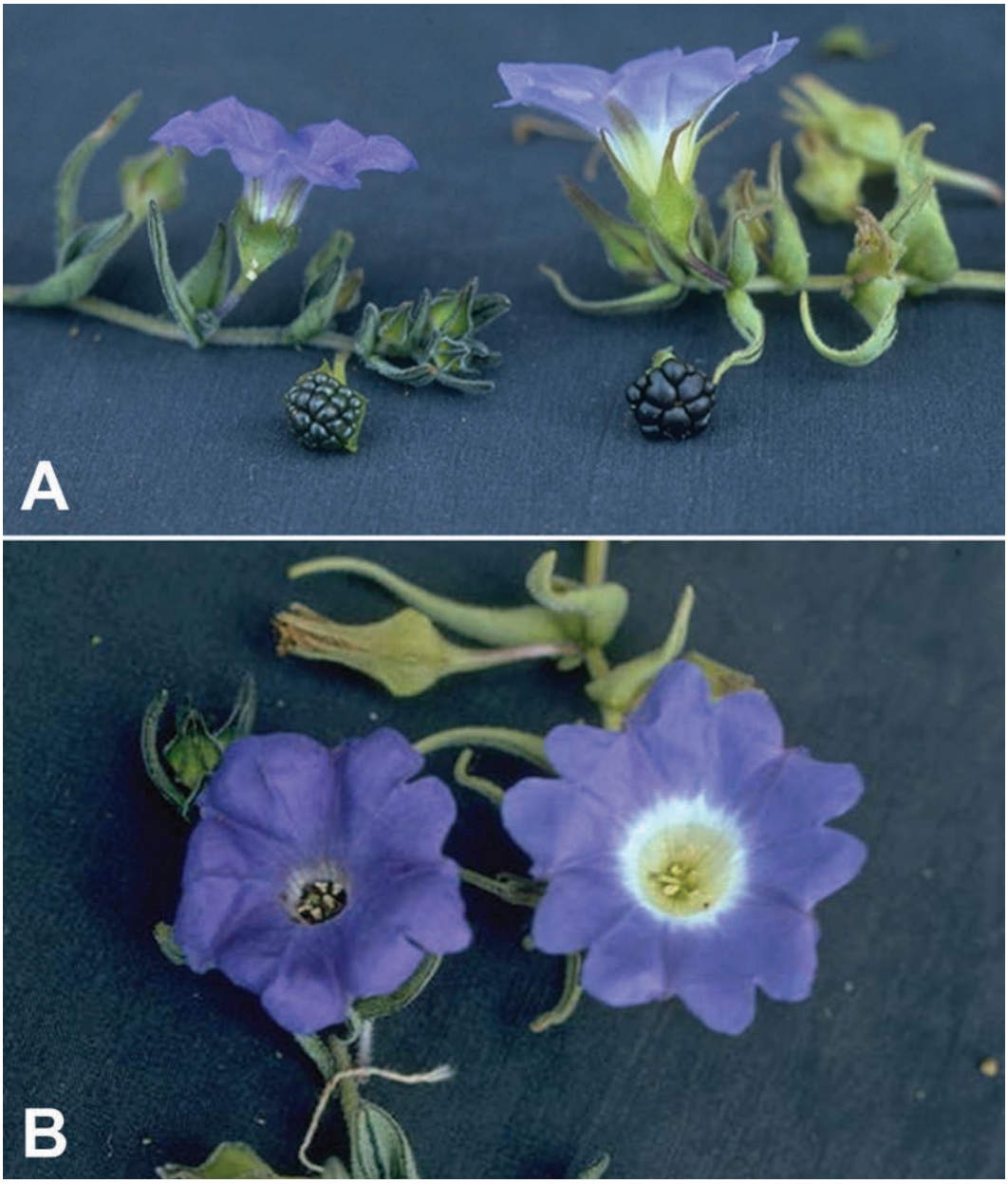


FIGURE 45. *Nolana elegans* compared to *N. rupicola*. **A**, Flowering branchlets with lateral view of corollas and mature ovaries of *N. elegans* (left) and *N. rupicola* (right); **B**, Frontal views of corollas in *N. elegans* (left) and *N. rupicola* (right).

5383 (GH); Quebrada de Yaquillas, 1884, *F. J. San Román s.n.* (SGO 55122); entre Blanco Encalada y Caleta Botija, 24°25'03"S, 70°32'03"W, 150 m.a.s.l., 4 October 2005, *F. Luebert & N. García 2617/1011* (F 2290709); Panul, 24°47'27"S, 70°32'33"W, 10–200 m.a.s.l., 7 October 2005, *F. Luebert & N. García 2678/1072* (F 2290736); Breas, 25°29'56"S, 70°24'03"W, 570 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2735/1129* (F 2290725); Los Puentes, a la entrada de la carretera a Quebrada Breas, 25°30'S, 70°25'W, 490 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2752/1146* (F 2290719,SGO 159457); Los Tórtolas, Sierra de San Pedro, 25°33'30"S, 70°35'45"W, 170 m.a.s.l., 12 October 2005, *F. Luebert & N. García 2765/1159* (F 2290690); Quebrada El Nueve, 3 October1953, *M. Ricardi 2720* (CONC 14510); Punta Rincon, 10 km al N Paposo, 5 m.a.s.l., 8 November 1985, *F. Schlegel 7973* (SGO 105238); Between Taltal and Paposo, 10 km N of Taltal, ascending Quebrada Cascabeles, 25°15'S, 70°30'W, 6 October 1991, *C. M. Taylor, C. von Bohlen, & A. Marticorena 10748* (F 2116662); Quebrada Los Yales, Paposo, 600 m.a.s.l., 25–26 August 1992, *J. C. Torres s.n.* (SGO 128746); Quebrada Los Yales, Paposo, 600 m.a.s.l., 25–26 August 1992, *J. C. Torres s.n.* (SGO 128781). **Atacama**: Dept. Freirina, 20–30 km al S de Freirina, camino a Quebradita, 300–500 m.a.s.l., 9 September 1949, *W. Biese 2616* (SGO 104254); 21 km W of Panamericana Hwy 5 on N route to Parque Nacional Pan de Azúcar, 26°08'S, 70°37'W, 85 m.a.s.l., 30 September 1998, *M. O. Dillon, D. Dillon, & V. Poblete 5606* (CONC,

E, F 2012856, GH); Parque Nacional Pan de Azúcar, Las Lomitas, 26°01'S, 70°36'W, 720–780 m.a.s.l., 11 November 1997, *M. O. Dillon & C. Trujillo C. 8014* (CONC 149968, E, F 2183318, GH, K, SGO 143688, US); Gruta Padre Negro, ca. 78 km NW of Copiapó, 26°47'48"S, 70°46'34"W, 24 m.a.s.l., 29 October 2009, *M. O. Dillon & R. Concha 9095* (CONC, F 2293453, SGO); Gruta Padre Negro, ca. 78 km NW of Copiapó, 26°47'48"S, 70°46'34"W, 24 m.a.s.l., 29 October 2009, *M. O. Dillon & R. Concha 9097* (F 2293451); Gruta Padre Negro, ca. 78 km NW of Copiapó, 26°47'44"S, 70°46'17"W, 82 m.a.s.l., 14 November 2009, *M. O. Dillon & A. P. Casareggio 9098* (E, F 2293468); Quebrada de la Zorra on Ruta C-10, 27°51'00"S, 71°04'50"W, 107 m.a.s.l., 25 October 2010, *M. O. Dillon 9163* (CONC, SGO); vicinity of Caldera, *E. E. Gigoux 30* (GH); Pan de Azúcar, Los Lomitas, 26°00'20"S, 70°36'19"W, 820 m.a.s.l., 14 October 2005, *F. Luebert & N. García 2820/1214* (F 2290722); Parque Nacional Pan de Azúcar, Quebrada Cerro Castillo, 13 October 1992, *M. Muñoz S. 3082A* (SGO 131621); hasta 12 km del camino acceso costero al Parque Nacional Pan de Azúcar, 26°08'S, 70°38'W, 31 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2800* (SGO 126125); Quebrada Coquimbo, 26°09'S, 70°45'W, 10 November 1987, *I. Paez s.n.* (CONC 143324); carretera Panamericana entre Chañaral y Caldera, Km 65, 23 October1965, *M. Ricardi, C. Marticorena, & O. Matthei 1450* (CONC 31170); Quebrada del León along the coast, ca. 20 km N of Caldera, 20 October 1938, 150 m.a.s.l., *C. R. Worth & J. L. Morrison 16141* (K). **Coquimbo**: ca. 5 km S of Tongoy, 30°17'S, 71°30'W, 50 m.a.s.l., 11 December 2004, *M. O. Dillon & G. Arancio 8688* (ULS); Punta Choros, 5 km hacia Carrizalillo, 29°12'58"S, 71°28'07"W, 9 October 2002, *A. Moreira M. 704* (SGO 149917); camino Guanaqueros a Tongoy, *M. Muñoz S. 1890* (SGO 108212); El Romeral, *M. Muñoz S. 1903* (SGO 108211); La Serena, Pt. Teatinos, 16 September 1947, *B. Sparre 2530* (SGO 98157); Coquimbo, Coastal hills N of La Serena, road to Chungungo, 29°33'17"S, 71°19'06"W, 138 m.a.s.l., 3 October 2010, *L. R. Landrum & S. S. Landrum 11517* (SGO 160515).

B4. ***Nolana jaffuelii*** I.M. Johnst., Contrib. Gray Herb. 112: 39. 1936. TYPE: CHILE. Antofagasta: Prov. Tocopilla, gravelly slope in hills near Tocopilla, somewhat fleshy herb, decumbent, flowers blue, 18 October 1925, *I. M. Johnston 3604* (Holotype: GH [00282338]). **Paratype**: CHILE. Tarapacá: Prov. Tarapacá, Iquique, Quebrada Huantajaya, ca. 700 m.a.s.l., September 1925, *E. Werdermann 757* (**Paratype**, B, not seen; Isoparatypes: BM [BM000941330], CONC [CONC 56100], E [E00130957], GH, K, SI 48529, SI003064, US [US 3312672, US00507022, US 1444768, US00053447]). Fig. 46–47.

Digital image: Holotype of *Nolana jaffuelii* from Harvard University Herbaria, Cambridge [GH00282338]. https://s3.amazonaws.com/huhwebimages/F07DE807582640A/type/full/282338.jpg

Annual *herbs* from a fleshy tap root, glabrescent; stems decumbent, 10–30 cm long, simple or branched from the base, 2–3 mm in diam., often with bluish or purple coloration. Basal rosette of *leaves*, blades oblanceolate to spathulate, 3–7 cm long, 8–15 mm wide, apically obtuse to rounded, base gradually attenuate, margins hyaline; petioles 20–40 mm long; cauline leaves on flowering stems geminate to subopposite, blades oblong-lanceolate or ovate, 12–30 mm long, 2–4(–8) mm wide, sessile, conspicuously decurrent, glabrous. *Inflorescences* of solitary flowers in upper leaf axils; pedicels 10–30 mm long, ascending. *Flowers* 5-merous; calyces 8–10 mm long, tube 5–6 mm in diam., lobes triangular, acuminate, 4–5 mm long, reticulate pattern, glabrous; corollas infundibularis, weakly zygomorphic, 13–20 mm long, limb 30–40 mm wide, violet, white band in throat, dark purple spot at the base; stamen filaments unequal. *Mericarps* 3-seriate, more than 20, 1–3 mm in diam., rounded to angular, sometimes with well-developed wings (cf. *Jiles 5326*); seeds 1–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Father Félix Jaffuel (b. 1874–d. 1939), a French priest who came to Chile in 1892 and became a teacher in Santiago in 1894. He taught science and mathematics, and, while traveling by ship to visit remote parishes in northern Chile, he collected around Tocopilla (1930–1931). Johnston was impressed with Jaffuel's collections and commemorated him with *Heliotropium jaffuelii* I.M. Johnst. (Boraginaceae).

Distribution and Ecology: Chile, Regions of Tarapacá and Antofagasta; (220–)700–900 m. It is recorded from sandy soils in near-coast habitats or, more rarely, from inland areas (Fig. 46); Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana jaffuelii represents the most northern member of the annuals with a basal rosette of leaves. It is represented by a few populations (Fig. 47A–B) to the north of *N. elegans*, but its distribution overlaps with that of *N. acuminata* near Antofagasta, Chile (Fig. 47A–B). In addition to *Nolana acuminata* and *N. jaffuelii*, a third species, *N. aplocaryoides*, was also recorded at that locality (Josefina Hepp, pers. comm.). The basal leaves are oblanceolate to spathulate and lack well-defined petioles (Fig. 48A, 49A). The herbage is glabrous or with sparce, simple, erect trichomes. The corollas can range from lavender with yellow throats (Fig. 47C) to blue with dark purple throats (Fig. 48B), not unlike those of *N. elegans*, a species to the south. The upper leaves and bracts are ovate to lanceolate and the succulent calyx envelopes the developing ovary (Fig. 48C); ripe mericarps (Fig. 48D) are rounded or irregularly angular to polyhedrons, wingless or with narrow, horizontal wings around the apical end.

The mericarps in *Nolana jaffuelii* have been the focus of detailed studies on their morphology and physiology (Cabrera, et al., 2015), and results suggest adaptations that allow for long periods of dormancy. These characteristics are likely present in other relatives living in the *lomas* formations.

A collection of *N. jaffuelii* was reported from Tacna, Peru in 1864 by R. Pearce (*s.n.*, BM000941326), the first year of the Chincha Islands War, also known as the Spanish-South American War or *Guerra hispano-sudamericana*, 1864–1866). In 1864, Peru's coastal Pacific territory extended south to the Río Loa, ca. 21°20'S latitude. No modern Peruvian collections with this combination of characters have been encountered in this study, and the species is here considered as endemic to Chile.

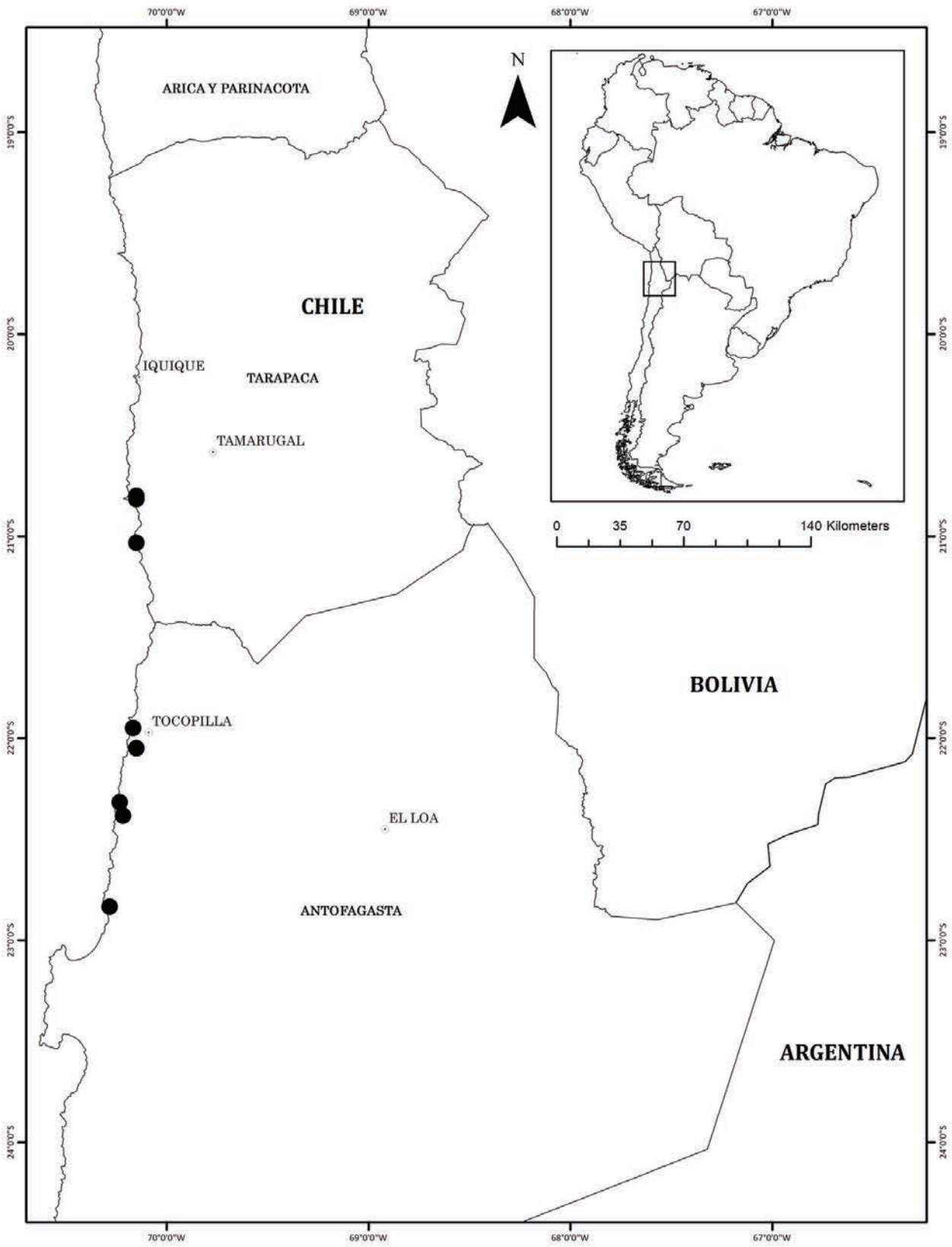


FIGURE 46. Distribution of *Nolana jaffuelii* I.M. Johnst.

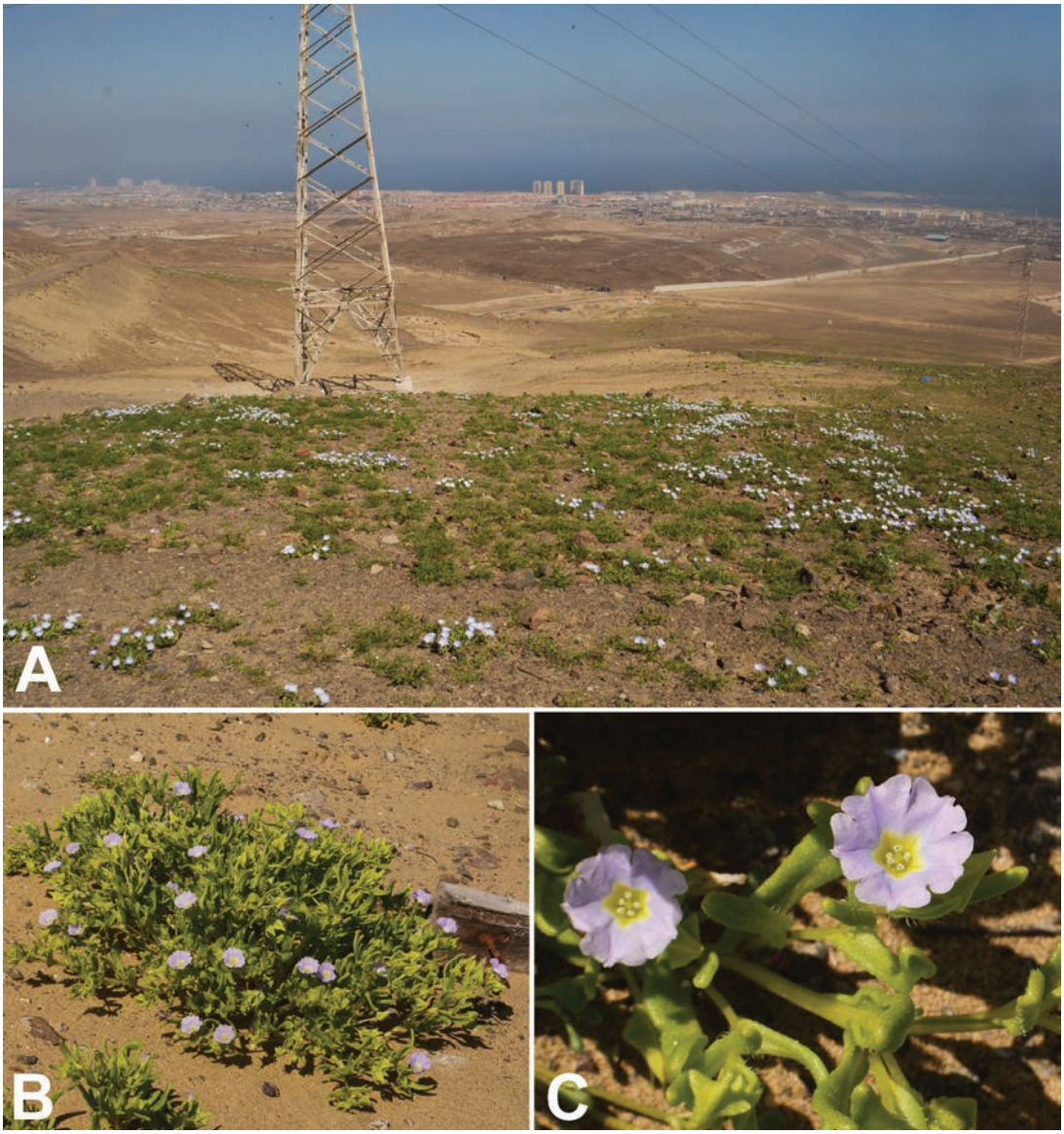


FIGURE 47. *Nolana jaffuellii* population east of Antofagasta, Chile. **A**, *N. jaffuelii*, *N. acuminata*, and *N. aplocaryoides*; **B**, Robust annual with basal leaves without well-defined petioles; **C**, Lavender corollas with yellow throats.

This taxon is likely related to *Nolana baccata*, a species that has a similar vegetative morphology; however, that species tends to have more flattened mericarps that form well-defined wings, and it has a more southern distribution. Previously, a group of collections from near Taltal were treated as *N. jaffuelii*; however, these are here referred to as *N. acuminata* (i.e., *Ch. von Bohlen V. 1298*; *Muñoz & Meza 2301*, *Teillier 452*, and *Teillier 481*). In 1936, Johnston [p. 40] commented that *N. jaffuelii* was a well-marked plant and probably most closely related to *N. elegans* of the Paposo region. He separated it from that species as being smaller in stature and glabrous.

Additional specimens examined: CHILE. **Tarapacá:** Prov. Iquique, Alto Patache, 800 m.a.s.l., 23 November 1997, *E. Belmonte 97-715* (CONC 143517), *97-724* (CONC 143505); camino de Iquique a Patillos, 17 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1331* (CONC 36114); Alto Punta Patache, *Pinto s.n.* (SGO 142972); vicinity of Iquique, 8 November 1914, *Mr. & Mrs. J. N. Rose 19448* (US 761968); Alto Punta Lobos, *R. Pinto s.n.* (SGO 142973); Alto Punta Patache, *W. Sielfeld 42* (SGO 143056). **Antofagasta**: Prov. Antofagasta, between Tocopilla and Antofagasta, roadside along Panamericana, 8 November 1991, *M. Ono et al. s.n.* (MAK 274957); Prov. Tocopilla, Cobija, Quebrada Aguada Cañas, *W. Biese 3083* (SGO 696688), *3084* (SGO 696689); Cerro Rosario, *M. R. Espinosa s.n.* (SGO 143257); Tocopilla, 27 October 1930, *F. Jaffuel 1004* (GH); Quebrada La Carmelita, Km 80, 22°03'S, 70°03'W, 750 m.a.s.l., 7 November 1969, *C. Jiles 5326* (CONC 102476); Cerro Copaca, 22°19'S, 70°14'W, 30 m.a.s.l., 28 September 1991, *M. Quezada & E. Ruiz 12* (CONC 121788); camino a Mina Manto de La Luna, 550 m.a.s.l., 28 September 1991, *M. Quezada & E. Ruiz 27* (CONC 121786); 10 km al N de Tocopilla,

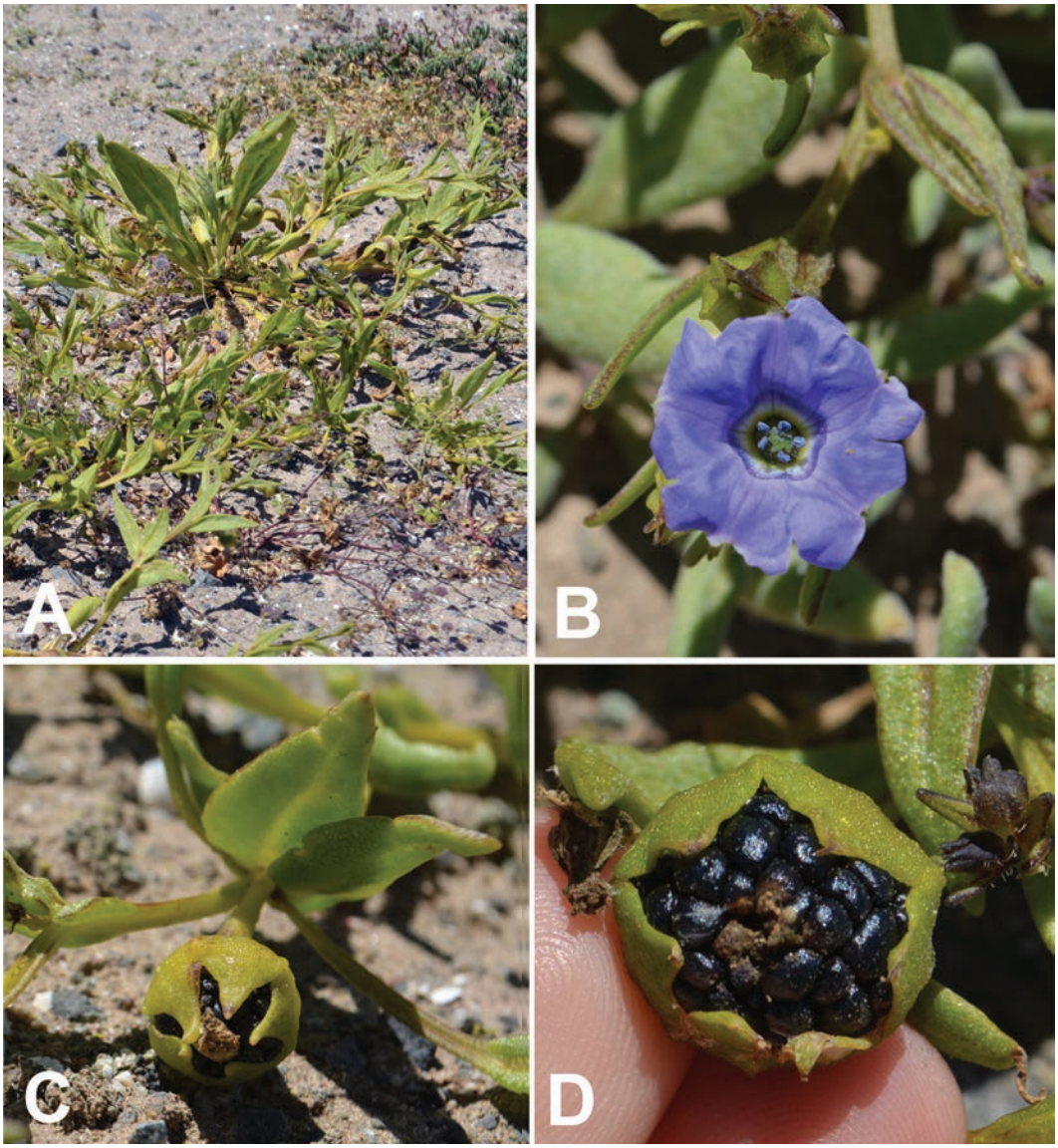


FIGURE 48. *Nolana jaffuellii*. **A**, Annual with narrow basal leaves; **B**, Blue corollas with dark purple throats; **C**, Leaves and bracts ovate to lanceolate; **D**, Calyx enveloping ripe mericarps.

220 m.a.s.l., 27 October 1985, *F. Schlegel 7730* (CONC 99989, SGO 105237). [PERU. Tacna, September 1864, *R. Pearce s.n.* (BM000941326)]. **No exact locality**: sin data, BM000941272.

B5. ***Nolana paradoxa*** Lindl., Bot. Reg. 10: tab. 865. 1824. TYPE: Based upon garden material raised from Chilean mericarps received from John Miers, who resided near Concon where the plant is common growing on pure sand. Fig. 49–55. Neotype designated here: CGE05021.

Digital image: No image is currently available via the internet; the image published here (Fig. 49) was provided by Cambridge University Herbarium, Cambridge [CGE05021].

Homotypic synonyms: *Periloba paradoxa* (Lindl.) Raf., Fl. Tellur. 4: 87. 1838; *Sorema paradoxa* (Lindl.) Lindl., Bot. Reg. 30: tab. 46. 1844.

Heterotypic synonyms: *Nolana atriplicifolia* D. Don, in Don [Sweet], Brit. Fl. Gard., ser. 2, 4: pl. 305. 1835. TYPE: CHILE. Based upon garden material raised from Chilean seed, no specimen located. *Nolana atriplicifolia* D. Don var. *cuneifolia* Dunal, Prodr. 13: 12. 1852. TYPE: CHILE. Valparaíso: Quintero, January 1830, "in arenosis salsis ad litus," *C. L. G. Bertero 1183* (Holotype: G [00137871]; Isotypes: BM [BM000941320], CONC [CONC 43376], F [F neg. 23238], FI [FI009589], GH); *Nolana napiformis* Phil., Anal. Univ. Chile 91: 30. 1895. TYPE: CHILE. Coquimbo: Coquimbo, November 1864, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 55140]; Isolectotype: SGO [SGO 55141]); *Nolana geminiflora* Phil. Anal. Univ. Chile 91: 27. 1895. TYPE: CHILE. Valparaíso: Algarrobo, April 1887, *R. A. Philippi s.n.* (Lectotype designated by

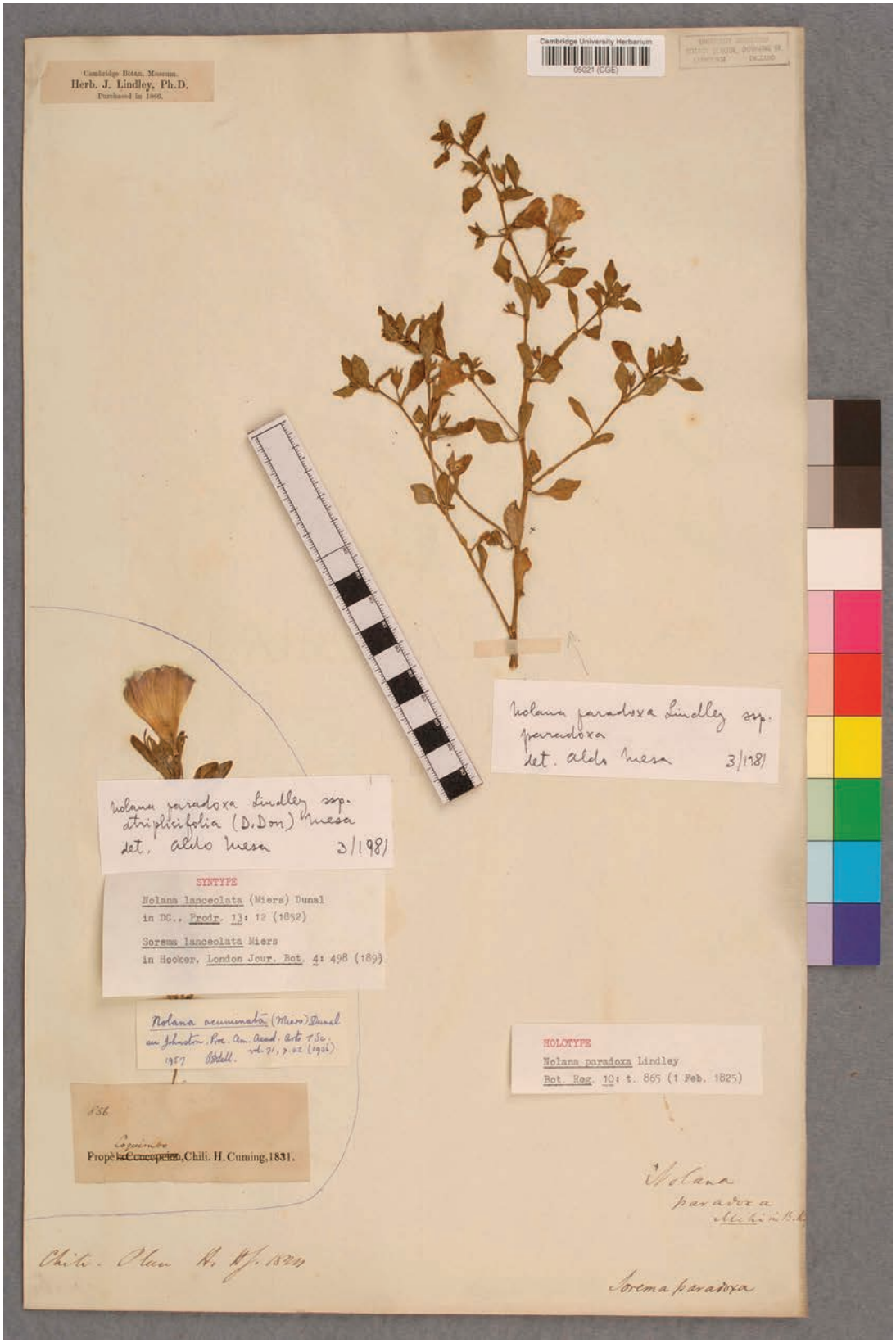


FIGURE 49. *Nolana paradoxa*. Neotype herbarium sheet, upper right, Cambridge University Herbarium, Cambridge, UK.

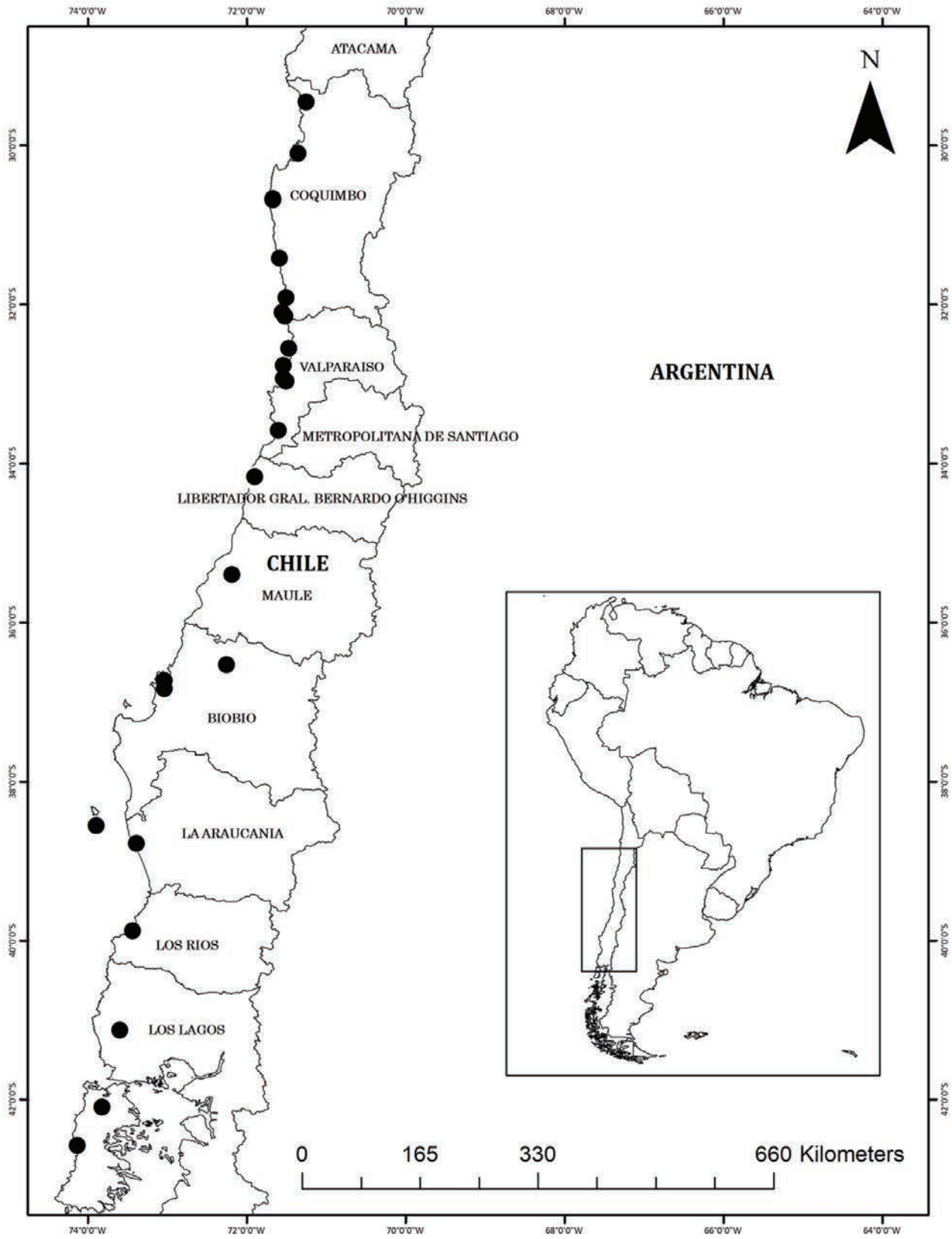


FIGURE 50. Distribution of *Nolana paradoxa* Lindl.

Mesa-M., 1981: SGO [55131]); *Nolana rupestris* Phil. ex Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 3. 1891; *Nolana rupestris* Phil., Anal. Univ. Chile 91: 28. 1895. TYPE: CHILE. Valparaíso: Curauma, prope Valparaíso, 33°09'S, 71°42'W, November 1882, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55116, SGO000004386]); *Nolana ochrocarpa* Phil. ex Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 3. 1891; *Nolana ochrocarpa* Phil., Anal. Univ. Chile 91: 33. 1895. TYPE: CHILE. Bío-Bío: Prov. Concepción, San Vicente, cerca de Talcahuano, 36°45'S, 73°10'W, January 1886, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55133]; Isolectotypes, K [K000532180], SGO [SGO 42677]); *Sorema petiolata* Phil., Linnaea 33: 207. 1864–1865. TYPE: CHILE. Valdivia: Corral, 39°53'S, 73°25'W, 1858, *H. Krause s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55148]; Isolectotypes designated by Mesa-M., 1981: G, not seen, P, not seen, S, not seen); *Nolana petiolata* (Phil.) Reiche, Anales Univ. Chile 125: 493. 1910; *Sorema littoralis* Miers, London Jour. Bot. 4: 370. 1845. TYPE: CHILE. Valparaíso: bay of Valparaíso, found growing sparingly on sandy beach within the spray of the sea, December–January 1831, *H. Cuming 627* (Lectotype designated by Mesa-M., 1981: K [K00053184]; Isolectotypes designated by Mesa-M., 1981: CGE, not seen, CONC [CONC 29159], E [E00130946, E00130947], K [K000532181, K000532183, K000532185]). *Nolana littoralis* Miers ex Dunal in DC., Prodr. 13: 12. 1852.

Annual or perennial *herbs,* floriferous stems elongate, prostrate and branched, succulent, woody, deciduous, pubescent with flaccid trichomes, rarely glabrous, thickened taproot. Basal *leaves* in a rosette, blades oval to elliptic, 2–5 cm long, 3–4 cm wide; petioles to 5 cm long; cauline leaves on flowering stems, alternate to geminate, venation thickened on underside; petioles often purplish, margins with multicellular, flagelliform trichomes with enlarged bases; leaves on floriferous stems 30–40 mm long, 4–10 mm wide, geminate, subopposite, elliptic, basally cordate to cuneate, apically rounded to obtuse, petiolate; all leaves erect to spreading, succulent, pale to medium green or sometimes with reddish tint, viscid with capitate-glandular trichomes. *Inflorescences* of solitary flowers, terminal and axillary; bracts like foliage; pedicels ca. 25 mm long, pubescent with curly, capitate-glandular trichomes. *Flowers* 5-merous; calyces campanulate, ca. 12–20 mm long, ca. 10 mm wide, 5-dentate, lobes unequal, ca. 6 mm long, lanceolate-acuminate; ciliolate; corollas infundibularis, weakly zygomorphic, (20–)25–45 cm long, limb 30–40 mm wide, pale to sky blue, rarely white, tube whitish-yellow with 3 dark veins on each petal, inside of corolla yellowish with 3 dark veins per petal, then followed with white zone, remainder pale to dark blue or blue-violet; stamens unequal; filament widened at the base, pubescent; nectary disc crateriform, margin sinuate; styles variable in length, but shorter than the filaments, gynobasic; filament capitate or peltate. *Mericarps* pyriform, angular to polyhedrons, (3–)6–8 mm long, 25 or more, unequal, 2- to 3-seriate; seeds 1–2(–3) per mericarp. Chromosome number: 2*n*=24.

Etymology: The epithet is from the Greek, *paradoxos*, suggesting conflicting or apparently contradictory situations. Lindley was perplexed by the dramatic difference between mericarps in *N. paradoxa* and the only other species known to him, *N. humifusa*. He commented that the fruit in the former consisted of 20, 1-seeded mericarps, 14–15 of which are abortive, whereas the latter species consistently has five mericarps typically with four seeds each.

Distribution and Ecology: Chile, Regions of Coquimbo, Valparaíso, O'Higgins, Maule, Bío-Bío, Araucanía, Rios, and Lagos, ranging ca. 1700 km; 5–20 m. It is recorded from near-ocean habitats and sand dunes and is rarely found in more interior habitats or at higher elevations (Fig. 50); Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Common name: *suspiro del mar*

Nolana paradoxa is a variable and widespread species growing in sandy soils near the ocean (Fig. 51A–B). Its distribution ranges ca. 1500 km from central Chile to Isla Chiloe at >42°S latitude. It has a thickened taproot (Fig. 4C), prostrate stems with bracts that subtend solitary flowers (Fig. 52A–B); it arises from a basal rosette of petiolate leaves (Fig. 53A) and has showy flowers with corollas up to 4 cm wide (Fig. 53B). The mericarps are numerous, often 25 or more (Fig. 53C), and they are corky and apparently buoyant in saltwater, which would aid in coastal dispersal. The receptacle clearly shows the scars at the attachment of individual mericarps (Fig. 53D).

The northern limit of *N. paradoxa* appears to be in the vicinity of Coquimbo (cf. *B. Sparre 2809*, *A. Cabrera 11387*, *A. M. Mora s.n.* [SGO 131747]), and the southern limit of *N. acuminata* appears to be in the same area. *Monsalve s.n.* from Pichidangui is included as *N. paradoxa* with some reservations. This region of overlap should be investigated further to establish the distributional limits of *N. paradoxa* and *N. acuminata*.

Nolana paradoxa was the second species, after *Nolana humifusa*, to be introduced and cultivated in Europe. It was most likely grown from mericarps sent to Francis Place by John Miers, who was living near Concón, Chile in 1822. The plant illustrated in Plate 2604 (Fig. 54) was drawn in May 1823 from plants obtained from Place's garden. The plant that Miers had access to (Fig. 55) was also from garden material on exhibit by the Horticultural Society and raised by Place. The correct publication date for Lindley's description of *Nolana paradoxa* in the Botanical Register is 1824, although it is cited as 1825 by numerous sources (e.g., Johnston, 1936: 43).

The taxonomic treatment of this species has varied, and some elements have been circumscribed as distinct species. Its extensive synonymy includes no fewer than eight taxa, including five described by R. A. Philippi. Philippi published *Nolana rupestris* (Philippi, 1895); however, as Johnston (1936) speculated that Philippi had prematurely distributed duplicates to Berlin for several new *Nolana* species, including *N. rupestris*, the herbarium name was picked up by Wettstein (1891). This sheet has ovate-lanceolate leaves

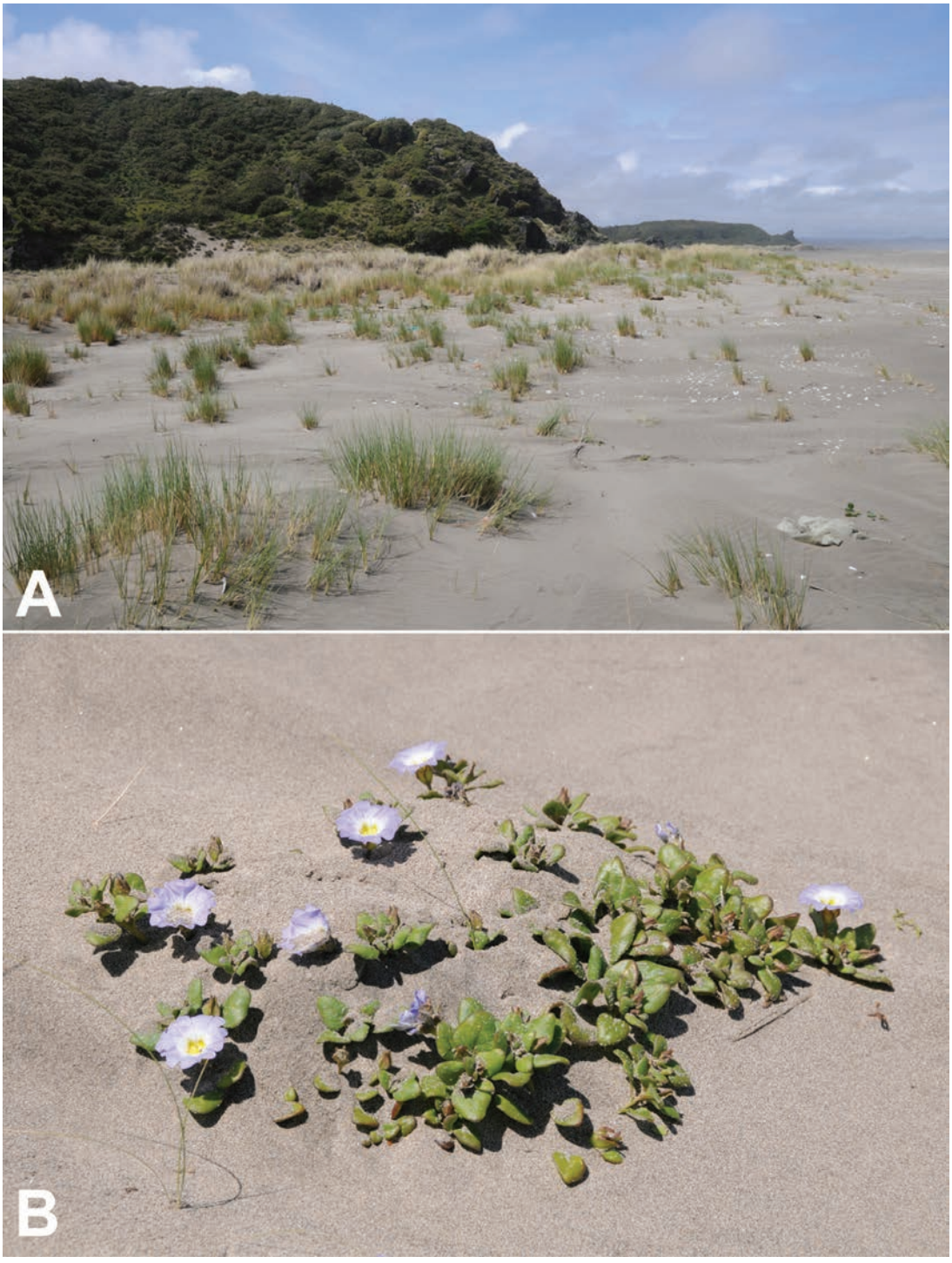


FIGURE 51. *Nolana paradoxa*. **A**, Near-ocean sand dunes on western side of Isla Chiloe, southern Chile; **B**, Annual, flowering individual on Isla Chiloe (*Dillon & Moreira 9213*).

FIGURE 52. *Nolana paradoxa*. **A**, Fruiting branch with pedicels nodding at maturity; **B**, Ovary with maturing mericarps.

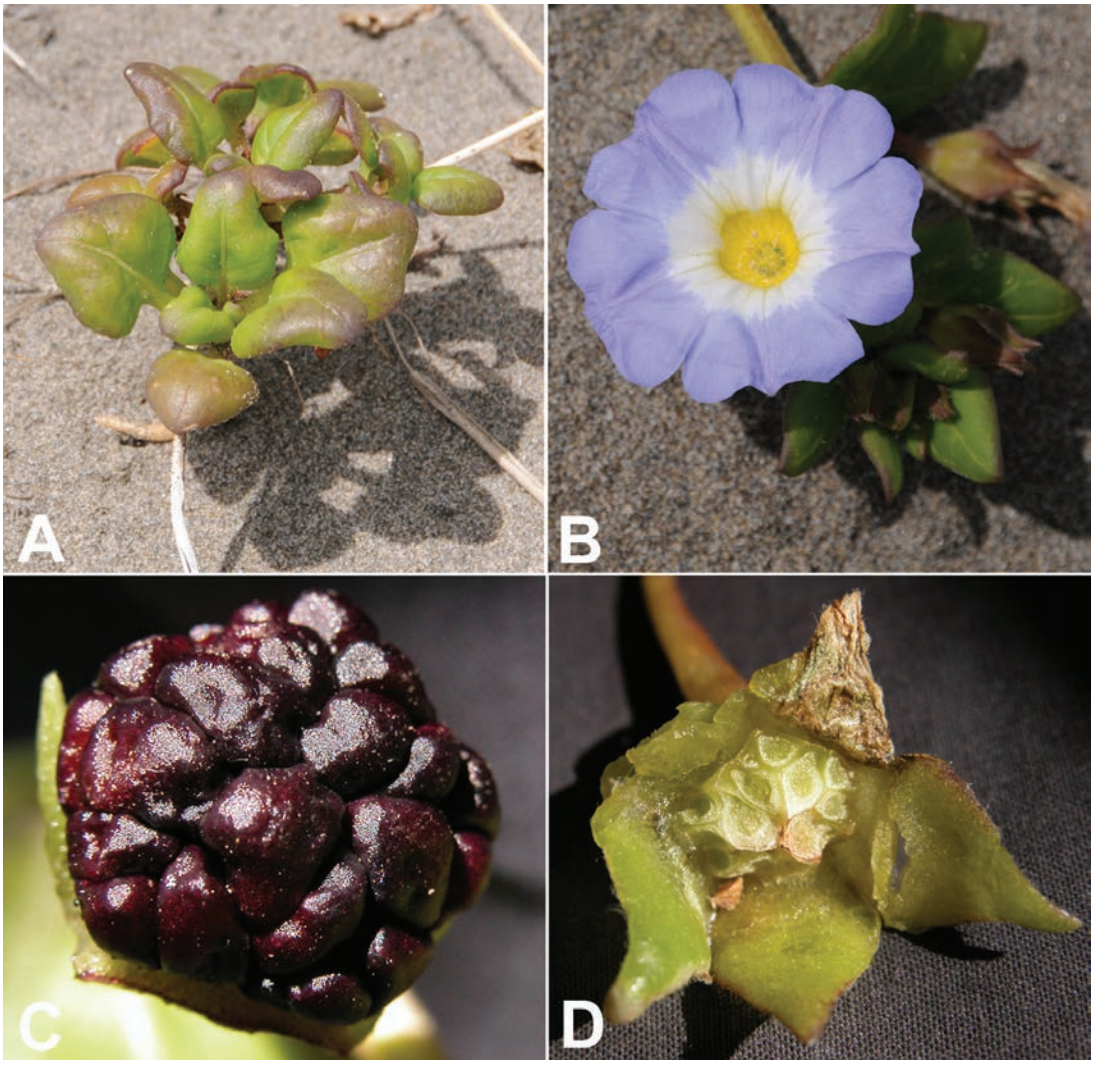


FIGURE 53. *Nolana paradoxa*. **A**, Basal rosette of petiolate leaves; **B**, Frontal view of corolla; **C**, Ovary with maturing mericarps.

4.5 cm long and ca. 2 cm wide, that are densely pubescent with flaccid, uniseriate trichomes. The calyx is up to 1.5 cm with the lobes to 8 mm long, and the corollas to 3 cm long. Initially, this sheet was annotated as *N. acuminata*; its overall morphology and distribution suggest that *N. paradoxa* is a better assignment. Two sheets designated as *Nolana napiformis*, *R. A. Philippi s.n.* (Lectotype, SGO 55140; Isolectotype, SGO 55141) were originally labelled in the handwriting of Philippi as *Sorema arenaria* Phil.; however, the sheets were subsequently annotated by Carlos Muñoz (March 1946) as *Nolana napiformis* Phil. These are diminutive plants with small, thickened roots 4–6 cm long.

Two species, *Nolana paradoxa* and *N. humifusa* (as *N. prostrata*), made their way into the horticultural trade. Artificial hybrids between these two species yielded *Nolana tenella* Lindl. (Fig. 17), that may still be found in cultivation (Johnston, 1936). Wider usage of artificial hybrids between *Nolana* species has been investigated (Freyre et al., 2005), and a few have been patented (see Hybridization). *Nolana paradoxa* is the most widely distributed species in the horticultural trade, and two corolla color morphs are marketed: "Bluebird", with blue corollas, and "Snowbird," with white corollas.

The author visited Isla Chiloé on 11 November 2011 and made collections of *Nolana paradoxa* for DNA analyses (*Dillon & Moreira 9213*). The following collection has a questionable location on the label: CHILE. **Aysén**: Prov. Capitán Prat. Cochrane, camino Internacional, 47°16'S, 72°03'W, 350 m.a.s.l., 6 February 2013, *O. Ojeda 6854* (CONC 180418). The locality data places the collection from an area unsuitable for any *Nolana* species (Sebastián Teillier, pers. comm.).

Additional specimens examined: CHILE. **Coquimbo**: Isla Damas, 29°14'04"S, 71°31'36"W, 30 m.a.s.l., 31 August 2002, *G. Arancio 14859* (CONC 157026); Prov. Choapa, Humedal Huentelauquén, 31°36'49"S, 71°33'46"W, 8 m.a.s.l., 13 October 2012, *A. Cea s.n.* (CONC 185214); Coquimbo, Peñuelas, *A. Cabrera 11387* (SGO 126636); Coquimbo, beachside playa near Estero Pachingo, Tongoy, 30°16'08"S, 71°29'48"W, 0–5 m.a.s.l., 11 December

FIGURE 54. Illustration of *Nolana paradoxa*, Plate 2604, drawn in May 1823 from cultivated plants.

FIGURE 55. Illustration of *Nolana paradoxa*, Plate 865, drawn in February 1825 [1824] from cultivated plants.

2004, *M.O. Dillon & G. Arancio 8686* (ULS); Coquimbo, Guayacán, *E.M.L. Kausel 5175* (SGO 137147); Pichidangui, 32°06'S, 71°33'W, *Monsalve s.n.* (SGO 132151); La Pampilla, *A. M. Mora s.n.* (SGO 131747); La Radio, entre La Serena y Coquimbo, *C. Muñoz P. & E. Pisano V. 3323* (SGO 118826); La Serena, *B. Sparre 2809* (SGO 98358). Dept. Illapel, Caleta Oscuro, *C. Marticorena, O. Matthei, & R. Rodríguez 294* (CONC 43022); Pichidangui, *F. Schlegel 3171* (CONC 44867); Prov. Elqui. Lagunillas, *F. Squeo 87-061* (CONC 112965). **Valparaíso**: Prov. Aconcagua, near Los Molles, *K. Beckett, M. Cheese, & J. Watson 4108* (SGO 94961). Prov. Petorca, Los Molles, camino entre la caleta y el Puquén, 15 m.a.s.l., 21 September 1991, *Ch. von Bohlen V. 1074* (SGO 131696), *1075* (SGO 131699); Viña del Mar, *O. Buchtien s.n.* GH); Chile prope Valparaíso, 1832, *H. Cuming 627* (BM00941323); Mun. La Ligua, Los Molles, 32°14'35"S, 71°30'53"W, 10 m.a.s.l., 17 October 1997, *U. Eggli & B. E. Leuenberger 2930* (B, CONC 136094, SGO 146162); Viña del Mar, Laguna Verde, 10 November 2004, *O. Fernández C. 1057* (CONC 162239); Valparaíso, 1856057, *P. Germain s.n.* (BM000941317); Las Cruces, 70 km S of Valparaíso, 10 m.a.s.l., 7 January 1939, *T. H. Goodspeed 23314* (GH, K); Quintero, Campiche, *L. H. Gunckel 39510* (CONC 129667); Los Molles, *L. H. Gunckel 23427* (CONC 129664); Playa de los Enamorados, *L. H. Gunckel 35712* (CONC 129663); Playa de las Conchitas, *L. H. Gunckel 36615* (CONC 129662); Ritoque, *L. H. Gunckel 43251* (CONC 129661); Reñaca, 19 October 1936, *F. Jaffuel & A. Pirion 3613* (GH); Playa de Concón, October 1937, *F. Jaffuel & A. Pirion 3949* (GH); Tunquén, *E. M. L. Kausel 4308* (SGO 123747), *4433* (SGO 123744), entre Tunquén and Mirasol, *E. M. L. Kausel 4440* (SGO 123745); Quintero, Playa Las Conchitas and Playa Los Enamorados, 35 m.a.s.l., 1 November 1990, *T. G. Lammers, C. M. Baeza P., & P. Peñailillo B. 7734* (CONC 113446, F 2055208); Valparíaso, December–January, *A. Mathews s.n.* (GH); Concón, *Herb. John Miers 343* (BM000941322, BM000941314); Valparíaso, San Antonio, 16 October 1927, *G Montero O. 216* (GH); Valparaíso, Cartagena, 10 m.a.s.l., 8 September 1935, *G. Montero O. 2445* (GH); Los Molles, camino hacia El Puquén, *M. Muñoz S. 1649* (SGO 137410); Tunquén, *H. Niemeyer F. & C. Fernández 9597* (SGO 151298); Valparaíso, Viña del Mar, 1885, *F. Philippi & A. Borchers s.n.* (BM000941316); Valparaíso, October, *C.A.W. Sandeman s.n.* (BM000076943); Dpto. Petorca, Los Molles, 32°14'S, 71°31'W, 20 m.a.s.l., 2 October 1960, *F. Schlegel 2962* (CONC 42572); Pichicuy, *E. Tepe, A. Marticorena & P. Pelser 1887* (CONC 167901, GH). **O'Higgins**: Prov. Cardenal Caro, Mun. Paredones, Bucalemu S of Pichilemu, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 3122a* (B). **Maule**: Vichuquén, Lipimavida, 20–25 January 1969, *P. Aravena 7* (US 3204373 ex SGO 103953); Talca, Constitución, *J. Arriagada T. s.n.* (SGO 165076); Curicó, Iloca, *L. H. Gunckel 43402* (CONC 149648). **Bío-Bío**: Prov. Arauco, Isla Mocha, *F. Behn s.n.* (CONC 25371); camino a Yani, *O. Parra & L. Torres 172* (CONC 153921). Prov. Concepción, San Pedro de la Paz, Michaihue, 36°51'32"S, 73°09'09"W, 5 m.a.s.l., *M. Acosta & M. Rosas 1119* (K); Dichato, *C. Junge s.n.* (CONC 4802); Bahía San Vicente, along road S of Avenida Las Golodrinas, 2 m.a.s.l., 22 October 1990, *T. G. Lammers, C. M. Baeza P., P. Peñailillo B., & N. Mazzeo 7504* (CONC 113331, F 20548); Prope la Concepción, October 1825, *J. Macrae s.n.* (K); Talcahuano, Isla Rocuant, 5 m.a.s.l., 10 November 1994, *M. Quezada & P. López 13* (CONC 134237); Isla Quiriquina, *M. Ricardi 9059* (CONC), *10917* (CONC); Isla Rocuant, *R. Rodríguez, P. Claret, & C. Sanhueza 4033* (CONC 165907); Rocoto, *B. Sparre 9964* (CONC 17740). Ñuble: Prov. Itala, Punta Mela, *C. M. Baeza P., P. López, & O. Parra 1995* (CONC 153920); Talcahuano, Parque Gualpén, *E. Weldt 228* (CONC 33493). **Araucanía**: Prov. Cautín, Coi-Coi, La Lobería, *C. Aedo 7200* (CONC 161500, MA); Cautín, Herb. *R. M. Middleton s.n.* (BM000941318); [Puerto] Saavedra, *L. H. Gunckel 21941* (CONC 129651). **Ríos**: Prov. Valdivia, Hueicolla, 40°09'S, 73°40'W, 3–10 m.a.s.l., 11 February 1988, *M. F. Gardner & S. G. Knees 4155* (K); Corral, *L. H. Gunckel 15156* (CONC 129647); **Los Lagos**: ca. 20 km S of Ancud on Ruta 5 and ca. 18 km E of junction with Hwy W-30 (W-250), 42°35'01"S, 74°07'54"W, 5 m.a.s.l., 11 November 2011, *M. O. Dillon & A. Moreira M. 9213* (F 2331765); Chiloé, playa Arenilla, Bahia Caulín, *M. T. Eyzaguirre s.n.* (SGO 152456); Isla Grande de Chiloé, Chiloé National Park, 30 km N of Cucao at mouth of Rio Anay, *M. Gardner 3588* (CONC 107178); Chiloé, 1896, *R. Maldonado s.n.* (BM0, 00941315); Ancud, Caulín, orilla de playa, 41°47'59"S, 73°35'39"W, 5 m.a.s.l., 20 February 2007, *M. Muñoz S. 4873* (SGO 154486); Chiloé, Playa Huenocoyhue, 4 m.a.s.l., 13 March 1969, *C. Ochoa 2708* (US 2946531); Chiloe, December 1873, *E. C. Reed* (K); Chiloé, Islas Desertores, Talcán, *C. Villagrán 3437* (SGO 128616). Without exact locality: Chile, 1879, *Herb. John Miers s.n.* (BM000941325); sin data, (BM000941319), sin data, 1904, *F. Philippi s.n.* (BM000021200); *Wilkes Explor. Exped. s.n.* (US 57460). Cultivated: GREAT BRITAIN. **Kew.** Royal Botanical Gardens, grown from seeds, *W. G. D'Arcy 17802* (F 211666). USA**. Illinois**. Chicago, 3311 N. Seeley Ave., 26 July 1987, grown from seeds, *T. Plowman 14512* (F 2090884). **Massachusetts**. Woburn, 1 September 1972, *T. Plowman s.n.* (AMES 30446, HUH01563470).

B6. **Nolana parviflora** (Phil.) Phil., Anal. Univ. Chile 91: 29. 1895. Fig. 56–59.

Basionym: *Sorema parviflora* Phil., F. Atac. 44 and Viage Des. Atac. 10: 218. 1860. TYPE: CHILE. Atacama: Copiapó, Caldera, *R.A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55113]).

Digital image: Lectotype of *Sorema parviflora* from Museo Nacional de Historia Natural, Santiago [SGO 55113]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004382

Homotypic synonymy: *Periloba parviflora* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 105. 1929; *Nolana parviflora* Phil., Anal. Univ. Chile. 91: 34. 1895. TYPE: CHILE. Atacama: Copiapó, Bandurrias, *G. Geisse s.n.* (Lectotype designated by Mesa-M., 1981: SGO [42669]). **Paratype**: CHILE. Atacama: Copiapó, Caldera, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [42670]; Isolectotype: US [1336135]).

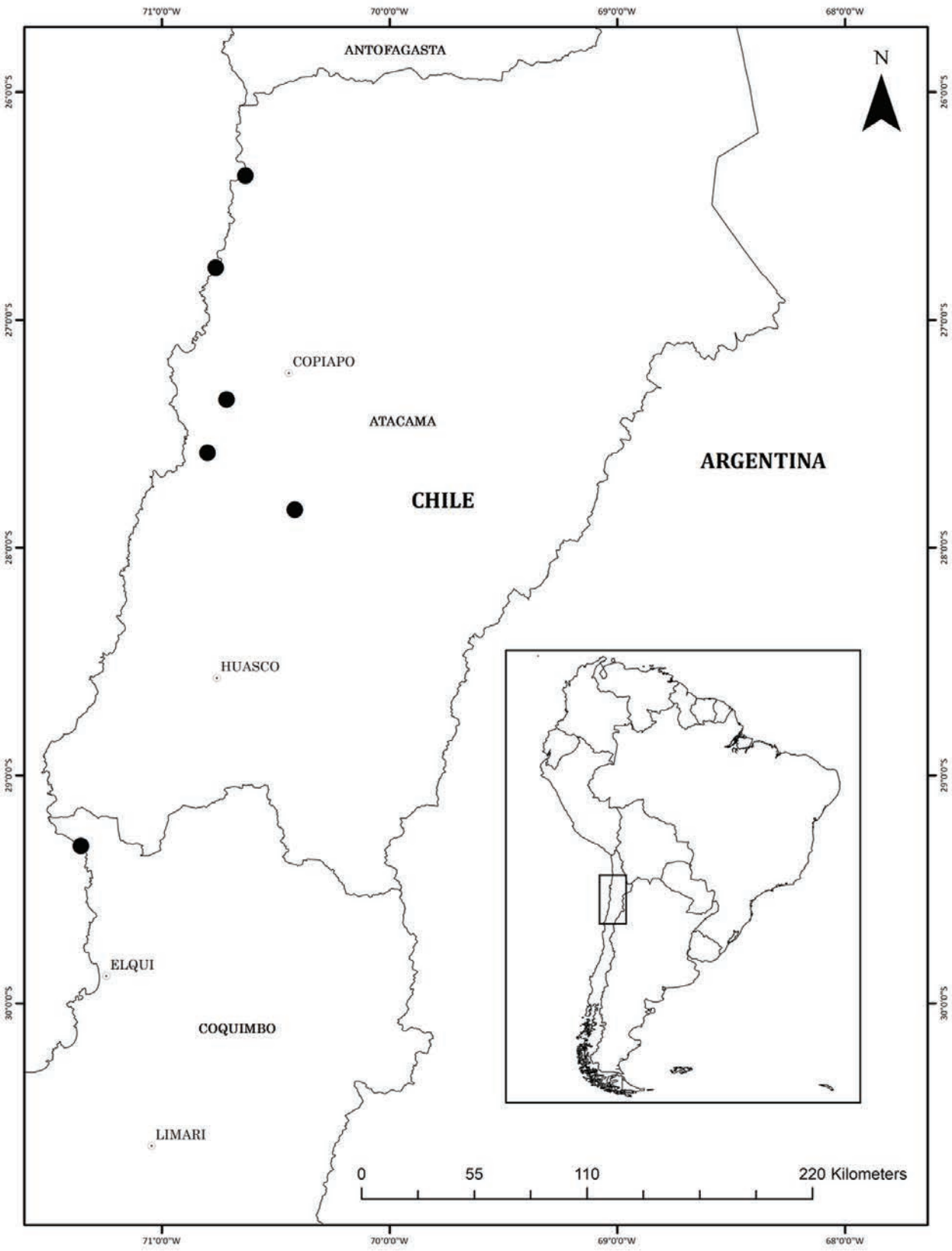


FIGURE 56. Distribution of *Nolana parviflora* (Phil.) Phil.

Decumbent to erect *annuals* to 10 cm tall. *Leaves* from a basal rosette, blades lanceolate-spathulate, 30 mm long, ca. 5 mm wide, margins strongly revolute, apically obtuse to rounded, basally cuneate, glabrous except for scattered flagelliform trichomes; cauline *leaves* on flowering stems, alternate, blades spathulate to oblong, 10–15 mm long, ca. 2 mm wide, apically obtuse, basally decurrent, glabrous, margins thickened. *Inflorescences* of terminal flowers, inconspicuous. *Flowers* 5-merous; calyces 6 mm long, ca. 5 mm wide, bases strongly protruding, keeled, lobes equal, lanceolate, ca. 4 mm long, ca. 2.5 mm wide, acute; corollas infundibularis, regular, 9–10(–12) mm long, limb 6–10 mm wide at throat, white, corolla lobes only slightly exceeding calyx lobes. *Mericarps* 10–15, biseriate, plump, medio-longitudinal keel, often projecting into an erect wing; seeds 1–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *parvus*, little, small, or puny, and refers to the short corollas, that just surpass the calyx lobes.

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 20–265 m.a.s.l. It is recorded from environments with sandy soils, near-coast habitats or, more rarely, from higher, inland areas (Fig. 56); Matorral Desértico Tropical Costero, Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Nolana parviflora is a decumbent or prostrate annual herb from sandy soils near the ocean (Fig. 57). The herbage of this species is decidedly yellowish green and not a deep green as in its congeners (Fig. 58A). It has a spreading habit (Fig. 58B), with flowering branches arising from its central rosette of leaves. Flowering branches have calyces that become reddish upon maturity (Fig. 59A). Another distinguishing character is the short, invariably white corollas that only slightly surpass the calyx lobes (Fig. 59B). This species is most like *N. baccata*, except for the character of diminutive white corollas. Mericarp size and surface markings are like those in *N. baccata*; however, they are not as angular as in that species, and have a medio-longitudinal keel frequently drawn out into a narrow erect wing (Fig. 59C). In dried collections, it is difficult to find suitable characters to separate *N. parviflora* and smaller forms of *N. pterocarpa* or *N. baccata*.

Additional specimens examined: CHILE. **Atacama**: Chañaral, 5 m.a.s.l., 22 February 1939, *A. A. Beetle 26153* (GH); ca. 13 km SSW of Chañaral, 26°26'33"S, 70°41'02"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9076* (CONC, SGO); ca. 14 km SW of Chañaral, 26°39'53"S, 70°43'02"W, 18 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha* (CONC, SGO); ca. 14 km SW of Chañaral, 26°27'29"S, 70°40'57"W, 30 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9088* (CONC, SGO); Ruta 5, ca. 40 km N of Caldera, 26°42'44"S, 70°44'17"W, 82 m.a.s.l., 14 November 2009, *M. O. Dillon & A. Casareggio M. 9099* (CONC, SGO); ca. 1 km SE from Bahia Inglesa on Ruta C-360, 27°06'03"S, 70°50'43"W, ca. 10 m.a.s.l., 30 September 2010, *M. O. Dillon 9132* (CONC, F 2331758, SGO); ca. 4 km from Caleta Barranquilla on Ruta C-370, 27°31'38"S, 70°51'31"W, 101 m.a.s.l., 25 October 2010, *M. O. Dillon 9156* (CONC, SGO); ca. 5 km SW from Bahia Salada on Ruta C-324, 27°40'27"S, 70°56'38"W, 34 m.a.s.l., 25 October 2010, *M. O. Dillon 9159* (CONC, SGO); Pajonales, October 1888, *G. Geisse s.n.* (Herb. Gunckel 7996; CONC 129683); camino a Bahía Salada, cerca del Cerro Chascón, 27°35'S, 70°48'W, 265 m.a.s.l., 18 October 2005, *F. Luebert & C. Becker 2895* (SGO 159451); Copiapó, 380 m.a.s.l., 14 September 1936, *G. Montero O. 3002* (GH); Km 917 S Obispito, 26°46'15"S, 70°45'49"W, 70 m.a.s.l., 29 September 2005, *M. Muñoz S. 4576* (E00936019, SGO 153603); Copiapó, Estación Travesía a 24 km al S.O. de Copiapó, 710 m.a.s.l., 24 September 1941, *C. Muñoz P. & G. T. Johnson 1895* (SGO 112649); Mina Candelaria, a 71 km al SO de Copiapó, hacia Bahía Salada, 23 September 1941, *C. Muñoz P. & G. T. Johnson 1934* (SGO 112166); Posada Los Pajaritos, *M. Muñoz S., I. Meza P., & E. Barrera M. 1035* (SGO 108657); Barquito, 26°22'S, 70°38'W, 50 m.a.s.l., 26 October 1941, *E. Pisano V. & R. Bravo F. 505* (CONC 144539, SGO 156431); Copiapó, Monte Amargo, 200 m.a.s.l., October 1924, *E. Werdermann 460* (A, BM000941332, CONC 55630, E 00130956, F 565282, K). **Coquimbo**: ca. 2 km W of Choros Bajos towards the coast, 29°18'32"S, 71°21'20"W, 20 m.a.s.l., 19 October 1997, *U. Eggli & B. E. Leuenberger 2962* (B, SGO 144076). **No exact locality**: Desert of Atacama, September–October 1890, *Th. Morong 1272* (E 00130966, F 166482, GH); s.d., 1904, *F. Philippi s.n.* (BM000941331).

B7. **Nolana pterocarpa** Phil. ex Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 3. 1891. Fig. 60–61.

Basionym: Nolana pterosperma Phil., Anal. Univ. Chile 91: 27. 1895. TYPE: CHILE. Atacama: Piedra Colgada [entre Caldera y Copiapó], September 1885, F. Philippi & A. Borchers s.n. (Lectotype designated by Mesa-M., 1981: SGO [55123]; Isolectotypes: GH [GH00282378], US [US 01336134, US00121962]).

Digital image: Lectotype of *Nolana pterosperma* from Museo Nacional de Historia Natural, Santiago [SGO 055123]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004385

Heterotypic synonyms: *Nolana stans* Phil., Anal. Univ. Chile 91: 31. 1895. TYPE: CHILE. Atacama, Piedra Colgada, [entre Caldera y Copiapó], September 1885, *F. Philippi & A. Borchers s.n.* (Lectotype designated by Mesa-M., 1981: SGO [42674]; Isolectotypes: BM [BM000941312], GH [GH00282369], K, SGO [SGO 55134]). *Periloba stans* (Phil.) I.M. Johnst., Contr. Gray Herb. 85:105. 1929.

Erect annual *herbs*; stems 12–40 cm long, branched from the base; taproot slender. Basal *leaves* lanceolate to spathulate, ca. 4 cm long, ca. 1 cm wide, petioles ca. 1 cm long, margins with short triangular trichomes, apically rounded, cauline leaves on flowering stems alternate, blades spathulate, short-decurrent on stems. *Inflorescences* of solitary flowers in the upper leaf axils, pedicels ca. 30 mm long, pubescent with flaccid multicellular trichomes. *Flowers* 5-merous; calyces 11–15 mm long, 5–10 mm wide; lobes 5–7 mm long, ca. 3 mm wide, acute; corollas infundibularis, regular, ca. 20 mm long, ca. 40 mm wide at mouth. *Mericarps* 8–15(–20), angular to polyhedrons, wings 3–4 mm long, light brown to black; seeds 1–5 per mericarp. Chromosome number: unknown.

FIGURE 57. *Nolana parviflora*. Yellowish individuals in large numbers in sandy soils SW of Chañaral, Chile, 28 October 2009.

Etymology: The species epithet is from the Greek, *pter-*, wing or winged, and *-carpa*, for fruited, and refers to the winged mericarps that are diagnostic for this species.

Distribution and Ecology: Chile, Region of Atacama; ca. 500 m.a.s.l. It is recorded from a few near-coast habitats or, more rarely, inland areas (Fig. 60); Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana pterocarpa is distinguishable with some difficulty, given that its overall habit is like that of *N. baccata,* and the winged mericarps are like those in *N. parviflora*, or, more rarely, as in *N. jaffuelii* (cf. *Jiles 5326*). One of my collections is assigned to this taxon with some doubts, and more detailed study of all these taxa will be necessary to clarify the species' boundaries.

Johnston (1936) commented on the variation exhibited in these plants, saying that young plants of *N. pterocarpa* are strikingly like flowering juvenile forms of *N. baccata* and are frequently separated from them with difficulty. He suggested that the corollas in *N. pterocarpa* are less deeply lobed than in *N. baccata*, and that the leaves are much more revolute at the margins. Johnston (1936) speculated that R. A. Philippi had prematurely distributed duplicates to Berlin for several new *Nolana* species, including *N. pterocarpa*. This herbarium name was picked up by Wettstein (1891) and subsequently described as *N. pterosperma* Phil. (1895). In his description, Philippi used an orthographic variant of the epithet, *pterosperma*, different from the herbarium name, *pterocarpa,* used in Wettstein's key. Johnston (1936) placed *Nolana stans* Phil., from Piedra Colgada between Caldera and Copiapó, in synonymy with *N. baccata*; however, it seems very robust for *N. baccata* and, overall, more closely resembles *N. pterocarpa*; the mericarps are angular, but not winged.

Additional specimens examined: CHILE. **Atacama**. Prov. Copiapó, Llano de los Lirios, 25 km S of Copiapó, 27°34'S, 70°26'W, 620 m.a.s.l., 2 December 1987, *M. O. Dillon & S. Teillier 5040* (CONC, E, F 1993968, GH, K, NY, SGO, US); Llano de La Jauja, frente a Sierra Los Nichos, 28°13'S, 70°48'W, 2 November 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2915* (SGO 126126), *2917* (SGO 126127); Carretera Panamericana entre Copiapó and Vallenar, km 55, 27°49'S, 70°31'W, 500 m.a.s.l., 26 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1509* (CONC 36113, F 1801921).

B8. ***Nolana reichei*** M.O. Dillon & Arancio, Arnaldoa 14: 207. 2007. TYPE: CHILE. Coquimbo: Prov. Limarí, Caleta El Toro, desembocadura de Río Limarí, 30°44'06"S, 71°41'58"W, 40 m.a.s.l., 11 December 2004, *M. O. Dillon & G. Arancio 8690* (Holotype: ULS; Isotypes: E, F 2329902, GH, SGO, US). Fig. 61–65.

Digital image: Isotype of *Nolana reichei* from the Field Museum, Chicago [F 2329902]. https://fm-digital-assets.fieldmuseum.org/2300/397/V0363371F.jpg

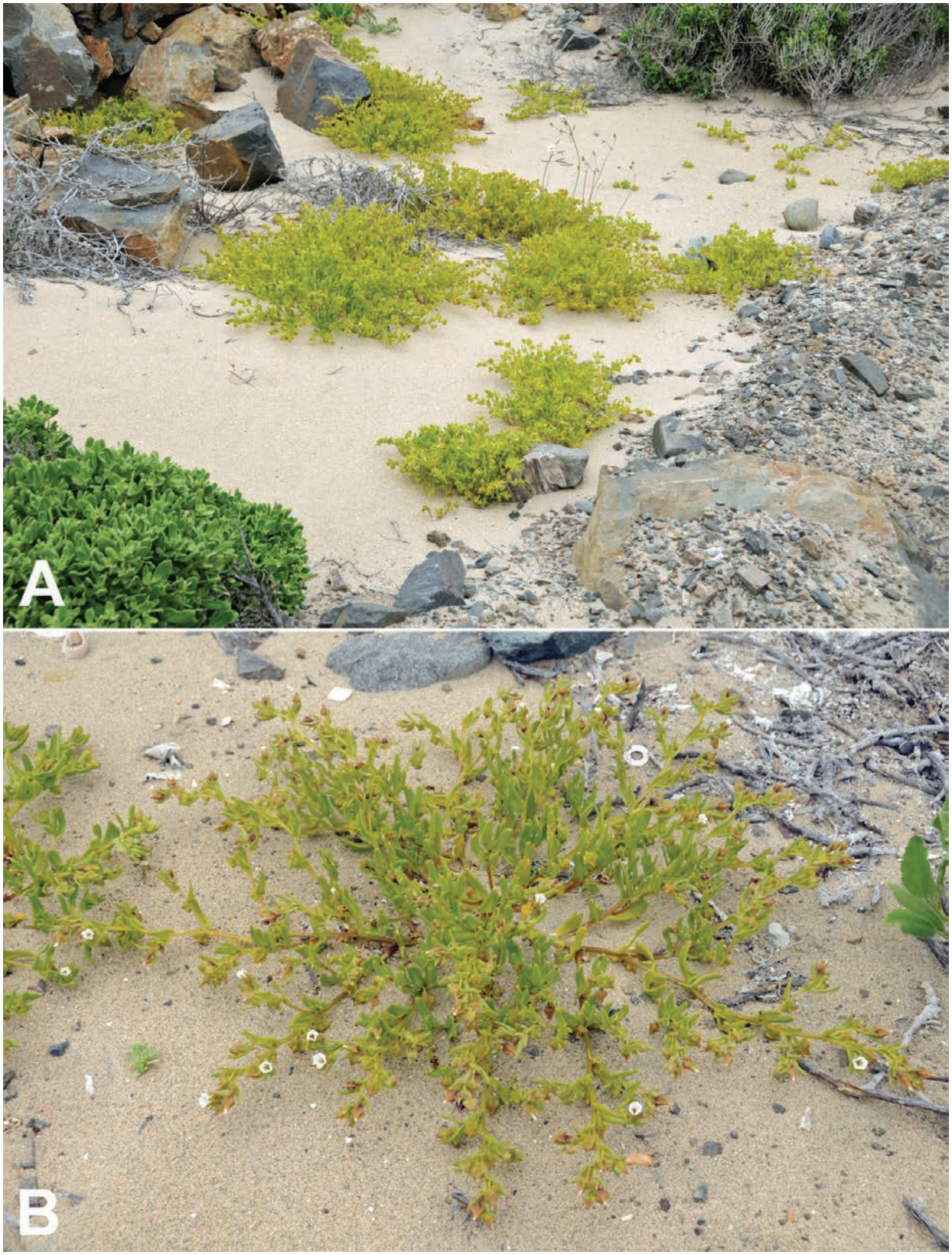


FIGURE 58. *Nolana parviflora*. **A**, Individuals growing in sandy soils SW of Chañaral, Chile, 28 October 2009; **B**, Annual with basal rosette of lanceolate-spathulate leaves.

FIGURE 59. *Nolana parviflora*. **A**, Flowering branch with maturing calyx becoming reddish; **B**, Frontal view of corolla; **C**, Mericarps with a medio-longitudinal keel.

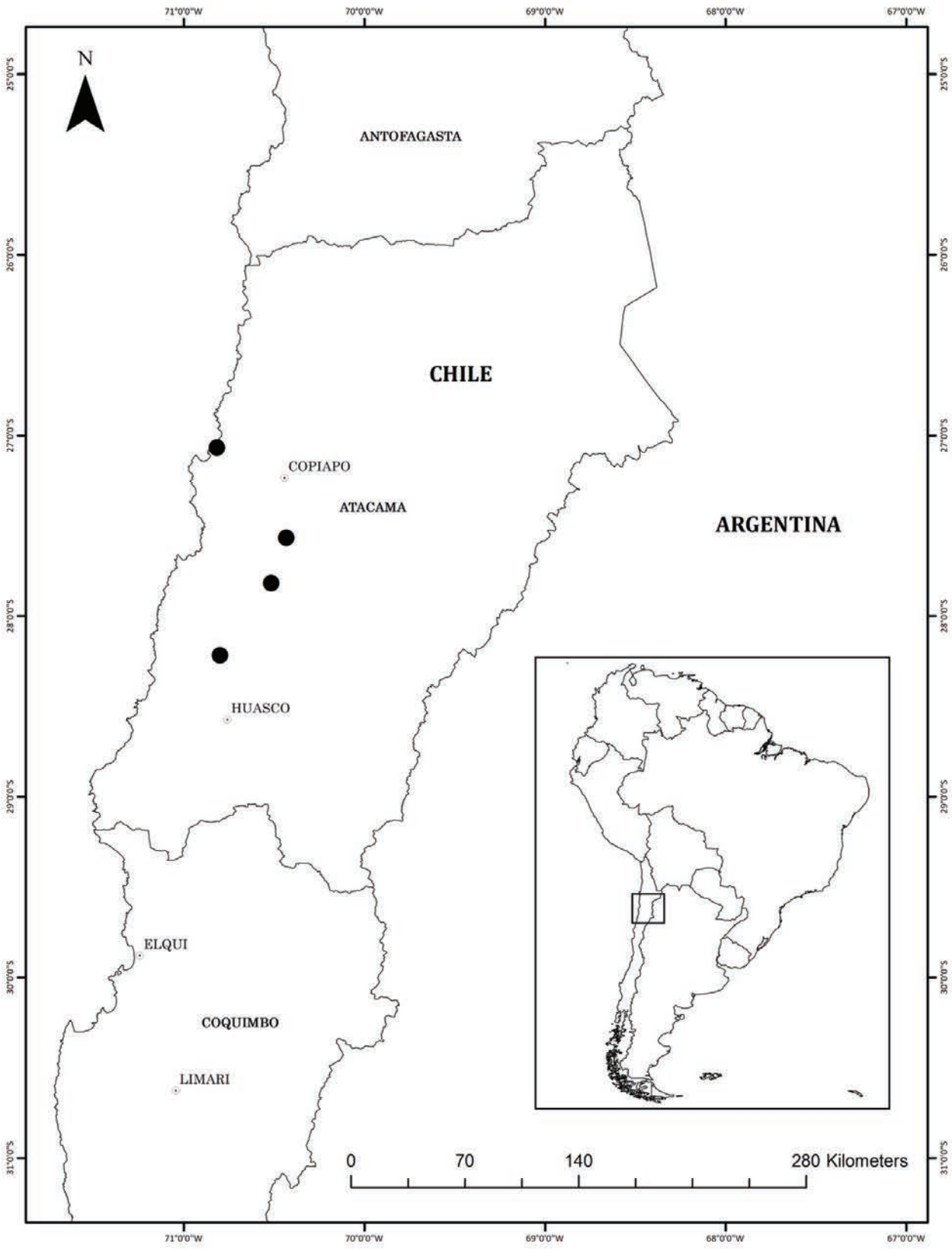


FIGURE 60. Distribution of *Nolana pterocarpa* Phil. ex Wettst.

FIGURE 61. Distribution of *Nolana reichei* M.O. Dillon & Arancio.

Succulent, perennial *herbs*; stems prostrate, flexulose, to 50 cm long, much-branched from a thick taproot, minutely glandular pubescent, reddish. Basal *leaves* spathulate to ovate, 10–12 cm long, 2–3 cm wide, basally cuneate, petiolate, 2–3 cm long; cauline leaves on flowering stems alternate, blades lanceolate, 23–33 mm long, 2–3 mm wide, succulent, apically acute, bases decurrent, margins entire, undulate, pubescent with stiff, multicellular trichomes. *Inflorescences* of solitary flowers in the leaf axils, terminal and axillary; pedicels filiform, 5–6 cm long, villous. *Flowers* 5-merous; calyces campanulate, ca. 5 mm wide at anthesis, glabrous, tube ca. 10 mm long, 5–6 mm wide; 5-lobed, lobes lanceolate, 5–7 mm long, 3–4 mm wide; corollas broadly infundibuliform, regular to weakly zygomorphic, 30–40 mm long, limb 40–50 mm wide, 5-lobed, lobes obtuse, 2.5–3.0 mm long, 9–10 mm wide, distinctive coloration pattern with concentric rings of purple distally, blue, black and ultimately deep yellow at the base, externally pubescent with capitate-glandular trichomes; stamens 5, included, filaments inserted on lower third of corolla, unequal, three 5–7 mm long, two 8–10 mm long, pilose at the bases; anther thecae ca. 4 mm long, 1.0–1.5 mm wide, creamy white to yellow; ovary glabrous, basal nectary, 5 carpels, style included, stigma capitate, green. *Mericarps* ca. 15, angular, 3.5–4.5 mm long, undulating surface, joined at the faces, included within the expanding calyx; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Karl Friedrich Reiche (b. 1860–d. 1929), a German botanist who emigrated to Chile and directed the botanical section of the Museo Nacional de Historia Natural (National Museum of Natural History) in Santiago from 1896 to 1911. Upon leaving Chile, he assumed a post in the Escuela de Altos Estudios México (1911–1923). From 1924 until his death in 1929, he worked in Munich, Germany as an independent investigator at the Botanische Staatssammlung. He produced a treatment of the Nolanaceae for his *Flora of Chile* (Reiche, 1910), and he was the first botanist to classify the species described here as *N. reichei*. Karl Reiche was also known as "Carlos" in Chile, and publications are sometimes cited under that name.

Distribution and Ecology: Chile, Region of Coquimbo; 20–500 m.a.s.l. It is recorded from a small area with sandy soils; near-coast habitats or, more rarely, from higher, inland areas (Fig. 62); Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Illustration: Fig. 62. Illustration of *Nolana reichei*. **A.** Habit; **B.** Opening corollas; **C.** Stamen; **D.** Calyx opened to expose gynoecium; **E.** Corolla dissected to expose bands of colors; **F.** Corolla; **G.** Flower and peduncle; **H.** Gynoecium with angular mericarps (*Dillon & Arancio 8690*, F by Nancy Klaud).

Common name: *suspiro de siete colores*

Nolana reichei has large, multicolored corollas with rings of color in the throat or limb. It is a well-known species to Chileans, who had most often applied the scientific name *N. lanceolata*. Its locality at Caleta del Toros is very near the southern margin of Fray Jorge (Fig. 63A), and many botanists have encountered this showy species (Fig. 63B). In Miers' description (1845: 498) of *Sorema lanceolata*, he states that the corolla "much resembles" that of *N. paradoxa*; however, its leaves are distinctive in shape and pubescence (Fig. 64A), the corolla is decidedly different in both lobe shape and coloration pattern (Fig. 64B), and it has stiff trichomes (Fig. 64C). The thickened taproot and basal leaves are typical for the group (Fig. 65A). The corolla has the same type of aestivation, with overlapping, twisted or contorted lobes (Fig. 65B). The mericarps are angular, and the dorsal surface is undulating (Fig. 65C). *Nolana paradoxa* has more petiolate leaves with ovate leaf blades, and the corollas have only a yellow spot in the throat. *N. reichei* is in an unresolved clade as the sister species to *N. paradoxa* (Dillon et al., 2007c).

The recognition of *N. reichei* comes after detailed study of the variation exhibited within *N. paradoxa* throughout its distributional range. Of the five *Nolana* species (Fig. 20) which were co-occurring at Caleta El Toro (i.e., *N. crassulifolia*, *N. werdermannii*, *N. reichei, N. rupicola*, and *N. sedifolia*), only *N. rupicola* (Fig. 20E) could be regarded as a member of *Sorema* (Dillon et al., 2007c). *Nolana rupicola* is distinguished from *N. reichei* by possessing thick, succulent, ovate leaves and cream-colored corollas lacking bands of colors in the limb.

Several collections from the immediate area of Fray Jorge were initially attributed to *Nolana paradoxa* or *N. acuminata*, (e.g., *B. Collantes T. s.n.*, CONC 129689; *Dillon et al. 5420*; *A. Kohler 183*; *J. Kummerow s.n.*, CONC 42634; *Ricardi 2099*; and *Werdermann 893*). After an examination of many collections, it appears likely that *Nolana reichei* is more widespread than the type locality near the ocean and may occur at 500–600 m.a.s.l. more distant from the ocean.

In Reiche's treatment of the Nolanaceae for the Flora of Chile (Reiche, 1910), he clearly recognized this species from the mouth of the Río Limarí near Fray Jorge, calling attention to the large corollas, up to 5 cm wide, with prominent dark coloration in the throat. He referred to the species with doubts ("*con duda refiero a esta especie*") as *Sorema* (*Nolana*) *lanceolata* Miers ex DC. (1845: 498) with its type (*Cuming 856*) from Coquimbo. When Johnston examined *Cuming 856*, he was convinced that Miers' new species, *N. lanceolata*, was identical to *N. acuminata*, and cited *Sorema lanceolata* as a synonym of *N. acuminata* (Johnston, 1936: 42).

Additional specimens examined: CHILE. **Coquimbo**: Prov. Limarí, Fray Jorge, 21 September 1963, *F. Behn s.n.* (CONC 28597); Fray Jorge, 450 m.a.s.l., September 1948, *B. Collantes T. s.n.* (CONC 129689); Parque Nacional de Fray Jorge, 30°42'S, 71°40'W, 480–500 m.a.s.l., 21 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5420* (E, F 2144378, HSP, SGO); Caleta El Toro, desembocadura del Río Limarí, 30°44'09"S, 71°42'02"W, 20 m.a.s.l., 22 October 2005, *M. O. Dillon, G. Arancio, J. M. Fariña, & P. Ossa 8747* (F 2329919, HSP); Llanos de a Laguna, partes de potrero al borde del camino a Fray Jorge, 240 m.a.s.l., 22 August 1948, *C. Jiles 672* (CONC 36164); Fray Jorge, September 1965, *A. Kohler 183* (CONC 129688); Fray

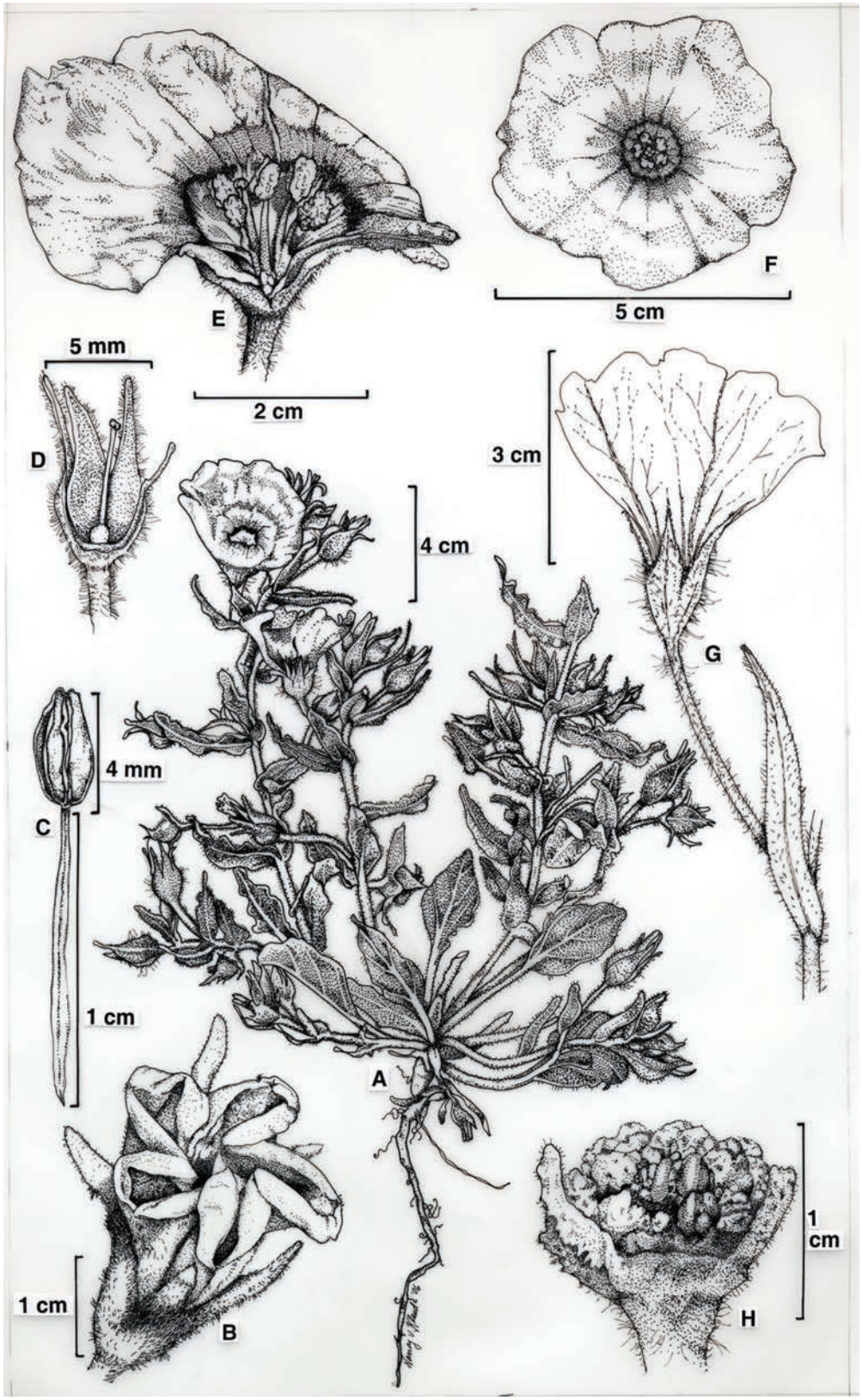


FIGURE 62. Illustration of *Nolana reichei*. **A**, Habit; **B**, Opening corollas; **C**, Stamen; **D**, Calyx opened to expose gynoecium; **E**, Corolla dissected to expose bands of colors; **F**, Corolla; **G**, Flower and peduncle; **H**, Gynoecium with angular mericarps. Drawn by Nancy Klaud.

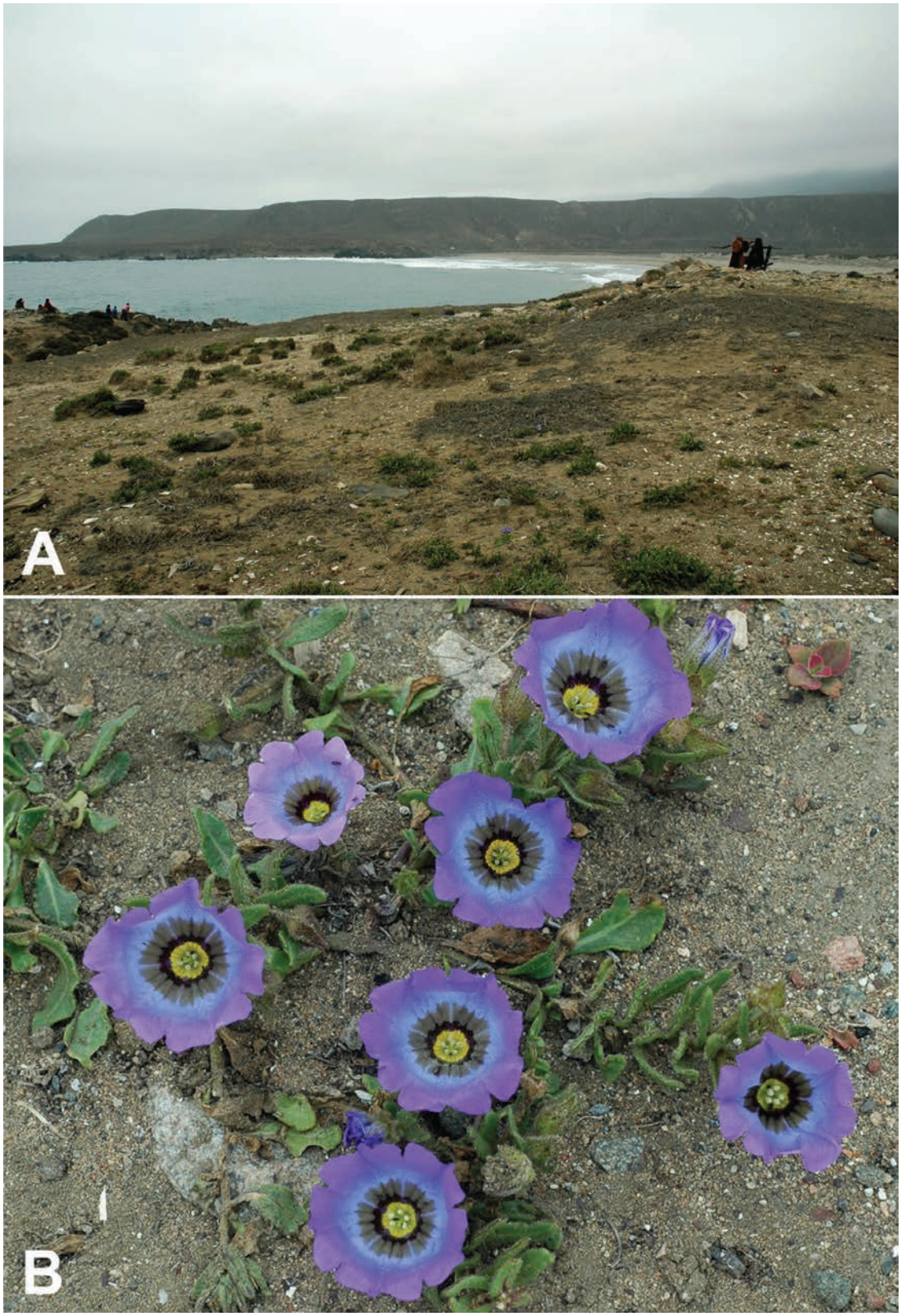


FIGURE 63. *Nolana reichei*. **A**, Type locality at south side of Río Limarí (Caleta El Toro), northern Chile; **B**, Habit of prostrate to decumbent radiating stems.

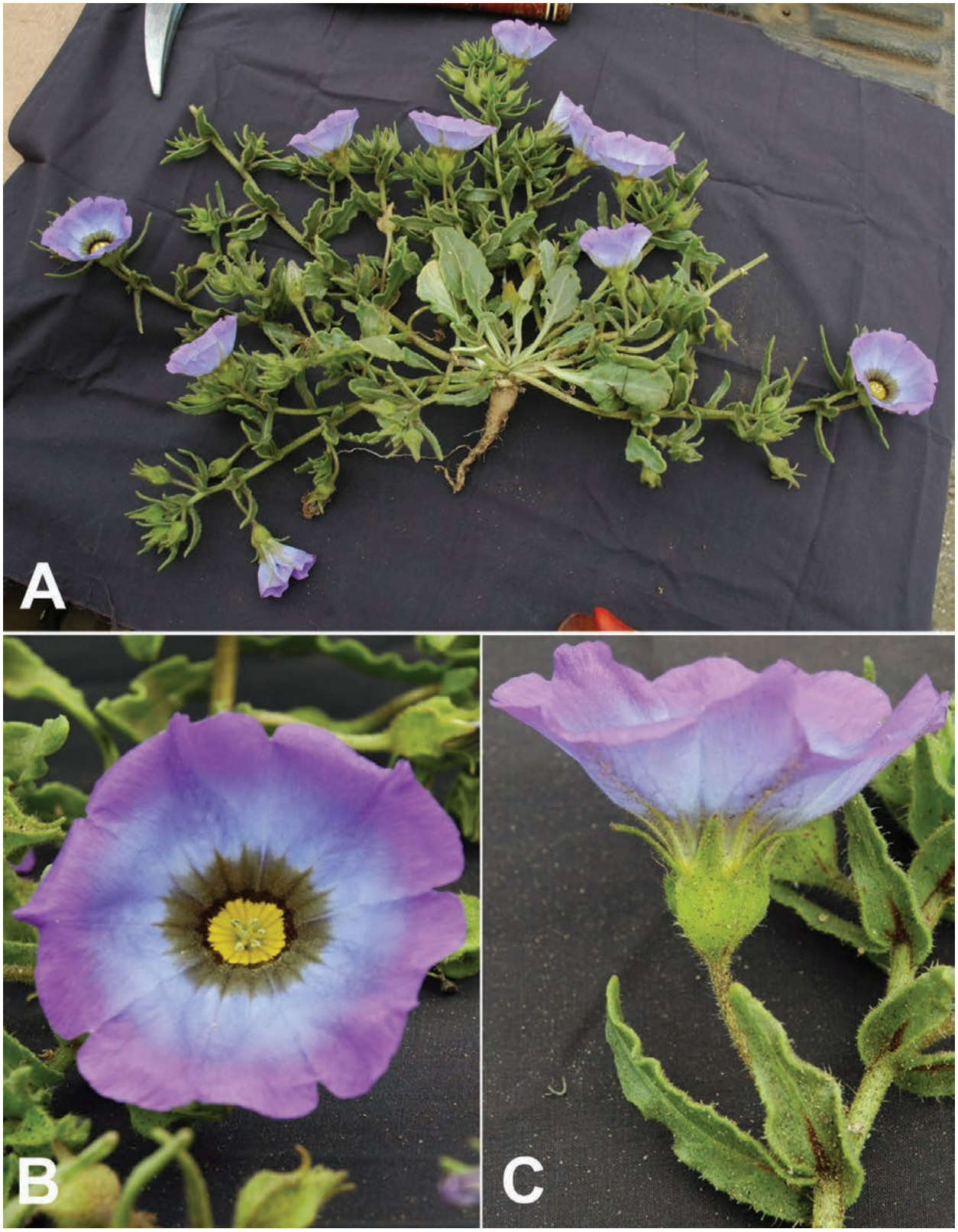


FIGURE 64. *Nolana reichei*. **A**, Plant removed from soil; illustrating basal rosette of leaves, flowering stems, and tap root; **B**, Frontal view of corolla displaying the bands of colors in the throat; **C**, Lateral view of flower.

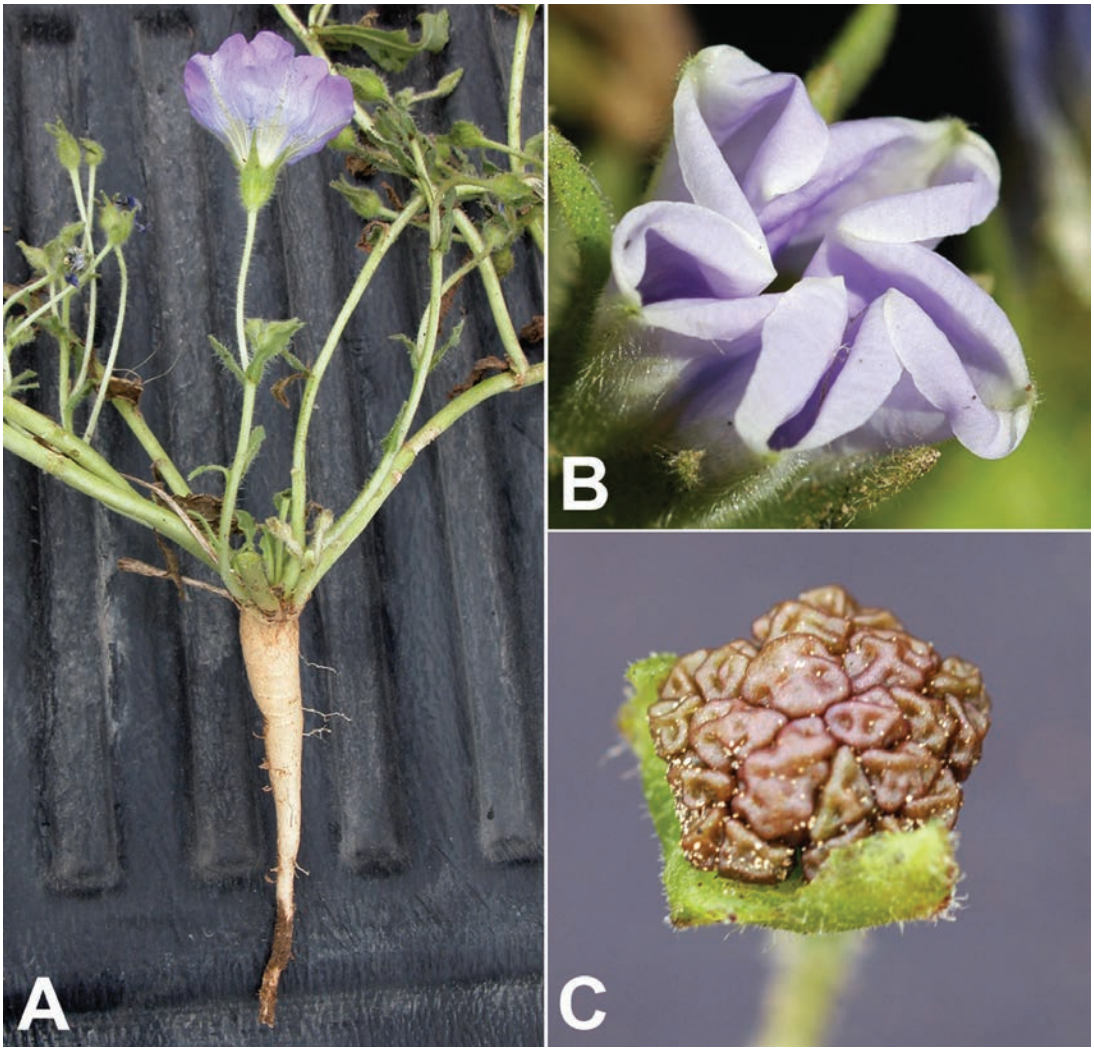


FIGURE 65. *Nolana reichei*. **A**, Taproot; **B**, Opening corollas; **C**, Ovary with angular mericarps.

Jorge, 30°40'S, 71°40'W, 300 m.a.s.l., September 1958, *J. Kummerow s.n.* (CONC 42634); Caleta El Toro, 30°43'53"S, 71°41'50"W, 10 m.a.s.l., 22 October 2005, *F. Luebert & C. Becker 2913* (E, F 2329918); desembocadura Rio Limarí, *C. Muñoz P. & E. Pisano V. 3433* (SGO 58383); *C. Muñoz P. 214* (SGO 57767, SGO 57768). Dept. Ovalle, Fray Jorge, 15 September 1947, *J. Ibáñez & G. Kuschel s.n.* (CONC 144821, SGO 130626); Fray Jorge (Limarí), 600 m.a.s.l., 5 October 1941, *G. H. Schwabe 230b* (SGO 57638); Fray Jorge, *M. Ricardi 2099* (CONC 12754); Loma de Fray Jorge, 17 August 1917, *C. J. F. Skottsberg & I. Skottsberg 844* (F 737490); Fray Jorge–Ovalle, 20 August 1917, *C. J. F. Skottsberg & I. Skottsberg 907* (F 737405); Fray Jorge, *B. Sparre 2917* (SGO 98438); Fray Jorge, Limarí, *E. Werdermann 893* (B, BM000941321, CONC 56159, E00130961, F 564338, GH, K, US 1444782, US 3310836); S end of Fray Jorge forest, 300–500 m.a.s.l., 10 November 1938, *C. R. Worth & J. L. Morrison 16425* (K). Sin data (SGO 58104).

B9. ***Nolana rupicola*** Gaudich., Voy. Bonite, Bot., t. 28. 1841. TYPE: CHILE. Coquimbo: [*non* Valparaíso], 1832, *C. Gaudichaud 67* (Lectotype designated by Mesa-M., 1981: P [0445257]; Isolectotypes: P [P04459131], F neg. 23243 ex G, G [G00383949]). Fig. 66–71.

Digital image: Lectotype of *Nolana rupicola* from the National Museum of Natural History, Paris [P0445257]. http://mediaphoto.mnhn.fr/media/1441360628341yblbe5aatFmEQsbm

Heterotypic synonyms: *Alona longifolia* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Coquimbo: *H. Cuming 887* (Holotype: CGE [05015]; Isotypes: BM (BM000992196), E [E00130950], K [K000532189]). *Sorema longifolia* (Lindl.) Miers, London Jour. Bot. 4: 498. 1845. *Nolana longifolia* (Lindl.) Miers ex Dunal in DC., Prodr. 13: 12. 1852; *Periloba longifolia* (Lindl.) I.M. Johnst., Contrib. Gray Herb. 85: 156. 1929; *Sorema bracteosa* Phil., Fl. Atacam. 43: 298. 1860. TYPE: CHILE. Atacama: Cachinal de la Costa

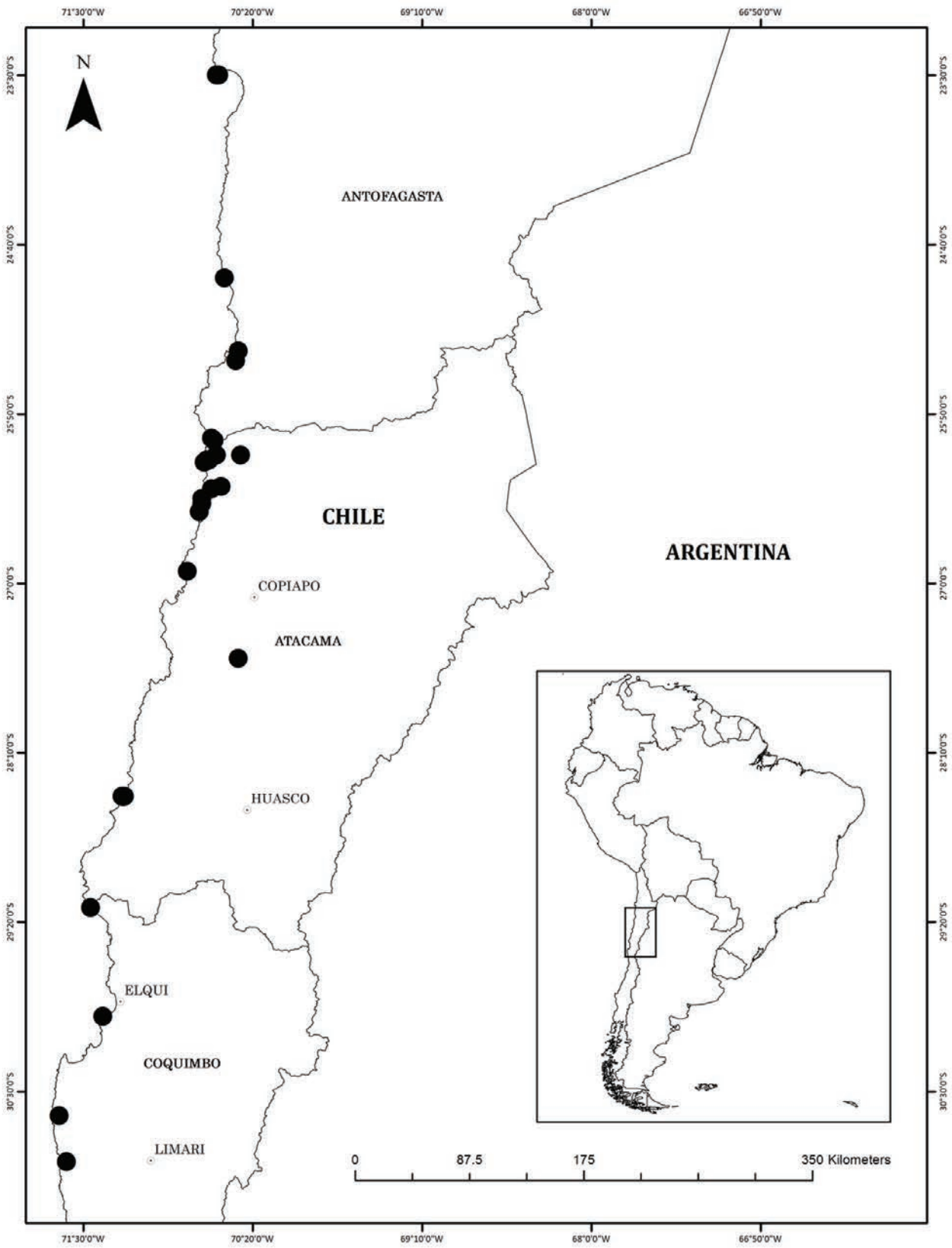


FIGURE 66. Distribution of *Nolana rupicola* Gaudich.

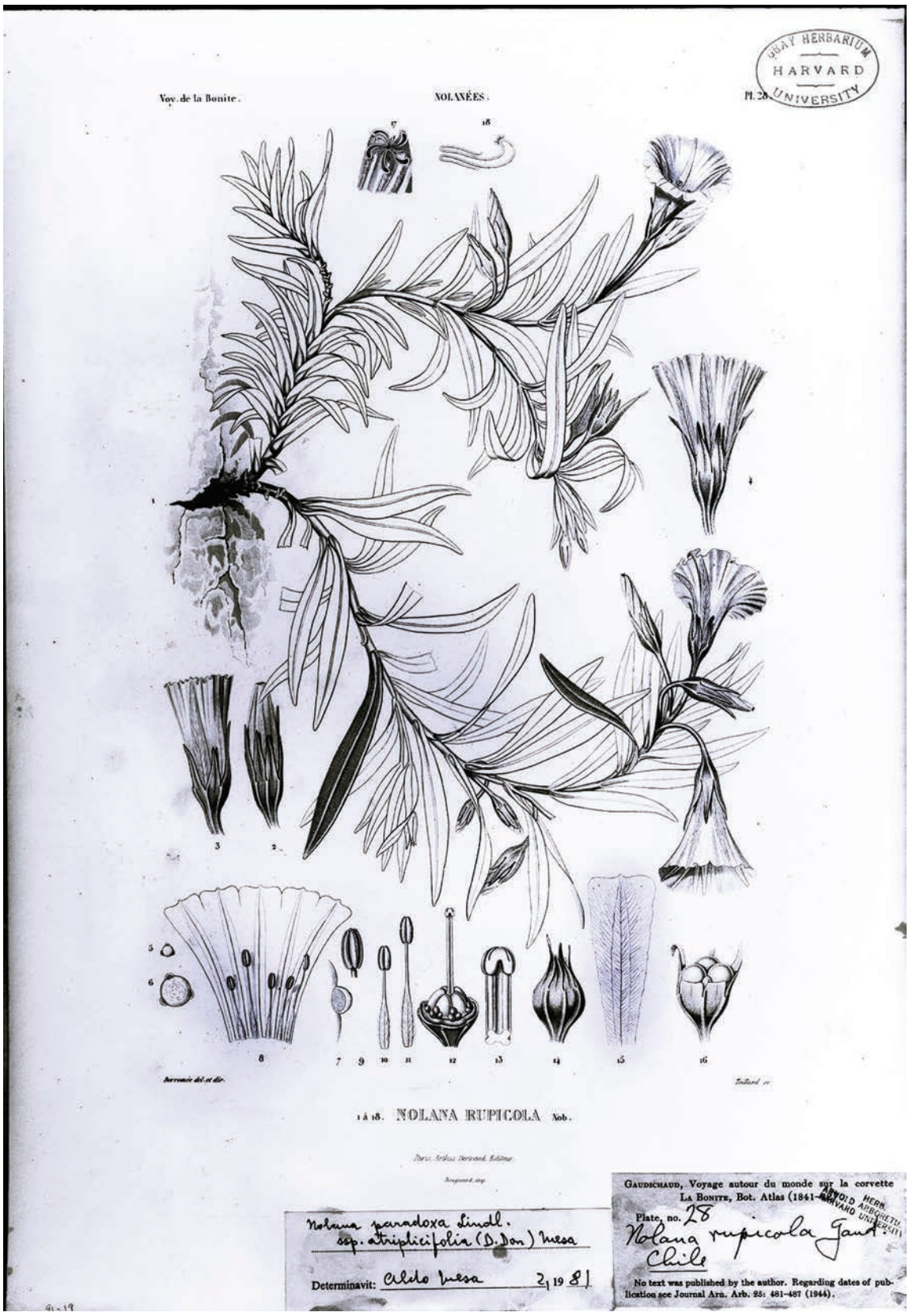


FIGURE 67. Illustration of *Nolana rupicola*, Plate 28. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 68. Illustration of *Nolana rupicola* as *Sorema lanceolata* Miers, Plate 108. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

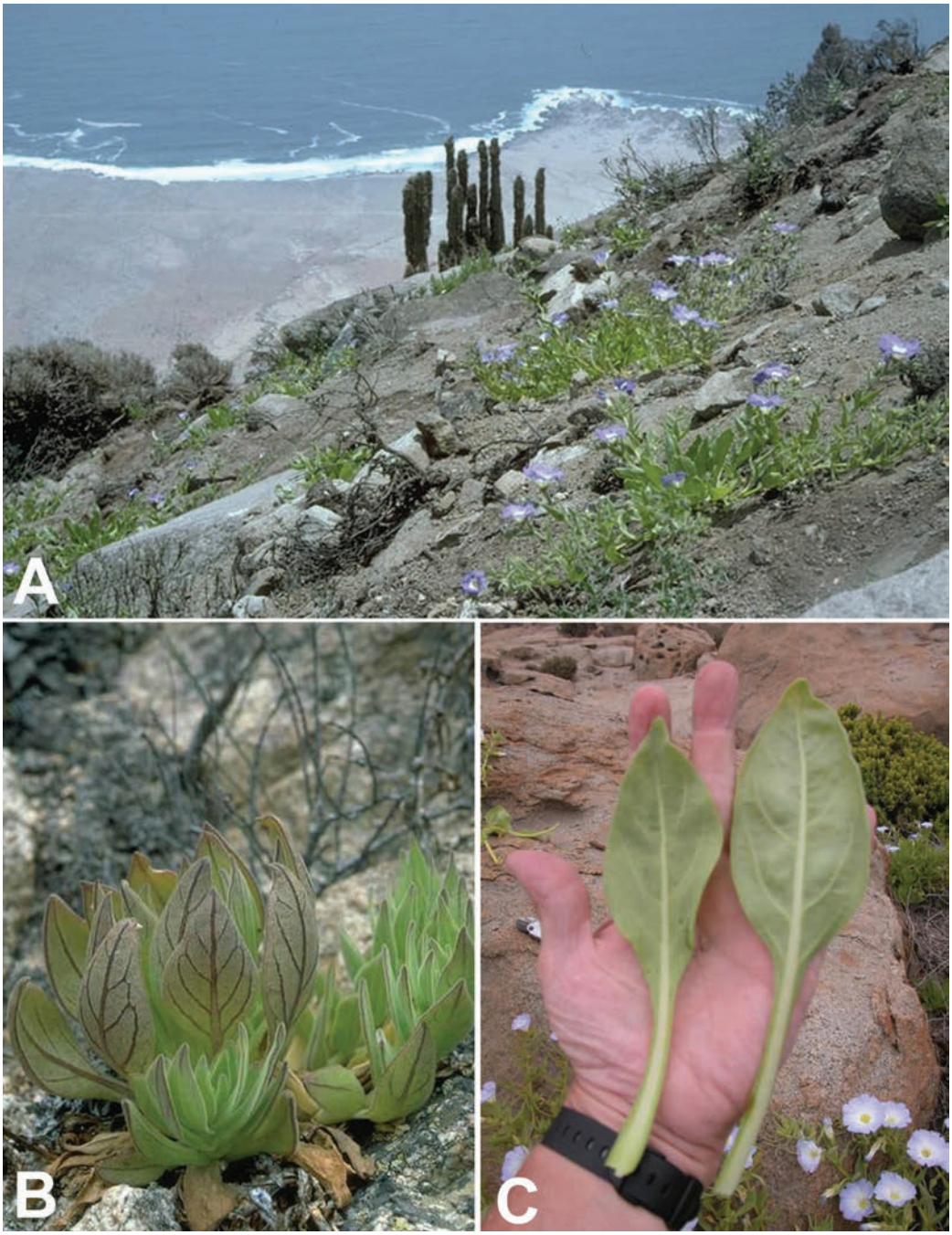


FIGURE 69. *Nolana rupicola*. **A**, Herbs growing in near-ocean habitats; **B**, Basal leaves with purple veins; **C**, Basal leaves with petioles.

y cerca del puerto de Coquimbo, December 1853, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55146, SGO000004396]; Isolectotype: SGO [SGO 55102, SGO000004397]). *Nolana triquetra* Koch & Bouché, Index Seminum [Berlin] 12. 1855, no type designated.

Annual to, more typically, perennial *herbs*, taproot fleshy; branches straight, prostrate, 40–60 cm long, fleshy, becoming woody, glandular pubescent. Basal rosette of *leaves*, blades oval, ovate to broadly lanceolate to elliptic, 2–10 cm long, 8–10 cm wide; petioles 5–7 cm long; cauline leaves on flowering stems alternate, blades lanceolate to ovate, bases sessile, auriculate to amplexicaul, not decurrent, apically obtuse, succulent, dull green, pubescent with capitate-glandular trichomes, viscid, aromatic. *Inflorescences* of solitary flowers, terminal and axillary; pedicels ca. 10 mm long. *Flowers* 5-merous; calyces ca. 20 mm long, campanulate, 5-dentate, teeth unequal, erect, lanceolate-acuminate; corollas infundibularis, regular to weakly zygomorphic, (20–)25–45 mm long, limb 40–50 mm wide, pale to sky blue; nectary disc patelliform, margin sinuate; styles variable in length but shorter than the

FIGURE 70. *Nolana rupicola*. **A**, Light blue corollas with yellow at the base; **B**, Prostrate flowering stems with flowers subtended by auriculate bracts, but not decurrent.

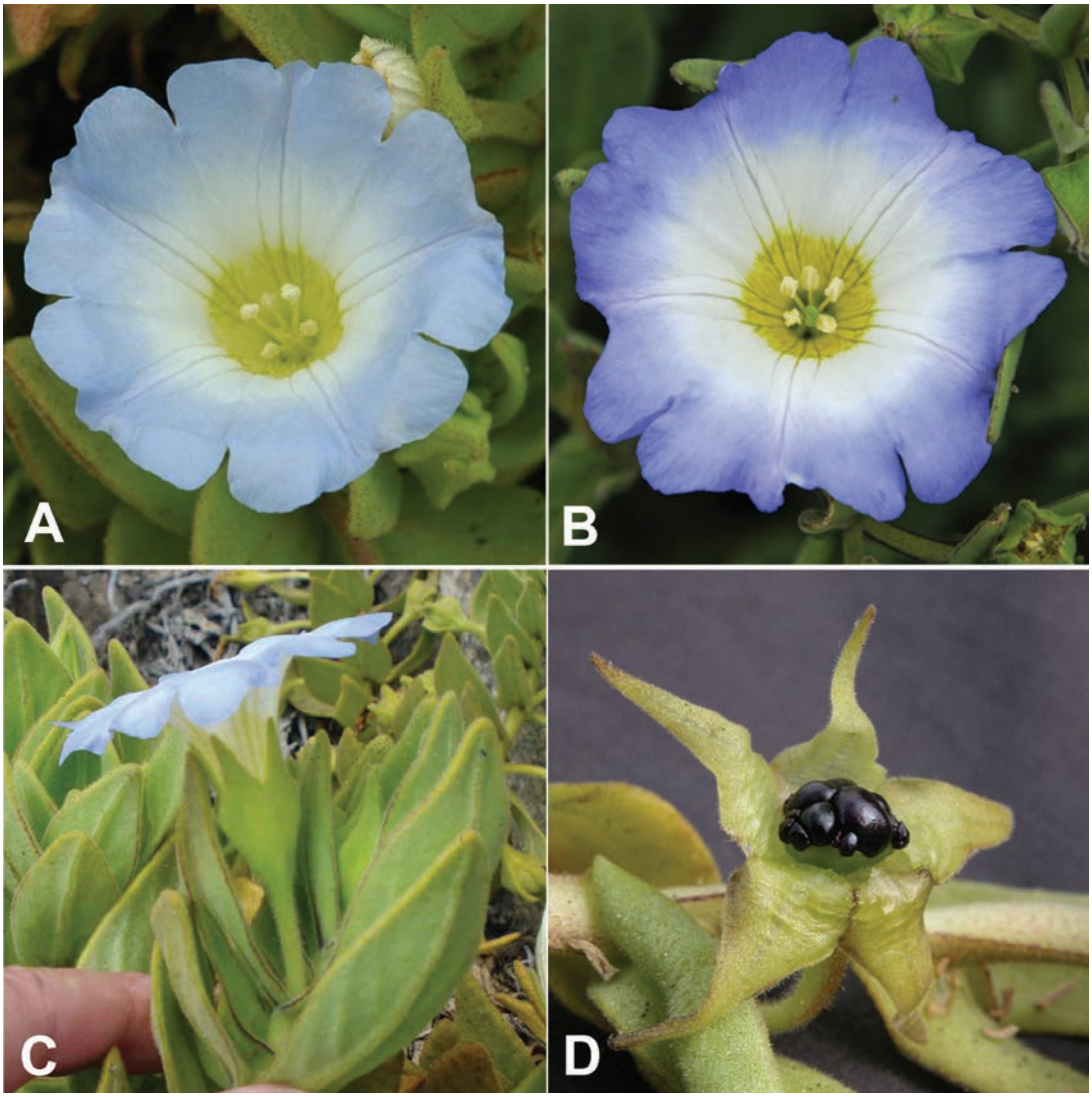


FIGURE 71. *Nolana rupicola*. **A**, Light blue corolla with yellow throat; **B**, Dark blue corolla with yellow throat; **C**, Thick succulent cauline leaves with indistinct abaxial veins; **D**, Maturing ovary on green receptacle.

stamens; gynobasic; stigma capitate or peltate. *Mericarps* 5 large, 4–6 mm long, polyhedrons, ca. 15 small, 3–4 mm long, spherical; seeds 2–7 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *rupes* or *rupestris*, referring to rocky or rock-dwelling, and describes the preferred habitat for this species.

Distribution and Ecology: Chile, Regions of Antofagasta, Atacama, and Coquimbo; 0–200(–780) m.a.s.l. It is recorded from environments with sandy/rocky soils; near-coast habitats or, more rarely, from more inland sites (Fig. 66); Matorral Desértico Tropical Costero, Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Illustrations: Figure 67. Illustration of *Nolana rupicola*, Plate 28. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944). Figure 68. Illustration of *Nolana rupicola* as *Sorema lanceolata*, Plate 108. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana rupicola is a spreading, perennial herb with a basal rosette of sticky-pubescent leaves, growing most generally in near-ocean habitats (Fig. 69A). The basal leaves often have purple veins (Fig. 69B) and are some of the largest leaves in the genus (Fig. 69C). The corollas are always light or pale blue with yellow at the base (Fig. 70A), and the flowering stems are prostrate with the flowers subtended by lanceolate leafy bracts, whose bases are auriculate but not decurrent (Fig. 70B). The corollas are showy to ca. 45 mm in diameter, completely white (Fig. 71A), or the distal

portion of the lobes are blue with yellow in the throats (Fig. 71B). The cauline leaves are thick and succulent with abaxial indistinct veins, and they are very sticky to the touch (Fig. 71C). The ovary has a green receptacle and smooth, shiny mericarps (Fig. 71D).

It appears to be closely related to *N. elegans*, a species with a similar basal rosette of leaves, purple stripes along the mid-veins, blue outer corolla, passing to white, then a yellow center, and white to yellow pollen. Identification of herbarium material is difficult, and differences in opinion can arise. Johnston annotated *A. A. Beetle 26136* (K) in duplicate as *N. elegans*, but the leaves and overall size do not fit that taxon well and is placed here under *N. rupicola*. Furthermore, in 2004, I identified *M. Muñoz S. 4077* (SGO) as *Nolana cf. paradoxa*; however, after examining many sheets of this taxon, here it is considered a white form of *N. rupicola*.

Johnston (1929: 105) commented that the generic name, *Periloba* Raf. (1838), was based upon *Nolana paradoxa*, as illustrated in the Botanical Magazine (1825) and the Botanical Register (1824). He also stated that the generic name, although legitimately established and unmistakable as to its application, had been incorrectly cited by numerous authors as a synonym of the liliaceous genus *Nothoscordum* Kunth (now placed in the Amaryllidaceae). When *Nothoscordum* was added to the list of *Nomina Conservanda* at the International Nomenclature Congress held in Brussels, Belgium in 1910, *Periloba* was listed as a *nomen rejiciendum*. *Periloba*, having the same type species as *Sorema* Lindl. (1844), is clearly synonymous with the latter genus, and hence, *Nolana* and *Gubleria* Gaudich. (1842–1846), based upon *Alona baccata*, is also a synonym (Table 2).

Johnston (1936: 41–42) related *N. rupicola* to *N. acuminata* and commented that the two had similar geographic ranges; however, the former possesses a shrubby perennial base. The leaves have abundant capitate-glandular trichomes, as well short non-glandular trichomes. This pubescence gives the leaves of *N. rupicola* a duller green tinge than its glandless relative, *N. acuminata*. The coarser leaves in *N. rupicola* are more elongate and strap-shaped and tend to have subauriculate, somewhat amplexicaul bases instead of the abruptly short-decurrent bases in *N. acuminata*. He noted that *N. rupicola* also was more restricted to fog-bathed cliffs and rocky places along the coast, whereas *N. acuminata* is more frequently found in sandy or gravelly locations. The mericarps of *N. rupicola* are indistinguishable from those of *N. acuminata*.

Additional specimens examined: CHILE. **Antofagasta**: Paposo, 1 December 2001, *C. Aedo 7050* (CONC 161705, MA); Taltal, 10 km N from Paposo, 24°55'54"S, 70°30'46"W, 16 m.a.s.l., 21 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 32* (E 00230546); Quebrada Anchuña, al N de Taltal, 18 September 1949, *W. Biese 2475* (SGO 96504); Quebrada Guanillos, 10 km al N del Cachinal de la Costa, 14 December 1949, 50–500 m.a.s.l., *W. Biese 3347* (SGO 75223); cercanías de Paposo, 25°00'34"S, 70°27'57"W, 20 June 2015, *K. Bull H. 671* (SGO 166637); ca. 60 km S of Taltal, near mouth of Quebrada de La Cachina, 20°00'S, 70°37'W, 50–100 m.a.s.l., 28 November 1988, *M. O. Dillon & D. Dillon 6039* (E, F 2144367, GH, SGO, US); ca. 9 km N of ThermoElectric plant N of Paposo, 24°57'S, 70°31'W, 70 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8675* (CONC 179100, F 2292797, SGO 158930); Punta Plata, 24°53'47"S, 70°31'33"W, 50 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9062* (F 2292854, SGO 158725); Rinconada de Paposo, 24°56'S, 70°29'W, 0–250 m.a.s.l., 1 December 1989, *O. Gálvez, A. Cornejo, & M. Villarroel O. 14* (SGO 127376); Sierra Esmeralda, cerca de Caleta Guanillos, 25°53'24"S, 70°39'11"W, 200 m.a.s.l., 13 October 2005, *F. Luebert & N. García 2784/1178* (F 2290703); La Higuera, NE de Paposo, 400–900 m.a.s.l., 19 September 1941, *C. Muñoz P. & G. T. Johnson 2932* (SGO 118407). **Atacama**: Huasco, Carrizal de Bajo, road to Llanos de Challe, 26°13'11"S, 71°08'44"W, 38 m.a.s.l., 7 December 2004, *P. Baxter, M. F. Gardner, P. Hechenleitner V., P. I. Thomas, & C. Zamorano E. 1902* (CONC 176879); Huasco, 26 December 1971, *K. Beckett, M. Cheese, & J. Watson 4696* (SGO 110035); Chañaral, hills to north, 22 February 1939, 100 m.a.s.l., *A. A. Beetle 26136* (GH, K); Chañaral, rock outcrops near coast, 23 February 1939, 5 m.a.s.l., *A. A. Beetle 26165* (GH, K); camino Ovalle a Serena, 20 km de Serena, 14 September 1948, *F. Behn s.n.* (CONC 8288); Cuesta de Huasco, 20 September 1949, *F. Behn s.n.* (CONC 8988); Camino a Carrizal Bajo, 9 November 2002, *M. Chamy & M. Piovano 11* (SGO 150486); Parque Nacional Pan de Azúcar, 26°09'S, 70°39'W, 100–200 m.a.s.l., 5 December 1987, *M. O. Dillon & S. Teillier 5085* (CONC, E, F 1994739, GH, SGO); ca. 18 km S. of Chañaral, 26°30'S, 70°43'W, ca. 70 m.a.s.l., 24 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5496* (CONC, E, F 2011627, GH, SGO); Parque Nacional Pan de Azúcar, Las Lomitas, 26°01'S, 70°36'W, 720–780 m.a.s.l., 11 November 1997, *M. O. Dillon & C. Trujillo C. 8005* (CONC 150007, E, F 2183322, GH, K, SGO 143690); Parque Nacional Pan de Azúcar, 26°07'S, 70°35'W, 200 m.a.s.l., 1 December 1997, *M. O. Dillon 8146* (CONC 149971, F 2182959, GH, SGO 143699); ca. 24 km S of Chañaral, near Villa Alegre, 26°30'25"S, 70°42'03"W, 50 m.a.s.l., 27 October 2004, *M. O. Dillon & M. Finger C. 8606* (CONC 179073, E, F 2327496, F 2329911, SGO 158698); ca. 12 km SW of Chañaral, 26°25'42"S, 70°41'41"W, ca. 6 m.a.s.l., 28 October 2009, M. O. *Dillon & R. Concha 9085* (F 2293471); 12 km S of Chañaral along Panamericana, 0–30 m.a.s.l., 27 November 1991, *U. Eggli & B. Leuenberger 1783* (B [2 sheets], SGO 145723); Huasco, 2 November 1930, *F. Jaffuel 1182* (GH); Travesía norte, cerca del mar, 600 m.a.s.l., 6 October 1966, *C. Jiles 4938* (CONC 103445); vicinity of Puerto de Chañaral, hills back of El Barquito, 26°23'S, 28–29 October 1925, *I. M. Johnston 4768* (GH); vicinity of Aguada Grande ["Cachinal de La Costa" of Philippi], near Antofagasta–Atacama provincial boundary, ca. 26°02'S, 16–18 December 1925, *I. M. Johnston 5770* (GH); Carrizal Bajo, July 1900, *T. King s.n.* (E00130963); rocas costeros al sur de Chañaral, 13 September 1965, *A. Kohler 115* (CONC 36028); camino de Caldera a Chañaral, Km 17,

frente a Barranquilla, 24 October 1971, *C. Marticorena, R. Rodríguez, & E. Wendt 1878* (CONC 36177); Orilla Playa Carrizal Bajo, 23 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1104* (SGO 108614); Carrizal Bajo, en camino costero al Norte, 30 October 1987, *M. Muñoz S. & I. Meza P. 2357* (SGO 137726); between Caldera and Chañaral, 10 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274056), 15 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274055); Carrizal Bajo, 1885, *F. Philippi & A. Borchers s.n.* (BM000941328); Puerto de Chañaral, 27 October 1941, 80–140 m.a.s.l., *E. Pisano V. & R. Bravo F. 531* (CONC 144192, SGO 156457); Huasco, lomas de Las Lozas, 14 November 1956, *M. Ricardi & C. Marticorena 3938* (CONC 24056); Parque Nacional Pan de Azúcar, frente Cerro Soldado, 15 m.a.s.l., 26°10'S, 70°40'W, 28 October 1991, *R. Rodríguez 2639* (CONC 125753); ca. 10 km N of Caldera, 26°50'S, 70°45'W, 4 October 1991, *C. M. Taylor, C. von Bohlen, & A. Marticorena 10692* (F 2116663); Parque Nacional Pan de Azúcar, 26°07'S, 70°25'W, 15 September 1992, *S. Teillier, P. Rundel, & P. García 2740* (F 2114622, SGO 129373); Barquito harbor, near Chañaral, 50 m.a.s.l., 18 November 1935, *J. West 3867* (GH); Huasco, back from town isolated on rock outcrops, 10–15 m.a.s.l., 26 October 1938, *C. R. Worth & J. L. Morrison 16221* (GH, K, US 3634881). **Coquimbo**: Coquimbo, September 1934, *C. Grandjot 993* (SGO 116580); Coquimbo, October 1929, *C. Elliot 525* (B, K [2 sheets]); Coquimbo, 28 February 1892, *O. Kuntze s.n.* (F 297512, US 701195); Elqui, Punta Tortuga, 25 m.a.s.l., 31 October 1990, *T.G. Lammers, C. M. Baeza P., & P. Peñailillo B. 7635* (CONC 113432, F 2055114); Coquimbo, 4 m.a.s.l., 27 September 1934, *G. Montero O. 1824* (CONC 112942, GH); El Faro, puerto de Coquimbo, 20–50 m.a.s.l., 14 September 1941, *C. Muñoz P. & G. T. Johnson 2772* (SGO 118264); Punta Choros, flores blancas, centro amarillo, 29°14'S, 71°27'W, 14 m.a.s.l., *M. Muñoz S. 4077* (SGO 146633); Coquimbo, *F. Philippi s.n.* (BM000941327); Coquimbo, 5–10 m.a.s.l., November 1923, *E. Werdermann 112* (BM000021198, E00130955, F 549236, GH). **No exact locality**: July 1900, *T. King 74* (E00130962); September–October 1890, *T. Morong 1227* (F 166468, GH).

Clade C

C1. ***Nolana balsamiflua*** (Gaudich.) Mesa, Fl. Neotrop. 26: 68. 1981. Fig. 72–75.

Basionym: *Alona balsamiflua* Gaudich., Bot. Voyage Bonite, Atlas tab. 107. 1851. TYPE: CHILE. Antofagasta: Prov. Antofagasta, Cobija, July 1836, *C. Gaudichaud 7* (Lectotype designated by Mesa-M., 1981: P [00605843]; Isolectotypes: CONC [CONC 29160], F 679043, F 1000372, FI-Webb [2 sheets], GH [GH0282364], P [P00605844, P00605846], US [US 1705994, US0021967, US 2343517, US00053345]).

Digital image: Holotype of *Alona balsamiflua* from the National Museum of Natural History, Paris [P00605843]. http://mediaphoto.mnhn.fr/media/14427652739002kQhcvGKmHb7yUCu

Erect to decumbent *shrubs* 30–150 cm tall; stems much-branched, densely leafy, pubescent with capitate-glandular trichomes. *Leaves* alternate, densely set, blades linear, 5–7 mm long, ca. 2 mm wide, pubescent with capitate-glandular trichomes, viscid, aromatic. *Inflorescences* of solitary flowers; pedicels ca. 2 mm long. *Flowers* 5-merous; calyces campanulate, 7–9 mm long, lobes equal, subulate; corollas infundibularis, regular, 30–45 mm long, limb 25–27 mm wide, pale lavender or lilac with yellowish throat, rarely white, margin revolute; stamens unequal, longer 12 mm long, shorter 9 mm long; filaments not widened at the base, glabrous; nectary disc patelliform, margin sinuate; style 5 mm long, terminal; stigma capitate. *Mericarps* 3–5, fused; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *balsamum*, a fragrant gum, and *flumen*, referring to dry streambeds where it occurs.

Distribution and Ecology: Chile, Region of Antofagasta; 500 m.a.s.l. It is recorded from rocky environments in near-coast habitats (Fig. 72); Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Illustration: Fig. 73. Illustration of *Nolana balsamiflua* as *Alona balsamiflua*, Plate 107. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana balsamiflua is a sprawling, shrubby species to over one meter tall and several meters wide (Fig. 74A–B). It has pungent, sticky foliage, large flowers (Fig. 75A–B), and connate mericarps (Fig. 75C–D). In the living state, its leaves are strongly aromatic, not unlike *N. rostrata*, where the leaves are resinous and sticky. Its distribution is restricted and covers no more that 100 km along the coast north of Antofagasta. *Nolana balsamiflua* is often recorded in sympatry with other *Nolana* species, such as *N. clivicola*, *N. dianae*, *N. linearifolia*, and *N. peruviana*. None of these congeners have foliar or floral morphology like *N. balsamiflua*.

A collection of *Nolana balsamiflua*, *C. Gaudichaud s.n.*, housed at Kew (K000532256), is labeled as an isotype; its label clearly has a date of 1844 and the locality as Cobija. It is assumed that this collection does represent an isotype; however, the veracity of the label should be investigated since it is known with certainty that Gaudichaud visited Cobija in 1836. The 1844 date may signify the publication date of the illustration, Plate 107. Another collection of *N. balsamiflua* by Gaudichaud (*C. Gaudichaud s.n.*), housed at the Universidad de Chile, Concepción herbarium (CONC 29160), is from Cobija with the date 1839; the veracity of the label data cannot be confirmed.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Tocopilla, Quebrada Aguada Cañas, 500–800 m.a.s.l., 16 October 1949, *W. Biese 2803* (SGO 696622); Quebrada above Playa de los Hornos, just N of Punta Hornos, 26 km S of Caleta Michilla, 22°55'S, 70°15'W, 300–350 m.a.s.l., 20 October 1988, *M. O. Dillon & D. Dillon 5726* (F 2045830); Quebrada Hornitos al N de Mejillones, 443 m.a.s.l., 13 March 2007, *L. Faúndez s.n.* (SGO 154419), *s.n.* (SGO 154420); Quebrada La Higuera, al sur de Tocopilla, 22°18'S,

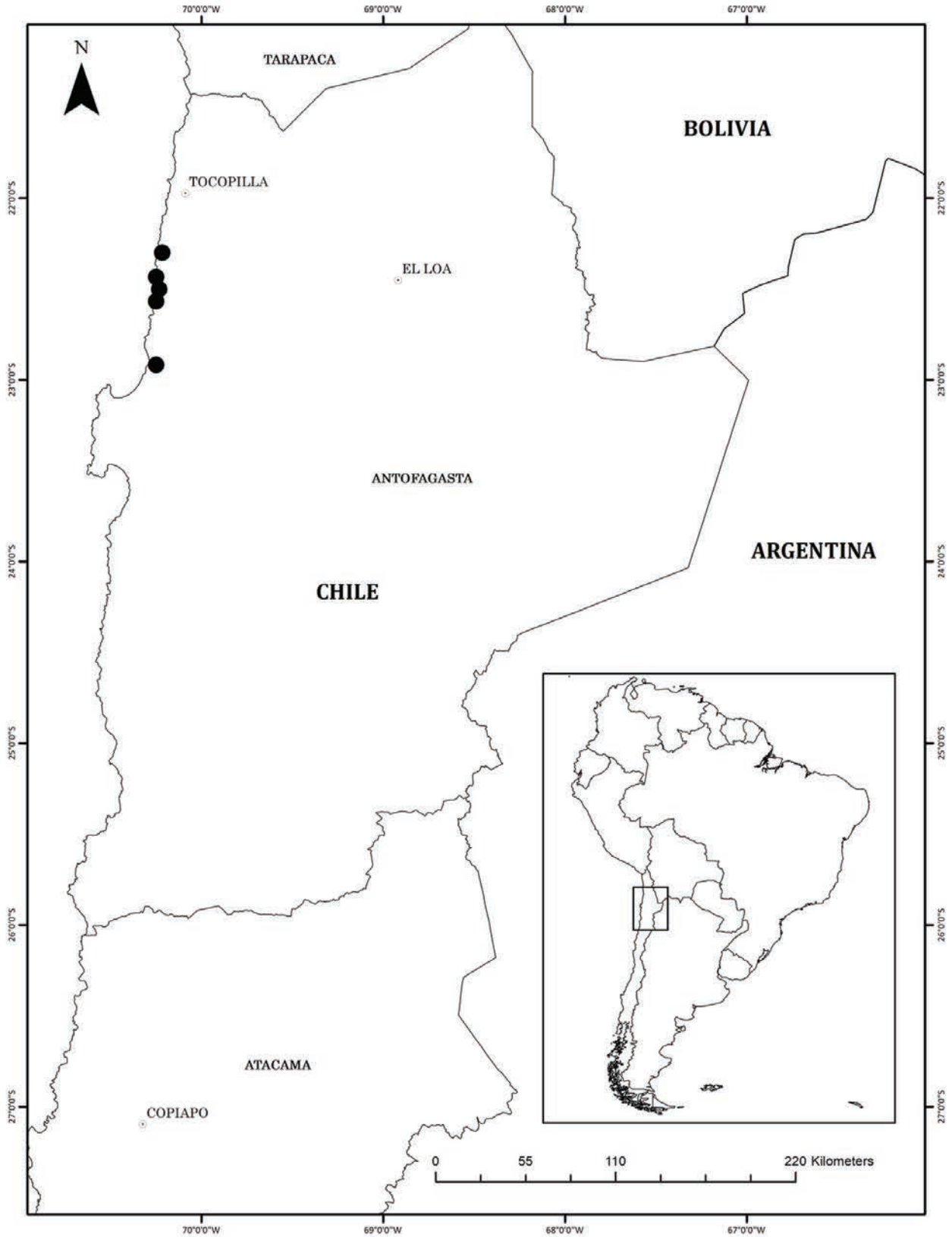


FIGURE 72. Distribution of *Nolana balsamiflua* (Gaudich.) Mesa.

FIGURE 73. Illustration of *Nolana balsamiflua* as *Alona balsamiflua*, Plate 107. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

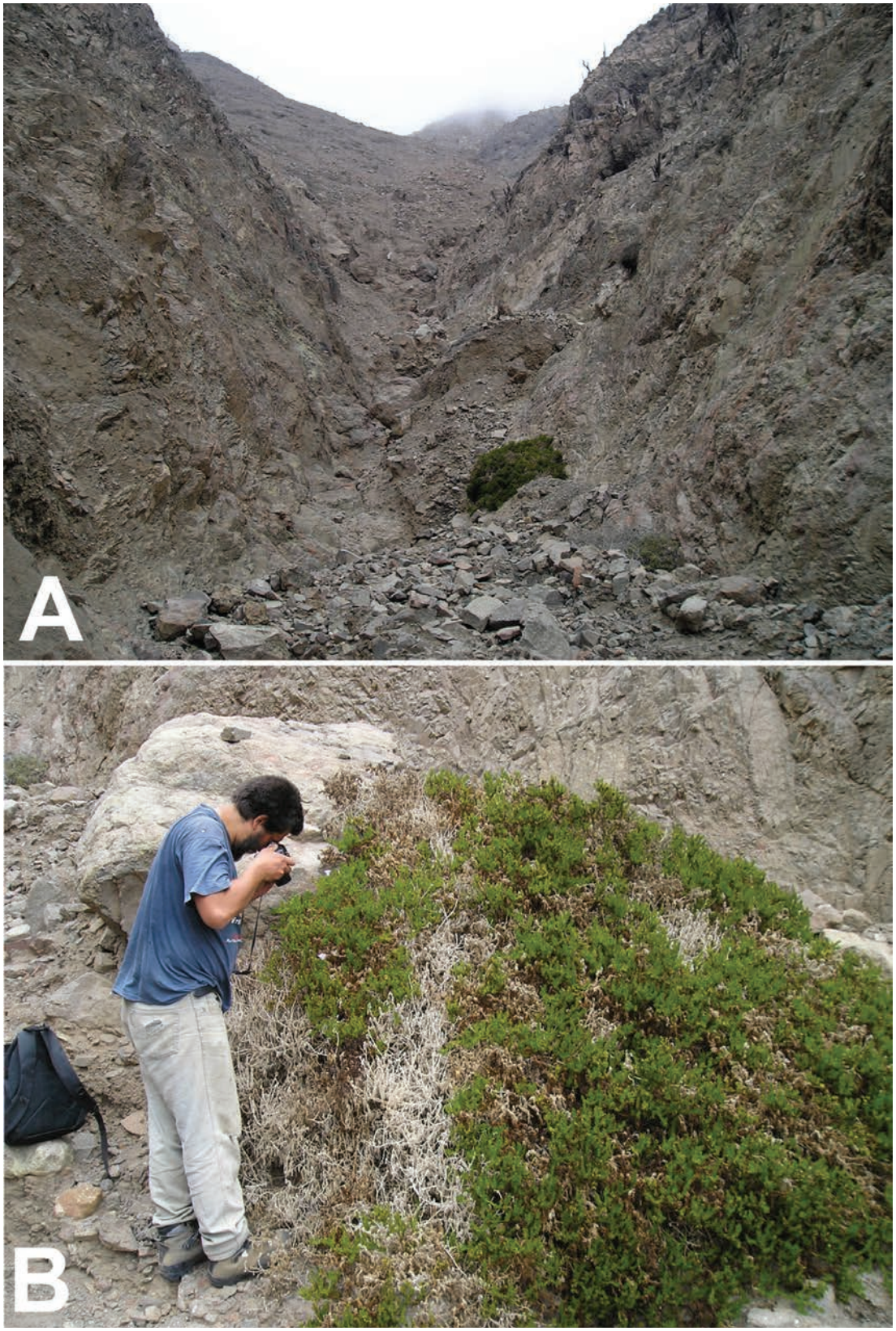


FIGURE 74. *Nolana balsamiflua*. **A**, Large shrubs in Quebrada La Higuera, south of Tocopilla, Chile; **B**, Large woody shrub with showy flowers.

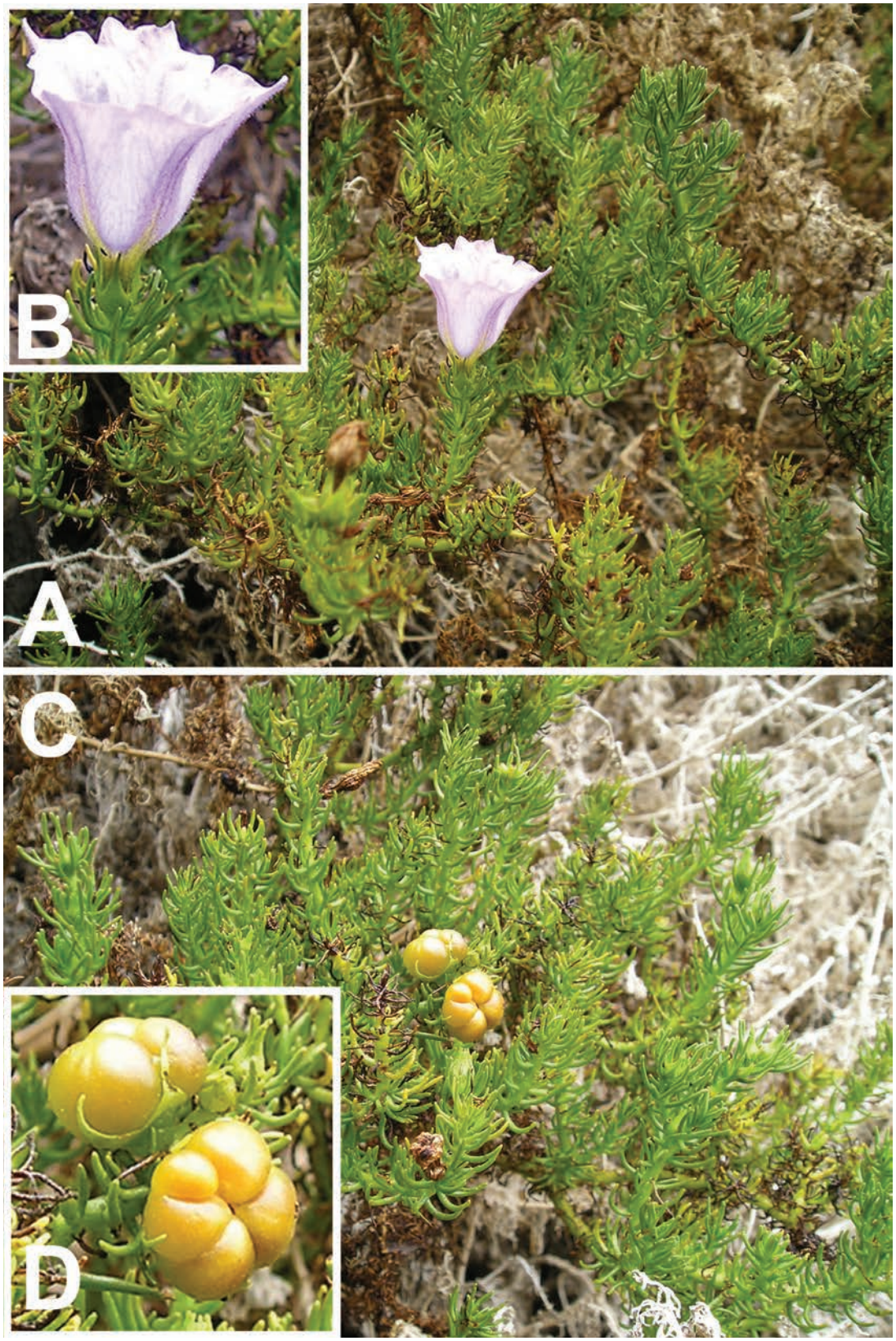


FIGURE 75. *Nolana balsamiflua*. **A**, Stems with pungent, sticky foliage; **B**, Large flowers; **C–D**, Connate mericarps.

70°13'W, 255 m.a.s.l., 30 September 2005, *F. Luebert, N. García, & N. Schulz 2576A/961A* (SGO 159440); Camino de Tocopilla a Antofagasta, Mina el Rincon, 22°30'S, 70°14'W, 315 m.a.s.l., 27 September 1996, *O. Matthei 489* (CONC 137093, SGO 152985); Caleta Buena, 22°26'S, 70°15'W, 30 m.a.s.l., 27 September 1996, *O. Matthei 492* (CONC 137096, SGO 152877); Cobija, 22 August 1969, 15 m.a.s.l., *O. Zöllner 3610* (CONC 119561).

C2. ***Nolana carnosa*** (Lindl.) Miers ex Dunal, Prodr. 13: 14. 1852. Fig. 76–79.

Basionym: *Alona carnosa* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Atacama: Peña Blanca, between Huasco and Coquimbo, *T. Bridges 1328* (Lectotype designated by Mesa-M., 1981: CGE [05010]; Isolectotypes: BM, [BM000941287], E [E00130901], K [K000532259]).

Digital image: Isolectotype of *Alona carnosa* from Royal Botanic Garden, Edinburgh [E00130901]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.e00130900

Homotypic synonym: *Nolana rostrata* (Lindl.) Miers var. *carnosa* (Lindl.) Mesa, Fl. Neotrop. Monogr. 26: 62. 1981.

Heterotypic synonyms: *Alona vernicosa* Phil., Fl. Atac. 44: 302. 1860. TYPE: CHILE. Atacama: en litori arenoso Caldera, December 1854, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55203, SGO000004347]; Isolectotype: W [W0074698], F [F neg. 33143, F 957135]); *Alona sedifolia* Phil., Anal. Mus. Nac. Bot. 2: 69. 1891. TYPE: CHILE. Atacama: [Tarapáca, Chiapa] [19°32'S, 69°12'W], 16 March 1885, *C. Rahmer s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55205]) [non *Nolana sedifolia* Poepp., 1829.] [Johnston, (1936: 20) notes the type of *Alona sedifolia* is "probably in fact from Caldera"]; *Alona grandiflora* Phil., Anal. Univ. Chile 91: 37. 1895. TYPE: CHILE. Atacama: no exact locality, *R. A. Philippi s.n.* (Holotype: SGO, not seen); *Osteocarpus brevifolius* Phil. Anal. Univ. Chile. 91: 40. 1895. TYPE: CHILE. Atacama: Caldera, *R. A. Philippi s.n.* (Holotype: SGO [42638, SGO000004391]); *Osteocarpus lepidophyllus* Phil., Anal. Univ. Chile. 91: 42. 1895. TYPE: CHILE. Atacama: Caldera, September 1885, *F. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55128, SGO000004393]). *Alona lepidophylla* Reiche, Anal. Univ. Chile. 125: 497. 1910; *Nolana lepidophylla* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 103. 1929.

Compact, densely branched *shrubs* to 50 cm tall, 1.0–1.5 m in diam.; stems branched, leafy, viscid, glabrescent, decumbent. *Leaves* alternate to fasciculate, blades oblong, 2–5(–30) mm long, 2–4 mm wide, trigonus, terete, concave abaxially, ascending, viscid, capitate-glandular trichomes, internodes densely crowded. *Inflorescences* of solitary flowers, terminal and axillary; pedicels minute. *Flowers* 5-merous; calyces ca. 10 cm long, plicate, bilabiate, tubular to narrowly-campanulate, buds pyriform, lobes linear, subulate, unequal; pedicels ca. 7 mm long, nodding in fruit; corollas infundibularis, regular, 30–40 mm long, limb ca. 25 mm wide, light blue to lavender, throat white, tube ca. 8 mm long; stigma green; anthers creamy white, unequal; filaments slightly widened and pubescent at the base; nectary disc crateriform, margins sinuous; style terminal; stigma peltate, bilobed. *Mericarps* (5–)7–8, 5–8 mm long, 4–5 mm wide; seeds 2–5 per mericarp. Chromosome number: 2*n*=24.

Etymology: The species epithet is from the Latin, *carnosus*, meaning fleshy, succulent, soft but firm, and is a descriptor for the leaves.

Distribution and Ecology: Chile, Region of Atacama; 0–250(–400) m.a.s.l. It is recorded from environments with sandy soils in near-coast habitats (Fig. 76); Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana carnosa forms dense, compact shrubs in near-ocean sandy habitats (Fig. 77A), such as those near Bahía Inglesa (Fig. 77B). The flowering stems arise from a central woody rootstock (Fig. 78A). Corollas are light blue to pink with white to cream-colored interior throats (Fig. 78B, 79A) and have a bilabiate calyx (Fig. 78C). The ovary enlarges within the calyx (Fig. 79B), and the mericarps are fused, with the apical style evident (Fig. 79C).

Nolana carnosa is closely related to *Nolana rostrata*, but there are diagnostic differences in the leaves, mericarps, and preferred habitats. These two species are largely geographically sympatric over their distribution; however, they typically occupy different habitats, with *Nolana carnosa* growing closer to the ocean, near sea-level, and it obtains some level of dominance in these environments.

Although *Osteocarpus lepidophyllus* and *O. brevifolius* were placed in synonymy with *N. rostrata* by Johnston (1936:18) and Mesa-M. (1981), their small leaves and leaf bases are more suggestive of *N. carnosa*. These synonyms are here treated as *Nolana carnosa*.

A question surrounds *E. M. L. Kausel 5452*, a collection that is filed under *N. filifolia* at SGO, with its label data indicating that it was collected at Cuesta Buenas Aires, Coquimbo. This collection has very short leaves approaching *N. carnosa*, and the mericarps do not appear to be fused, as in *N. filifolia*. Furthermore, all other *Nolana* collections made by Kausel on 9 October 1971 are from areas farther north, between Domeyko and Vallenar. For these reasons, this collection is more likely a representative of *N. carnosa*, and its label data may be in error. Another collection, *H. Cuming 863*, is questionably from Coquimbo; the original provenance must be established.

Morales and Montanola (2018) investigated *Nolana carnosa* for potential micropropagation and development for horticultural use. They stated that their intention was to develop a new ornamental with abundant white to deep blue flowers, evergreen foliage, and compact growth.

Additional specimens examined: CHILE. **Atacama**: Caldera, 10 m.a.s.l., 19 February 1939, *A. A. Beetle 26111* (K); Caldera, 5 m.a.s.l., 21 February 1939, *A. A. Beetle 26129* (K); "Coquimbo", questionable locality, *H. Cuming 863* (E001900); Copiapó, 2–3 km E of Caldera, 27°05'S, 70°48'W, 50 m.a.s.l., 3 December 1987, *M. O. Dillon & S. Teillier 5051* (CONC, E, F 1993977, GH, K, SGO, US); Bahía Inglesa, 27°08'S, 70°51'W, 0–10 m.a.s.l., 28

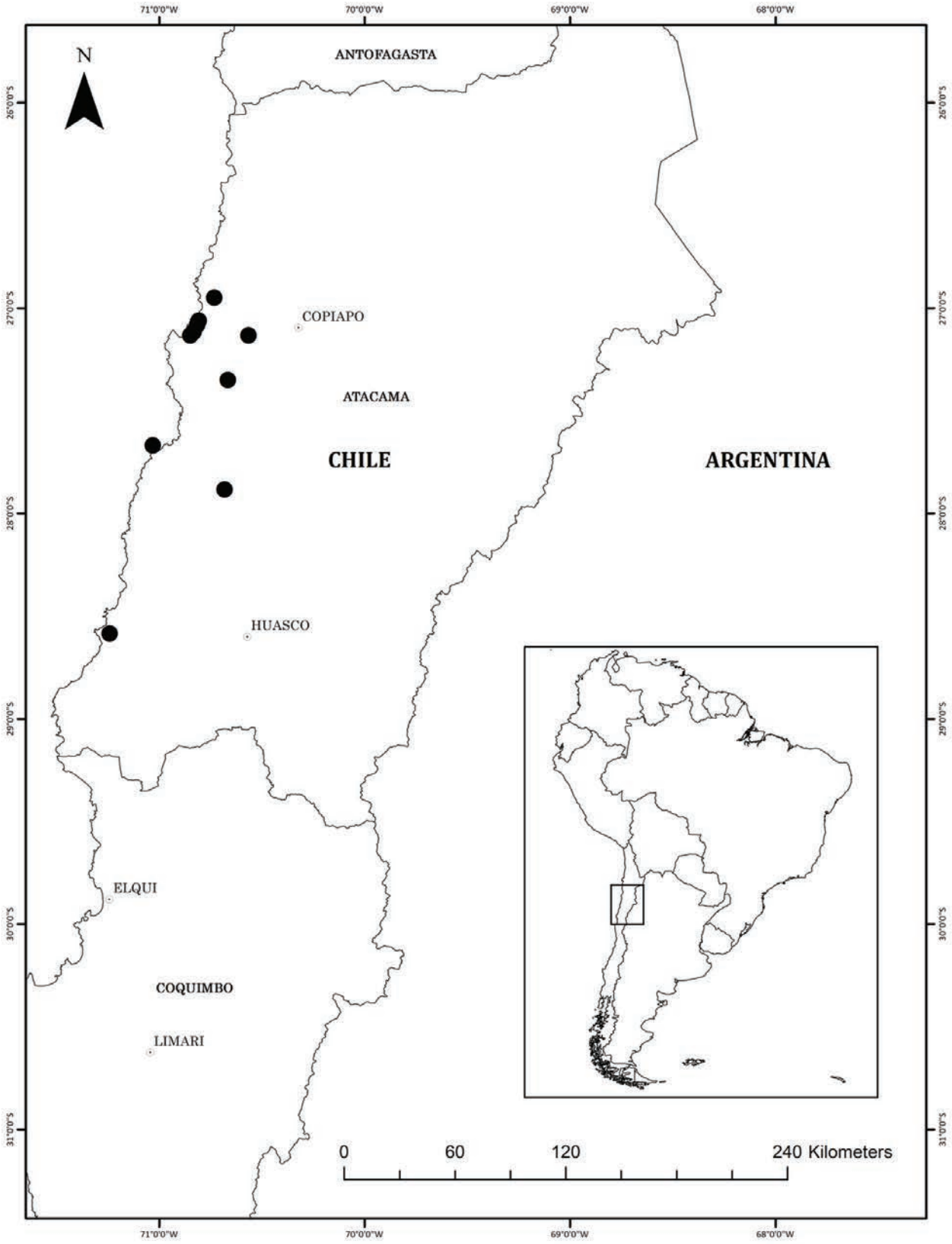


FIGURE 76. Distribution of *Nolana carnosa* (Lindl.) Miers ex Dunal.

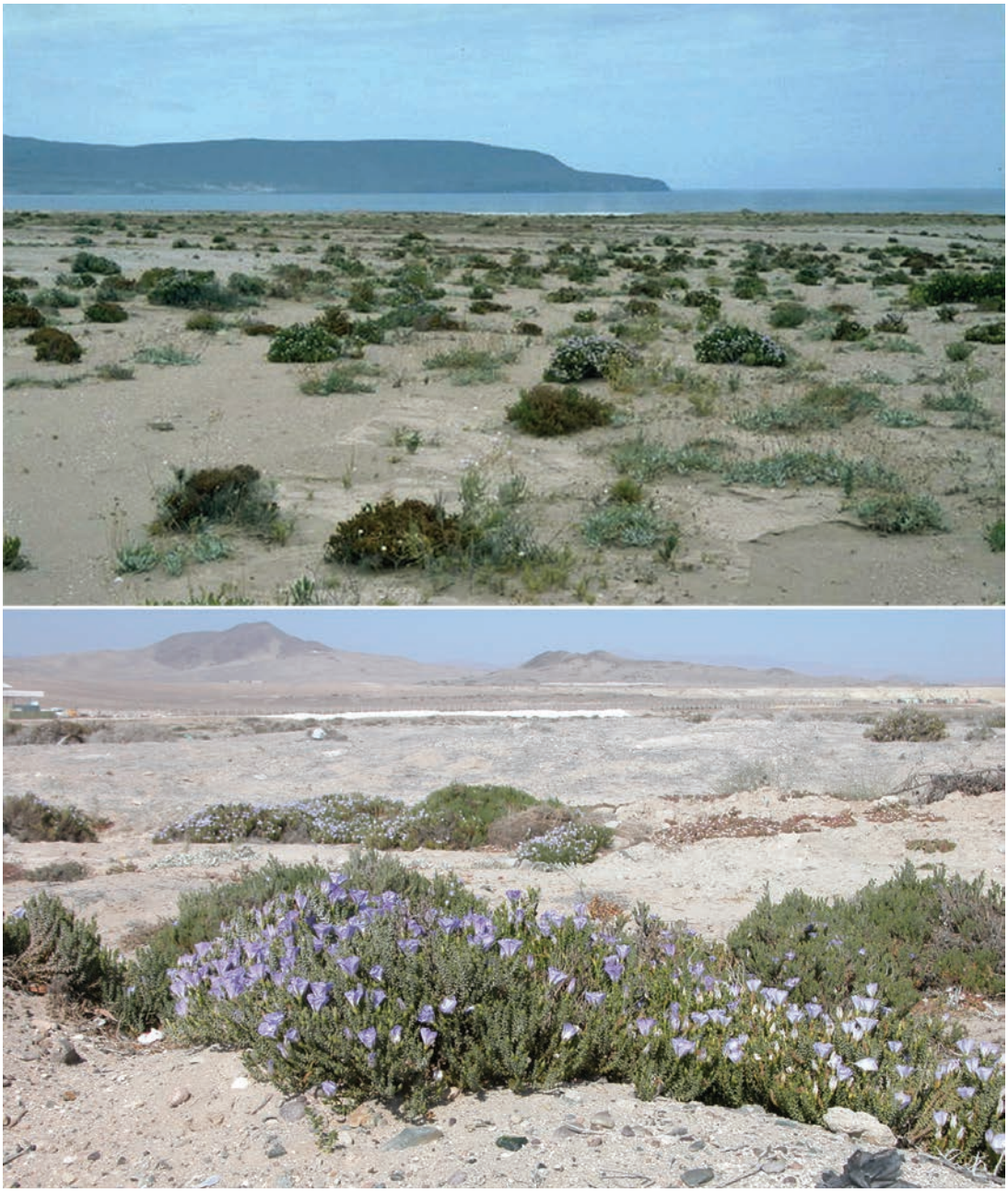


FIGURE 77. *Nolana carnosa*. **A**, Shrubs in sandy habitats at Bahía Inglesa; **B**, Spreading branches.

November 1988, *M. O. Dillon & D. Dillon 6047* (CONC, E, F 2144371, GH, NY, SGO, US); near Bahía Inglesa, 27°07'S, 70°50'W, 50 m.a.s.l., 24 November 1997, *M. O. Dillon & C. Trujillo C. 8093* (CONC 150022, E, F 2183311, GH, K, SGO 143707, US); northern entrada to Caldera, 27°03'42"S, 70°48'30"W, 10 m.a.s.l., 27 October 2004, *M. O. Dillon & M. Finger C. 8610* (F 2292840, SGO 158941); road to Aguada Tongoy, 13.5 km SSW of Huasco, 28°35'06"S, 71°14'33"W, 250 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8656* (F 2292783, SGO 158913); ca. 20 km N of Carrizal Bajo, 27°49'45"S, 71°05'01"W, 13 m.a.s.l., 15 October 2011, *M. O. Dillon & J. Guerra 9210* (CONC 179091); ca. 5 km ESE of Caldera, immediately S of Bahía Inglesa en route to Puerto Viejo, 27°07'27"S, 70°48'56"W, ca. 67 m.a.s.l., 30 September 2010, *M. O. Dillon 9134* (CONC, F 2324458, SGO); Quebrada El León, 26°57'33"S, 70°44'15"W, ca. 237 m, 30 October 2010, *M. O. Dillon 9173* (CONC, F 2331763, SGO); Bandurrias, September 1886, *G. Geisse s.n.* (SGO 72453); Caldera, 1889/90, *G. Geisse s.n.* (SGO 55202). Caldera, October 1887, *G. Geisse s.n.* (SGO 72448); vicinity of Caldera, *E. E. Gigoux s.n.* (GH); Caldera, 22 November 1925, *I. M. Johnston 5047* (GH, K, US 1473989); Panamericana a ca. 8 km al N de Caldera, 19 September 1966, *E. M. L. Kausel 5084* (SGO 79437); Dunas cerca de Caldera, 14 September 1965, *A. Kohler 114* (CONC 38331); Caldera, *A. Kohler 116* (CONC 129560);

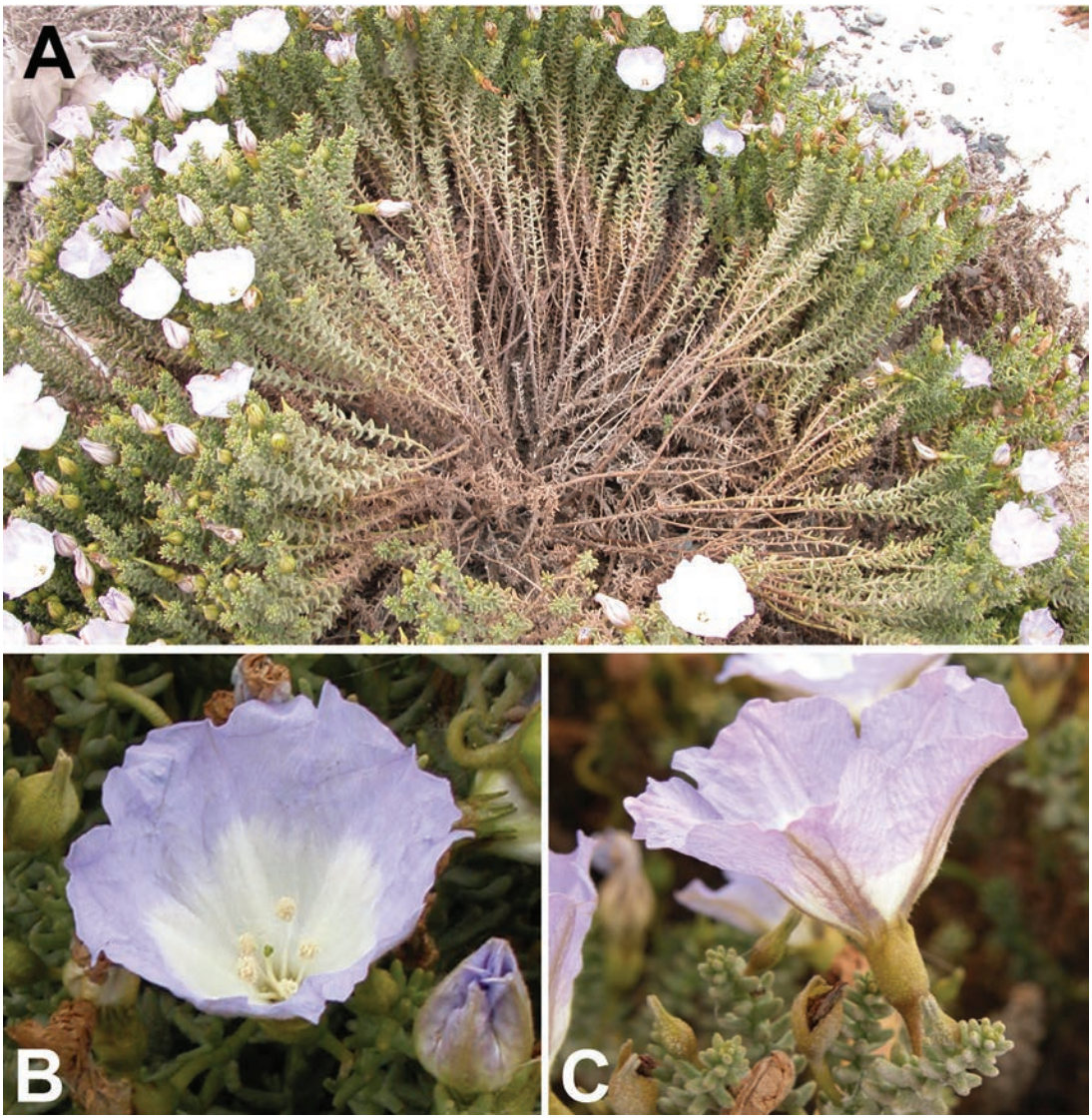


FIGURE 78. *Nolana carnosa*. **A**, Stems from a central woody rootstock; **B**, Light blue to pink corollas with white to cream-colored interior throats; **C**, Bilabiate calyx.

Pampa entre Vallenar y Copiapó, 14 September 1965, *A. Kohler 139* (CONC 33113); Travesía, cerca de Estancia Castilla, September 1965, *A. Kohler 159* (CONC 33084, US); Quebrada El León, 26°57'S, 70°44'W, 240 m.a.s.l., 16 October 2005, *F. Luebert & C. Becker 2846* (F 2290704, SGO 159441); Morro de Caldera, Playa Las Manchas, 27°08'S, 70°34'W, 0 m.a.s.l., 17 October 2005, *F. Luebert & C. Becker 2869* (F 2290691, SGO 159449); Llanos de Caldera, a 50 km de Copiapó, 150 m.a.s.l., 23 September 1941, *C. Muñoz P. & G. T. Johnson 1888* (SGO 112643); Camino de Copiapó a Caldera, Km 37, cerca de Punta Picasso, 160 m.a.s.l., 24 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1854* (CONC 36143); camino de Caldera a Copiapó, Km 5, 24 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1871* (CONC 36144); Planicies al N del valle de Copiapó, 13 October 1992, *M. Muñoz S. 3061* (SGO 131468); Camino a Aguada Tongoy, 28°34'01"S, 71°17'38"W, 72 m.a.s.l., 28 October 2002, *M. Muñoz S. 4230* (SGO 149465); 3 km separación Camino Los Colorados a Carrizal Bajo, *M. Muñoz S., I. Meza P., & E. Barrera M. 1071* (SGO 108667); Roqueríos al N de Caldera, en Santuario de Santa Gemita, 27°05'S, 70°49'W, 1 November 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2864* (SGO 126139); Bahía Inglesa, 30 September 1993, *M. Ono & K. Suzuki s.n.* (MAK 274036); between Caldera and Chañaral, 15 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274037); Caldera, *R. Pearce s.n.* (K000532260); Caldera, 1904, *F. Philippi s.n.* (BM000941288); Chañarcito Carrizal, September 1885, *F. Philippi s.n.* (SGO 55204), Chañarcito, 24 September 1885, *F. Philippi & A. Borchers s.n.* (BM000941285); Copiapó, Quebrada de Gertrudis, 400 m.a.s.l., 25 November 1941, *E. Pisano V. & R. Bravo F. 823* (CONC 144191, SGO 156623); Bahía Inglesa, 27°07'S, 70°51'W, 2 m.a.s.l., 14 January 1987, *F. Schlege 8093* (CONC 115654); Punta Cachos, 20 February 1998, *W. Sielfeld 67* (SGO 143054); ca. 1 km N of Caldera, 27°03'S, 70°49'W, ca. 100 m.a.s.l., 26

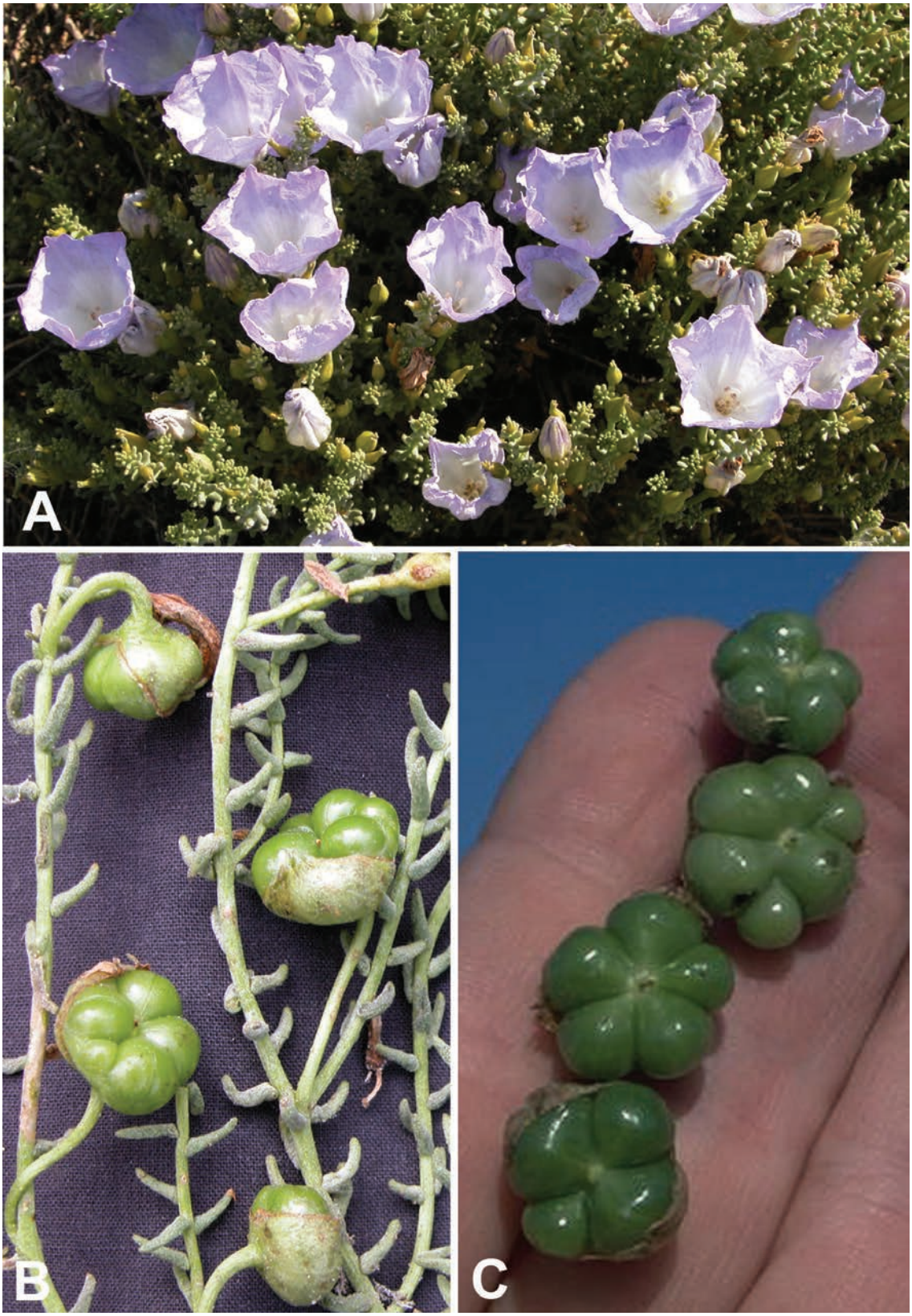


FIGURE 79. *Nolana carnosa*. **A**, Corollas have clear, white throats without guides; **B–C**, Mericarps fused with the apical style.

October 2000, *S. Teillier & M. O. Dillon 4928* (F 2324456); alrededores de Caldera, 3 August 1967, *C. Villagrán 119* (CONC 33273); Caldera, 10 m.a.s.l., September 1924, *E. Werdermann 383* (BM000941351, CONC 109124, F 565205, GH, K); entre Copiapó y Caldera, 16 September 1968, *O. Zöllner 2812* (CONC 129559); Caldera, August 1864, sin coll., (BM00941266). Without Exact Locality: Chile, 1890, *G. Geisse s.n.* (SGO 42656); Chile, Atacama, September–October 1890, *T. Morong 1274* (F 18075, F 166483, K, US 1417072).

C3. ***Nolana coelestis*** (Lindl.) Miers *ex* Dunal, Prodr. 13: 13. 1852. Fig. 80–85.

Basionym: *Alona coelestis* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Atacama: Prov. Huasco, "mountains near the town of Freirina, valley of Huasco", *T. Bridges 1329* (Lectotype designated by I. M. Johnston, 1936: CGE [015012]; Isolectotypes: BM [BM000941291], E [E00130909], K).

Digital image: Isolectotype of *Alona coelestis*, right side, *Bridges 1329* from Royal Botanic Garden, Edinburgh [E00130909]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.e00130909

Heterotypic synonyms: *Alona ericifolia* Miers, London J. Bot. 4: 500. 1845. TYPE: CHILE. Atacama: Huasco, *T. Bridges 1323* (Holotype: K [000532254]; Isotype: BM [000021195, frag]). *Nolana ericifolia* (Miers) Miers *ex* Dunal, Prodr. 13: 14. 1852. *Alona coelestis* var. *ericifolia* (Miers) W. Brandt, Bot. Jahrb. Syst. 69(2): 157. 1938; *Alona floribunda* Phil., Anal. Univ. Chile 43: 525. 1873. TYPE: CHILE. Atacama: Huasco, October 1866, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [42655]; Isolectotypes: G, not seen, F neg. 23237, GH, SGO [SGO 55183]).

Shrubs or subshrubs, 30–50 cm tall; stems erect, branched, densely leafy, glandular-pubescent, viscid. *Leaves* alternate, blades linear, (3–)10–25 mm long, 1–2 mm wide, fasciculate, margins strongly revolute, concave adaxially, densely villous with capitate-glandular trichomes, not sticky to the touch. *Inflorescences* of solitary flowers, terminal to subterminal, axillary; pedicels 10–20 mm long. *Flowers* 5-merous; calyces campanulate, (8–)13–15 mm long, pilose with curly trichomes, lobes triangular to subulate, equal; corollas infundibularis, regular, 30–35(–45) mm long, limb ca. 40 mm wide, blue distally, inner throat white with yellow; stamens unequal, 12–14 mm long; anthers glandular pubescent; nectary disc patelliform, margin sinuate; style terminal, ca. 14 mm long, truncate. *Mericarps* 3(–4), fused, 5–8 mm in diam.; seeds ca. 4 per mericarp. Chromosome number: unknown.

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 100–800 m.a.s.l. It is recorded from open environments with sandy soils (Fig. 80); Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Illustration: Fig. 81. Illustration of *Nolana coelestis*. Plate 106. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944). Fig. 82. Illustration of *Nolana coelestis* as *Alona coelestis* Lindl., Edwards's Botanical Register, vol. 30: t. 46 (1844) [S. A. Drake].

Nolana coelestis is a woody shrub to a half meter tall (Fig. 83), with showy flowers and pubescent foliage (Fig. 84A–B, 85B). The open flower reveals anthers and style (Fig. 85A). It is diagnosed by a combination of characters, including large, blue corollas nearly 4 cm wide with inner yellowish throats (Fig. 85B), actinomorphic calyces with dense curly trichomes (Fig. 85C–D), and three to four fused mericarps (Fig. 85E). It is most often confused with *N. filifolia*, another species with actinomorphic calyces; however, the leaf arrangement, leaf blade shape, and pubescence in these two species are very different. In *N. filifolia*, the leaves are narrowly linear, glandular and without elongate, curly trichomes that are common to *N. coelestis*.

Lindley described *Alona coelestis* from garden-grown material and published in Edwards's Botanical Register under plate 46 with a colored painting by his dedicated artist, Sarah Anne Drake (b. 1803–d.1857). Lindley cited two collections, *Bridges 1329* and *Cuming 857*, and, when Johnston published his monograph, he cited the collection by Bridges. He concluded that the species was best represented by cultivated individuals grown from Bridges' mericarp collections from near Freirina, valley of Huasco. The sheet from CGE [15012] is not currently available via the internet, and the E isolectotype sheet is referenced above.

Additional specimens examined: CHILE. **Atacama**: Huasco, 2 November 1930, *F. Jaffuel 1173* (GH); Huasco, 2 November 1930, *F. Jaffuel 1190* (GH); Huasco, 28°29'13"S, 71°10'06"W, 149 m.a.s.l., 25 August 2015, *P. Medina 3285* (CONC 187178); Vallenar, cercanías de Vallenar, 28°43'07"S, 70°48'11"W, 895 m.a.s.l., 20 October 2014, *P. Medina & F. Gamboa 358* (CONC 187209); Ruta C-46 entre Huasco y Vallenar, 28°32'07"S, 71°01'3"W, 272 m.a.s.l., 22 October 2014, *P. Medina & F. Gamboa 467* (CONC 187324); N of Vallenar along Panamericana, 24 October 1991, *M. Ono s.n.* (MAK 274948); Huasco, October 1866, *Reed s.n.* (BM000941289). **Coquimbo**: Quebrada de Juan Soldado, 10 November 1958, *E. Bailey s.n.* (SGO 132742); cerro grande de La Serena, 1 October 1971, *K. Beckett, M. Cheese, & J. Watson 4024* (SGO 110093); Coquimbo, November 1930, *Bro. Claude-Joseph 5440* (US 1470539), La Serena, October 1926, *Bro. Claude-Joseph 4418* (US 1284364); La Serena, *Bro. Claude-Joseph 4584* (US 1283882); Los Cerrillos, 300 m.a.s.l., September 1948, *B. Collanthes T. s.n.* (CONC 129554); Coquimbo, February 1882, [H.M.S. Alert], *Coppinger s.n.* (K); Coquimbo, 1831, *H. Cuming 857* (E00130908, K [2 sheets]); Punta Arrayán, ca. 20 km N of La Serena, 29°42'S, 71°19'W, 140–150 m.a.s.l., 22–23 September 1988, *M. O. Dillon, D. Dillon & V. Poblete 5436* (E, F 2011541); Coquimbo, [500–700 ft], September 1927, *C. Elliott 91* (K); Prov. Elqui, 10 km W of the Panamericana on gravel road to El Tofo and Chungungo, 2 km W of the culmination of the road at turnoff to El Tofo, 9 km above Chungungo, 29°26'55"S, 71°15'16"W, 580 m.a.s.l., 25 October 1997, *U. Eggli & B. E. Leuenberger*

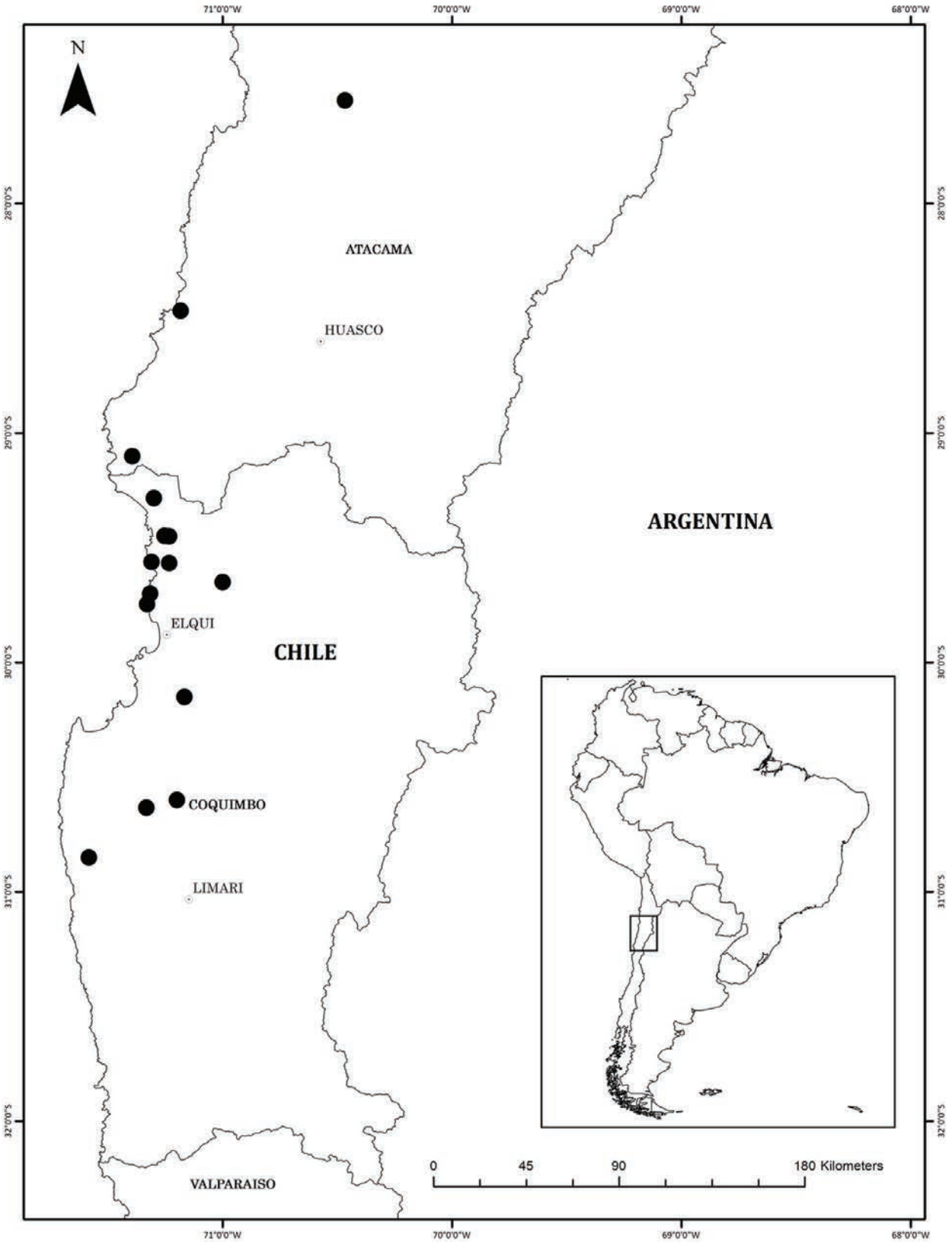


FIGURE 80. Distribution of *Nolana coelestis* (Lindl.) Miers ex Dunal.

FIGURE 81. Illustration of *Nolana coelestis*. Plate 106. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 82. Illustration of *Nolana coelestis* as *Alona coelestis* Lindl., Edwards's Botanical Register 30, plate 46. (1844).

FIGURE 83. *Nolana coelestis*. Shrubs with showy flowers and pubescent foliage. Photograph by María Teresa Eyzaguirre.

3030a (B); carretera La Serena al Norte, Km 24, Loma Las Perdices, 14 October 1961, *A. Garaventa H. 4297* (CONC 49156); "in maritimis," 8 October 1836, *C. Gay 1205* (SGO 55207); Coquimbo, 1835, *C. Gaudichaud 66* (CONC 29161, FI, P, not seen); Puerto Coquimbo, October 1889, *G. Geisse s.n.* (SGO 72449); Coquimbo, 1889/90, *G. Geisse s.n.* (GH, SGO 55190); 10.1 km N of road to Romeral, N of La Serena, ca. 0.5 km W of Panamericana, 29°44'45"S, 71°19'46"W, 100 m.a.s.l., 1 August 2000, *L. R. Landrum & S. S. Landrum 9823* (SGO 146805); Mineral El Tofo, Bahía Cruz Grande, 16–21 September 1960, *E. M. L. Kausel 4576* (SGO 79434); Punta de Teatinos, a 3 km al Norte, 10–50 m.a.s.l., 7 September 1942, *C. Muñoz P. & E. Pisano V. 3254* (SGO 118650); 4 km Sur de Caleta Hornos, 21 October 1984, *M. Muñoz S. 1929* (SGO 108210), *M. Muñoz S. 1930* (SGO 108209); Subida S Cuesta Buenos Aires, 29°34'S, 71°20'W, 27 October 1991, *M. Muñoz, S. Teillier, & I. Meza P. 2633* (SGO 126128); Coquimbo, 1888, *F. Philippi s.n.* [*1904*] (BM000992195); La Serena, Cerro Los Loros, 27 June 1940, *R. Santesson 794* (K); Cuesta de Buenos Aires, 29°34'S, 71°14'W, 500 m.a.s.l., 20 September 1961, *F. Schlegel 3902-1* (CONC 425884); Cuesta de Buenos Aires, 29°34'S, 71°14'W, 350 m.a.s.l., 10 October 1975, *M. Silva s.n.* (CONC 44041); Cuesta Buenos Aires, 540 m.a.s.l., 29 August 1948, *R. Wagenknecht H. 304* (CONC 129555); Choros Bajos, 50 m.a.s.l., 26 July 1973, *O. Zöllner 6927* (CONC 129556). Data Absent: CONC 14025, CONC 129553.

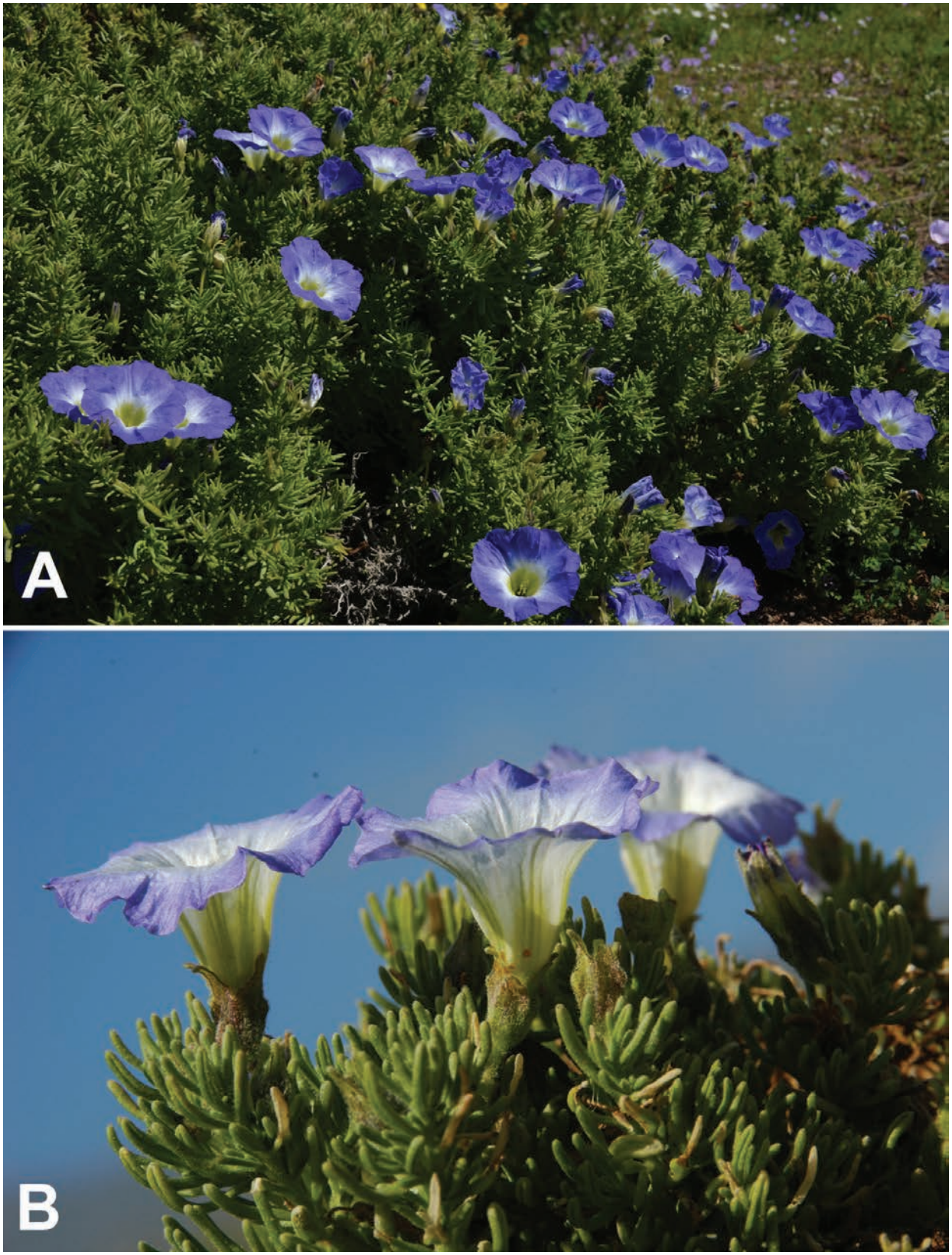


FIGURE 84. *Nolana coelestis*. **A**, Flowers and foliage; **B**, Lateral view of flowers with actinomorphic calyces. Photographs by María Teresa Eyzaguirre.

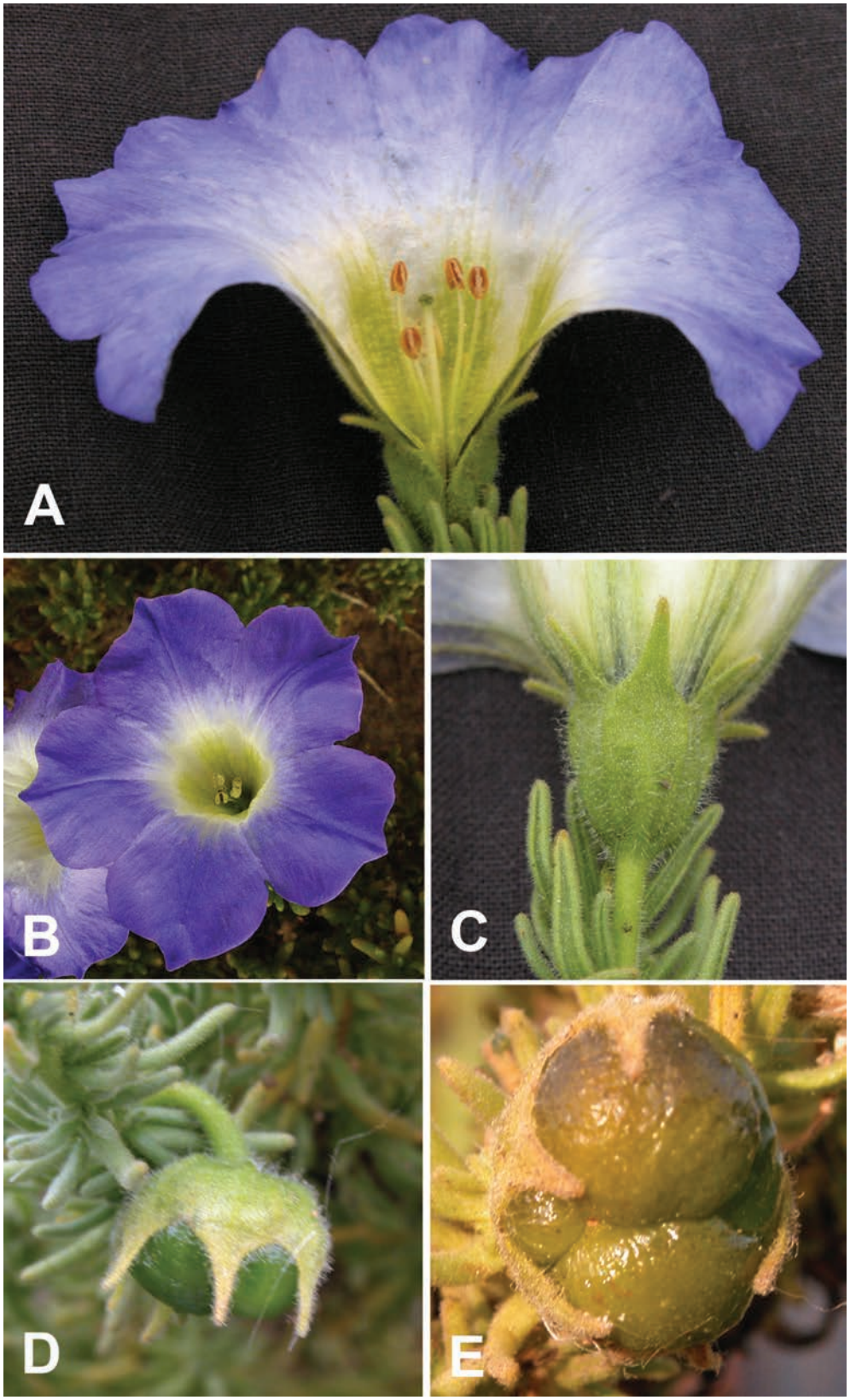


FIGURE 85. *Nolana coelestis*. **A**, Open flower reveals anthers and style; **B**, Corollas ca. 4 cm wide with inner yellowish throats; **C–D**, Actinomorphic calyces with dense curly trichomes; **E**, Three to four fused mericarps.

C4. ***Nolana filifolia*** (Hook. & Arn.) I.M. Johnst., Rev. Chilena Hist. Nat. 34: 231. 1930. Fig. 86–90.

Basionym: *Convolvulus filifolius* Hook. & Arn., Bot. Beechey Voyage 1: 35. 1830. TYPE: CHILE. Coquimbo: Coquimbo, Capt. F. W. Beechey Voyage, *A. Collie & G. T. Lay* s.n. (Lectotype designated here: G [005319-1, G00383957]).

Digital image: Lectotype of *Convolvulus filifolia* from Conservatoire et Jardin botaniques de la Ville de Genève, Geneva [G00383957]. http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=287621&base=img&lang=en

Homotypic synonym: *Alona filifolia* (Hook. & Arn.) I.M. Johnst., Contrib. Gray Herb. 112: 20. 1936.

Heterotypic synonyms: *Fabiana grandiflora* Dunal, Prodr. 13: 591. 1852. TYPE: CHILE. Coquimbo: les cerros environs de La Serena, *C. Gay 2* (Lectotype designated by Mesa-M., 1981: G-DC [00202707]; Isolectotypes: GH [GH00282331], P [P00605448, P00605449, P00605450]); *Alona glandulosa* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Coquimbo: Coquimbo, 1825, *J. Macrae s.n.* (Holotype: CGE [05014]; Isotypes: G [G 005319-2, G00383960], F neg. 23241, K [K000532257]); *Nolana chastenayana* Gaudich., Voy. Bonite, Atlas, pl. 33. 1842. TYPE: CHILE. Based upon material gathered in Coquimbo, no specimen located, Bonite Atlas pl. 33. 1842; *Ipomoea cruckshanksii* Choisy, Prodr. 9: 389. 1845. TYPE: CHILE. Coquimbo: Coquimbo, *A. Cruckshanks s.n.* (Holotype: K); *Osteocarpus foliolosus* Phil., Anal. Univ. Chile 91: 42. 1895. TYPE: CHILE. Coquimbo: cerca Ovalle en Valle Quebrada del Ingenio, January 1883, *F. Philippi s.n.* (Holotype: SGO).

Shrubs 20–60(–120) cm tall; stems erect, branched basally, pale green, densely leafy. *Leaves* alternate to fasciculate, blades linear, 5–15 mm long, ca. 1 mm wide, terete, strongly concave adaxially, viscid, capitate-glandular trichomes, aromatic, without elongate trichomes. *Inflorescences* of solitary flowers, axillary on branchlets; pedicels 5–12 mm. *Flowers* 5-merous; calyces narrowly campanulate, 8–20(–25) mm long, 5–11 mm wide, glabrous to densely pubescent, regularly lobed, lobes linear to long attenuate, (3–)5–7(–10) mm long, margins revolute; corollas infundibularis, regular, (15–)30–40(–50) mm long, limb (20–)30–60 mm wide, tube basally pale blue, apically sky blue, rarely completely white; stamens unequal, longer 11–15 mm long, shorter 9–13 mm; filament widened and pubescent at the base; nectary disc crateriform; style ca. 15 mm long, terminal; stigma peltate, (2-) 5-lobate. *Mericarps* 5–6, fused; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *filifolius*, or thread-leaved, and is a good descriptor for the leaves of this species.

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 15–600(–1300) m.a.s.l. It is recorded from open environments with sandy soils (Fig. 86); Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006). It was reported to be growing on granite near Coquimbo; however, this has not been confirmed.

Illustration: Fig. 87. Illustration of *Nolana filifolia*. Plate 33. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944). Fig. 88. Illustration of *Nolana filifolia* as *Alona rostrata*. Carlos Muñoz Pizarro, Flores silvestres de Chile, Ediciones de la Universidad de Chile by Eugenio Sierra Rafols (1966).

Nolana filifolia is a showy shrub (Fig. 89A) with large blue corollas and narrowly cylindrical, terete, resinous leaves that are sticky to the touch (Fig. 89B), and actinomorphic calyces that nod as they mature (Fig. 89C). In some individuals, the fusion of mericarps is complete (Fig. 90A), and the apical style is visible when the mature corolla is removed (Fig. 90B).

William Jackson Hooker (b. 1785–1865 d.) and George Walker Arnott (b. 1799–d. 1868) described *Convolvulus ? filifolius* in recounting the collections made on Captain Beechey's voyage (1841). Plants were collected by botanists and naturalists assigned to the voyage, including George Tradescant Lay (b. 1799–d. 1845), Alexander Collie (b. 1793–d. 1835), Alexander Cruckshanks (coll. 1825–1856), and James Macrae (coll. 1925; also cited as Macray, McRay, McRae). In the text, Hooker and Arnott (1841: 35) stated why they assigned their new species to *Convolvulus* Tournefort: "We regret that for want of perfect materials we can give but an unsatisfactory account of this interesting plant. Our best specimens are from Mr. Cruckshanks and judging by the flower (for they have no fruit) they appear to belong to the present genus. But the plant is quite shrubby and woody, much branched, and somewhat clammy."

Judging from the misidentifications, *Nolana filifolius* has been confused with *N. rostrata*, which does have similar leaves; however, the latter species has zygomorphic calyces that separate these two species. They share broadly sympatric distribution ranges, but are seldom found in the same environments. The illustrations made by Eugenio Sierra Ràfols (b. 1919–d. 1999) in Carlos Muñoz Pizarro's books explain this confusion. His drawings and a painting are labeled as *Alona rostrata*; however, the calyx and all of the leaves are clearly drawn, and conform in all ways with the species diagnosis for *N. filifolia* adopted here. In his first book, *Sinopsis de la Flora Chilena* (Muñoz, 1959), the illustrations were drawn by Sierra Ràfols from specimens collected by Muñoz. One illustration says *Nolana sp.* and the other *N. rostrata*; however, both are here considered *N. filifolia*, since they are clearly drawn with actinomorphic calyces. The vouchers have been examined in this study (i.e., *C. Muñoz P. 4294* and *C. Muñoz P. 4154*). In his second book, *Flores Silvestres de Chile* (Muñoz, 1966), Muñoz documented that Sierra Ràfols had collected material of *Nolana filifolia* that was perhaps used for the painting in Fig. 88 (i.e., *E. Sierra Ràfols s.n.,* SGO 75652, SGO 75653, SGO 75657).

Several populations are distinctive in their overall morphology. For example, a population 12–13 km south of Freirina and southeast of Huasco (i.e., *M. O. Dillon & J. Guerra 8655, U. Eggli & B. E. Leuenberger 3020*)

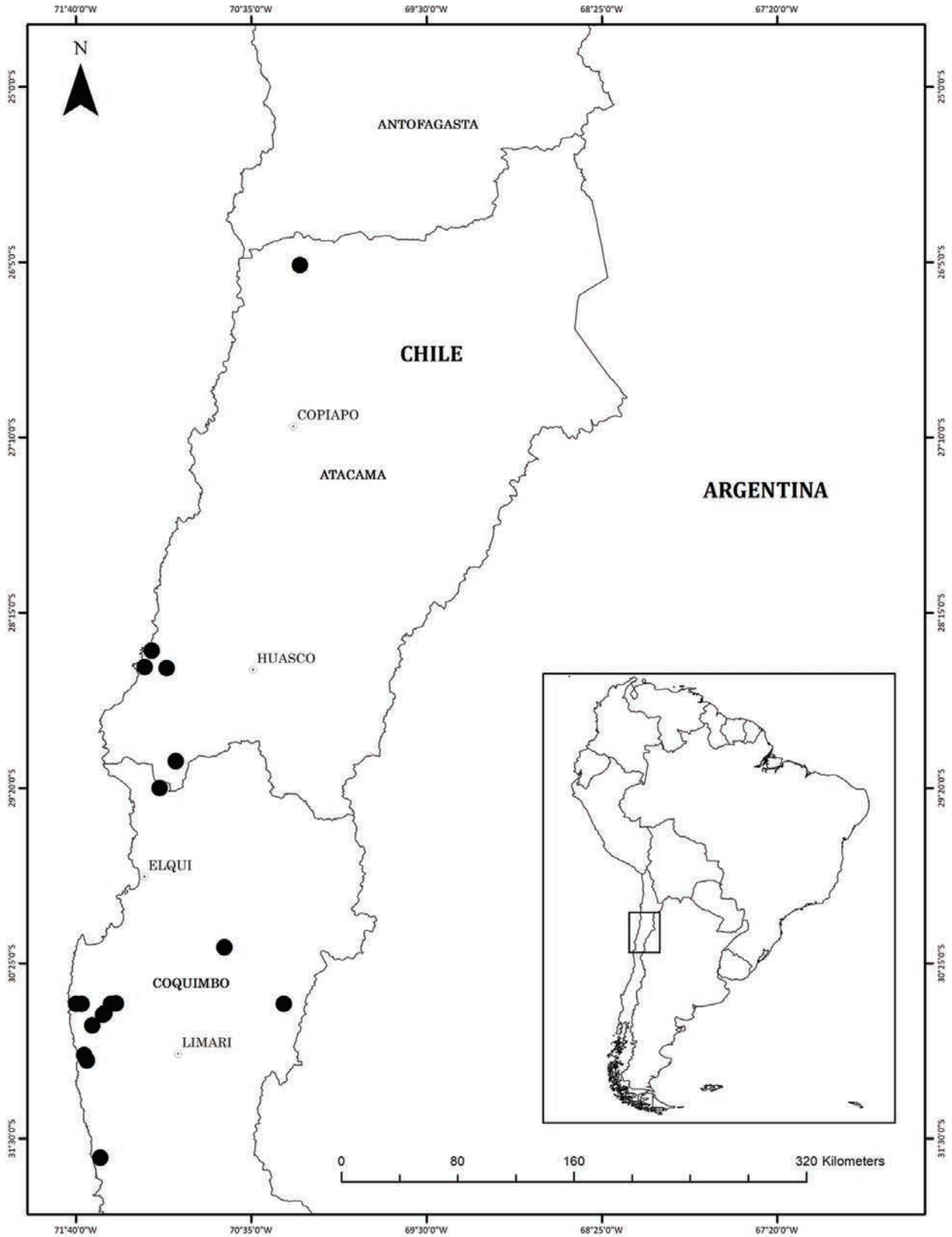


FIGURE 86. Distribution of *Nolana filifolia* (Hook. & Arn.) I.M. Johnst.

FIGURE 87. Illustration of *Nolana filifolia*. Plate 33. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 88. Illustration of *Nolana filifolia* as *Alona rostrata*. Carlos Muñoz Pizarro, Flores silvestres de Chile, Ediciones de la Universidad de Chile. Drawn by Eugenio Sierra Rafols (1966).

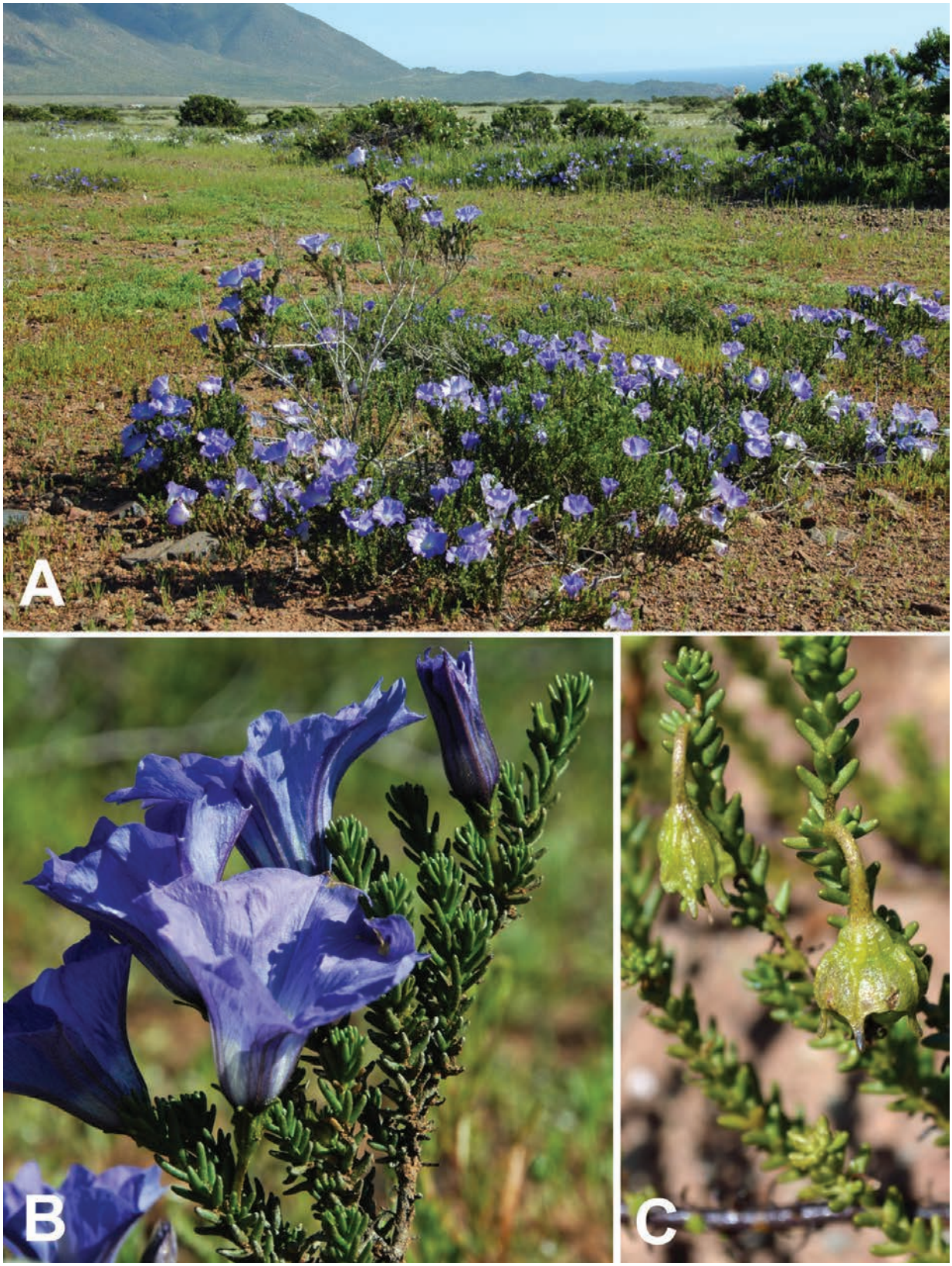


FIGURE 89. *Nolana filifolia*. **A**, Large shrubs with showy flowers; **B**, Blue corollas with narrowly cylindrical, resinous leaves; **C**, Actinomorphic calyces nodding in maturity. Photographs by María Teresa Eyzaguirre.

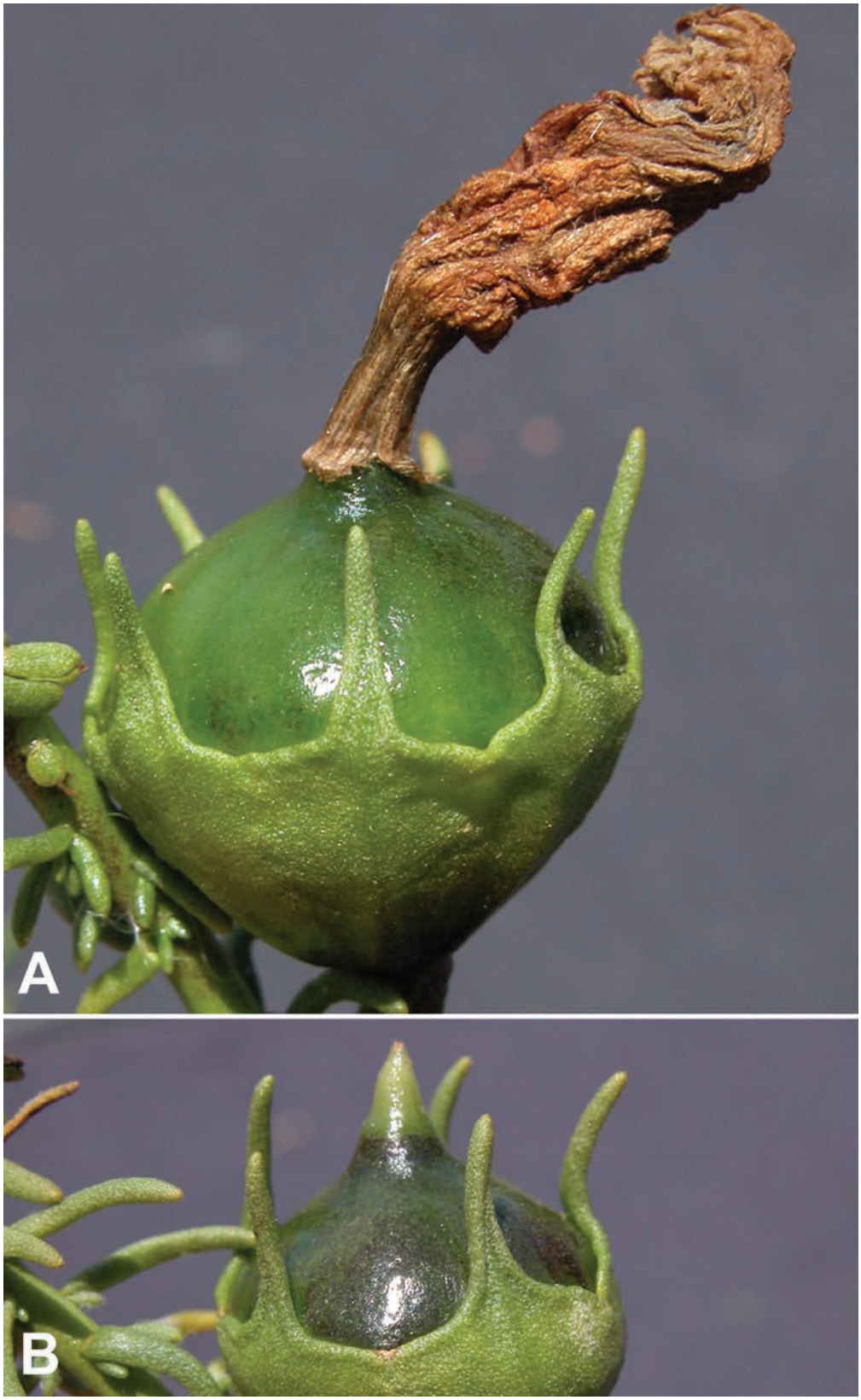


FIGURE 90. *Nolana filifolia*. **A**, Fusion of mericarps is complete; **B**, Corolla removed reveals apical style.

has densely villous calyces, and the latter collection was originally determined as *N. coelestis*. Their label data is repeated here: "Few-branched shrublets to 40 cm; stems pale green, rather woody and tough; leaves narrowly terete, medium grass-green, strongly concave adaxially; flowers funnel-shaped, sepals somewhat spreading, olive-green; corolla tube basally pale blue, apically sky-blue. Plants viscid and somewhat unpleasantly aromatic."

Additional specimens examined: CHILE. **Atacama**: Prov. Copiapó, 50 km al sur de Copiapó, 27°46'S, 70°29'W, 600 m.a.s.l., *Ch. von Bohlen 296* (CONC 129072). Prov. Huasco: Freirina, 20–30 km al S de Freirina, 300–500 m.a.s.l., 9 September 1949, *W. Biese 2583* (SGO 104234); Quebrada Honda, falda occidental del Co. J. Soldado, 200–300 m.a.s.l., 4 November 1949, *W. Biese 3038* (SGO 96995); road to Aguada Tongoy; ca. 13 km SSW of Huasco, 28°35'06"S, 71°14'33"W, ca. 250 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra 8655* (F 2292784, SGO 158914); Mun. Freirina, 12 km S of Freirina on gravel road towards Torres de Labrar, Quebrada del Negro, 28°35'31"S, 71°06'22"W, 600 m.a.s.l., 23 October 1997, *U. Eggli & B. E. Leuenberger 3020* (B, CONC 146116, SGO 146018); Huasco, 15 August 1966, *G. Montero O. 7568* (CONC 112943); Huasco, 14 August 1966, *G. Montero O. 7573* (CONC 31612); 2 km al poniente, Fundo El Pino, *Muñoz S. 1935* (SGO 108207); Quebrada del Pretil, 14 November 1956, *M. Ricardi & C. Marticorena 3947* (CONC 24063); Huasco, 10 km E, *S. Teillier 920* (SGO 141770). **Coquimbo:** Elqui, 3 km N of Caleta Hornos, 29°35'51"S, 71°15'02"W, 100 m.a.s.l., 19 December 2003, *M. Acosta & M. F. Leon 114* (K); Huasco, Aguada de Tongoy, 47.5 km NE of Vallenar, 28°32'24"S, 71°10'53"W, 200 m.a.s.l., 4 January 2002, *M. Acosta, M. F. Leon, & P. Leon-Lobos 029* (K); Cerca de La Higuera, 18 September 1958, *E. Bailey s.n.* (SGO 132732); La Rinconada, 17 September 1952, *E. Barros V. s.n.* (CONC 14026); Fray Jorge, 10 August 1972, *M. Bassano s.n.* (SGO 137635); road between La Serena and Vallenar, *K. Beckett, M. Cheese, & J. Watson 4053* (SGO 110101); Costa de Fray Jorge, 30 October 1963, 450 m.a.s.l., *F. Behn s.n.* (CONC 28593); La Serena, Pan de Azúcar, *A.L. Cabrera 11424* (CONC 24177, SGO 126652); Km 220, 29 October 1974, *D. Contreras & E. Caviedes 0109* (SGO 134441); El Palmar, 9 September 1974, *D. Contreras & E. Caviedes 0197* (SGO 134442); Pichidangui, October 1958, *O. Correa F. 50* (K); entrada de Fray Jorge, 2 km de Ruta 5, 30°36'17"S, 71°30'39"W, 250 m.a.s.l., 11 December 2004, *M. O. Dillon & G. Arancio 8689* (ULS); Choapa, ca. 3 km S of Huentelauquén along Pan-American Highway (5), 31°39'S, 71°34'W, 60 m.a.s.l., 29 November 1987, *M. O. Dillon & S. Teillier 4973* (F 1994556); Coquimbo, 200–300 ft, 25 September 1927, *C. Elliot 5* (E00130906, K); Elqui Valley, 25 September 1927, [3000–4000 ft], *C. Elliott 94* (E00130897, K); Coquimbo, sea-level, October, *C. Elliott 513* (K); Cerros de La Herradura, 12 September 1991, *C. Fernández & H. Niemeyer F. 91-118* (SGO 127488); Fray Jorge, 27 November 1951, *J. Fröden 233* (BM000941303); entre Vallenar y La Serena, 20 October 1961, *A. Garaventa H. 4290* (CONC 49155); Bosque de Fray Jorge, *A. Garaventa H. 4753* (CONC 50264); Termas de Socos, *A. Garaventa H. 5560* (CONC 48724); Cerrillos, September 1934, *C. Grandjot 250* (SGO 116574); Coquimbo, Jul–Aug 1856, *W. H. Harvey s.n.* (K); Ovalle–Cerrillos, 19 September 1952, *C. Hempel s.n.* (CONC 13252); Fray Jorge, 15 September 1947, *J. Ibáñez & G. Kuschel s.n.* (SGO 130627); Alcones, 28 September 1947, *C. Jiles 322* (CONC 31173), *C. Jiles 323* (CONC 36154); Llanos de La Laguna, 240 m.a.s.l., 9 August 1948, *C. Jiles 673* (CONC 36151); Serón, 1200 m.a.s.l., *C. Jiles 3167* (CONC 36155); Huanaqueros, 18 November 1961, *C. Jiles 4024* (CONC 36152); Llanos La Chimba, September 1962, *C. Jiles 4283* (CONC 36153); Llanos San Julian, September 1962, *C. Jiles 4283* (CONC 32949); Socos, 19 September 1963, *C. Jiles 4480* (CONC 32952); Hurtado–Huanpulla, 600 m.a.s.l., 22 March 1964, *C. Jiles 4511* (CONC 36146); Termas de Socos, 16 September 1966, *E. M. L. Kausel 5178* (SGO 137149); altiplanicie al S de Guayacán, 11 October 1966, *E. M. L. Kausel 5261* (SGO 137148); Quebrada del Teniente a Las Palmas, 12 October 1971, *E. M. L. Kausel 5447* (SGO 80554); entre Ovalle y Panamericana, 20 September 1967, *E. M. L. Kausel 5326* (SGO 137150); Fray Jorge, September 1965, *A. Kohler 181* (CONC 129547); Prov. Elqui, Ruta Norte 5, at 6 km N of Los Hornos, 29°35'51"S, 71°15'24"W, 100 m.a.s.l., 22 January 2003, *M. Leon & M. Narria 068* (K); Playa Las Estacas, entre Coquimbo y Guanaqueros, 10 m.a.s.l., 29 September 1984, *A. Landero 495* (CONC 115511); La Serena, 15 m.a.s.l., 18 September 1950, *U. Levi-Heins 760* (CONC 129557); Vicuña, Cuesta del Churqui, 700–800 m.a.s.l., *G. Looser 4304* (CONC 134576); Dept. Illapel, Carretera Panamericana, 13 km al Norte de Mantos de Hornillos, Quebrada Pajaritos, 31°01'S, 71°36'W, 280 m.a.s.l., *C. Marticorena, O. Matthei, y R. Rodríguez 361* (CONC 43024); carretera Panamericana, 3 km al sur de Huenteuquén, 16 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1406* (CONC 40703, F 1811788); Dept. La Serena, Cuesta de Buenos Aires, 350 m.a.s.l., 20 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1619* (CONC 40707, F 1811789); Dept. Ovalle, Camino de Carretera Panamericana a Termas de Socos, 1 km antes de las Termas, 17 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1443* (CONC 36786); Dept. La Serena, entre Mineral Los Cristales y La Laja, 1300 m.a.s.l., 22 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1740* (CONC 36149); Ovalle a Socos, Km 22, frente al Embalse Santa Rosa, 30°40'S, 70°23'W, 250 m.a.s.l., 11 February 1988, *C. Marticorena, T. Stuessy, & M. Baeza P. 9961* (CONC 136313); Canela Baja, 31°15'12"S, 71°36'45"W, 50–80 m.a.s.l., December 2008, *P. Medina 929* (SGO 162312); Pichidangui, 32°06'S, 71°33'W, 15 October 1957, *G. Monsalve s.n.* (SGO 132146); Al pie de un cerrito a 4.5 km entrada sur Choros Bajos desde Ruta 5, 29°20'S, 71°09'W, 220 m.a.s.l., 4 September 2000, *M. Muñoz S. 4071* (SGO 146627); Camino Ovalle a Ruta 5 pasado Valle El Encanto, 30°39'50"S, 71°25'16"W, 226 m.a.s.l., 11 October 2004, *M. Muñoz S. 4477* (SGO 152745); Prov. Limarí, Termas de Socos, 30°43'28"S, 71°29'26"W, 96 m.a.s.l., 11 October 2004, *M. Muñoz S. 4487* (SGO 152758), flor azul, *M. Muñoz S. 4488* (SGO 152759); Quebrada de El Jardín,

cerca de la Punta de Teatinos, 8 September 1942, *C. Muñoz P. & E. Pisano V. 3275* (SGO 118676); Huentelauquén, 13 September 1957, *C. Muñoz P. 4154* (SGO 119413); Al pié de la Cuesta El Mirador, *C. Muñoz P. 4294* (SGO 118486); Punta de Teatinos, September 1965, *C. Muñoz S. 3* (SGO 135260); Los Llanos de El Jardín, al N de La Serena, 25 October 1987, *M. Muñoz S. & I. Meza P. 2219* (SGO 137724); sur de Coquimbo, frente Camping Morrillos, *M. Muñoz S. 2473* (SGO 123051); 5 km antes de Pichasca desde Serón, 30°22'S, 70°49'W, 820 m.a.s.l., 2 September 2000, *M. Muñoz S. 4061* (SGO 146617); Llanos Compañia, 25 September 1915, *R. Ochoa s.n.* (CONC 129552); Dept. Illapel, Pichidangui, 32°09'S, 71°31'W, 15 m.a.s.l., 18 November 1960, *J. Petersen s.n.* (CONC 42600); Dept. Ovalle, Quebrada Teniente, 19 September 1952, *M. Ricardi 2071* (CONC 12726); Llanos de Barraza, 26 February 1965, *M. Ricardi 5267* (CONC 29989); Dept. Ovalle, camino de Socos a Ovalle, Llanos de Barraza, 12 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1235* (CONC 31171); Prov. Aconcagua. Pichidangui, 18 November 1960, *F. Schlegel 3169* (SGO 73295). Dept. Illapel, Pichidangui, 32°09'S, 71°31'W, 15 m.a.s.l., 18 November 1960, *J. Petersen s.n.* (CONC 42600); al Norte de los Vilos, 31°45'S, 71°30'W, 10 m.a.s.l., 21 September 1960, *F. Schlegel 2806* (CONC 42601); Fray Jorge, 30°40'S, 71°40'W, 300 m.a.s.l., September 1958, *F. Schlegel 4296* (CONC 42635), *F. Schlegel 4380* (CONC 42632); cerca de La Serena, 29°59'S, 71°20'W, 50 m.a.s.l., 22 April 1959, *F. Schlegel 5235* (CONC 42585); Coquimbo, Huentelauquén, 21 September 1963, *E. Sierra Ràfols s.n.* (SGO 75652, SGO 75653, SGO 75657); Coquimbo, Est. Fray Jorge o Ovalle, 20 August 1917, *C. J. F. Skottsberg & I. Skottsberg 1449* (F 737404). Vicinity of La Serena, 9 October 1914, *Mr. & Mrs. J. N. Rose 19264* (US 761811); Coquimbo, (1500 ft), 1 November 1981, *R. T. Schuh & N. I. Platnick 4* (US 2933403); La Serena, 25 September 1947, *B. Sparre 2737* (SGO 98306); Prov. Elqui, ca. 10 km S of Tongoy, 30°30'S, 71°30'W, 30 October 1991, *C. M. Taylor, C. von Bohlen, & A. Marticorena 10641* (CONC 128879, F 2116664); Caleta Manso, 9 km N Huentelauquén, 31 October 2000, *S. Teillier & C. Márquez 4849* (CONC 150887); Dep. Ovalle, Fray Jorge, 300 m.a.s.l., November 1925, *E. Werdermann 928* (BM000941304, B, CONC 56185, E00130905, F 568925, GH, K, US 1474336); La Serena, ca. 60 km N of La Serena, 1 November 1938, 100 m.a.s.l., *C. R. Worth & J. L. Morrison 16321* (GH, K); Huentelauquén, 17 September 1970, *O. Zöllner 4353* (CONC 129549); Guanaqueros, 100 m.a.s.l., 24 July 1973, *O. Zöllner 6908* (CONC 129545). **No exact locality**: CHILE, 1790, *T. Haenke s.n.* (Herb. Bohemiae 2195; F 1532704).

C5. ***Nolana rostrata*** (Lindl.) Miers ex Dunal, Prodr. 13: 14. 1852. Fig. 91–95.

Basionym: *Alona rostrata* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Atacama: near Vallenar, *T. Bridges 1326* (Holotype: CGE [05018]; Isotypes: BM [BM000941344], E [E00130877], K [K000532226], P [P00605863].

Digital image: Isotype of *Alona rostrata* from Royal Botanic Garden, Edinburgh [E00130877]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.e00130877

Homotypic synonyms: *Osteocarpus rostratus* (Lindl.) Phil., Gartenflora 33: 356, taf. 1175. 1884.

Heterotypic synonyms: *Alona fonckii* Phil., Anal. Univ. Chile 91: 36. 1895. TYPE: CHILE. Coquimbo: La Higuera, January 1886, *F. S. Fonck s.n.* (Holotype: SGO [55199, SGO000004336]; Isotype: BM [BM000941366]. *Alona obtusa* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Coquimbo: Coquimbo, *T. Bridges 1327* (Holotype: CGE, not seen; Isotypes: BM [BM000941343, BM000021196], E [E00130878], K [K000532264]; *Alona miersii* Phil. ex Wettst. (1891) Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 3. 1891; *Alona miersii* Phil., Anal. Univ. Chile 91: 35. 1895. TYPE: CHILE. Atacama: Chañarcillo, 24 September 1885, *R. A. Philippi s.n.* (Holotype: SGO [55188, SGO000004338]; Isotypes: K [K000532261, K000532263], US [US 1336132, US00121968]); *Alona phylicifolia* Phil. ex Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 3. 1891. *Alona phylicifolia* Phil., Anal. Univ. Chile 91: 36. 1895. TYPE: CHILE. Atacama: Caldera, September1879, *P. Ortega s.n.* (Holotype: SGO [55191]); *Osteocarpus lepidophyllus* Phil., Anal. Univ. Chile 91: 42. 1895. TYPE: CHILE. Atacama: Caldera, September 1885, *F. Philippi s.n.* (Holotype: SGO [055128]); *Nolana lepidophylla* (Phil.) I.M. Johnst., Contr. Gray Herb. 85: 103. 1929; *Osteocarpus brevifolius* Phil., Gartenflora 33: 356. 1884. TYPE: CHILE. Atacama: Atacama, *R. A. Philippi s.n.* (SGO [42638, SGO000004375]); *Rayera teretifolia* Gaudich., Bot. Voyage Bonite, Atlas tab. 108. 1851–1852. No type designated.

Shrubs, 40–60(–150) cm tall, stems branched, erect to prostrate, pubescent with capitate-glandular trichomes, viscid. *Leaves* alternate, blades linear, 5–20 mm long, 1–2 mm wide, terete, pubescent with capitate-glandular trichomes, viscid. *Inflorescence* of terminal and axillary flowers, buds pyriform, pedicels 1–4(–10) mm long. *Flowers* 5-merous; calyces tubular to campanulate, 8–13 mm long, bilabiate, viscid, 5-dentate, teeth subulate, unequal; corollas infundibularis, regular, 25–30(–45) mm long, limb 40–45 mm wide, blue to violet, center white, rarely completely white, tube 5–7 mm; stamens unequal, longer ca. 15 mm long, shorter ca. 13 mm long; filaments widened and pubescent at the base; nectary disc crateriform, margins sinuous; style ca. 20 mm long, terminal, bilobed. *Mericarps* (5–)7–8, rounded, 4–6 mm in diam.; seeds 2–7 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *rostratus*, provided with a long beak, and refers to the prolonged apices on the flower buds.

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 800–1200 m.a.s.l. It is recorded from open environments with sandy soils and mixed shrubs (Fig. 91); Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

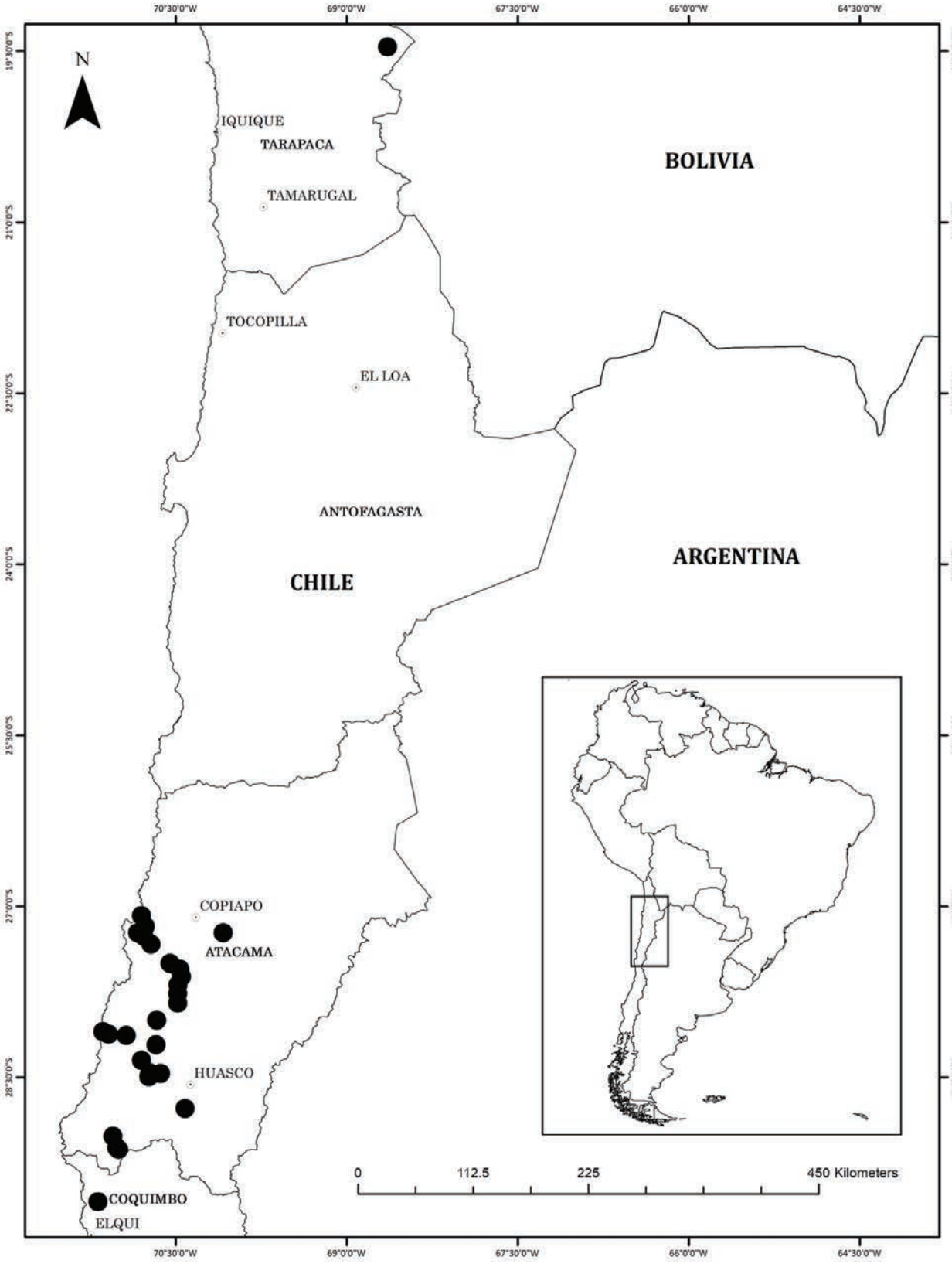


FIGURE 91. Distribution of *Nolana rostrata* (Lindl.) Miers ex Dunal.

Illustration: Fig. 92. Illustration of *Nolana rostrata* as *Rayera teretifolia*, Plate 108. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana rostrata is a showy species, typically an erect shrub up to one meter tall, that is much-branched from the base (Fig. 93A, Fig. 95C). In the region of Totoral and Carrizal Bajo, individuals have spreading, prostrate stems (Fig. 93B). The flowers exhibit actinomorphic calyces with two to three lobes on one side (Fig. 94A) and one or two lobes on the opposite side (Fig. 94B). The flowers are blue with a clear white proximal portion in the throat (Fig. 94C) and attract pollinators of various types. The maturing mericarps display the zygomorphic calyx all forced to one side (Fig. 95A). The leaves are sticky or resinous (Fig. 95B) and identical to those in *Nolana filifolia* from farther south. The roots are woody (Fig. 95C).

The prostrate forms of *Nolana rostrata* have been confused with *N. filifolia*; however, the calyces and mericarps serve to distinguish these taxa. Initially, several sheets were annotated as *N. filifolia* based upon the similarity of its leaves (e.g., *M. O. Dillon 9165*; *M. O. Dillon & M. Finger C. 8663; U. Eggli & B. E. Leuenberger 2594*; *F. Luebert & C. Becker 2900,* and *E. Pisano V. & R. Bravo F. 796*). These unique populations are here considered within the variation of *N. rostrata* but should be investigated in detail with marker data.

Though considered conspecific with *Nolana carnosa* by Mesa-M. (1981), *N. rostrata* is distinguished by its more linear leaf blades that are not expanded at the base, shorter pedicels, and its blue corollas. *N. carnosa* is restricted to more near-ocean habitats; however, it has been observed growing in complete sympatry with *N. rostrata* in the vicinity of Bahía Inglesa (cf. *Dillon 9133* and *9134*).

Osteocarpus lepidophyllus Phil. was transferred to *Nolana* by Johnston (1929: 103), who stated that he accepted it in *Nolana* with its lobed fruit breaking apart at maturity forming 3–10 mericarps. *In situ* these mericarps are uniseriate and broadly joined together ventrally. He also mentioned other synonyms, *Alona* Lindl. (1844), *Rayera* Gaudich. (1842–1846), *Velpeaulia* Gaudich. (1842) and *Osteocarpus* Phil.

Philippi prematurely distributed duplicates to Berlin of several new *Nolana* species, and his herbarium names, *Alona miersii* Phil. and *A. phylicifolia* Phil. were published by Wettstein (1891). These collections were subsequently fully described by Philippi (1895).

Several collections with unusual distributions from far outside its natural range require further investigation. Two 1968 collections by F. Behn are attributed to Antofagasta, Quebrada Taltal, *F. Behn s.n.* (CONC 36140) and *F. Behn s.n.* (CONC 36141). Three collections by O. Zalensky in 1968, are attributed to Tarapacá, *O. Zalensky XV-836* (SGO 78527), *O. Zalensky XV-841a* (SGO 78528), and *O. Zalensky XV-849* (SGO 78529). These records in Tarapacá are well outside of the northern range and elevations for this species; it has been suggested that there are problems with these five collections concerning the legitimacy of the label data, or perhaps they are from cultivated plants (Sebastián Teillier, pers. comm.).

Additional specimens examined: CHILE. **Atacama**: Prov. Copiapo, Dept. Chañaral, carretera Panamericana, Quebrada Peralillo, 26°14'S, 70°25'W, 500 m.a.s.l., 6 October 1966, *C. Jiles 4945* (CONC 36808); Panamericana, 15 km N Vallenar, 28°27'43"S, 70°43'30"W, 640 m.a.s.l., 27 October 2002, *M. Ackermann 520* (B [B1000092813], CONC 157555, SGO 150995]); Dept. Copiapó, Cerros Hacienda Castilla, 28 October 1965, *F. Behn s.n.* (CONC 30859); Camino entre Copiapó y Vallenar, 650 m.a.s.l., 7 September 1991, *Ch. von Bohlen V. 1332* (SGO 133411; 50 km S de Copiapó, *Ch. von Bohlen V. s.n.* (SGO 163967); Carretera Panamericana, 30 km N de Vallenar, 17 September 1957, *A. Cabrera 12638* (K [2 sheets]); camino a Carrizal Bajo, 9 November 2002, *M. Chamy & M. Piovano 10* (SGO 150485); 23 km N of Vallenar, *O. F. Clarke 6-04* (CONC 158528); Vallenar, October 1927, *Bro. Claude-Joseph 5024* (US 1422137); ca. 40 km NW of Copiapó, ca. 32 km SSE of Caldera, 27°20'S, 70°43'W, ca. 200 m.a.s.l., 24 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5464* (F 2012171); road to Aguada Tongoy, ca. 9 km S of Huasco, 28°32'28"S, 71°10'54"W, 100 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8652B* (F 2292787, SGO 158917); ca. 5 km S of Caldera, immediately S of Bahía Inglesa en route to Puerto Viejo, ca. 67 m.a.s.l., 30 September 2010, 27°07'27"S, 70°48'56"W, *M. O. Dillon 9133* (CONC, SGO); south of Carrizal Bajo, 28°06'46"S, 71°09'15"W, 45 m.a.s.l., *M. O. Dillon 9165* (CONC, SGO); southern edge of Parque Nacional de Llanos de Challe, 28°19'15"S, 71°09'03"S, 26 October 2010, *M. O. Dillon 9168* (CONC, SGO); E of coastal road, W of Totoral at Junction of northern & southern entrances to Totoral, 27°52'10"S, 70°59'23"W, 108 m.a.s.l., 5 October 2011, *M. O. Dillon 9201* (CONC 179097, SGO); route to Carrizal Bajo, 27°51'41"S, 71°04'29"W, 125 m.a.s.l., 5 October 2011, *M. O. Dillon 9202* (CONC 179096; SGO); ca. 7 km SE of Carrizal Bajo, 28°07'21"S, 71°05'20"W, 150 m.a.s.l., 29 November 2004, *M. O. Dillon & M. Finger C. 8663* (SGO 158948); Quebrada Agua Chica, ca. 9 km N of Vallenar, 28°29'S, 70°44'W, 700 m.a.s.l., 2 December 1987, *M. O. Dillon & S. Teillier 5025* (CONC, E, F 1993952, GH, K, SGO, US 3470029); 2 km S of Aeropuerto Desierto de Atacama, ca. 22 km S of Caldera, 27°15'54"S, 70°46'48"W, 260 m.a.s.l., 27 October 2004, *M. O. Dillon & M. Finger C. 8611* (CONC 179090, SGO 158942); ca. 99 km S of Copiapó, ca. 50 km N of Vallenar, 28°12'52"S, 70°40'23"W, 500 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8615* (CONC 179083, SGO 158952); Mun. Huasco, 2 km E of Carrizal Bajo towards the Panamericana, 28°06'01"S, 71°08'23"W, 20 m.a.s.l., *U. Eggli & B. E. Leuenberger 2594* (B, CONC 132088, SGO 145806); 41 km S of Copiapó towards Vallenar, 27°41'22"S, 70°28'51"W, 650 m.a.s.l., 9 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2873* (B, CONC 138498, SGO 146034); 137 km S of Copiapó, 28°29'43"S, 70°44'08"W, 600 m.a.s.l., 9 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2876* (B [2 sheets],

FIGURE 92. Illustration of *Nolana rostrata* as *Rayera teretifolia*, Plate 108. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

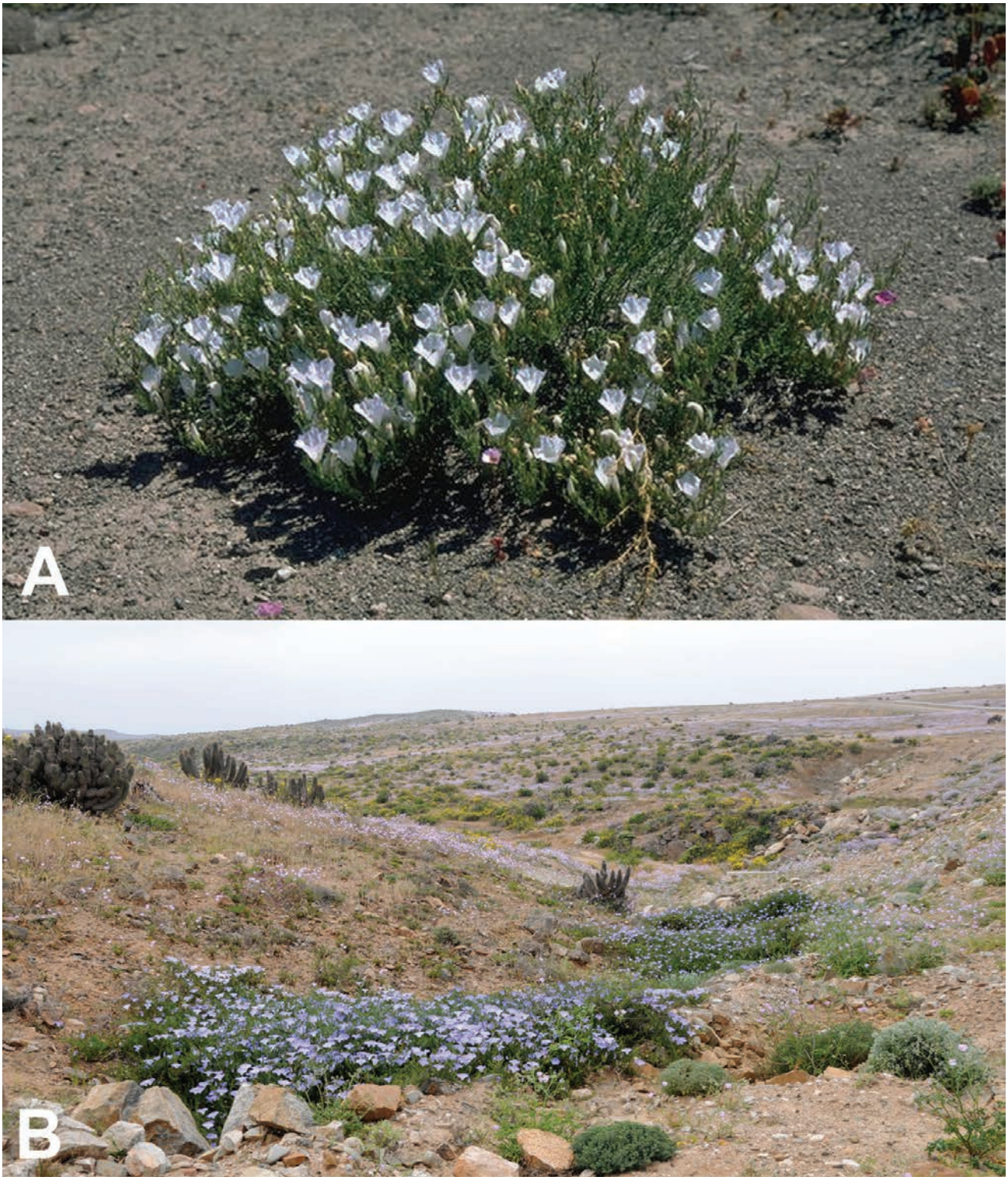


FIGURE 93. *Nolana rostrata*. Growth forms: **A**, Erect shrubs, branched from base; **B**, Spreading, prostrate stems in the region of Totoral and Carrizal Bajo, Chile.

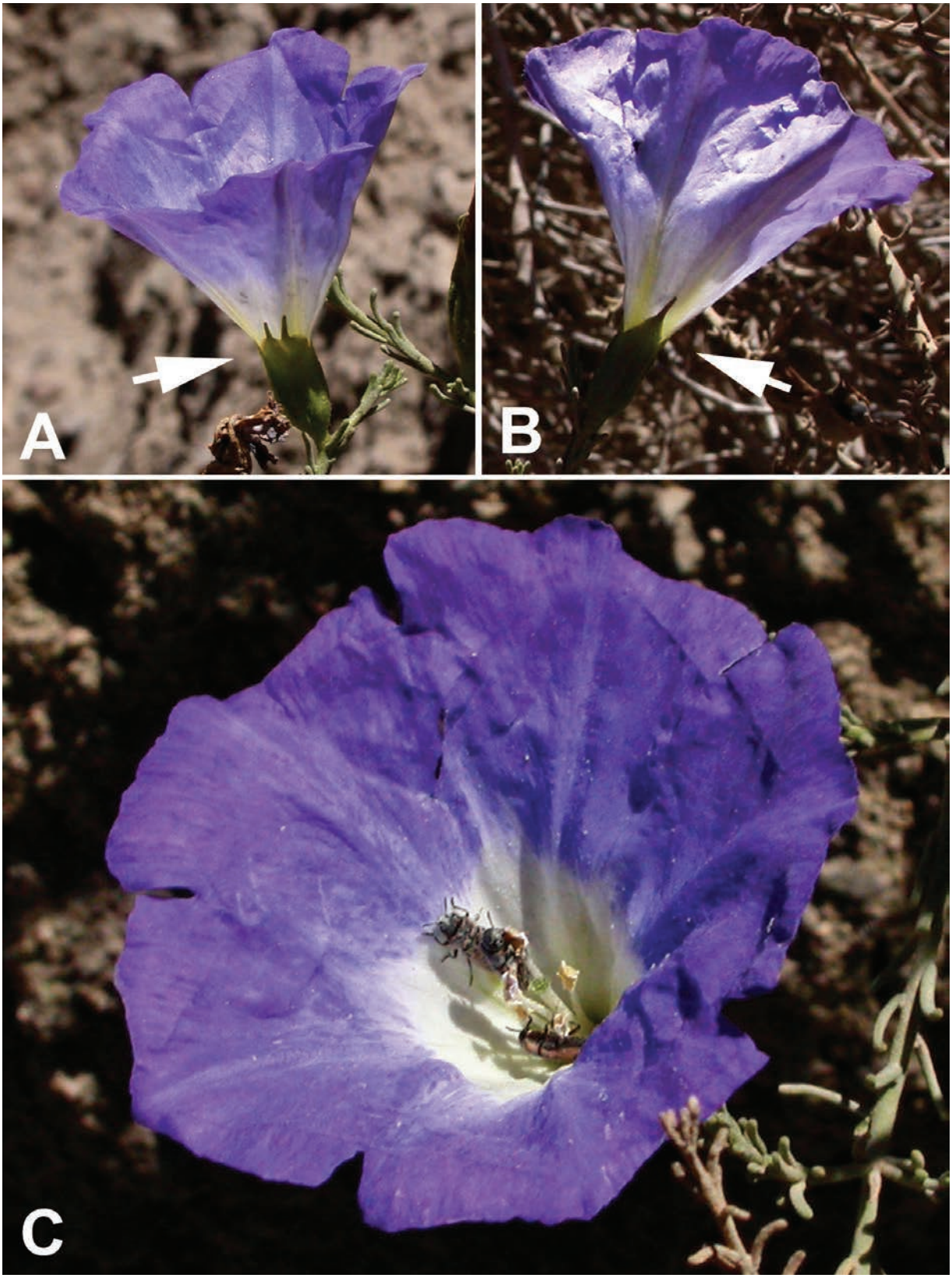


FIGURE 94. *Nolana rostrata*. **A–B**, Actinomorphic calyces with lobes on one side (see arrows) and one or two lobes on the opposite side; **C**, Blue corollas with clear white throat and pollinators.

FIGURE 95. *Nolana rostrata*. **A**, Maturing mericarps; **B**, Leaves are resinous and sticky; **C**, Roots woody and stems much branched from the base.

CONC 139500, SGO 146076); 8 km E of Alto del Carmen on gravel road towards El Transito and Conay, 28°46'38"S, 70°25'02"W, 880 m.a.s.l., 24 October 1997, *U. Eggli & B. E. Leuenberger 3031* (B, CONC 146115, SGO 145969); Quebrada El León, 26°57'S, 70°44'W, 9 October 2004, *M. T. Eyzaguirre 7* (SGO 167455); cruce Canto del Agua, Ruta 5 Norte, 28°19'39"S, 70°42'11"W, 530 m.a.s.l., 9 October 2004, *M. T. Eyzaguirre 45* (SGO 167485). Prov. Huasco, Cuesta Pajonales, ca. 10 km of Incaguasi along Pan Americana Hwy 5, 29°08'S, 71°00'W, 1030 m.a.s.l., 2 December 1987, *M. O. Dillon & S. Teillier 5006* (CONC, E, F 1993990, GH, SGO, US); ca. 11 km N of Vallenar, 28°28'S, 70°39'W, 600–620 m.a.s.l., 23 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5454* (CONC, E, F 2012180, GH, K, NY, SGO, US); 9 km S of Est. Chacritas, 580 m.a.s.l., 24 November 1991, *U. Eggli & B. E. Leuenberger 1744* (B, SGO 141274); Cerros Bandurrias, October 1888, *G. Geisse s.n.* (CONC 129564); Estancia Castilla, 17 September 1965, *G. Gleisner 60* (CONC 34542); Cuesta Cardón, 800 m.a.s.l., 25 October 1951, *C. Jiles 2079* (CONC 36139); sur de Copiapó, 19 September 1952, *C. Jiles 2186* (CONC 43007); Travesía, 19 September 1952, *C. Jiles 2187* (CONC 36147), *C. Jiles 2188* (CONC 36148); *C. Jiles 2223* (CONC 36150); Travesía Norte, 27°31'S, 70°26'W, 500 m.a.s.l., 6 October 1966, *C. Jiles 4934* (CONC 34663, CONC 102441); Travesía, 27°33'S, 70°28'W, 520 m.a.s.l., 5 November 1969, *C. Jiles 5278* (CONC 102353); Panamericana, 20 km S de Caldera, 19 September 1966, *E. M. L. Kausel 5088* (SGO 137154); Panamericana, Caldera, 20 km S, 19 September 1966, *E. M. L. Kausel 5089* (SGO 137153); Panamericana, 20 km S de Caldera, 19 September 1966, *E. M. L. Kausel 5090* (SGO 137156); Panamericana, ca. 36 km al N de Vallenar, cerca Chacritas, 18 September 1966, *E. M. L. Kausel 5098* (SGO 79441); Domeyko a Vallenar, 9 October 1971, *E. M. L. Kausel 5472* (SGO 80557); ca. Copiapó, 9 October 1971, *E. M. L. Kausel 5477* (SGO 80563); Copiapó, 9 October 1971, *E. M. L. Kausel 5478* (SGO 80560); Yerbas Buenas [cerca Carrizal], January 1872, *T. King s.n.* (SGO 75657); entre Vallenar y Copiapó, 15 September 1965, *A. Kohler 159* (CONC 129562); 4 km N of Vallenar, 550 m.a.s.l., 29 October 1990, *T. G. Lammers, C. M. Baeza P., & P. Peñailillo B. 7615* (CONC 113419, US 3222417); Huasco, Ruta Norte 5, 0.5 km N of Cuesta Pajonales and 107 km N of La Serena, 1280 m.a.s.l., 7 January 2003, *M. Leon & M. Narria 1147* (K); Huasco, 12.8 km NE of Árbol de Marañón, 19.8 km from Vallenar, 767 m.a.s.l., 8 January 2003, *M. Leon & M. Narria 061* (K); Camino entre Carrizal Bajo y Huasco, frente a La Herradura, 26°06'S, 71°09'W, 30 m.a.s.l., 19 October 2005, *F. Luebert & C. Becker 2900* (F 2290700, SGO 159446); Portezuelo Cardones, 27°28'S, 70°23'W, 800 m.a.s.l., 8 January 1973, *C. Marticorena, O. Matthei, & M. Quezada 592* (CONC 38722, F 1803539); camino de Almirante Latorre a La Serena, Km 2, 950 m.a.s.l., 18 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1536* (CONC 37016); camino de Copiapó a Caldera, Km 37, Cerca de Punta Picasso, 160 m.a.s.l., 24 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1855* (CONC 36142); Carretera Panamericana, entre Vallenar y Copiapó, 20 km al S de Copiapó, Llano Seco, 27°31'S, 70°26'W, 730 m.a.s.l., 6 February 1988, *C. Marticorena, T. Stuessy, & M. Baeza P. 9806* (CONC 107163); Carretera Panamericana, entre Copiapó y Vallenar, 10 km al S de Travesía, Llano Churque, 27°37'S, 70°27'W, 550 m.a.s.l., 10 February 1988, *C. Marticorena, T. Stuessy, & M. Baeza P. 9924* (CONC 136315); Estación Travesía a 24 km al S.O. de Copiapó, 710 m.a.s.l., 24 September 1941, *C. Muñoz P. & G. T. Johnson 1898* (SGO 112652), *1902* (SGO 112138); alrededores del Mineral de Chañarcillo, Copiapó camino de Bandurrias, 10 February 1944, *C. Muñoz P. 4010* (SGO 119740); Cuesta Pajonales, 27 October 1984, *M. Muñoz S. 2014* (SGO 108206); 1 km antes desvío a Algarrobal, Vallenar a Copiapó, 21 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1001* (SGO 108630); 5 km al N de camino de entrada a Carrizal Bajo, 26 October 1987, *M. Muñoz S. & I. Meza P. 2228* (SGO 137723); Totoral, 5 km por el camino hacia la mina, 29 October 1987, *M. Muñoz S. & I. Meza P. 2347* (SGO 137722); Llanos de Llampos, 27°14'S, 70°05'W, 29 October 1991, 1300 m.a.s.l., *M. Muñoz S., S. Teillier, & I. Meza P. 2720* (SGO 126138); Vallenar a Carrizal Bajo, 28°21'S, 70°48'W, 2 November 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2885* (SGO 126137); camino a Carrizal Bajo, Km 50, 28°08'S, 70°56'W, 2 November 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2940* (SGO 126136); Llano Seco, ca. 20 km S of Copiapó, 5 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274057); Punta de Vacas, ca. 70 km N of Copiapó, 2 November 1991, *M. Ono, N. Ohga, & T. Masuzawa s.n.* (MAK 274947); Caldera, (1885), *F. Philippi s.n.* [1904] (BM000941342); Chañarcillo, September 1885, *R. A. Philippi s.n.* (SGO 55193); Quebrada La Gertrudis, entre Totoral y Puerto Viejo, 350 m.a.s.l., 25 November 1941, *E. Pisano V. & R. Bravo F. 822* (CONC 144443, SGO 156622); Quebrada de Totoral (Boquerones), 160–180 m.a.s.l., 24 November 1941, *E. Pisano V. & R. Bravo F. 796* (CONC 144457, SGO 156606); Quebrada La Gertrudis, entre Totoral y Puerto Viejo, 25 November 1941, *E. Pisano V. & R. Bravo F. 822* (CONC 144443); Hacienda La Compañia, al S de Vallenar, 420 m.a.s.l., 9 December 1941, *E. Pisano V. & R. Bravo F. 961* (SGO 156691); Caldera–Copiapó, 12 November 1987, *K. H. Rechinger & W. Rechinger 63624* (B), *63625* (B); ca. 50 km antes de Copiapó, camino Vallenar–Copiapó, 25 September 1952, *M. Ricardi 2223* (CONC 12878); Sur de Incahuasi, camino Vallenar–Serena, 16 February 1968, *R. Ricardi 5549* (CONC 36145); Travesía, 7 November 1956, *M. Ricardi & C. Marticorena 3798* (CONC 23926); Barros Luco, 8 November 1956, *M. Ricardi & C. Marticorena 3809/197* (CONC 23937, F 2048635); Barros Luco, 8 November 1956, *M. Ricardi & C. Marticorena 3820* (CONC 23947); Vallenar, Quebrada a 10 km al sur, camino a La Serena, 12 November 1956, *M. Ricardi & C. Marticorena 3903* (CONC 24022); 30 km al norte de Vallenar, 17 September 1957, *M. Ricardi & C. Marticorena 4389/744* (CONC 24936); 5 km al sur de Vallenar, 9 October 1958, *M. Ricardi & C. Marticorena 4848/1233* (CONC 25642); Entre Vallenar y Copiapó, 30 January 1963, *M. Ricardi, C. Marticorena, &*

O. Matthei 506 (CONC 27972); Carretera Panamericana, 19 km al norte de Copiapó, 22 February 1969, *M. Ricardi & O. Parra 93* (CONC 33004); Prov. Elqui, Cuesta Pajonales, 29°08'S, 70°59'W, 1150 m.a.s.l., 31 October 1991, *R. Rodríguez 2777* (CONC 125848); Carretera Panamericana, frente a Punta de Díaz, 19 February 1970, *R. Rodríguez y P. Rivera 58* (CONC 34933); Huasco, 28°23'41"S, 70°21'23"W, 1639 m.a.s.l., 1 December 2005, *M. Rosas 3163* (K); Vallenar, camino Mina Algarrobo, *J. Saá L. s.n.* (CONC 129548); La Serena–Vallenar, 800 m.a.s.l., November 1975, *G. Schilling R. s.n.* (CONC 129546); Valle Carrizal Bajo, 11.5 km de Caleta Exp., 75 m.a.s.l., 12 November 1985, *F. Schlegel 7999* (CONC 115643, SGO 105232); 5.8 km N of Domeyko, *B. B. Simpson 29-XI-04-3* (CONC 160018); Panamericana, 70 km N of Vallenar, 28°00'S, 70°40'W, 500 m.a.s.l., 8 April 1994, *C. M. Taylor, & A. Pool 11526* (CONC 143606, SGO 147788); Panamericana, Km 750, cruce Chañarcillo, 27°51'S, 70°29'W, 7 October 1987, *S. Teillier 860* (CONC 143322, SGO 141772); Vallenar, Cuesta de Pajonales, 29°07'S, 71°01'W, 10 September 1987, *S. Teillier 1025* (CONC 143321, SGO 141773); El Bronce, 1850 m.a.s.l., *S. Teillier & J. Delaunoy 5561* (CONC 166851); Alto del Carmen, 800 m.a.s.l., November 1923, *E. Werdermann 150* (BM000941347, CONC 129563, E00130805, F 549274, K); Tierra Amarilla, 1000 m.a.s.l., September 1924, *E. Werdermann 412* (BM000941346, CONC 109129, E00130896, F 565234, K); ca. 30 km E of Vallenar, San Felix road, 24 October 1938, 200 m.a.s.l., *C. R. Worth & J. L. Morrison 16218* (K, US 3634878); 40 km al norte de Vallenar, *O. Zöllner 1705* (CONC 129551); Bandurrias, 850 m.a.s.l., 25 September 1976, *O. Zöllner 9300* (CONC 129550); Bandurrias, 22 September 1977, *O. Zöllner 9803* (CONC 129565); Travesía, 21 September 1969, *C. Zuleta s.n.* (CONC 129566). **Coquimbo**: 26 km N of Portezuelo Tres Cruces, 40 km N of Hurtado, 30°04'48"S, 70°43'55"W, 1 November 1977, *T. Ayers, A. Muñoz M., & R. Scott. 1544* (SGO 143825); Dept. Elqui, Cerca de Vicuña, 19 September 1963, *G. Gleisner 125* (CONC 43005); near Cuesta de Pajonales, 26 October 1971, *K. Beckett, M. Cheese, & J. Watson 4159* (SGO 94954); Mineral Los Plomos, 16 km de Tres Cruces, 900–1200 m.a.s.l., 3 November 1949, *W. Biese 2928* (SGO 674907); La Serena, October 1927, *Bro. Claude-Joseph 5021* (US 1422134), *5033* (US 1422144); Pajonales, 29°10'S, 71°03'W, 27 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2681* (SGO 126135); La Serena, September 1952, 60 n, *L. E. Peña s.n.* (CONC 129561); El Tofo, camino a Crus Grande, 10 October 1958, *M. Ricardi & C. Marticorena 4926/1311* (CONC 25721); Quebrada Marqueza, *E. J. Tepe, A. Marticorena, & P. B. Pelser 1798* (CONC 167842); Quebrada San Carlos, 5 km al oeste de Vicuña, a los pies del Cerro Tololo, Valle del Rio Elqui, 30 December 1974, 600–800 m.a.s.l., *C. Villagrán, R. Torres, & R. Osorio s.n.* (SGO 123683). **No exact locality**: CHILE, north Chile, *W. Lobb 433* (K); December 1873, *E. C. Reed s.n.* (K000532262); *F. Philippi s.n.* [1904] (BM000941348); Caldera, September 1900, *F. Philippi s.n.* [1904] (BM000941345).

C6. ***Nolana stenophylla*** I.M. Johnst., Contrib. Gray Herb. 85: 103. 1929. TYPE: CHILE. Antofagasta: Dept. Taltal, on the rocky and bushy alluvial fan at the mouth of the quebrada just below Aguada del Cardon, 30 November 1925, *I. M. Johnston 5272* (Holotype: GH [00282344]). Fig. 96–99.

Digital image: Holotype of *Nolana stenophylla* from Harvard University Herbaria, Cambridge [GH00282344]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282344

Homotypic synonym: *Alona stenophylla* (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 22. 1936.

Lax *shrubs*, 15–30(–50) cm tall, 1–2 m in diam., hispid to villous with abundant multicellular, capitate-glandular trichomes; stems 10–20 cm long, 1.5–2.5 mm wide, decumbent, internodes 1–3 cm long, densely leafy. *Leaves* alternate to fasciculate, blades linear, 15–30 mm long, 1.3–2.3 mm wide, concolorous, apically rotund, basally attenuate, densely pubescent with capitate-glandular trichomes. *Inflorescence* of solitary flowers in leaf axils; pedicels 10–30 mm long, hispid, ascending, recurved in fruit. *Flowers* 5-merous; calyces cupulate, 15–20 mm long, enlarged in fruit, tube ca. 6 mm long, 8–10 mm in diam., lobes lanceolate, acuminate; corollas infundibularis, regular to weakly zygomorphic, 28–35 mm long, limb 30–40 mm wide; stamens unequal, the longer ca. 7 mm long, the shorter ca. 4 mm; filaments glabrous; style terminal, ca. 1 cm long, nectary disc patelliform, margin sinuate. *Mericarps* 3(–5), uniformly 3 mature mericarps, unequal, the largest ca. 6 mm long, ca. 4 mm wide, umbonate, shiny; seeds 1–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *stenos*, narrow, and *-phyllus*, -leaved, and refers to the linear leaves typical for this species.

Distribution and Ecology: Chile, Regions of Antofagasta; 50–500(–950) m.a.s.l. It is recorded from rocky, alluvial fans in near-coast habitats (Fig. 96); Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana stenophylla is a prostrate, spreading shrub up to 2 m in diameter (Fig. 97A). Superficially, it resembles the sympatric *N. linearifolia*; both species have large, showy lavender or purple corollas (Fig. 97B, 98A) and linear, terete leaves (Fig. 98B). It is readily distinguished; *N. stenophylla* has equal calyx lobes (Fig. 99A), whereas *N. linearifolia* has deeply cut, unequal calyx lobes (Fig. 99A) and five, small, unfused mericarps. *Nolana stenophylla* invariably has three large, fused mericarps (Fig. 99B–D).

When Johnston described this species (Johnston 1929: 104), he made extensive comments and provided these insights: "This new species is probably most closely related to *N. gayana*, agreeing with that species in the form of its corolla and in its elongate leaves. The nutlets in *N. stenophylla*, however, are twice as large and are acuminate at the apex and the narrower more succulent leaves are very obscurely if at all revolute. The nutlets in the new species are very characteristic. They are simply parts of a disrupted 4- to 5-lobed fruit. The ventral half of the nutlet, by which it is affixed, is strongly convex or angled and after becoming detached is irregularly roughened. The back is prominently

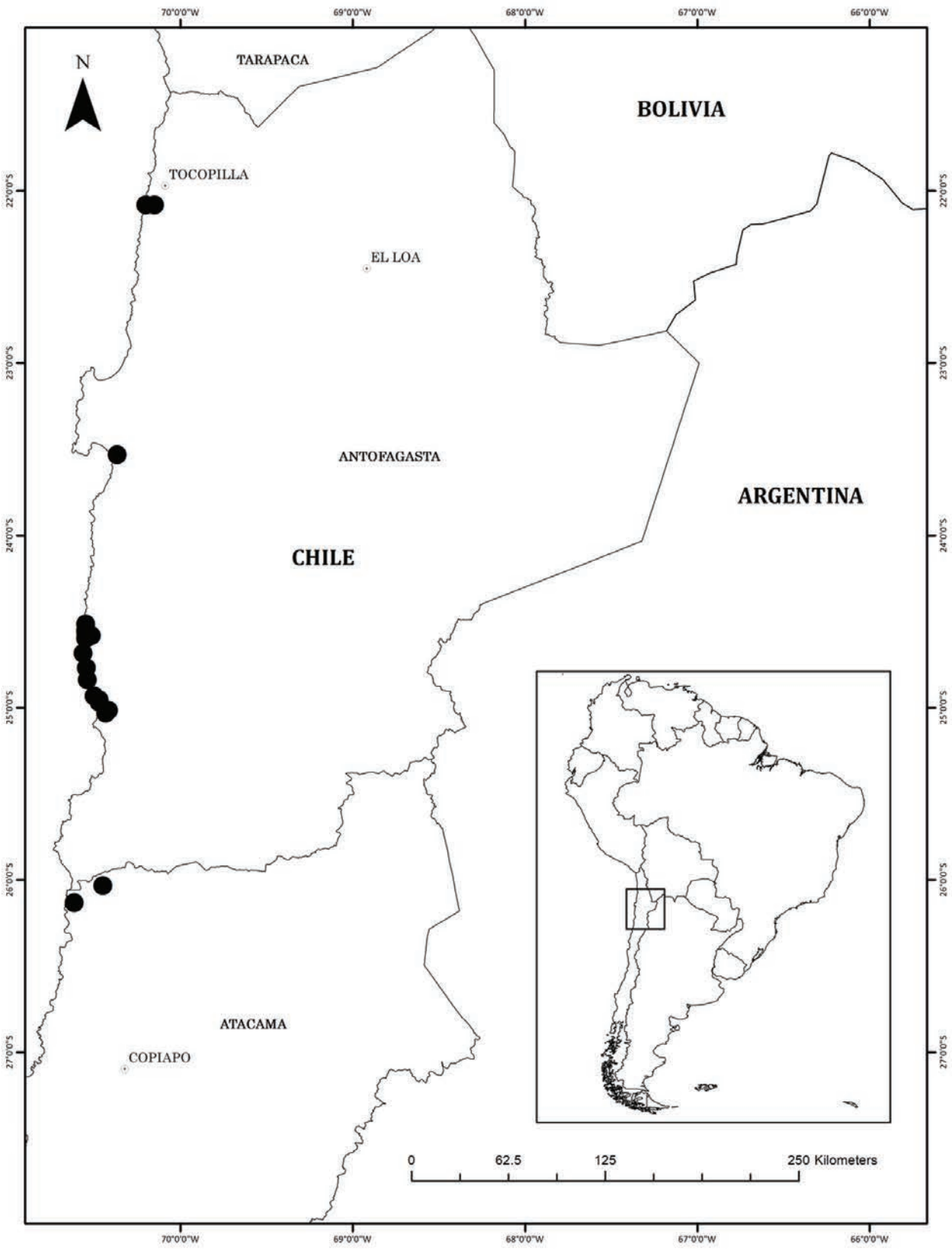


FIGURE 96. Distribution of *Nolana stenophylla* I.M. Johnst.

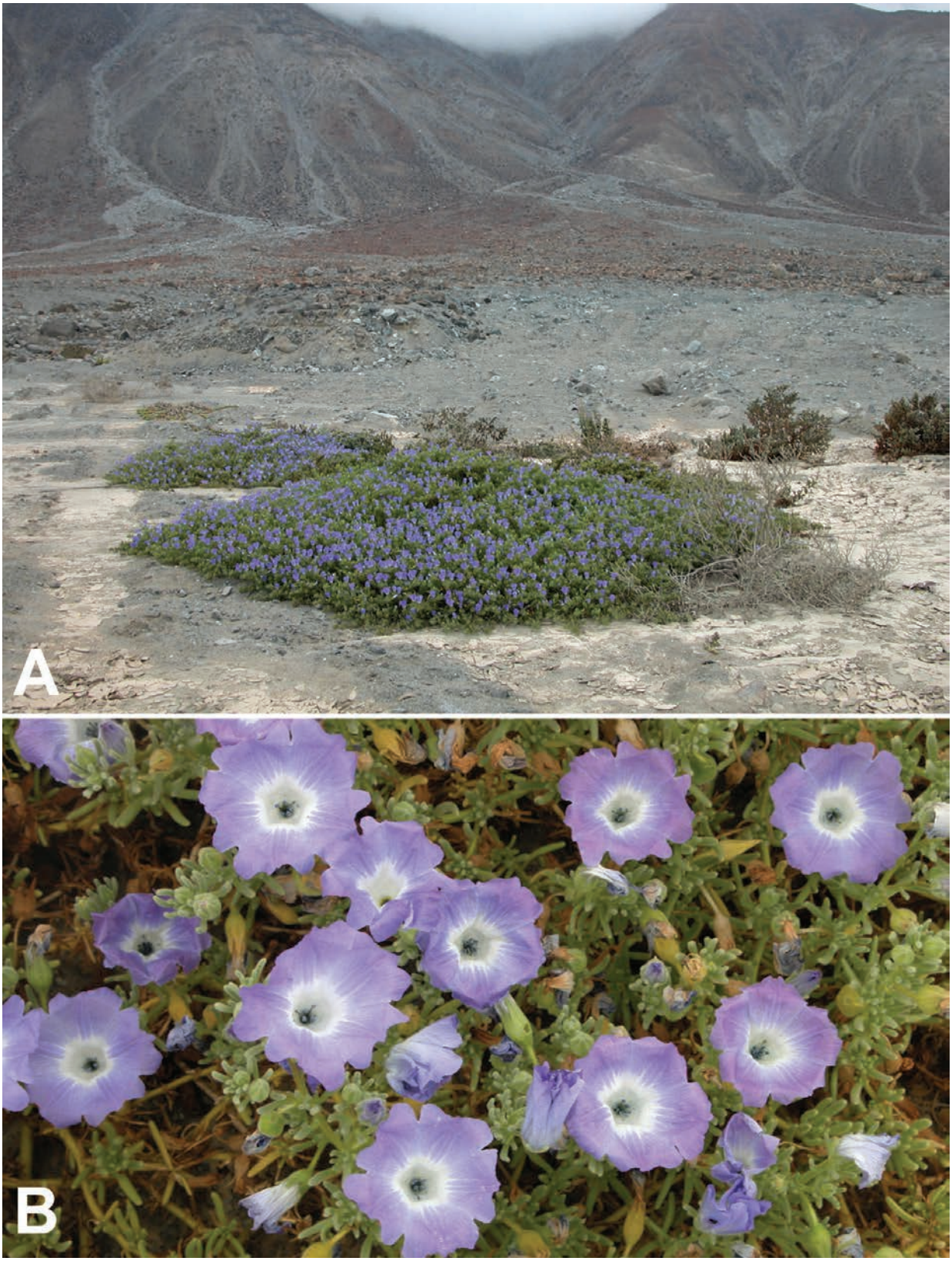


FIGURE 97. *Nolana stenophylla*. **A**, Prostrate, spreading shrubs; **B**, Showy lavender to purple corollas.

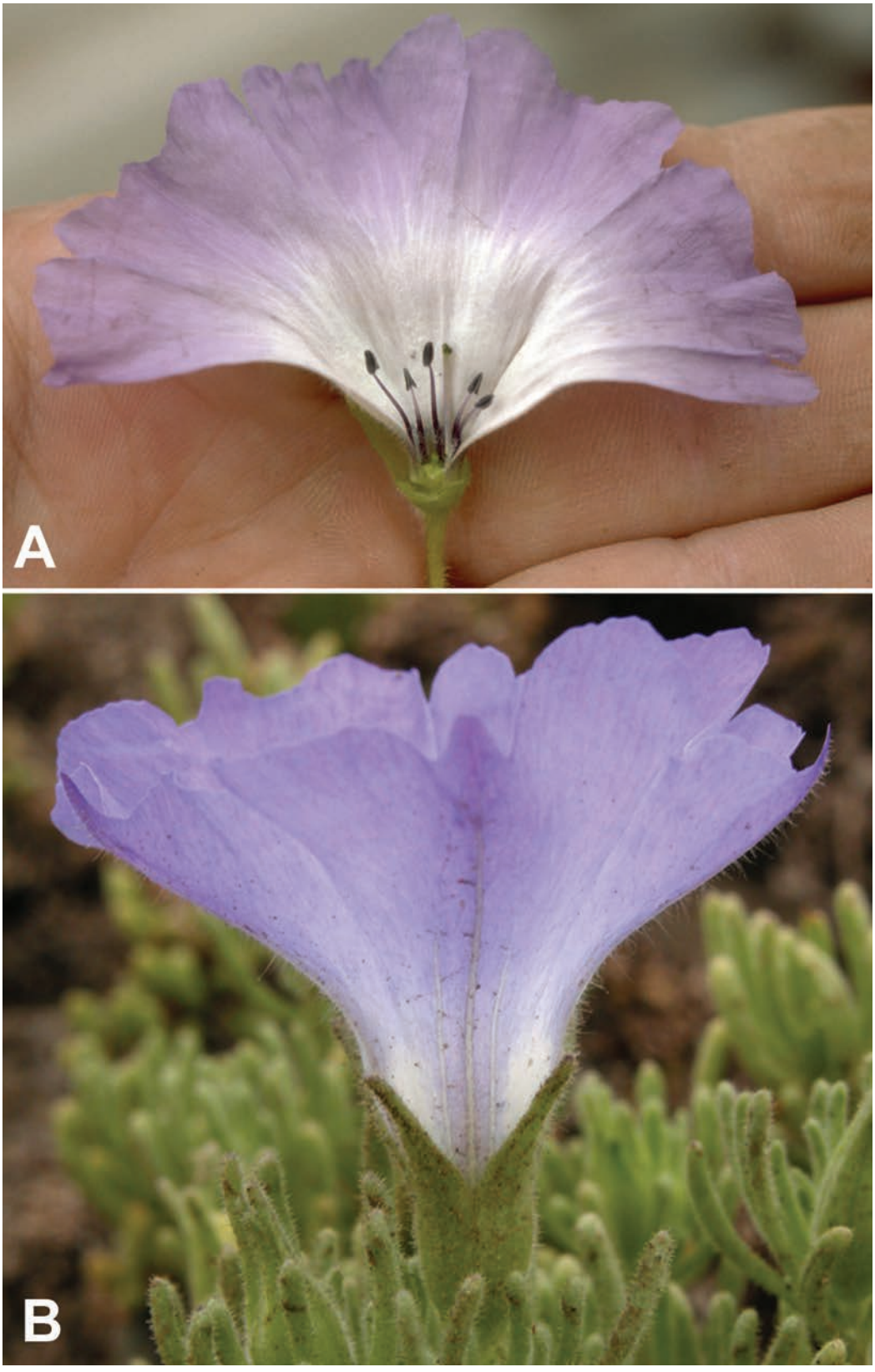


FIGURE 98. *Nolana stenophylla*. **A**, Dissected flower exposing unequal anthers and style; **B**, Lateral view of flower.

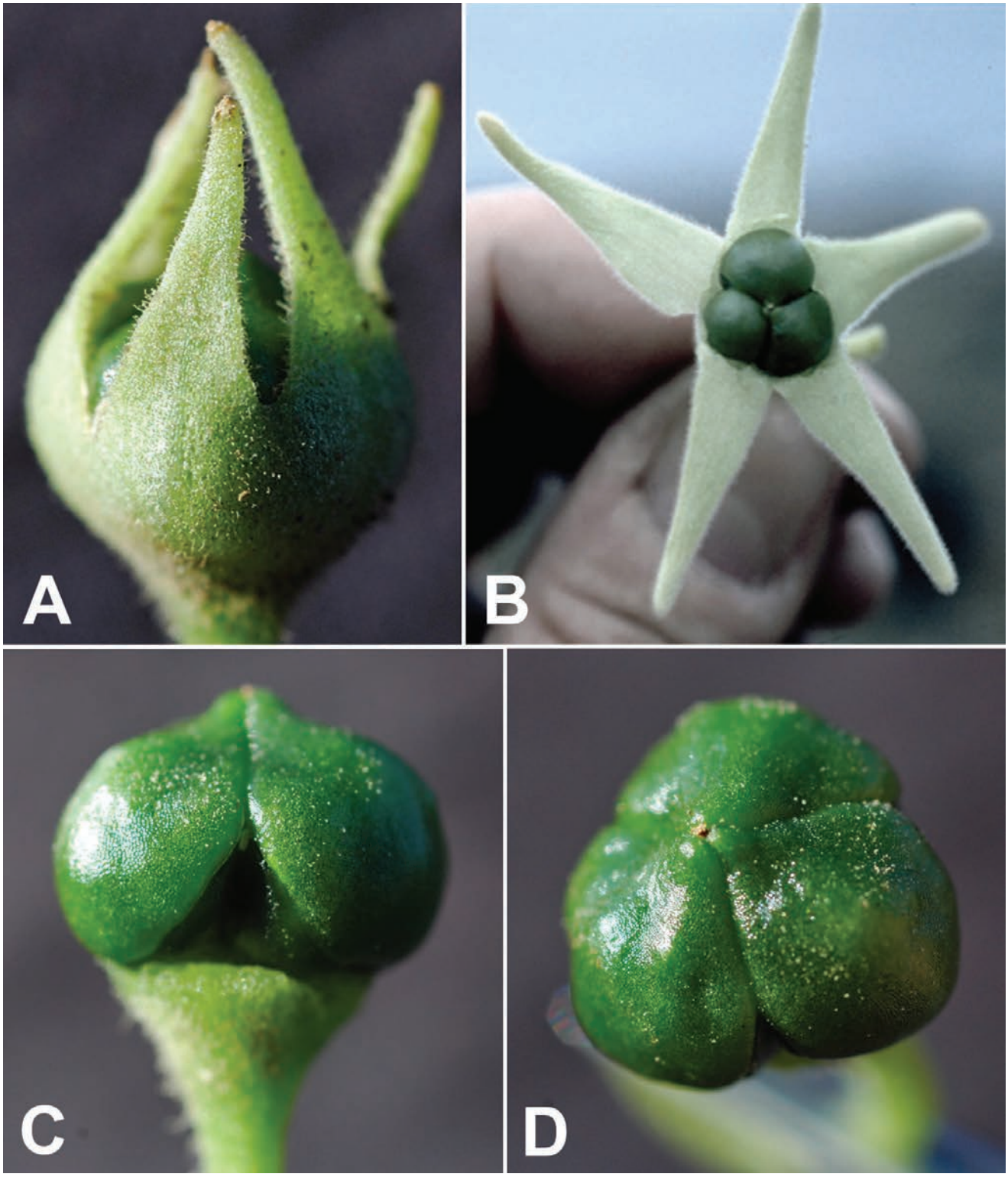


FIGURE 99. *Nolana stenophylla*. **A**, Calyx lobes all equal and cut nearly to the base; **B**, Three large, fused mericarps; **C**, Lateral view of gynoecium; **D**, Frontal view of fused mericarps and apical style.

umbonate and quite smooth. The tip of the nutlet is drawn up into a beak 1–2 mm long. The nutlets in *N. gayana* are affixed by a medioventral areola and are ellipsoid. The leaves, stems and calyces in the new species are rather abundantly glandular-villous."

The analysis by Dillon et al. (2009) placed *N. stenophylla* firmly within the clade including other taxa considered as *Alona* by Johnston. He initially described this species within *Nolana*, but by 1936, Johnston had changed his opinion and transferred *Nolana stenophylla* to *Alona*, commenting that it was a distinct species with its closest relative, perhaps, in *Alona coelestis*. Johnston stressed the importance of the apical style as opposed to the gynobasic style in *Nolana*. The DNA data suggested that *N. stenophylla* is most closely aligned with *N. balsamiflua*, also its nearest geographic neighbor, in a strongly supported clade that includes *N. carnosa*, *N. coelestis*, *N. filifolia*, and *N. rostrata*.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, cercanías de Paposo, 25°00'34"S, 70°27'57"W, 20 June 2015, *K. Bull H. 672* (SGO 166645); Quebrada Paposo, 950 m.a.s.l., 7 December 1987, *M. O. Dillon & S. Teillier 5117* (CONC, E, F 2010702, GH, SGO, US); near Quebrada Botija, 24°31'S, 70°34'W, 90–100 m.a.s.l., 4 October 1988, *M. O. Dillon & D. Dillon 5630* (CONC, E, F 2013660, GH, SGO); near Quebrada Botija, 24°31'S, 70°33'W, 18 December 1987, *M. O. Dillon 5351* (CONC, F 2010907, GH); vicinity of Miguel Díaz, 100–350 m.a.s.l., 15 December 1987, *M. O. Dillon & S. Teillier 5295* (CONC, E, F 2010893, GH, K, SGO, US 3470027); vicinity of Aguada Miguel Díaz, 24°36'S, 70°33'W, 250–450 m.a.s.l., 14 November 1988, *M. O. Dillon & D. Dillon 5909* (CONC, E, F 2144375, GH, SGO, US); Quebrada Rinconada, 25 October 1988, *M. O. Dillon, D. Dillon, & M. Villarroel O. 5743* (CONC, E, F 2045807, GH, K, SGO, US); aguada directly W of Quebrada de Iscuña, 20–30 m.a.s.l., 7 October 1988, *M. O. Dillon & D. Dillon 5662* (F 2014402); near Quebrada Cañas, 24°35'S, 70°31'W, ca. 100 m.a.s.l., 7 October 1988, *M. O. Dillon & D. Dillon 5663* (F 2014401); near Quebrada Cañas, 24°35'S, 70°31'W, ca. 100 m.a.s.l., 7 October 1988, *M. O. Dillon & D. Dillon 5664* (F 2014400); 5 km N of Paposo, 24°58'06"S, 70°28'18"W, 10 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8622* (CONC 179077, F 2329905, SGO 158721); 36 km N of Paposo ThermoElectric plant, in front of Quebrada Panul, 24°41'05"S, 70°33'52"W, 100 m.a.s.l., 1 November 2004, *M. O. Dillon & M. Finger C. 8637* (CONC 179078, F 2329907, HSP, SGO 158717); 27 km N of Paposo, 24°46'13"S, 70°32'42"W, 90 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8680* (CONC 179106, F 2292802, SGO 158925); 20 km N of Paposo, in front of Quebrada Médano, 24°50'21"S, 70°32'25"W, 50 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9064* (F 2292851, SGO 158728); Paposo, 25°03'S, 70°30'W, 10 October 1983, *M. Elgueta 30* (SGO 145506); Paposo, *C. Jiles 4964* (CONC 43019); Cachinales, 39 km S of Paposo, 25°09'S, 70°26'W, 150 m.a.s.l., 16 September 1991, *L. R. Landrum, A. Morales, & S. S. Landrum 7496* (F 2116639); Panul, 24°47'27"S, 70°32'33"W, 10–200 m.a.s.l., 7 October 2005, *F. Luebert & N. García 2679/1073* (F 2290682); Caleta Botija, 24°31'S, 70°34'W, 5 m.a.s.l., 7 October 2005, *A. Marticorena, M. Rosas, & P. Guerrero 704* (CONC 190471); Quebrada El Rincón, 24°57'17"S, 70°28'17"W, 90 m.a.s.l., 2 October 2005, *M. Muñoz S. 4673* (SGO 153702); Paposo, El Rincón, *M. Ricardi 2658* (CONC 14475); Miguel Diaz, 24°32'S 70°39'W, 6 November 2006, *N. Schulz 35* (SGO 154754); Sector "El Gaucho", *S. Teillier, P. Rundel, & P. García 2888* (SGO 129367); Sector "El Gaucho", 25°26'S, 70°35'W, 50 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2916* (F 2114615, SGO 129370). Prov. Tocopilla, Quebrada ca. 15 km E of Tocopilla, 25°05'S, 70°09'W, 520–550 m.a.s.l., 18 October 1988, *M. O. Dillon & D. Dillon 5709* (CONC, E, F 2014371, GH, SGO).

Clade D

D1. ***Nolana arenicola*** I.M. Johnst., Contrib. Gray Herb. 112: 29. 1936. TYPE: PERU. Tacna: Prov. Tacna, ca. 650 m.a.s.l., August 1925, *E. Werdermann 730* (Holotype: GH [GH00282362]; Isotypes: A [A00282362], B [B 100248499], BM [BM000021205, E [E00259359], F [F 564175], G [G00383939], K [K000532283], NY [NY312358], S [S04-2768], U [U0005236], UC [UC289204], US [US 1444766, US00121956, US 3312681, US00507017]). Fig. 100–101.

Digital image: Holotype of *Nolana arenicola* from Harvard University Herbaria, Cambridge [GH00282363]. https://s3.amazonaws.com/huhwebimages/EFE032CFA1CA49F/type/full/282363.jpg

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. subsp. *spathulata* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 136. 1981.

Robust annual *herbs*, 20–100 cm tall; root 12–16 cm long, 6–8 mm in diam., stems erect, 5–8 mm in diam., pubescent with capitate-glandular trichomes to glabrescent, branches 7–18 cm long, 1.2–3.0 mm in diam., conspicuously pubescent with curly, capitate-glandular trichomes. *Leaves* alternate, blade lanceolate-spathulate, 18–45 mm long, 6–18 mm wide, succulent, margins entire, apically acute, pubescent with capitate-glandular trichomes, basally cuneate to attenuate; petioles 7–16 mm long, densely pubescent with curly, capitate-glandular trichomes, sclerified. *Inflorescences* of solitary flowers; pedicels 7–12 mm long. *Flowers* 5-merous; calyces 11–15 mm long, 5.0–6.5 mm diam., campanulate, densely pubescent with capitate-glandular trichomes outside, base of lobes colored, inter-lobular space hyaline, lobes 4.5–6.0 mm long, 1–2 mm wide, apically spathulate, acute, zygomorphic; corollas rotate to briefly infundibularis, regular, 20–30 mm long, limb ca. 20 mm long, blue; stamens unequal, two 13–14 mm long, fused half the length, three 11–12 mm long, fused half the length; nectary ca. 6 mm wide; styles 7.5–9.5 long. *Mericarps* 6–10, 1-seriate, polyhedrons, joined laterally, 5 larger 5–6 mm long, 4–5 mm wide, black, shiny; seeds 3–6 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *arena*, pertaining to sand, and *-cola*, dweller or exists only, in this case, in sand.

Distribution and Ecology: Peru, Departments of Arequipa, Moquegua, and Tacna, ranging ca. 500 km; 200–900 m.a.s.l. One historical record from Arica, Chile;

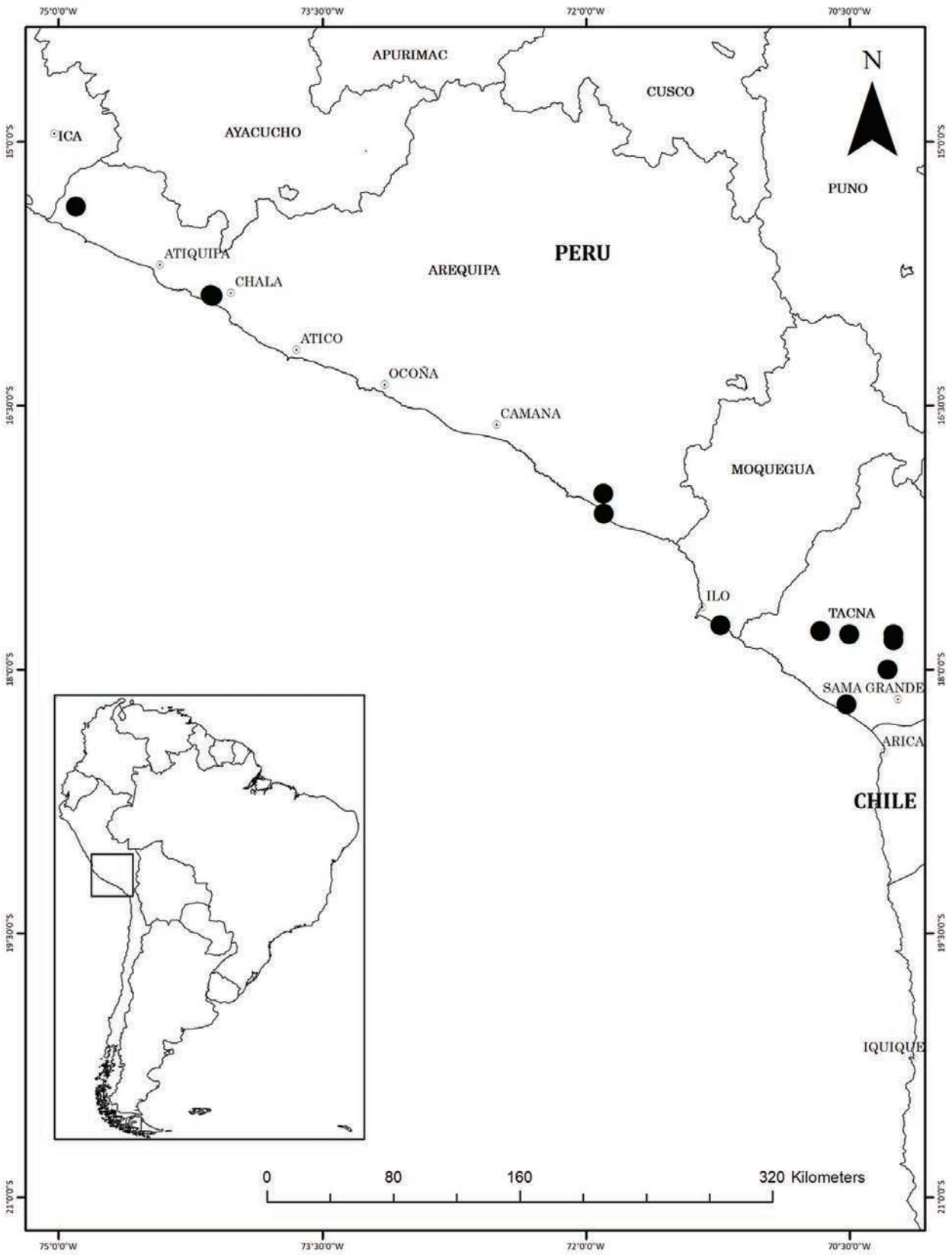


FIGURE 100. Distribution of *Nolana arenicola* I.M. Johnst.

FIGURE 101. *Nolana arenicola*. **A**, Erect herbs to one meter tall; **B**, Calyx lobes have expanded apices and showy blue corollas.

however, there are no modern collections of this species from northern Chile and its attribution to Arica may have been a labeling error of a collection from 1880. It is recorded from sandy soils in the coastal Peruvian Desert (Fig. 100).

Nolana arenicola is an erect herb reaching one meter tall when sufficient moisture is available (Fig. 101A). The calyx lobes have expanded apices and showy, blue corollas (Fig. 101B). It has been confused with its nearest congener, *N. spathulata*, with whom it shares a similar calyx with enlarged apices and five large mericarps. These two are differentiated with difficulty; *N. arenicola* generally possesses smaller leaves with rounded or angular bases, not cordate or reniform as in *N. spathulata*. The distribution of *N. arenicola* and *N. spathulata* are sympatric at various localities. Since the primary observable difference between *N. arenicola* and *N. spathulata* seems to be the leaf bases, more detailed studies will be necessary to confirm the taxonomic status of this species.

The historical record from 1880 for *Nolana arenicola* is cited as from Arica; however, no other collections from that area have been seen in this study. Fieldwork in the region also failed to find any populations of this taxon in Chile. The type collection of *Nolana arenicola*, *E. Werdermann 730*, was originally labeled *Nolana parvifolia* Phil., a name associated as a synonym of *N. humifusa*.

Additional specimens examined: CHILE. **Arica & Parinacota**: Arica, December 1880, *P. Ortega s.n.* (GH, SGO 30844, SGO 30845). PERU. **Arequipa**: Prov. Caravelí., Dist. Cháparra, Lomas de Cháparra, 15°52'34"S, 74°07'23"W, 287 m.a.s.l., 2 May 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7780* (HSP 8844); Lomas de Cháparra, 15°52'34"S, 74°07'23"W, 287 m.a.s.l., 2 May 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7781* (HSP 011902, HUT 60401). **Tacna**: Prov. Tacna, between Sama and Tacna, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11650* (K, USM 80812); Lomas de Sama Grande, Yarada, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11663* (K, USM 80813); Lomas de Tacna, 800–900 m.a.s.l., 4 October 1957, *R. Ferreyra 12524* (USM 80810); Lomas de Tacna, 800–900 m.a.s.l., 4 October 1957, *R. Ferreyra 12518* (USM 80811); Sama Grande, 60 km al N de Tacna, 700 m.a.s.l., 7 October 1957, *R. Ferreyra 12643* (USM 80814); cerca Tacna, 500–600 m.a.s.l., 5 October 1957, *R. Ferreyra 12527* (USM 80809); Tacna, cerca a Puquio, 800–900 m.a.s.l., 30 April 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19807* (USM 45685); Lomas de Sama, Km 1243–1244, 700–800 m.a.s.l., 1 May 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19811* (USM 75859); Lomas de Sama, 10 km N of Tamasiri, 200 m.a.s.l., 25 November 1957, *P. C. Hutchison 1847* (F 1555880, K, US 2406448, USM); on the Pan-Americana Hwy, ca. 25 km S of Camiara, 10 km N of Tamasiri, 630 m.a.s.l., 26 November 1964, *P. C. Hutchison & J.K. Wright 7156* (F 1641561, USM 80819); Tacna, September 1864, *R. Pearce s.n.* (BM000941265); Lomas de Tacna, 700 m.a.s.l., 29 November 1959, *C. Vargas C. 13052* (CUZ, USM 80818); Lomas de Tacna, 500–600 m.a.s.l., 28 October 1966, *C. Vargas C. 18064* (CUZ).

D2. ***Nolana chancoana*** M.O. Dillon & Quip., Arnaldoa 14(2): 177. 2007. TYPE: PERU. Arequipa: Prov. Caravelí. Dist. Atico. Lomas of Atico, prostrate herb; flowers lavender, 16°14'S, 73°39'W, 2 November 1983, *M. O. Dillon & D. Dillon 3836* (Holotype: HUSA; Isotypes: F [F 1950515], HAO, destroyed, E, GH, NY, SGO, TEX, US). Fig. 102–105. Digital image: Isotype of *Nolana chancoana* from The Field Museum, Chicago [F 1950515]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.f0361462f

Succulent, annual *herbs*; stems prostrate, 12–50 cm long, much-branched, glabrous. *Leaves* alternate, blades linear to oblanceolate, 10–40 mm long, 2.0–6.5 mm wide, glabrous, succulent, trigonus, apically acute to obtuse, bases cuneate; petioles 1–3 mm long. *Inflorescences* of solitary flowers in upper leaf axils, pedicels filiform, glabrous, 7–20 mm long. *Flowers* 5-merous; calyx suburceolate, 10–15 mm wide at anthesis, glabrous, tube 5–10 mm long; 5-lobed, lobes deltoid, equal, 6–10 mm long, 4–8 mm wide; corollas infundibularis, zygomorphic, 12–17 mm long, limb 15–20 mm wide, blue to violet, or whitish, internally deep purple, veined, glabrous, externally glabrous, 5-lobed, lobes acute, 5–8 mm long, 2–4 mm wide; stamens 5, filaments inserted on lower third of corolla, unequal, three 2–3 mm long, two 3.5–4.5 mm long, pilose at the bases; anther thecae 1.5–2.0 mm long, 1.0–1.5 mm wide; ovary glabrous, basal nectary, 5 carpels, style included, stigma capitate, green, ca. 1 mm in diam. *Mericarps* ca. 20, 3-seriate, 5, 8.5–9.0 mm in diam., 5, 2–4 mm in diam., 10, ca. 1 mm in diameter, maturing within the expanding calyx, surfaces wrinkled, black, shiny; seeds 1–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dra. Magda Chanco (b. 1941–), a professor of botany and curator at the Universidad Nacional Mayor de San Marcos and Museo de Historia Natural 'Javier Prado' in Lima, Peru. She has worked tirelessly for her institution with undergraduate education and participation in student mentoring.

Distribution and Ecology: Peru, Departments of Arequipa and Ayacucho, ranging ca. 400 km; 30–300(–450) m.a.s.l. It is recorded from sandy soils in near-ocean sites and, more rarely, from interior sites more distant from the coast (Fig. 103).

Nolana chancoana is a distinctive species with stems radiating from a central taproot (Fig. 104A–B). It has glabous, narrow, strap-shaped leaves, and showy flowers of various colors from deep blue to white, with internal purple veins or guides in the throat (Fig. 104C). The glabrous leaves and glabrous, globose calyces with triangular lobes are distinctive (Fig. 105A). The mericarps are irregularly shaped and mature from pale to black with brightly lustrous or nitid surfaces (Fig. 105B–C).

Ferreyra (1962) treated the material here referred to as *N. chancoana* under the epithet *N. coronata*; however, an examination of the type of the latter species showed it to be distinct from *N. chancoana*. *Nolana coronata* is readily distinguished by its larger, ovate to lanceolate leaves with obvious petioles and its consistent five angular mericarps with the interior faces connate in fruit.

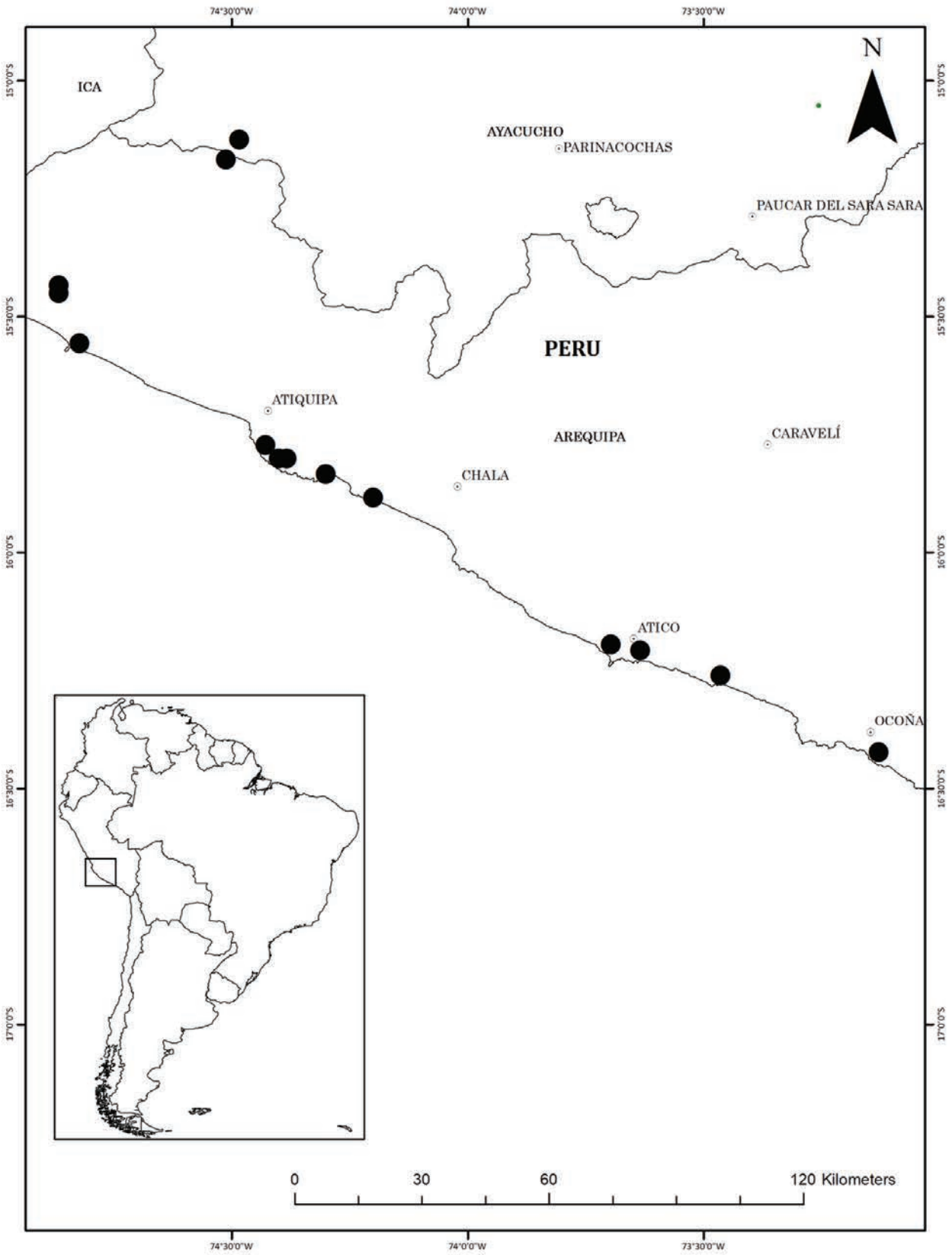


FIGURE 102. Distribution of *Nolana chancoana* M.O. Dillon & Quip.

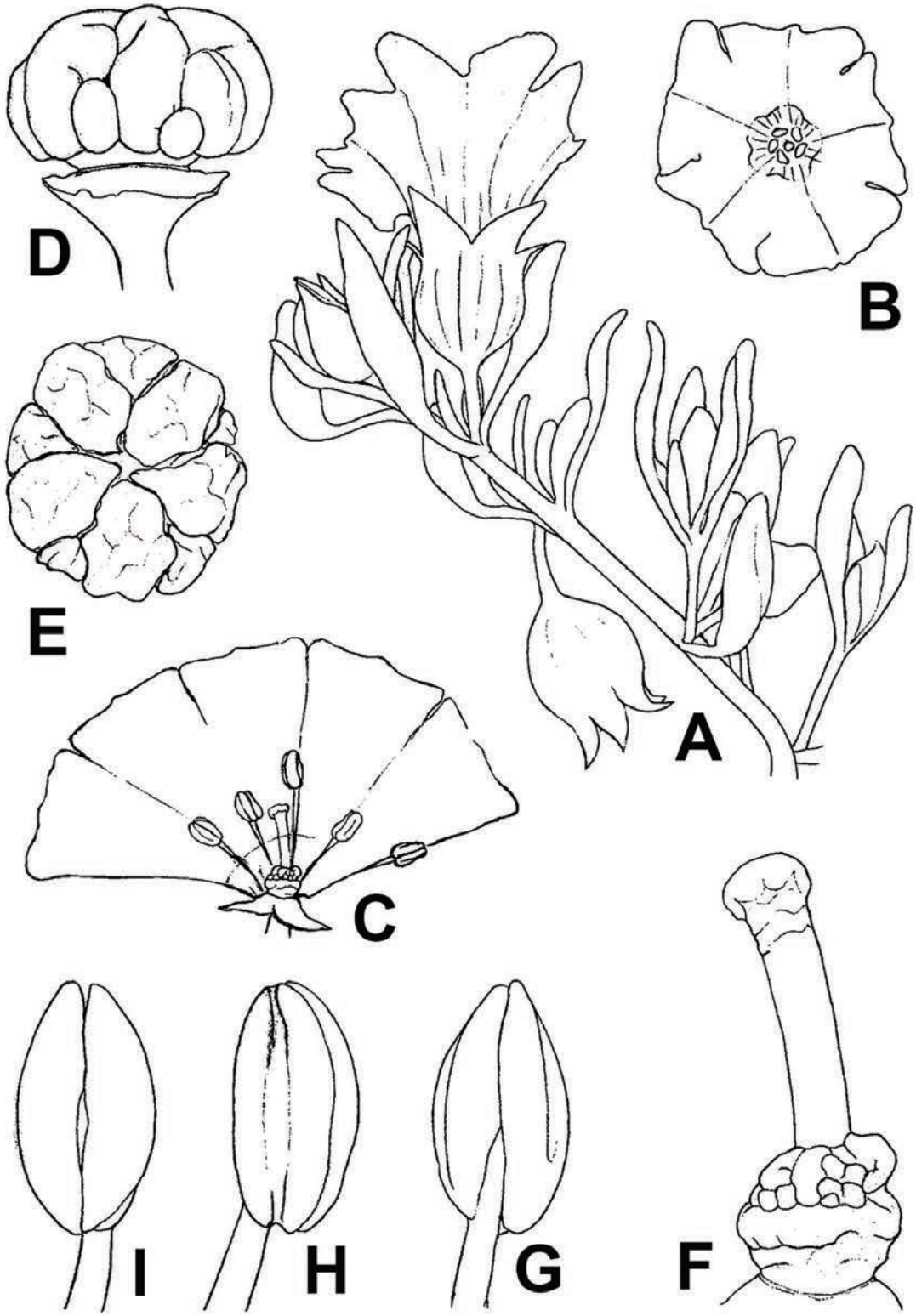


FIGURE 103. Illustration of *Nolana chancoana*. **A**, Flowering and fruiting branch; **B**, Frontal view of corolla; **C**, Dissected flower showing anthers, gynoecium, and stigma; **D**, Lateral view of gynoecium; **E**, Dorsal view of gynoecium; **F**, Gynoecium and stigma; **G**, Dorsal view of anther thecae; **H**, Lateral view of anther thecae; **I,** Ventral view of anther thecae. Drawn by Edgardo Ortiz Valencia.

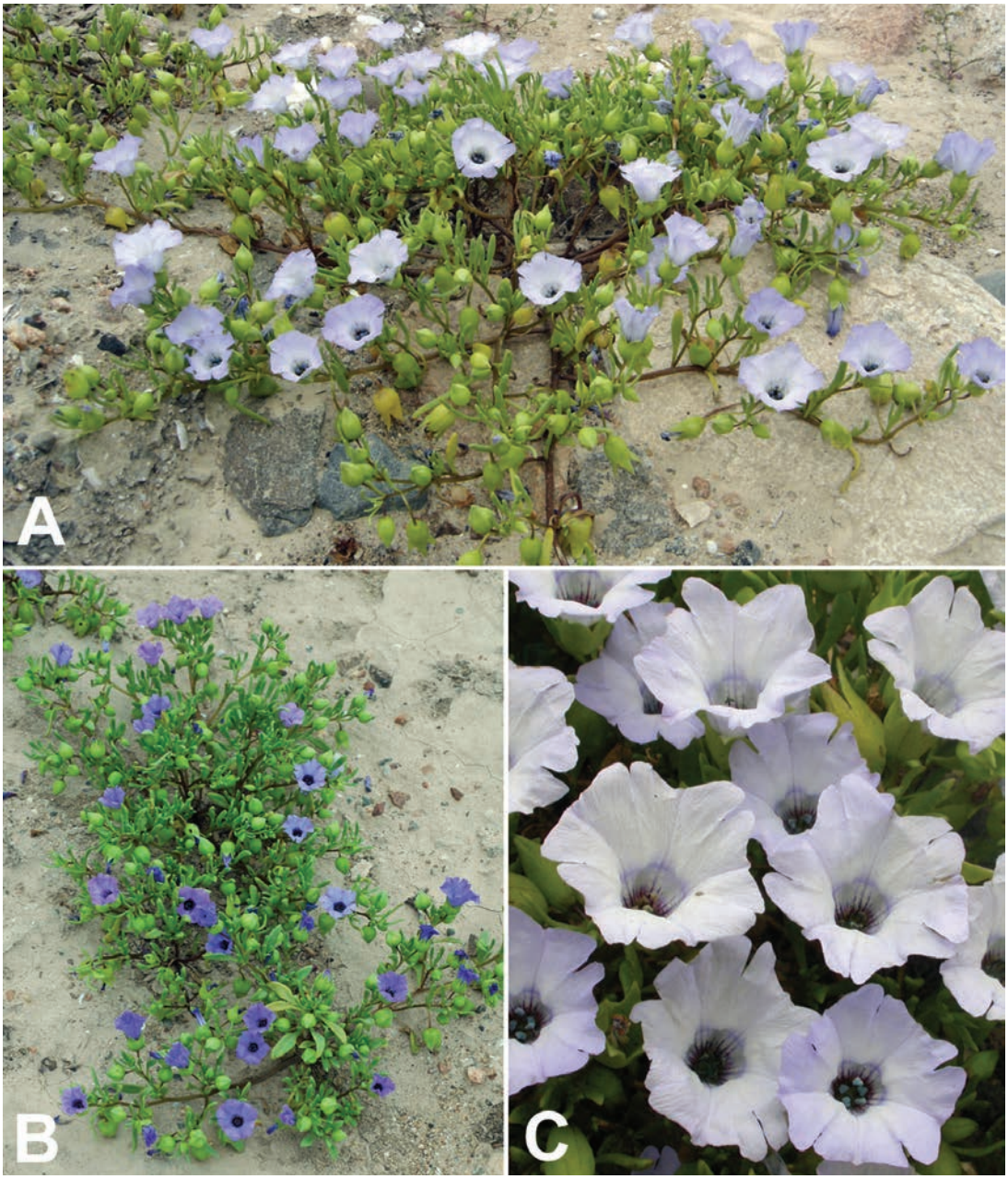


FIGURE 104. *Nolana chancoana*. **A–B**, stems radiating from a central taproot; **C**, Corollas with internal purple veins or guides in the throat.

With molecular marker data, *Nolana chancoana* was recovered in a clade that included other species with inflated, globose calyces, including *N. inflata* and *N. weissiana*. These two species are readily distinguished by their deep purple corollas, and very different petiolate, pubescent basal leaves.

Additional specimens examined: PERU. **Arequipa**: Prov. Caravelí. Dist. Atico. Lomas of Atico, ca. 48 km SE of Chala, ca. 100 m.a.s.l., 8 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3262* (CONC, E, F 1934760, GH, NY, SGO, US); Lomas of Jahuay, ca. 89 km S of Nazca, ca. 15 km N of Chaviña, ca. 30 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3772* (E, F 1950162, GH, US); Lomas of Atiquipa, ca. 10.5 km N of turn-off to Atiquipa, 150–200 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3778* (E, F 1950160, GH, SGO, US, USM 74599); ca. 7 km N of Chala, 15°50'S, 74°18'W, 110 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8200* (F 2198751); Prov. Camaná, Ocoña, Norte de Ocoña, ca. Km 767, 16°26'S, 73°08'W, 300 m.a.s.l., 12 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8760* (F 2319994, HSP 005095, HUSA 6270, HUT, US, USM); 16°16'S, 73°28'W, 300 m.a.s.l., 12 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8766* (F 2330879, HSP 005099, HUSA 6267, HUT, US, USM); Bella Unión, Sur de Nazca entre Km 518 y Km 590, 15°26'S, 74°52'W, 80–310 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen,*

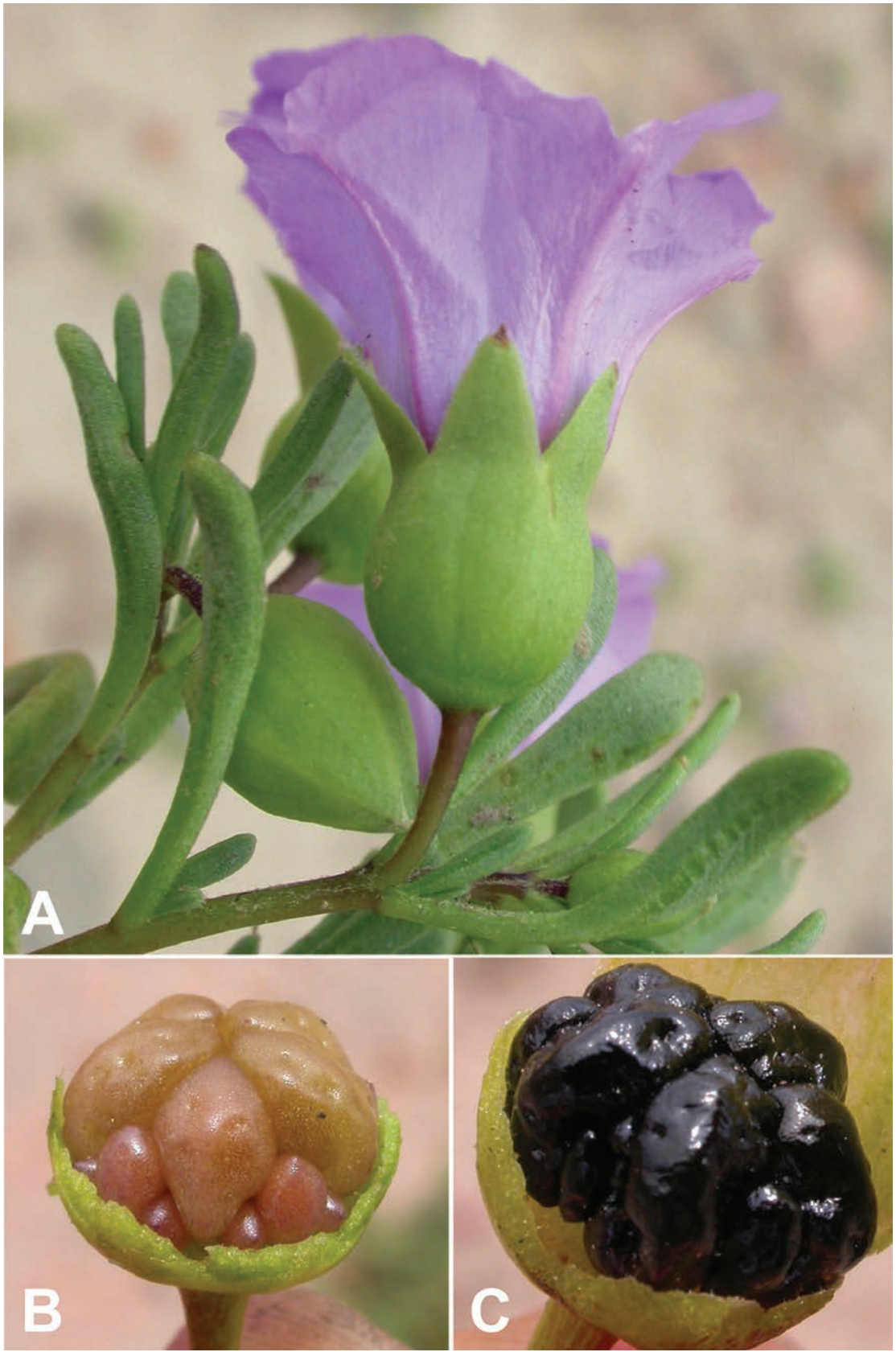


FIGURE 105. *Nolana chancoana*. **A**, Glabrous leaves and globose calyces with triangular lobes; **B–C**, Mericarps maturing from pale to black.

V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8789 (F 2330877, HSP 005112, HUSA 6278, HUT, US, USM); Chala, al S de Santa Rosa, 15°49'13"S, 74°20'17"W, 283–300 m.a.s.l., 14 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8871* (F 2330863, GH, HSP 005173, HUSA 6298, US); Entre Atico and Camaná, 16°10'S, 73°48'W, 50 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8912* (F 2330876, GH, HSP 005198, HUSA 6245, HUT, US, USM); 16°13'S, 73°42'W, 30 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8914* (F 2330862, GH, HSP 005200, HUSA 6244, HUT, US, USM); Entre Atico and Camaná, 16°13'S, 73°42'W, 30 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8919* (F 2330878, GH, HSP 00506, HUSA 6480, HUT, US, USM). Prov. Caravelí, Lomas de Atico, entre Chala y Camaná, 50–100 m.a.s.l., 3 December 1955, *R. Ferreyra 11727* (USM 81290); Lomas de Cápac, cerca a Chala, 100–150 m.a.s.l., 3 December 1955, *R. Ferreyra 11745* (GH, USM 81096); Lomas de Atiquipa, 300–400 m.a.s.l., 2 May 1983, *R. Ferreyra 19830* (USM 50480); PanAmerican Hwy 652 S of Lima at "Cali" gas station, 6 km S of Chala, Lomas de Cápac, 200 m.a.s.l., 13 September 1957, *P. C. Hutchison 1288* (USM 81095); entre Silaca y Ocoña, 15°49'06"S, 74°23'32"W, 203 m.a.s.l., 20 August 2006, *V. Quipuscoa S., M. Laura Q,. & Y. Cano B. 3379* (HSP 000613, HUSA 562); Atiquipa, Silaca, Km 590 de la Panamericana Sur, Tanaka and Atiquipa, 15°48'42"S, 74°23'48"W, 291 m.a.s.l., 19 November 2007, *V. Quipuscoa, M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3557* (HSP 000688, HUSA 7529, USM); Dist. Atiquipa, ca. a Agua Salada, Km 591 Panamericana Sur, 16°46'19"S, 74°25'42"W, 245 m.a.s.l., 27 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6621* (HSP 8804); Malco, 15°10'00"S, 74°30'43"W, 590 m.a.s.l., 28 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7573* (HSP 011331); Lomas cerca de Chala, 22 August 1957, *K. Rahn 063* (USM 54294); Atiquipa, October 1863, *A. Raimondi s.n.* (GH ex B, USM 10856); Acarí, Lomas de Pongo, 300 m.a.s.l., 2 August 1947, *O. Velarde 523* (USM 81097); Km 586 Panamericana Sur, Lomas 6 km N of Atiquipa, 450–860 m.a.s.l., 3 October 1997, *M. Weigend & H. Förther 97/692* (F 2211309), *97/693* (F 2211308, HUT 34262), *97/694* (F 2211307). **Ayacucho**: Prov. Lucanas, Dist. Santa Lucía, entre Malco y Huanca, 15°08'24"S, 74°27'47"W, 684 m.a.s.l., 28 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7585* (HSP 011835).

D3. ***Nolana chapiensis*** M.O. Dillon & Quip., Arnaldoa 14(2): 180. 2007. TYPE: PERU. Arequipa: Prov. Arequipa, Dist. Polobaya, entre La Gruta y el Santuario de Chapi, [16°45.51'S, 71°19.72'O], 2300 m.a.s.l., 25 November 2000, *V. Quipuscoa S. & L. Cáceres M. 2495* (Holotype: HUSA [5044]; Isotypes: F 2229849, GH, US). Fig. 106–109.

Digital image: Isotype collection of *Nolana chapiensis* from the Field Museum, Chicago [F 2229849]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.f0361461f

Succulent *shrubs*; stems to 50 cm long, much-branched, decumbent, to ca. 1.2 m long. *Leaves* subopposite, erect, blades elliptic, 8–15 mm long, 2.0–3.5 mm wide, succulent, entire, pubescent with stiff capitate-glandular trichomes, ca. 0.25 mm long, apically obtuse, bases cuneate; petioles 0.8–3.5 mm long to sessile. *Inflorescences* of solitary flowers in upper leaf axils, pedicels filiform, 3–6 (–12) mm long, densely pubescent with stiff, capitate-glandular trichomes. *Flowers* 5-merous; calyces campanulate, 3.0–3.5 mm wide at anthesis, pubescent with capitate-glandular trichomes, tube 2.5–3.0 mm long, 2.5–3.5 mm wide, 5-lobed, lobes lanceolate, equal, 3–6 mm long, 1.5–2.0 mm wide; corollas infundibularis, regular, 16.5–20.0 mm long, limb 5.0–8.5 mm wide; lobes 2–3 mm long, retuse, light purple, internally glabrous, externally pubescent with capitate-glandular trichomes; stamens 5, included, filaments inserted on lower third of corolla, unequal, three 9–11 mm long, two ca. 12–14 mm long, pilose at the bases; anther thecae 2.0–2.5 mm long, 1.0–1.5 mm wide, purple, glabrous; ovary glabrous, basal nectary, 5 carpels, style included, 7–9 mm long, stigma capitate, green, ca. 1 mm in diam. *Mericarps* 5, globose, unequal, 3.5–4.5 mm long, 5–7 mm in diam., included within the persistent calyx; seeds 3–4(–5) per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates the Santuario of Our Lady of Chapi where the religious icon, Virgin de Chapi, resides southwest of Arequipa. Legend has it that the shrine of the Virgin de Chapi was being moved by a priest in 1790, and, allegedly, it grew so heavy that it became impossible to go any farther. In 1884, the statue was transferred to a rustic chapel, and a Mercedarian missionary built a church (completed in 1897) and promoted pilgrimages from Arequipa. The sanctuary is called the "Little Lourdes" because of a great number of miraculous healings for those who have completed the long pilgrimage from Arequipa during the first week of May. In 2001, the church was damaged by an earthquake and has since been rebuilt.

Distribution and Ecology: Peru, Departments of Arequipa and Moquegua, inland localities ca. 60 km from the coast; 2200–2400 m.a.s.l. (Fig. 106). It is recorded from interior arid localities with characteristic vegetation for southern desert sites that receive rains.

Nolana chapiensis is a shrubby species confined to interior arid sites that include the emblematic cactus, *Browningia candelaris* (Meyen) Britton & Rose (Cactaceae) (Fig. 107A–B). The stems are reddish, glandular- pubescent, with small elliptic leaves that lack a well-defined petiole (Fig. 108A). The corollas have a distinctive form, abruptly expanding above the calyx (Fig. 108B) with guides in the throat (Fig. 108C–D). The corollas are very similar to those in *Nolana rhombifolia* (Fig. 150A–B) and, interestingly, they both occur in areas with similar rainfall patterns and shared community members (Pinto and Luebert, 2009). The pedicels are densely glandular-pubescent and nod in fruit (Fig. 108E). There are uniformly five mericarps, that are smooth and shiny (Fig. 108F). It most closely resembles

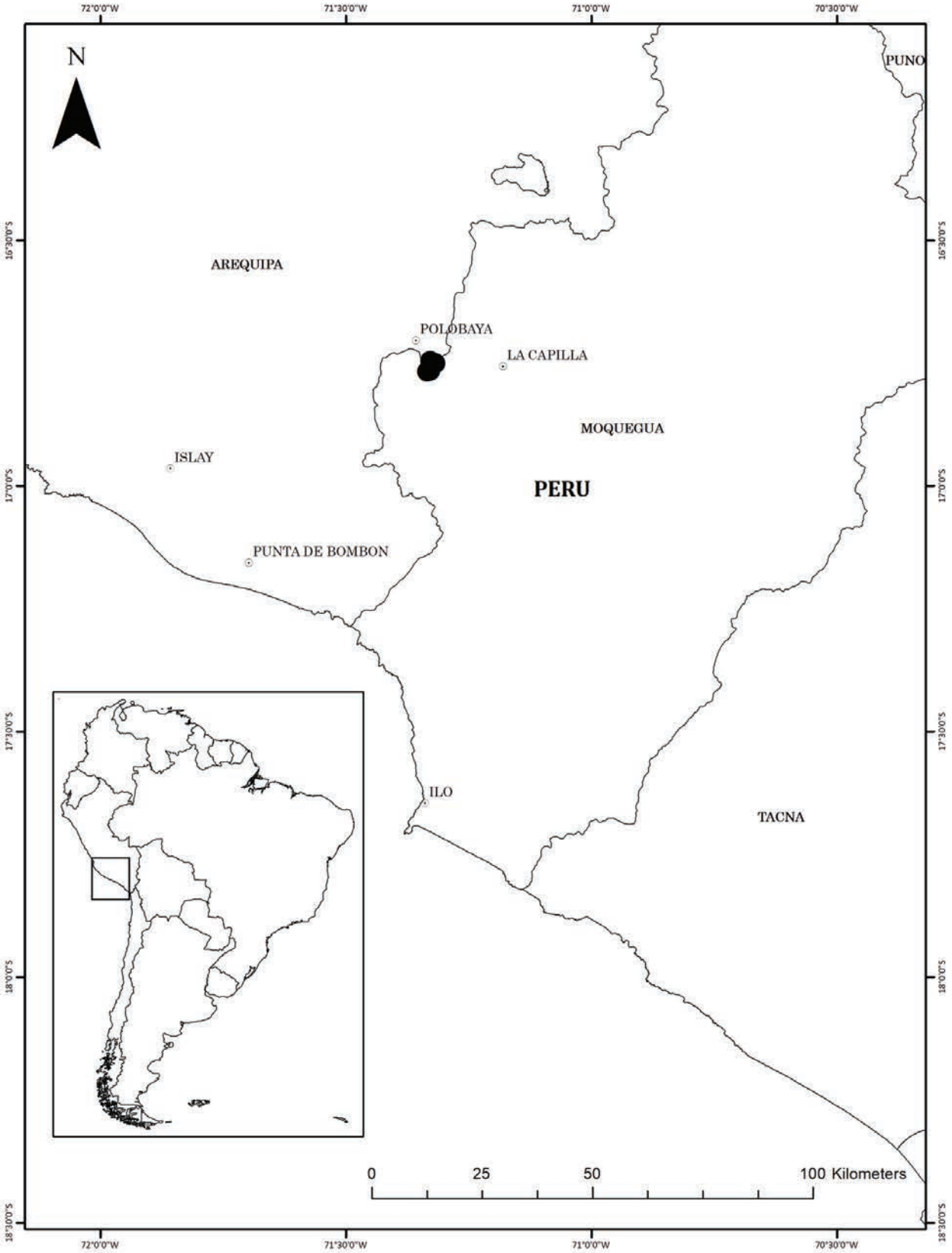


FIGURE 106. Distribution of *Nolana chapiensis* M.O. Dillon & Quip.

FIGURE 107. *Nolana chapiensis*. **A**, Habitat south of Chapi, Chile, with *Browningia candelaris* (Cactaceae); **B**, Flowering shrubs.

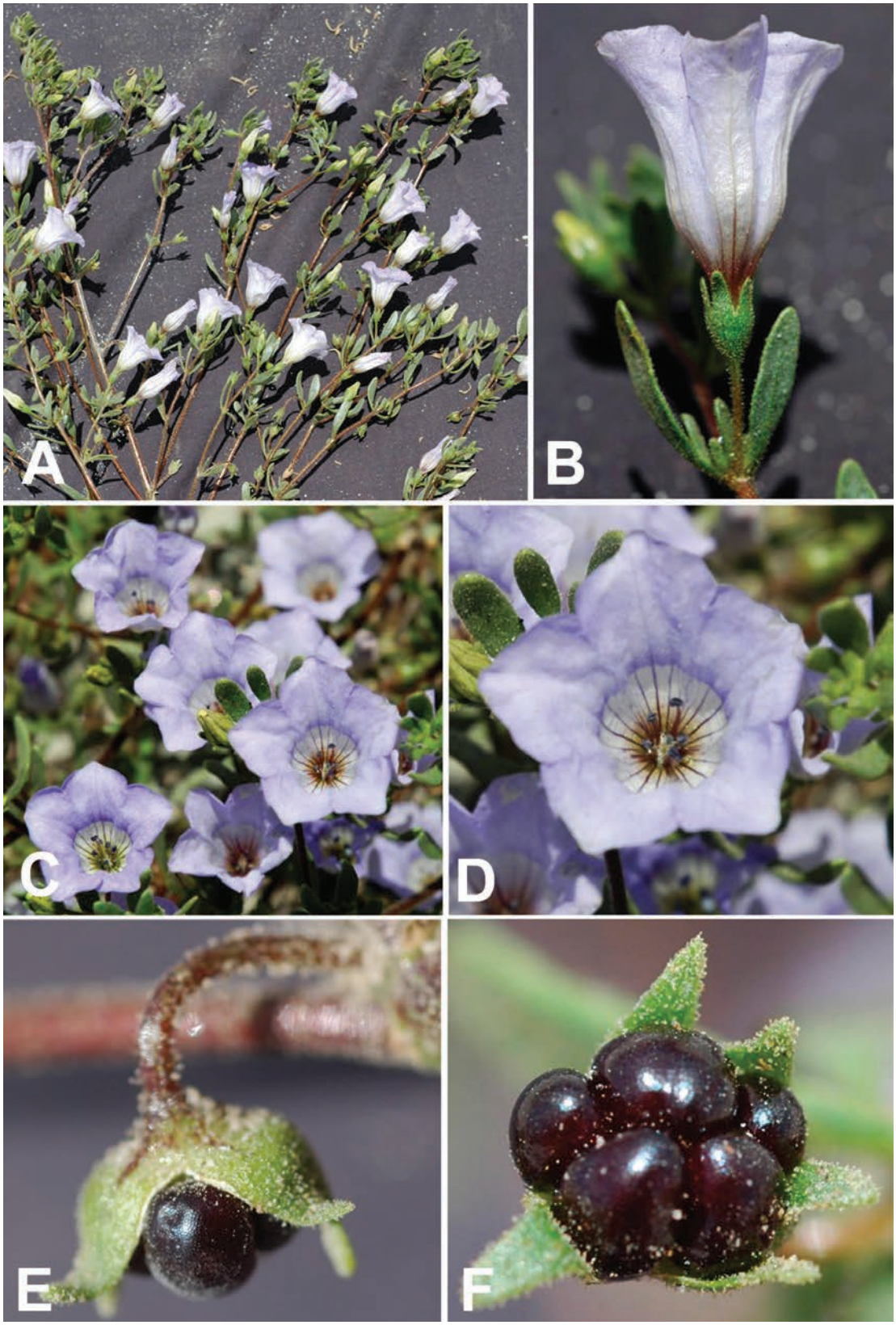


FIGURE 108. *Nolana chapiensis*. **A**, Flowering stems with small elliptic leaves; **B**, Corolla abruptly expanding above the calyx; **C–D**, Corollas with guides in the throat; **E**, Nodding, densely glandular pubescent pedicels; **F**, Mericarps.

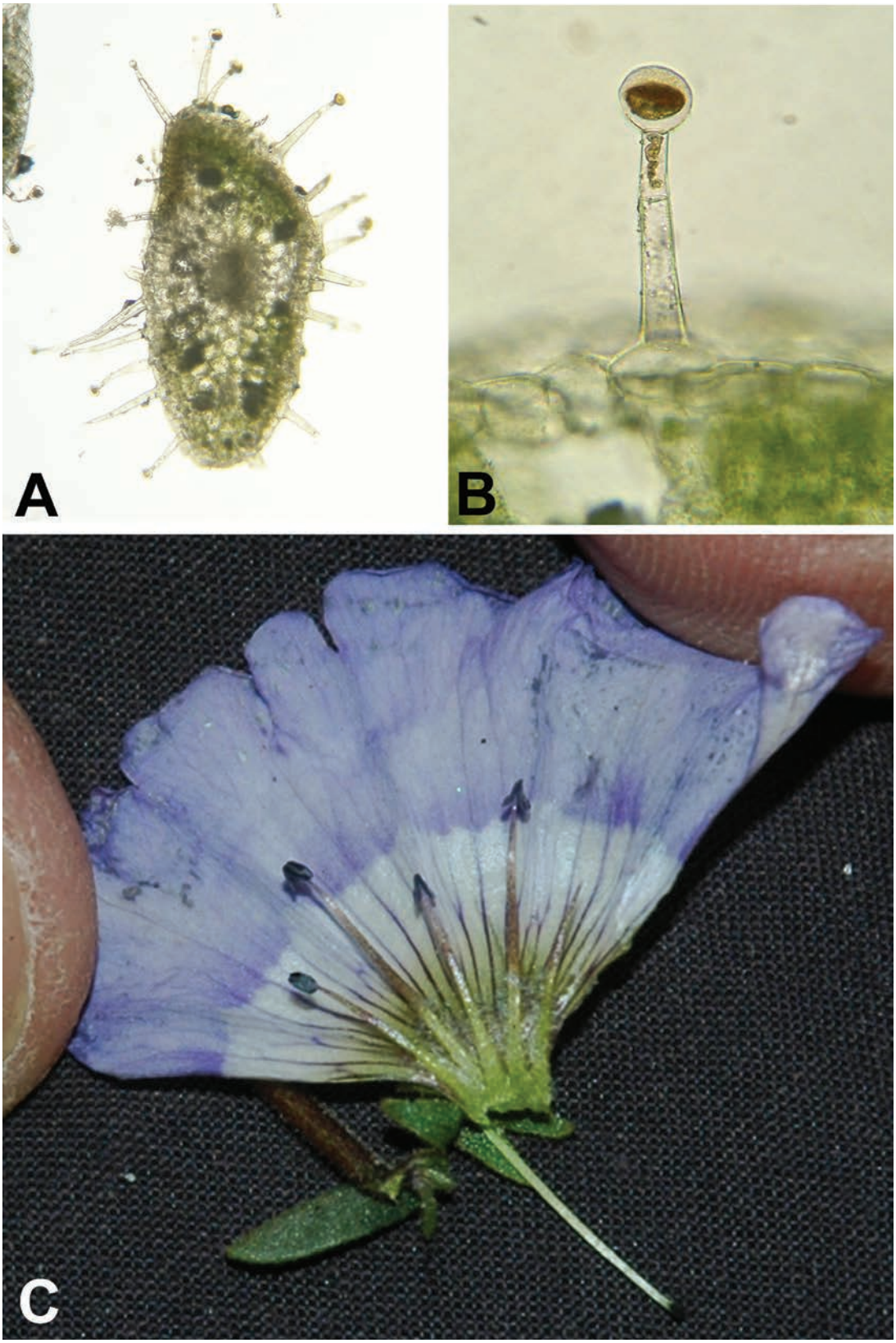


FIGURE 109. *Nolana chapiensis*. **A**, Cross-section of leaf; **B**, Stalked, gland-tipped trichome; **C**, Dissected flower.

N. laxa and *N. weberbaueri,* both species with petiolate, lanceolate to ovate leaves, and distributions in the vicinity of Lima and Ica, respectively. *Nolana laxa* is distinguished by typically possessing three large mericarps (Fig. 131A), whereas *N. chapiensis* invariably possesses five mericarps (Fig. 108F). The leaves, stems and floral parts are all densely pubescent with capitate-glandular trichomes on both abaxial and adaxial surfaces (Fig. 109A). Trichomes are of variable size, but all have a capitate apical cell (109B). The dissected corolla illustrates the position of the unequal anther filaments and their pubescent bases (Fig. 109C).

Utilizing the GBSSI waxy marker, Dillon et al. (2007c) determined that *N. chapiensis* is grouped within a largely unresolved clade of Peruvian species that includes *N. scaposa, N. lezamae, N. humifusa, N. aticoana, N. urubambae*, *N. spathulata* and *N. laxa*. Further studies will be necessary to establish the relationships among this group of species.

Additional specimens examined: PERU. **Arequipa**: Prov. Arequipa. Alrededores de la Gruta de la Virgin de Chapi, 16˚45'S, 71˚19'W, 2240 m.a.s.l., 23 November 2005, *M. O. Dillon, S. Leiva G., V. Quipuscoa S., M. Zapata C., E. Ortiz V., G. Castillo P., & M. Corrales M. 9019* (CONC, E, F 2276623, GH, HSP 005289, HUSA 6378, HUT, US 3512557); a 4 km del Santuario de Chapi, camino a la Gruta, 16˚45'S, 71˚19'W, 2250 m.a.s.l., 20 October 2002, *V. Quipuscoa S., M. O. Dillon, L. Cáceres M., G. Castillo P., M. Laura Q., Y. Cano B., & Y. Chilque G. 2785* (HSP 000318, HUSA 4043, HUT 40135); Polobaya, abajo de la Gruta de la Virgin de Chapi, 16˚46'S, 71˚20'W, 2260 m.a.s.l., 14 December 2002, *V. Quipuscoa S., N. Hidalgo A., D. Sotomayor M., M. Rodríguez, & A. Hopkins 2850* (HSP 000324, HUSA 4082, HUT 40136); Dist. Polobaya, cerca al ojo de agua Chapi, 16˚44'55"S, 71˚19'32"W, 2330 m.a.s.l., 12 May 2017, *V. Quipuscoa S., I. Treviño Z. M. Balvin A., D. Rodríguez P. S. Huamani Q., & G. Rosado A. 5421* (HSP 8724). **Moquegua**: Prov. General Sánchez Cerro, Dist. La Capilla, 1 km del río Chapi, 16˚45'54"S, 71˚19'37"W, 2233 m.a.s.l., 12 May 2017, *V. Quipuscoa S., I. Treviño Z. M. Balvin A., D. Rodríguez P. S. Huamani Q., & G. Rosado A. 5418* (HSP 12020).

D4. ***Nolana galapagensis*** (Christoph.) I.M. Johnst., Contrib. Gray Herb. 112: 32. 1936. Fig. 110–112.

Basionym: *Periloba galapagensis* Christoph., Nyt Mag. Naturvid. 70: 89, 1932. TYPE: ECUADOR. Islas Galápagos: Galápagos Islands, Isla Santa Cruz (Indefatigable Island), *B. Rorud 15* (Holotype: O, not seen; Isotype: US [US 1528972, US00121966]).

Digital image: Isotype of *Periloba galapagensis* from the National Museum of Natural History, Washington, D.C. [US 1528972]. http://n2t.net/ark:/65665/3b25e2fb9-0124-471c-8722-ab49d1520070

Shrubs to ca. 2 m tall; stems soft-ligneous, erect to decumbent, densely leafy, internodes not evident, minutely puberulent. *Leaves* alternate to fasciculate, blades linear-spathulate to oblanceolate or ovate, 5–35 mm long, 3–6 mm wide, glabrous, succulent, apically rounded, bases cuneate; petioles ca. 5 mm long. *Inflorescences* of solitary flowers clustered at the branch apex, axillary on branchlets; pedicels 1–9 mm long; glandular-pubescent. *Flowers* 5-merous; calyx oblong, tube 2–3 mm long, 2.5–3.0 mm wide, lobes oblong, ca. 4 mm long, ca. 1 mm wide, unequal, apically obtuse; corollas hypocrateriformis, zygomorphic, l2–20 mm long, tube ca. 4 mm wide, limb ca. 10 mm wide, white. *Mericarps* (10–)15–25, 2- to 3-seriate, 8–20 small, 1–2 mm long below middle of gynobase, 3–5 larger, 2–3 mm long, black, conspicuously faveolate-reticulate; seeds unknown. Chromosome number: 2*n*=24.

Etymology: The species epithet indicates the place of origin for this Galápagos Island endemic.

Distribution and Ecology: Ecuador, Galapagos Islands; Isla Caamaña, San Cristobal, Santa Cruz, Santa María, Seymour, and Tortuga; 0–500 m.a.s.l. (Fig. 110). It is endemic to coastal dunes and rocky areas near the ocean. Potentially, it can dominate the "Littoral Zone" that begins at the ocean's edge and includes many halophytes (Wiggins and Porter, 1971).

Common name: *Galapagos clubleaf*.

Nolana galapagensis is a distinctive shrubby species within the flora of the Galapagos Islands, growing in proximity to the ocean (Fig. 111A). It is decidedly woody with a thick trunk with bark, 8–10 cm in diameter (Fig. 111B). It is the only species to be observed coexisting with sea lions (Fig. 112A). The succulent leaves are weakly petiolate, glabrous, and fasciculate (Fig. 112B). The calyx has succulent, unequal lobes with obtuse apices (Fig. 112C) and small, white, tubular flowers (Fig. 112D). Small, white, tubular flowers are also encountered in continental species, especially the northern Chilean species, *N. sedifolia*, but the leaves and calyx characters are not similar (Fig. 347). Furthermore, molecular studies suggest relationships to *N. lycioides*, a species that does not share even a superficial resemblance (Dillon et al., 2009).

Additional specimens examined: ECUADOR. Islas Galápagos: Isla Santa Cruz, Isla Caamaña, ca. 4 km ESE of Puerto Ayora, 00˚45'32"S, 90˚16'46"W, 25 February 2004, *M. O. Dillon 8504* (F 2330858); Isla Santa Cruz, Turtle Bay, (Bahía de Tortuga), 0–10 m.a.s.l., 12 October 1966, *U. & I. Eliasson 266* (K); Isla Caamaño (= Jensen Island, Academy Bay), 0–5 m.a.s.l., 18 March 1967, *U. & I. Eliasson 1623* (BM000941305, K); Santa Cruz (= Indefatigable, Chaves), beach at Tortuga Bay, *L. A. Fournier 184* (US 2853461); North Seymour Island, 12 June 1932, *J. T. Howell 10002* (GH, US 2604259); Indefatigable Island, 24 March 1939, *T. W. J. Taylor 97* (K); Isla Santa Cruz, on lava peninsula along S shore of Tortuga Bay, 15–16 km W of Academy Bay, margins of sand dunes at E end of bay, 11 February 1964, *I. L. Wiggins 18699* (GH, K). Isla Floreana (Charles Island), easterly facing slopes of sand dunes, Bahía Cormorant, 2–6 m.a.s.l., 14 February 1967, *I. L. Wiggins & D. M. Porter 563* (GH).

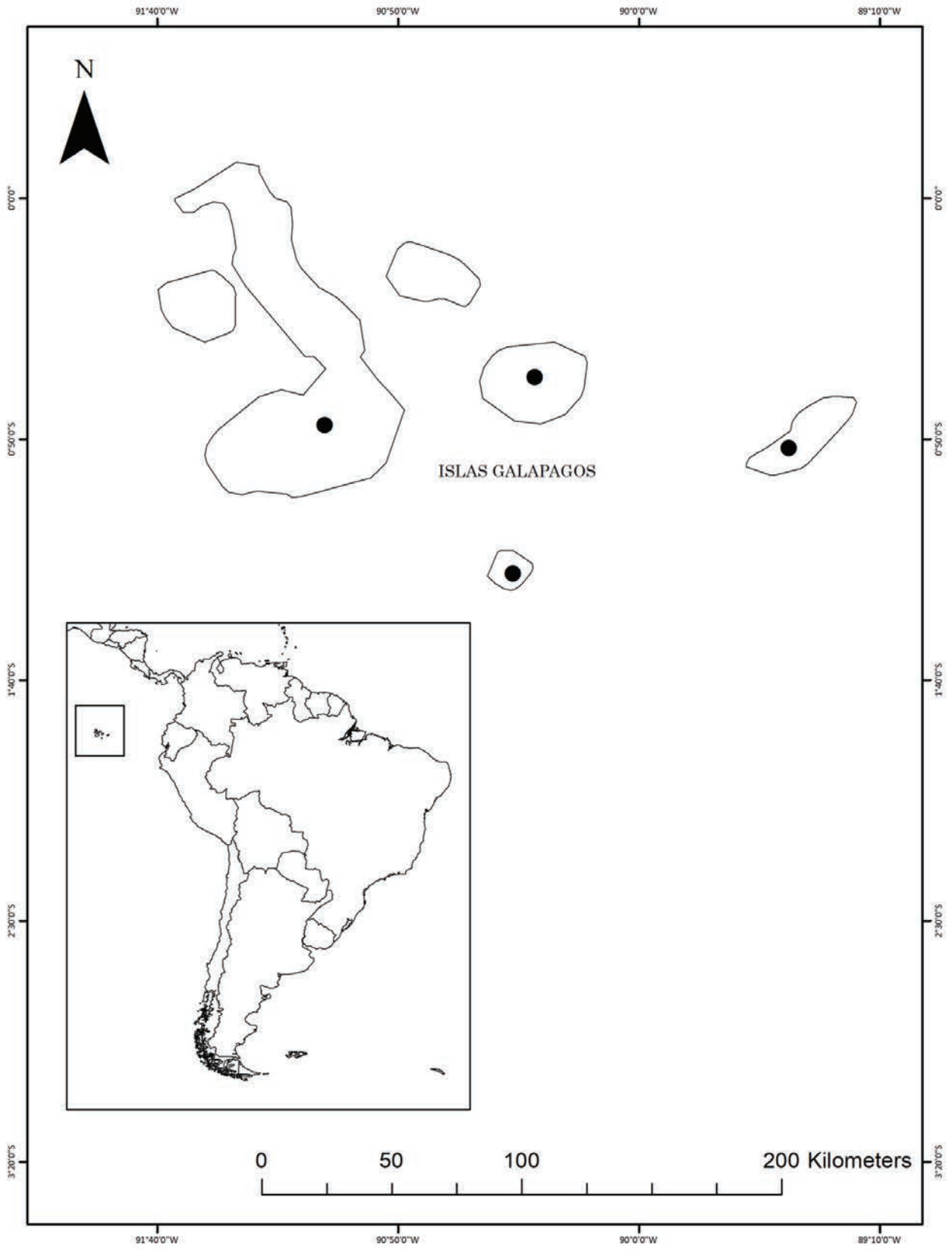


FIGURE 110. Distribution of *Nolana galapagensis* (Christoph.) I.M. Johnst.

FIGURE 111. *Nolana galapagensis*. **A**, Large shrubs near ocean sites; **B**, Trunk with bark.

D5. ***Nolana hoxeyi*** M.O. Dillon & Quip., Harv. Pap. Bot. 28(1): 2. 2023. TYPE: PERU. Tacna: Prov. Tacna, Dist. Sama, ca. 2 km Sur de Puerto Grau, carratera costanera, 18˚00'35"S, 70˚52'43"W, 112 m.a.s.l., 19 Noviembre 2021, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., & J. Muñuico M. 8027* (Holotype: HSP [12376]; Isotypes: HSP [12377], F 2330851, HUT, USM). Fig. 113–116.

Shrubs, 50–100 cm tall; stems intricately branched, erect, 50 cm long, young branches densely velutinous to villous, occasionally capitate-glandular. *Leaves* alternate, fasciculate, blades elliptic to linear-oblanceolate, 7–11 mm long, 1.0–1.5(–2.0) mm wide, densely strigose, succulent, base attenuate, apex rounded to obtuse; petioles sessile to subsessile, canaliculate. *Inflorescences* compact or densely racemose, 30–40 cm long; flowers subtended by leaf-like bracts, 4–5 mm long, ca. 1 mm wide, strigose; pedicels cylindrical, densely pubescent, strigose, 1–5 mm long. *Flowers* 5-merous; calyx narrowly campanulate, 2.0–3.5 mm wide at anthesis, densely strigose, 5-lobed, tube 1.5–2.0 mm long, 2.0–2.5 mm in diam., lobes lanceolate, unequal, 2.5–3.0 mm long, 1.0–1.5 mm wide, apex acute; corolla zygomorphic, infundibuliform, 15–20 mm wide at anthesis, 10–13(–15) mm long, light lavender or lilac, throat clear, externally and internally glabrous; stamens 5, included, filaments inserted on lower third of corolla, unequal, two filaments 9–10 mm long, three filaments 6–8 mm long, glabrous; anther thecae light purple, ca.1 mm long, ca. 1 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 0.5–1.0(–1.5) mm wide, basal nectary, carpels 7–9, style included, 7–9 mm long, stigma bilobed, light green, ca. 0.5 mm long. *Mericarps* 7–10(–12), 2-seriate, round, black, rugose-punctate, 2.0–2.5 mm long, 3 or 4 large, 7 or 8 smaller, included within expanding calyx; seeds 1–5 per mericarp. Chromosome number: unknown.

Etymology: The epithet of *Nolana hoxeyi* commemorates Paul D. Hoxey (b. 1971–), a prolific collector and author of publications on the Cactaceae, especially the genera of Central and South America. His photographs and documentation were critical in locating populations of this new species. He splits his residency between Cambridge, England, and Arequipa, Peru.

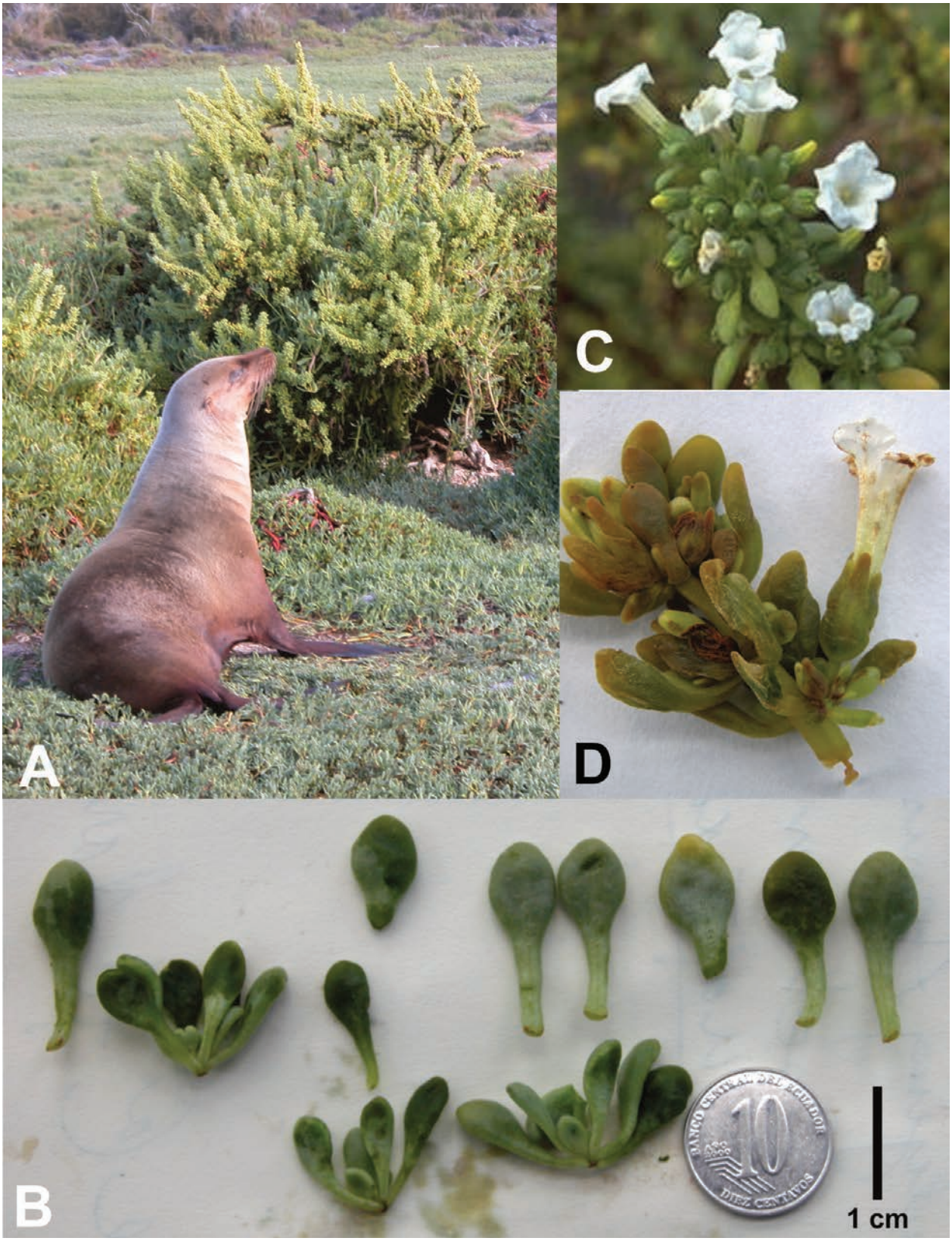


FIGURE 112. *Nolana galapagensis*. **A**, Sea lion lounges among shrubs; **B**, Succulent leaves; **C–D**, Flowers.

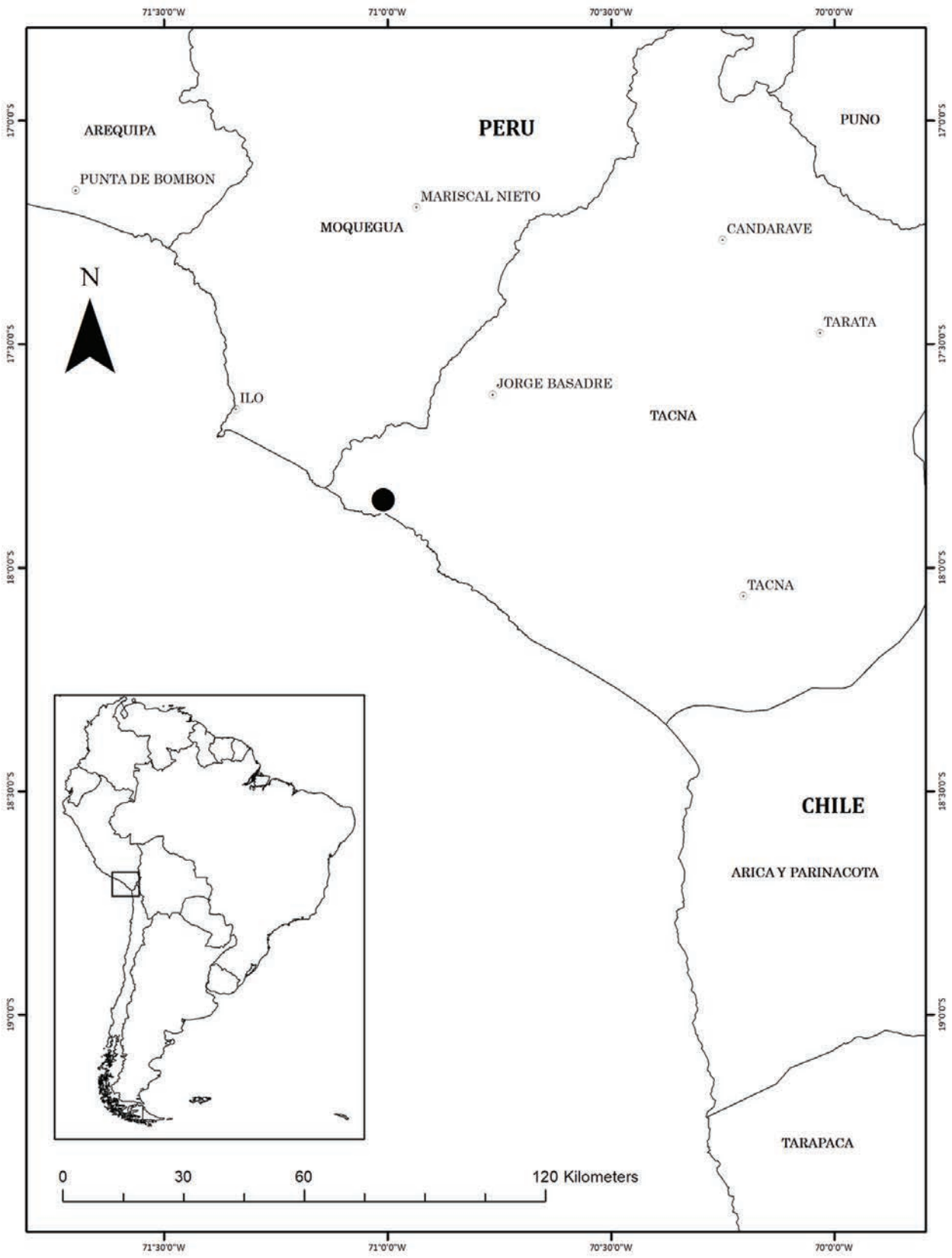


FIGURE 113. Distribution of *Nolana hoxeyi* M.O. Dillon & Quip.

Distribution and Ecology: Peru, Department of Tacna; 100–600 m.a.s.l; restricted to sandy soils, most commonly from near-ocean localities near sea level, and to ca. 10 km inland reaching 600 m.a.s.l. (Fig. 113).

Nolana hoxeyi is known from a small area in the Province of Sama, recorded from near-ocean habitats from 100 to 600 m.a.s.l., and within a few kilometers of the ocean (Fig. 115A). It is decidedly different with its sinuate stems and densely set fasciculate leaves (Fig. 115B). There are no evident internodes, only stems covered with dense leaves on all surfaces. This species is decidedly woody with strong trunks to 5 cm in diameter (Fig. 115C). The apical portion of the stems develop into dense, racemose inflorescences, which appear spicate with many flowers over the apical 20–50 cm (Fig. 116A–D).

Nolana hoxeyi was first recognized as potentially new while examining photographs of the two G. K. Muller collections identified as *Nolana lycioides* (*Mueller & Chávez 3591*, USM 81298) and another identified as *N. coelestis* (*Mueller et al. 12236*, USM 64133), a Chilean species quite unrelated and differing in many fundamental morphological characteristics. Both sheets were collected in the Morro de Sama region. When living plants were encountered on 19 November 2021, it was obvious that they represented a species new to science (Dillon and Quipuscoa, 2023).

Nolana hoxeyi does not closely resemble any other *Nolana* species, but it does share some characteristics with *N. samaensis*. These two species share similar mericarp shape and size but differ in mericarp number. The densely leafy stems and distinct, densely racemose inflorescences are unique in *N. hoxeyi*. The most common inflorescences in *Nolana* are solitary flowers borne in leaf axils, but sometimes, as in *N. inflata* and *N. weissiana*, they display weakly cymose inflorescences; the inflorescence of *N. scaposa* is easily recognized and well-developed. The only other *Nolana* species with such densely set leaves are *N. galapagensis*, *N. onoana* of northern Chile, and *N. tricotiflora* of southern Peru.

Additional specimens examined: PERU. Tacna: Morro Sama, September 1980, 250 m.a.s.l., *G. K. Muller & R. Chávez 3591* (USM 64133, not seen); Morro de Sama, 6 August 1985, *G. K. Muller, G. Krebs, & R. Chávez 12236* (USM 81298, not seen).

D6. ***Nolana inflata*** Ruiz & Pav., Fl. Peruv. 2: 7, tab 112a. 1799. TYPE: PERU. Arequipa: Prov. Camana, *J. Tafalla s.n.* (Lectotype designated by Dillon and Quipuscoa, 2023: MA [815130] ; Isolectotypes: B [B W03450-010], F [F 712544, F 843609, F 845149], FI-Webb [FI009586], G [G00383940, G00303942, G00383943], HAL [HAL115089], K [K000532 269], MA [MA815125, MA815126, MA815127, MA815 129, MA815131, MA817979, MA817682, MA817683], MPU [MPU0012109], P [P00605856]). Fig. 117–121.

Digital image: Lectotype of *Nolana inflata* from Royal Botanical Garden, Madrid [MA815130]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.ma815130

Heterotypic synonymy: *Nolana ventricosa* Ruiz & Pav., Fl. Peruv. 2: 7. 1799. Rejected name.

Perennial *herbs* with a large taproot; stems decumbent, 9–38 cm long, 1.5–3.0 mm in diam., prostrate. Blades of basal *leaves* in rosette lanceolate to oblanceolate, rarely spathulate, 45–230 mm long, 10–85 mm wide, hirsute with capitate-glandular trichomes, apices obtuse to acute, basally attenuate, margins irregularly dentate, penninerved; midrib with 5–7 lateral nerves; petioles ca. 30 mm long; flowering stems prostrate to ascending, cauline leaves alternate or rarely opposite, blades subovate-rounded to oblong-elliptic, 20–25 mm long, 15–20 mm wide; petiole 2–7 mm long. *Inflorescences* weakly cymose; pedicels 6–14 mm long, hirsute-glandular. *Flowers* 5-merous; calyx campanulate-globose, 10–15 mm long, 7–10 mm in diam., hirsute-glandular outside, tube campanulate, 5.5–8.0 mm long, 6–8 mm wide, obscurely veined; lobes triangular, acute, 3.5–5.0 mm long, 3.0–4.2 mm wide; corollas infundibularis, regular to weakly zygomorphic, 16–25(–32) mm long, 13–20 mm wide, pinkish-lilac to deep purple, pilose, lobes subequal, obtuse, tube short, densely villous inside; stamens unequal, united with tube for 1/2 the length, two 8.5–14.0 mm long, three 7–12 mm long, densely villous basally; style gynobasic, 8–11 mm long; stigma capitate-lobate; nectary disc patelliform. *Mericarps* 5–10, 2-seriate, reniform, sometimes angled or with scattered sharp, conic protrusions, unequal, black, shiny, the five larger 3–6 mm long, 2.0–4.5 mm wide, five smaller 1–4 mm long, 1.2–3.5 mm wide; seeds 1–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *inflatus*, meaning bladdery, thin, membranous, or swollen, and refers to the overall form and texture of the calyx.

Distribution and Ecology: Peru, Departments of Ancash, Arequipa, and Lima, ranging >850 km; (12–)100–300(–800) m.a.s.l. It is recorded from a wide range of environments, including near-coast sites in southern Peru, with outliers in central and northern Peru (Fig. 117).

Illustration: Fig. 118. Illustration of *Nolana inflata* from the Royal Botanical Expedition to the Viceroyalty of Peru, plate 112. H. Ruiz-López & J. Pavón (1777–1816). Drawn by Francisco Pulgar (1799).

Nolana inflata has a distinctive basal rosette of leaves and prostrate stems that form inflorescences with many flowers (Fig. 119A–B). Basal leaves are densely pubescent, succulent, and with obvious venation on the abaxial surfaces (Fig. 120A). Flowers are subtended by modified leaflets, and the calyx is globose and appears inflated (Fig 120B). Opening the calyx reveals the connate mericarps (Fig. 120C–D).

The corollas of *Nolana inflata* are highly infested by red spider mites, such as *Tetranychus cinnabarinus*, and the dense trichomes may protect the maturing gynecium from attack by insects (Fig. 121A–B). While postulating the function of a morphological trait, it is undeniable that these trichomes provide an obstacle to predation.

This species is morphologically like *N. weissiana*, a near geographic neighbor, as suggested by marker data (Dillon et al., 2007c; Tu et al., 2008). Further studies may confirm that these taxa are conspecific, but *N. inflata* has clear nomenclatorial priority. The discovery of a population in the

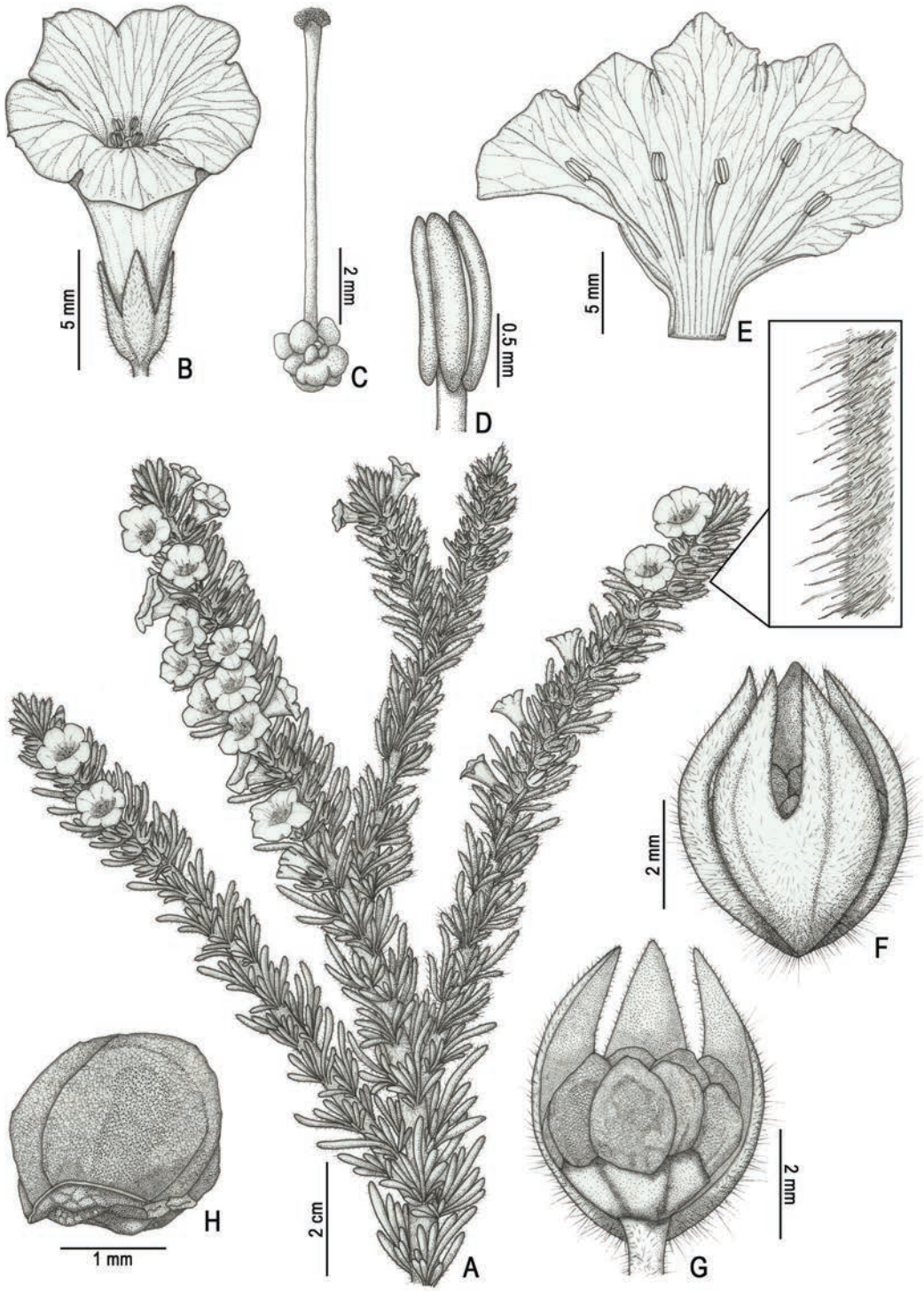


FIGURE 114. Illustration of *Nolana hoxeyi*. **A**, Habit with enlargement of surface pubescence; **B**, Flower; **C**, Gynoecium and style; **D**, Anther; **E**, Dissected corolla; **F**, Calyx; **G**, Dissected calyx with mericarps; **H**, Mericarp. Drawn by Maricruz Bedoya Cuno.

FIGURE 115. *Nolana hoxeyi*. **A**, Type locality; **B**, Habit with sinuate stems and densely set fasciculate leaves; **C**, Woody trunk.

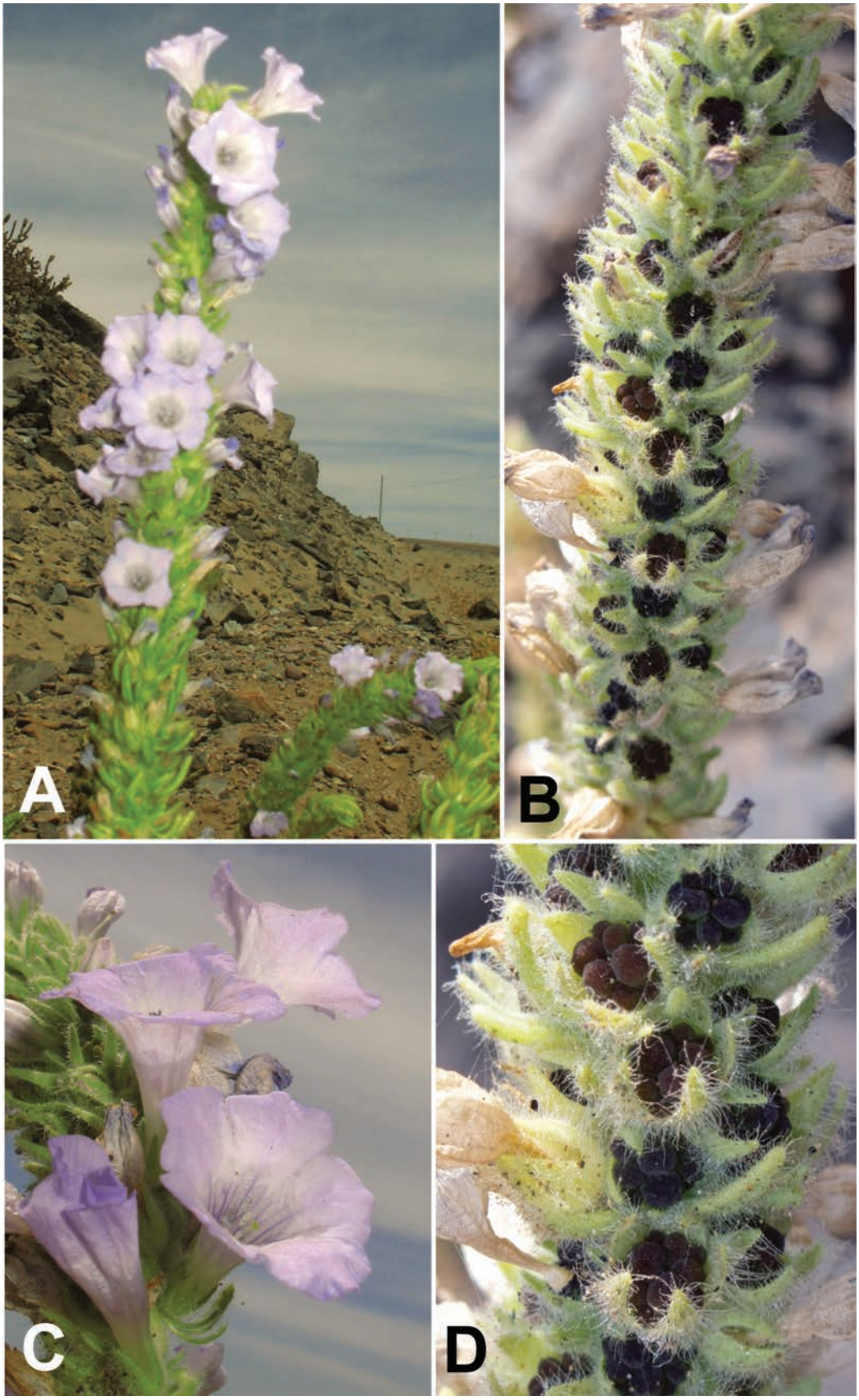


FIGURE 116. *Nolana hoxeyi*. **A**, Racemose inflorescence; **B**, Closeup of fruiting inflorescence; **C**, Flowers; **D**, Mericarps.

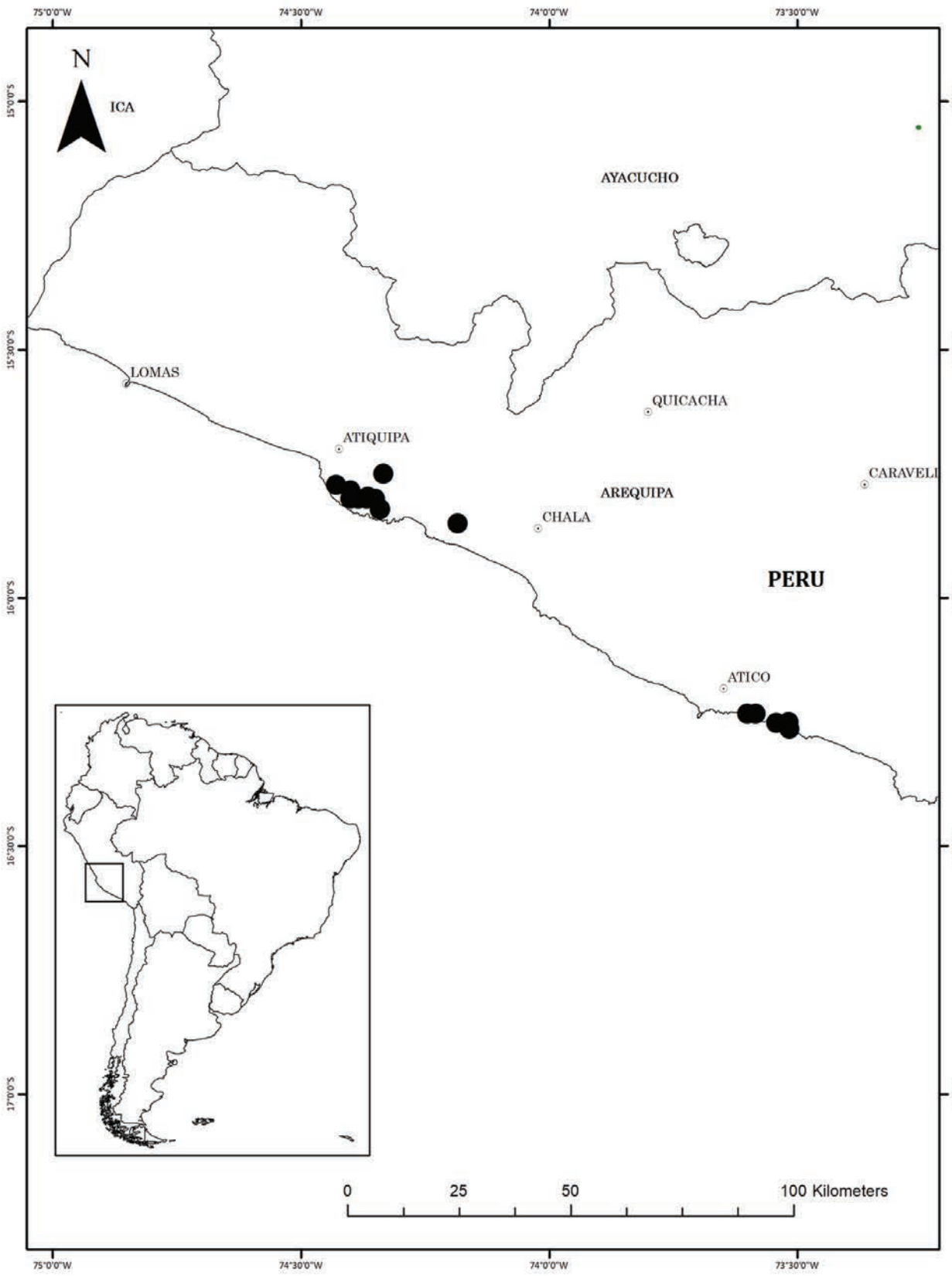


FIGURE 117. Distribution of *Nolana inflata* Ruiz & Pav.

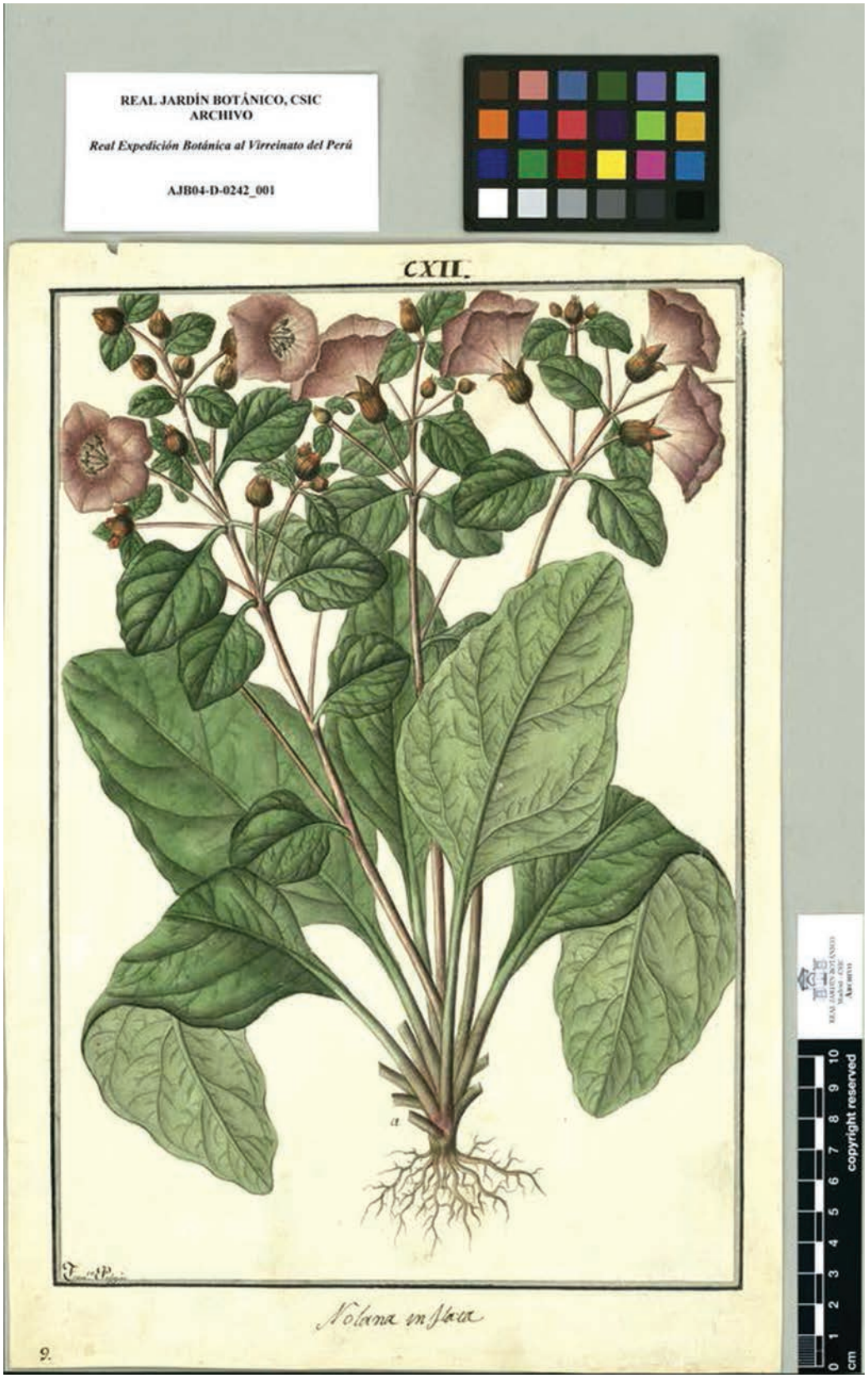


FIGURE 118. Illustration of *Nolana inflata* from the Royal Botanical Expedition to the Viceroyalty of Peru, plate 112, H. Ruiz & J. Pavón (1777–1816). Drawn by Francisco Pulgar (1799).

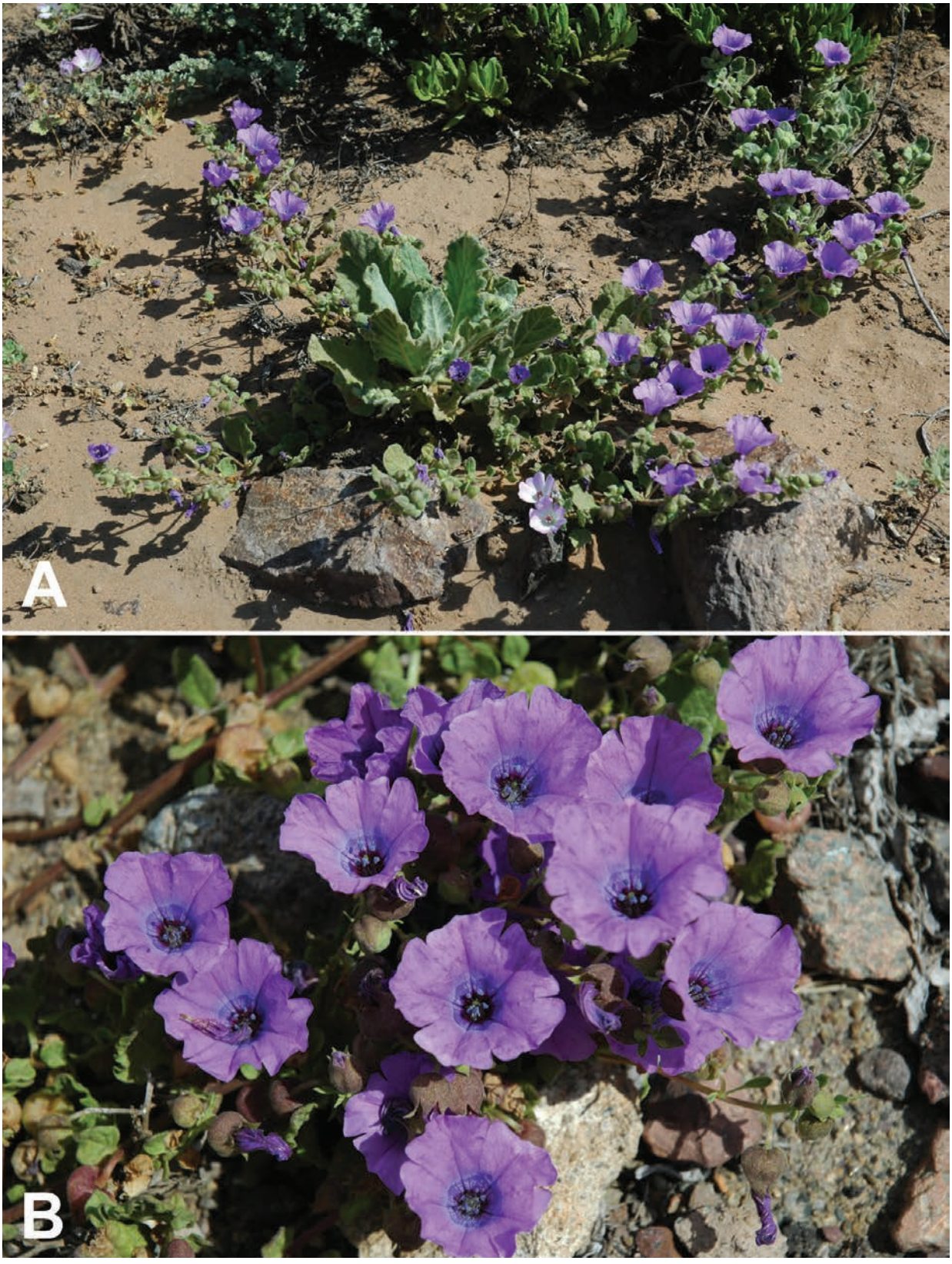


FIGURE 119. *Nolana inflata*. **A**, Basal rosette and prostrate stems forming inflorescences; **B**, Dense inflorescences.

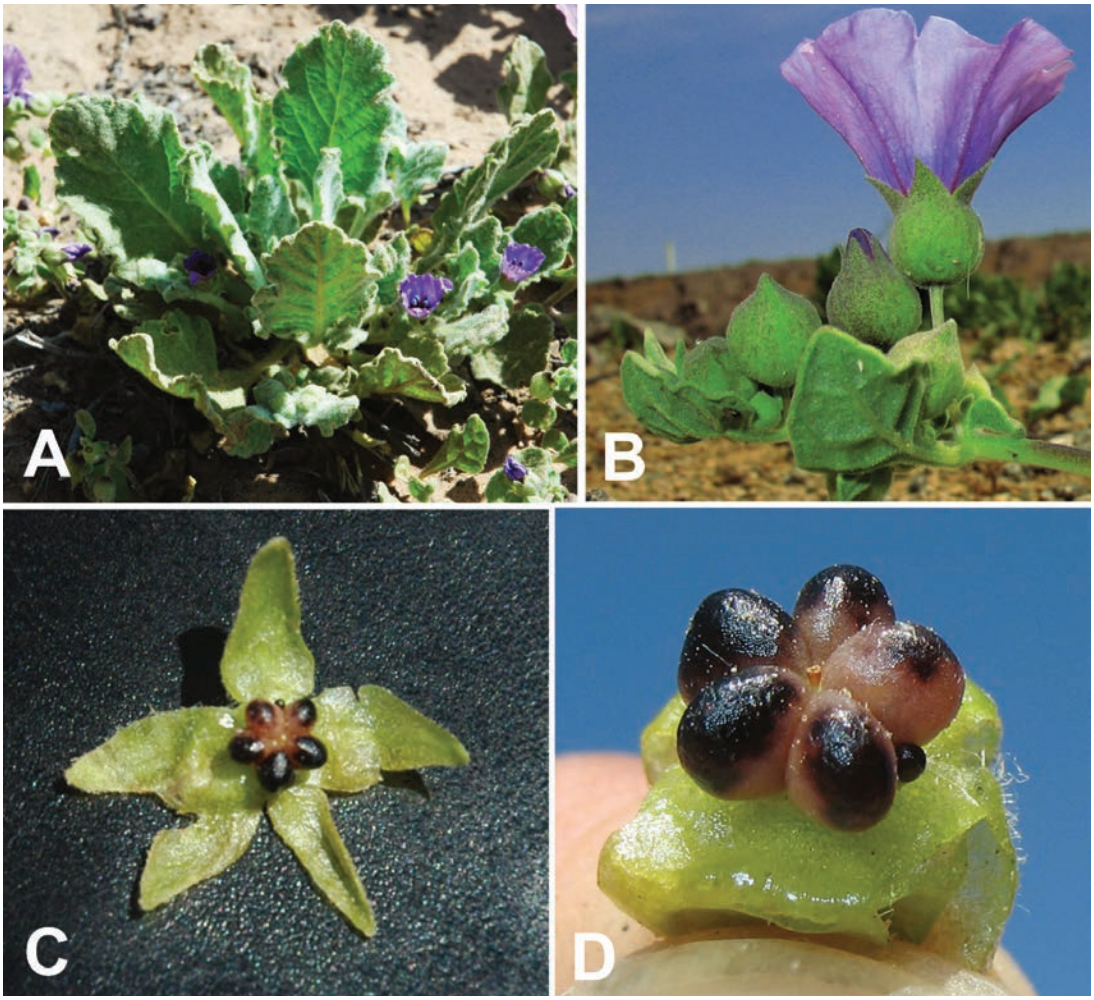


FIGURE 120. *Nolana inflata*. **A**, Densely pubescent basal leaves with prominent venation on the abaxial surfaces; **B**, Globose calyx with triangular lobes; **C**, Open calyx reveals five prominent, connate mericarps; **D**, Ripening mericarps.

Department of Ancash may well suggest that *N. inflata* had a more widespread distribution in the near past.

Mesa-M. (1981) designated a collection from MA as the lectotype; however, there are no fewer than nine duplicate collections. From these, a single collection has here been chosen as the lectotype, and the additional sheets are all considered isolectotypes.

Johnston (1936: 50) observed that the mericarps of some of the nutlets have several stout, subulate appendages, nearly 0.5 mm long, on their dorsal surfaces. These have been observed and recorded.

Additional specimens examined: PERU. **Ancash**. Prov. Huaylas, Huascaran National Park, western flank of Cordillera Blanca, Alpamayo–Cashapampa trail, 8°48'00"S, 77°45'00"W, 3500 m.a.s.l., 31 July 1954, *W. Rauh & G. Hirsch P2015* (F 1578068). **Arequipa**: Prov. Caravelí, 12 km S of Atico at Km 711 along Pan-American Hwy 1, 90 m.a.s.l., 26 February 1994, *E. F. Anderson, J. McAuliffe, K. & F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7967* (F 2143986); between Km 594 and Km 595 N of Chala along Pan-Americana Hwy 1, 15°48'53"S, 74°21'16"W, 240 m.a.s.l., 27 February 1994, *E. F. Anderson, J. McAuliffe, K .& F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7974* (F 2143992); Lomas of Atiquipa, ca. 10.5 km N of turn-off to Atiquipa, Km 584 S of Lima, 270–600 m.a.s.l., 2 November 1983, *M. O. Dillon & D. Dillon 3801* (CONC, E, F 1950516, GH, SGO, US, USM); Lomas of Atico; ca. 8 km S of Atico along Pan-American Highway, Km 706–707 S of Lima, 2 November 1983, *M. O. Dillon & D. Dillon 3844* (CONC, E, F 1950512, GH, K, USM); ca. 11 km S of Atico, 16°16'S, 73°31'W, 50 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8203* (E, F 2198754, GH); Lomas de Atiquipa, ca. 5 km N of turnoff to Atiquipa on PanAm, 15°48'S, 74°24'W, 230 m.a.s.l., 3 March 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8246* (F 2199347, US 3692755); Atiquipa, N de Atiquipa, Km 593, 15°49'S, 74°23'W, 270 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8805* (F 2776728, HSP 005125, US 3512466);

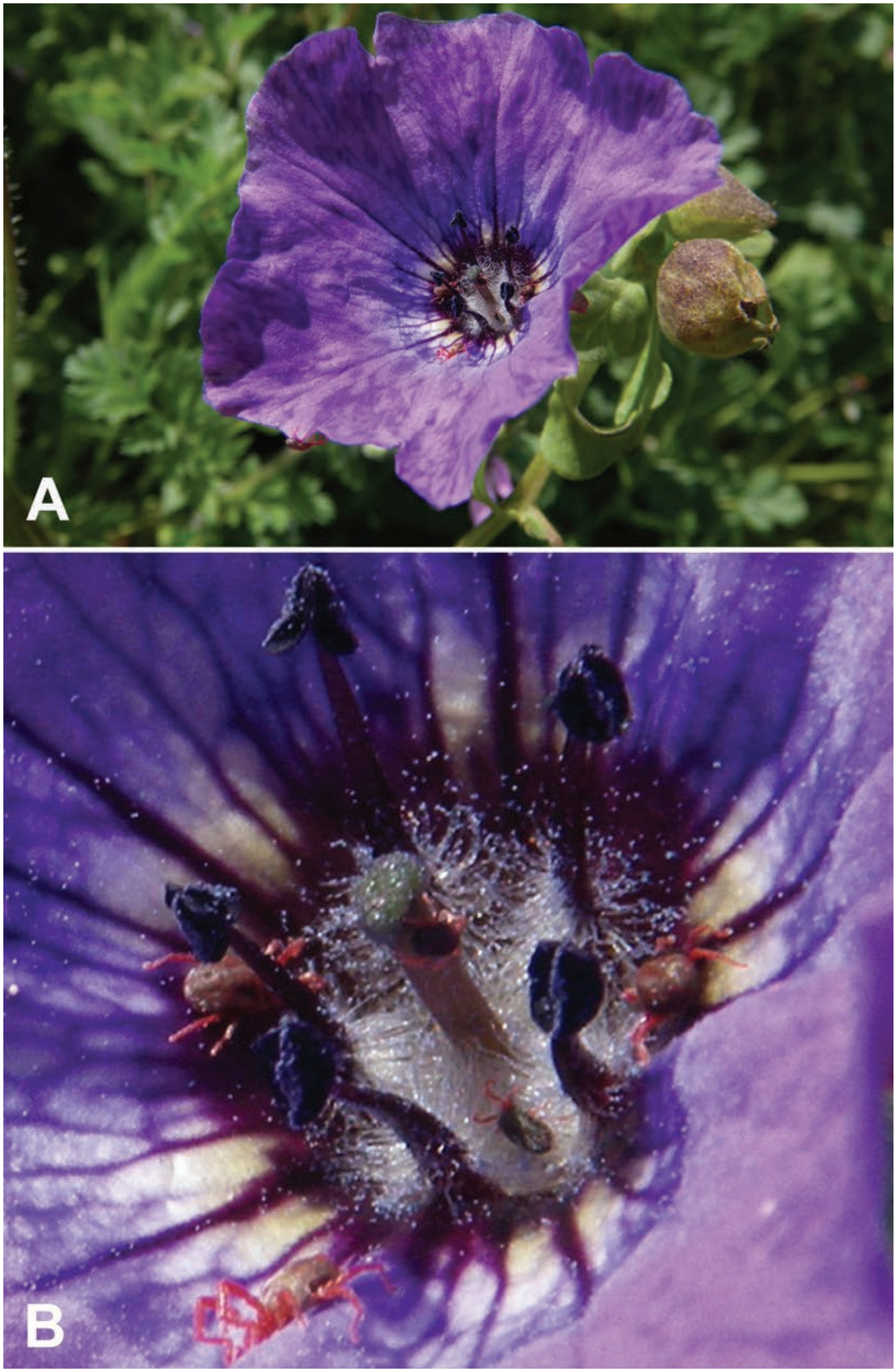


FIGURE 121. *Nolana inflata*. **A**, Corollas infested with red spider mites; **B**, Dense trichomes protecting maturing gynecium from attack by insects.

Atiquipa: a 2 km E del cementerio de la Comunidad de Atiquipa, 15°45'49"S, 74°20'56"W, 496 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8832* (F 2276733, HSP 005143, US 3512496); Caravelí: Chala, al sur de Santa Rosa, 15°49'13"S, 74°20'17"W, 283–300 m.a.s.l., 14 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8874* (F 2276735, HSP 005176, US 3512499); Chala, al Sur de Chala, 15°52'S, 74°11'W, 230 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8880* (F 2276696, HSP 005182, US 3512530); Atico, entre Atico y Camana, formación de Lomas, 16°13'S, 73°42'W, 30 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8916a* (F 2276700, HSP 005202, US 3512534); Atico, entre Atico y Camana, 16°13'S, 73°42'W, 30 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8916b* (F 2276701, HSP 005203, US 3512535); entre Puerto Inca Y el pueblo de Santa Rosa, 243 m.a.s.l., 16 November 2013, *C. Fernández A. & M. Fernández Z. 58* (HSP 003238); Atiquipa, 250–300 m.a.s.l., 20 October 1946, *R. Ferreyra 1488* (USM); Lomas de Atiquipa, 250–300 m.a.s.l., 14 November 1949, *R. Ferreyra 6472* (F 1442796, US 1998714, USM 81153); Atiquipa, 280–300 m.a.s.l., 9 November 1952, *R. Ferreyra 8811* (USM); Atiquipa, 12 December 1956, 200–300 m.a.s.l., *R. Ferreyra 12115* (USM); Atiquipa, 100–200 m.a.s.l., 20 December 1959, *R. Ferreyra 13952* (USM); Atiquipa, 200–300 m.a.s.l., 20 November 1967, *R. Ferreyra 17149* (USM); Atiquipa, 300–400 m.a.s.l., 2 May 1983, *R. Ferreyra 19833* (USM); Atiquipa, 15 km N of Chala, [1000 ft], 24 October 1975, *P. Holt 164* (K); Silaca, Km 590 de la Panamericana Sur, 15°48'42"S, 74°23'48"W, 291 m.a.s.l., 19 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3545* (HSP 000346); Dist. Atiquipa, ca. a Agua Salada, Km 591 Panamericana Sur, 15°46'19"S, 74°25'42"W, 245 m.a.s.l., 27 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6629* (HSP 011444); cerca a la plaza de Atiquipa, 15°47'47"S, 74°21'52"W, 305 m.a.s.l., 28 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6639* (HSP 011451); entre Santa Rosa and Chala, ca. Km 605, 15°49'20"S, 74°20'24"W, 277 m.a.s.l., 29 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., M. Bedoya C., & W. Ancalla C. 6688* (HSP 011469, HUT 60412); Entre Chala y Santa Rosa, ca. Km 606 Panamericana, 15°49'15"S, 74°20'22"W, 287 m.a.s.l., 29 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., M. Bedoya C., & W. Ancalla C. 6707* (HSP 8820, HUT 60428); Lomas de Atico, 16°15'22"S, 73°31'10"W, 443 m.a.s.l., 2 December 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6845* (HSP 011527); Dist. Atico, Panamericana Sur Km 720 al sur de Atico, 16°13'04"S, 73°32'29"W, 12 m.a.s.l., 3 December 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6852* (HSP 011529, HUT 60411); Dist. Atiquipa, Silaca Km 596 Panamericana Sur, 15°48'31"S, 74°23'59"W, 229 m.a.s.l., 30 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7651* (HSP 011861); Dist. Atiquipa, ca. al desvío a Atiquipa, 15°48'16"S, 74°22'01"W, 276 m.a.s.l., 30 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7657* (HSP 011863, HUT 60409); Atiquipa, 17 November 1957, *O. Tovar 2700* (USM 81161); Atiquipa, 17 November 1957, *O. Tovar 2707* (USM 81156); Lomas de Atico, 600 m.a.s.l., 31 October 1966, *C. Vargas C. 18212* (CUZ), *18224* (CUZ); Lomas de Chala, 31 October 1966, *C. Vargas C. 18240* (CUZ); Lomas de Atiquipa, 400–500 m.a.s.l., 1 November 1966, *C. Vargas C. 18260* (CUZ); 11 km S of Atico, Km 712 Panamericana Sur, ca. 50 m.a.s.l., 4 October 1997, *M. Weigend & H. Förther 97/754* (F 2211300); 8 km N of Atiquipa, 100–200 m.a.s.l., 20 September 1938, *C. R. Worth & J. L. Morrison 15637* (F 1488300, K). **Lima**: Prov. Canta, Dist. Santa Rosa de Quives, camino entre Trapiche y Macas, 11°41'22"S, 76°56'09"W, 550–650 m.a.s.l., 24 August 2011, *P. Gonzáles & E. Castañada 1578* (E00700853, USM 258162); 7 km NE of Trapiche, 800 m.a.s.l., 4 August 1957, *P. C. Hutchison 1018* (USM 81176).

D7. ***Nolana insularis*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 49. 1936. Fig. 122–124.

Basionym: *Periloba insularis* I.M. Johnst., Contrib. Gray Herb. 95: 32. 1931. TYPE: PERU. Ica: Cresta de la Isla San Gallán, November 1919, *R. C. Murphy 3472* (Holotype: BKL, not seen; Isotype: GH [GH00282343]).

Digital image: Isotype of *Nolana insularis* from Harvard University Herbaria, Cambridge [GH00282343]. https://s3.amazonaws.com/huhwebimages/9A3E6A873A79431/type/full/282343.jpg

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 133. 1981.

Perennial *herbs* becoming distinctly woody, spreading caudex; stems prostrate, sparsely branched, 5–20 cm long, 1.5–3.0 mm in diam., canescent, densely villous with capitate-glandular trichomes and dendritic trichomes, or, more rarely, glabrescent. *Leaves* alternate, blades ovate to obovate, 10–15 mm long, 6–8 mm wide, thick and fleshy, apically rounded, basally attenuate; both surfaces densely covered with capitate-glandular trichomes and dendritic trichomes; petioles 5–10 mm long. *Inflorescences* of solitary flowers; pedicels ca. 10 mm long, deflexed in maturity. *Flowers* 5-merous; calyces globose, ca. 10 mm long, 6–7(–8) mm in diam., 2- to 3-lobed; lobes ca. 5 mm long, acute; corollas infundibularis, regular, ca. 20 mm long; tube cylindrical, ca. 5 mm long, limb ca. 10 mm wide; filaments 3–4 mm long, bases densely villous; nectary disc patelliform, elevated gynobase. *Mericarps* 15–20, 2- to 3-seriate, 1.0–2.5 mm long, polyhedrons; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *insula*, meaning island, and *insularis*, pertaining to islands.

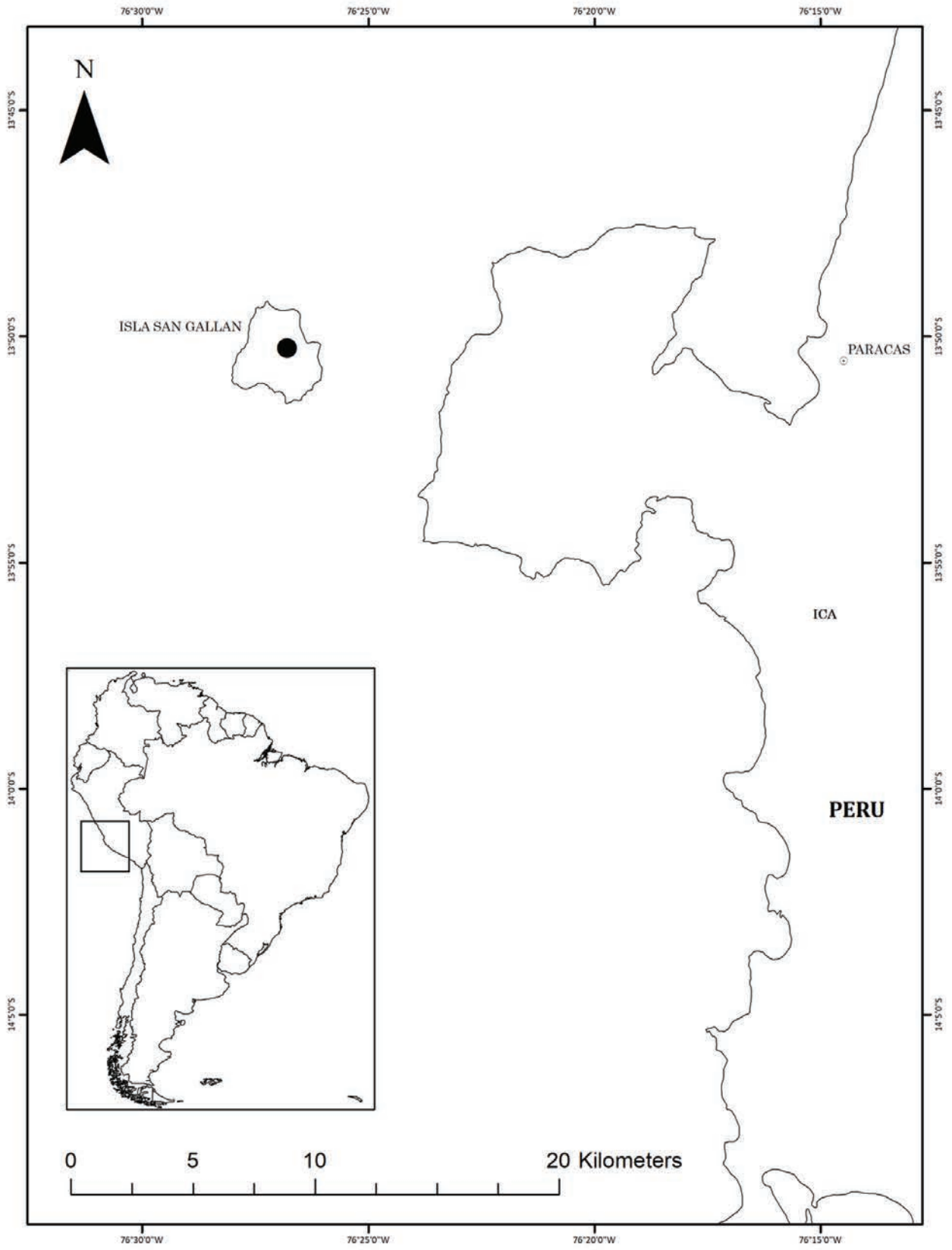


FIGURE 122. Distribution of *Nolana insularis* (I.M. Johnst.) I.M. Johnst.

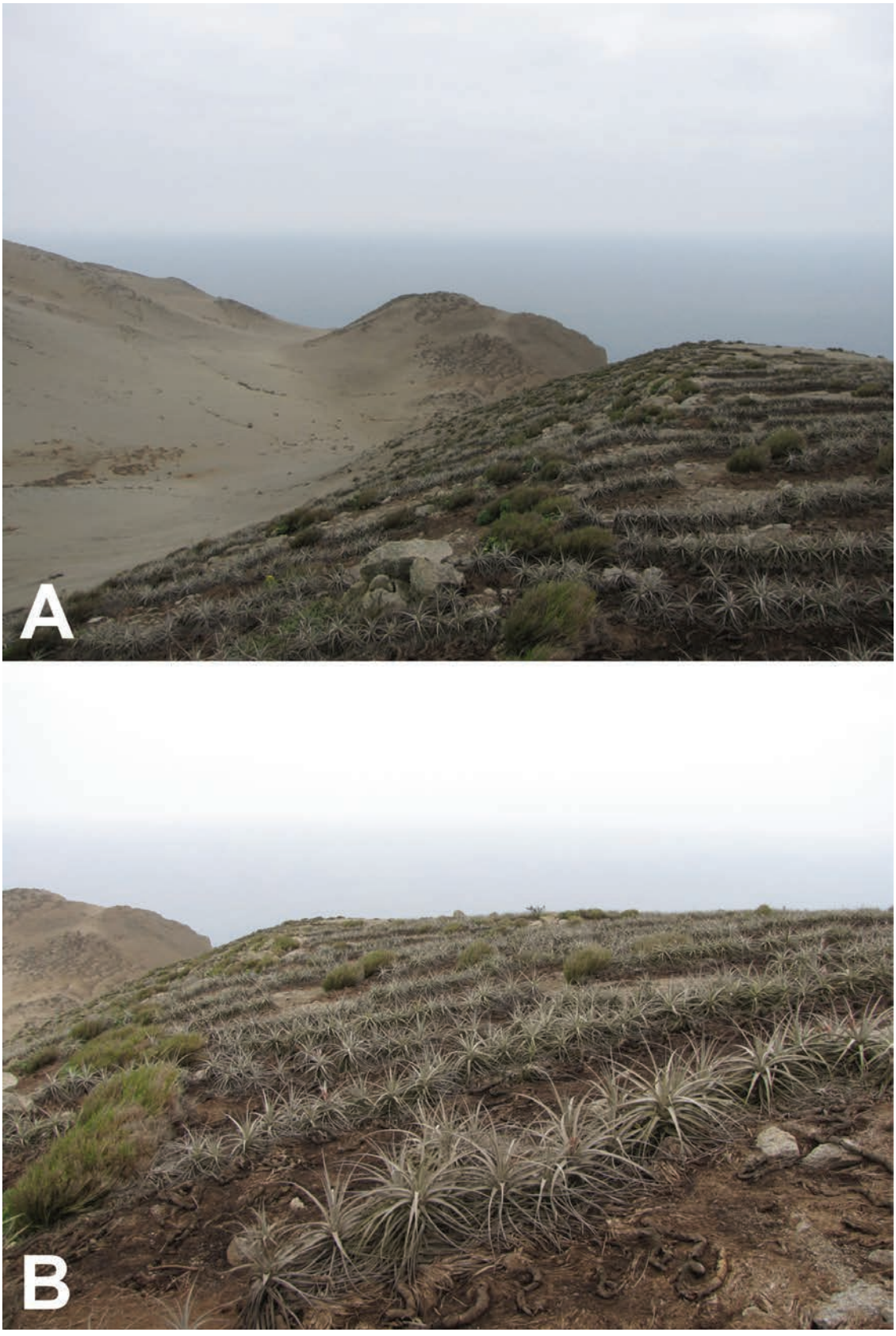


FIGURE 123. *Nolana insularis*. **A–B**, Vegetation dominated by *Tillandsia latifolia* Meyen. Photographs by Joanna Alfaro Shigueto.

FIGURE 124. *Nolana insularis*. Woody stem apex illustrating bilabiate calyx and flower. Photograph by Joanna Alfaro Shigueto.

Distribution and Ecology: Peru, Department of Ica, restricted to Isla San Gallán (13°53'30"S, 76°27'02"W) southwest of the port of Pisco and ca. 5 km west of the Paracas Peninsula (Fig. 122). It is only recorded from Isla Gallán, an island about 4 km long, that is lower at its north end and slopes generally upward to the south, culminating at the southern end in cliffs or headlands that reach an altitude of ca. 400 m.a.s.l.

Nolana insularis is a perennial and is one of the small number of species that make up the island's flora, which is dominated by *Tillandsia latifolia* Meyen (Fig. 123A–B). The photograph is not of the highest quality, but it does display the salient morphological features of this species, including the woody stem, densely pubescent succulent leaves, and the bilabiate calyx and corollas (Fig. 124). It most closely resembles *N. willeana*, from the Lomas de Amará, ca. 120 km to the southeast in Ica.

Nolana insularis is one of a small community of plants restricted to the upper reaches of Isla San Gallán. Robert Cushman Murphy (b. 1887–d. 1973), an ornithologist from the American Museum of Natural History, visited Isla San Gallán in November 1919, and his collections yielded 17 species of ferns and flowering plants, including *Nolana insularis* and *Polyachyrus nesites* I.M. Johnst. (Johnston, 1931). In 2009, the island was visited by Dra. Joanna Alfaro Shigueto and her research team from ProDelphinus (Lima), who were performing an ornithological survey. She provided several photographs of the plants she encountered, including *Nolana insularis* (Fig. 124). No plant specimens were made.

Additional specimens examined: Known only from the type collection; no additional herbarium material has been located.

D8. ***Nolana latipes*** I.M. Johnst., Contrib. Gray Herb. 112: 30. 1936. TYPE: PERU. Arequipa: Prov. Islay, Mollendo, dry sandy places at lower edge of Loma Formation, 20–200 m.a.s.l., flowers bright blue, 3 October 1902, *A. Weberbauer 1498* (Holotype: B; Isotype: GH [GH00282370]). Fig. 125–128.

Digital image: Isotype of *Nolana latipes* from Harvard University Herbaria, Cambridge [GH00282370]. https://s3.amazonaws.com/huhwebimages/C8392470A8A047A/type/full/282370.jpg

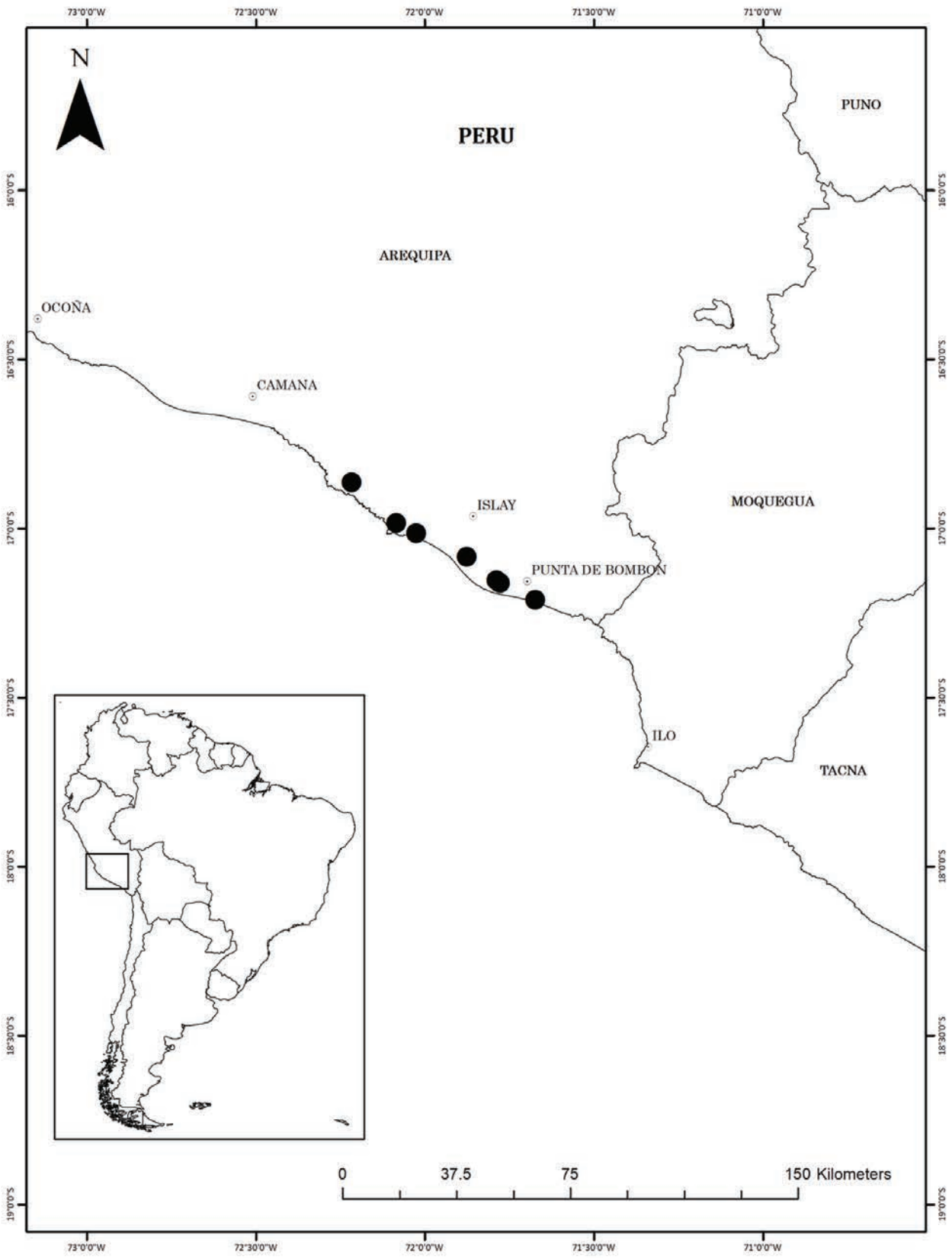


FIGURE 125. Distribution of *Nolana latipes* I.M. Johnst.

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 133. 1981.

Heterotypic synonym: *Nolana ivaniana* Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 3. 1955. TYPE: PERU. Arequipa: Prov. Islay, lomas entre Mollendo y Matarani, 150–200 m.a.s.l., 29 November 1955. *R. Ferreyra 11564* (Holotype: USM [242132, USM000560]).

Annual *herbs*, semisucculent, inconspicuously puberulent-glandular to glabrescent; stems branched, decumbent, 10–50 cm long, 2–5 mm in diam. *Leaves* alternate, blades oblanceolate to ovate-oblong, 15–40(–70) mm long, 5–18(–30) mm wide, apex obtuse, base gradually attenuate, subsessile, pubescent with capitate-glandular trichomes. *Inflorescences* of solitary flowers, pedicels 10–30 mm long, glabrescent. *Flowers* 5-merous; calyces 12–15 mm long, 4–5 mm in diam., campanulate, villous with capitate-glandular trichomes, tube 3–4 mm long, lobes cut to the base, zygomorphic, bilabiate, lobes ascending, linear-lanceolate, 7–10 mm long, 1.0–1.5 mm wide at the base, acuminate; corollas infundibularis, 15–20 mm long, 16–20 mm wide, violet, purple or, occasionally, all white forms, tube 3–5 mm long, 1.0–1.5 mm wide, densely villous inside; stamens unequal 3–6 mm long, united with the tube almost 1/2 the length; nectary patelliform, 10-dentate, 2–3 mm in diam.; styles gynobasic, 4–5 mm long. *Mericarps* 10–20, black, five 3.5–4.0 mm long, rugose, appearing much like raisins; seeds 3–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *latipes*, with a broad foot or stalk, and refers to the elevated receptacle where the mericarps attach.

Distribution and Ecology: Peru. Department of Arequipa ranging <50 km; 20–650 m.a.s.l. (Fig. 125). It is recorded from sandy soils, coastal *Lomas* formations (Dillon, 1997).

Nolana latipes is distinctive with lime-green herbage (Fig. 126A–B) and oblong leaf blades with a sessile base (Fig. 124C). Even though individuals can approach one meter in diameter, it is decidedly an annual with a large taproot and is restricted to sandy soils. Robust annuals are densely branched and with white corollas and long pedicels (Fig. 127A–B). The corollas range from white to lavender or light blue (Fig. 128A), and the densely pubescent calyx lobes are deeply cut to the base (Fig. 128B–C). The gynoecium is composed of mericarps with deep wrinkles, appearing like raisins (Fig. 128D), not unlike those of *N. pallidula* and *N. chancoana*. The calyx lobes in *N. latipes* are clearly bilabiate and reflexed at the apices; they lack the swollen or expanded apices of *N. arenicola*, *N. pallidula*, and *N. spathulata*.

Johnston (1936: 31) commented upon this new species, stating that it possessed angular, black, and rugose mericarps, five large ones attached broadly on their faces and seated in sockets of the pyramidal gynobasic ovary. Smaller wedge-shaped mericarps are fitted in between, both above and below, the five principal mericarps.

Ferreyra (1961) compared *Nolana latipes* with *N. ivaniana*, and emphasized the longer pedicels and the less pubescent, long attenuate calyx lobes in typical *N. latipes*. After examining several populations in the field and many herbarium collections, it became impossible to maintain *N. ivaniana* as distinct from *N. latipes*. The types of these two species are from within the same small geographic area. Due to this change in status, the results presented in Tu et al. (2008), with *N. ivaniana* as terminal taxa (*Dillon et al. 8973*), are valid for *N. latipes*. Those results, therefore, suggested that *N. latipes* is resolved in a clade with other southern Peruvian species, including *N. arenicola*, *N. scaposa*, and *N. spathulata* (Tu et al., 2008). Cesar Vargas annotated his sheet in the Cusco herbarium (*Vargas 8470*, CUZ) as *Nolana sessilifolia* Vargas, which is an herbarium name that was never formally published.

Additional specimens examined: PERU. **Arequipa**: Prov. Islay, 7 km W of Cocachacra, 40 m.a.s.l., 24 October 1983, *M. O. Dillon & D. Dillon 3695* (F 1950173, GH); ca. 2 km N of Matarani, 16°59'S, 72°05'W, 150 m.a.s.l., 23 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8219* (E, F 2198762, GH, US); Mollendo: Alrededores de Catarindo, 17°01'S, 72°02'W, 5–10 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva, V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8973* (E, F 2276712, GH, HSP 005251, US 3512508); S of Mollendo, 17°01'S, 72°00'W, 100 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8985* (E, F 2276595, GH, HSP 5259, US 351208); Lomas de Mollendo, frente al mar, 7 October 1957, 100–200 m.a.s.l., *R. Ferreyra 12591* (USM); Lomas de Mollendo, frente al mar, 100–200 m.a.s.l., 7 October 1957, *R. Ferreyra 12600* (USM); ca. 1 km de carretera Mollendo–Mejía, 24 April 2019, *M. Quispe T. 196* (HSP 12015); alrededores del INDEHI-UNSA, Catarindo, 17°01'00"S, 72°02'09"W, 20 November 2002, *V. Quipuscoa S., N. Hidalgo A., D. Sotomayor M., & M. Rodríguez Z. 2823* (F 2293641, US 3620892); Catarindo, 17°01'02"S, 72°02'01"W, 0–20 m.a.s.l., 5 December 2002, *V. Quipuscoa S. & M. O. Dillon 2849* (HSP 000536, HUT 40134); ca. Km 157 carretera Costanera Punta de Bombón–Ilo, 17°12'41"S, 71°40'22"W, 7 m.a.s.l., 28 October 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6244* (HSP 8768, HUT 60425); Dist. Mollendo, alrededores del terminal terrestre de Mollendo, 17°00'48"S, 72°01'26"W, 152 m.a.s.l., 4 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., M. Bedoya C., & W. Ancalla C. 6464* (HSP 011388, HUT 60407); ca. 200 m al S de La Pampilla, 17°09'10"S, 71°47'13"W, 50 m.a.s.l., 13 January 2018, *V. Quipuscoa S. & M. Balvin A. 6862* (HSP 12039); Mollendo, sea level–500 ft, August–September 1932, *D. B. Stafford 56* (K); Lomas de Mollendo-Matarani, 100–300 m.a.s.l., 11 August 1949, *C. Vargas C. 8470* (CUZ); 1 km from Islay, 100 m.a.s.l., 28 September 1938, *C. R. Worth & J. L. Morrison 15709* (F 1488319, K); 8 km S of Mollendo, 3 m.a.s.l., 28 September 1938, *C. R. Worth & J. L. Morrison 15736* (GH, K).

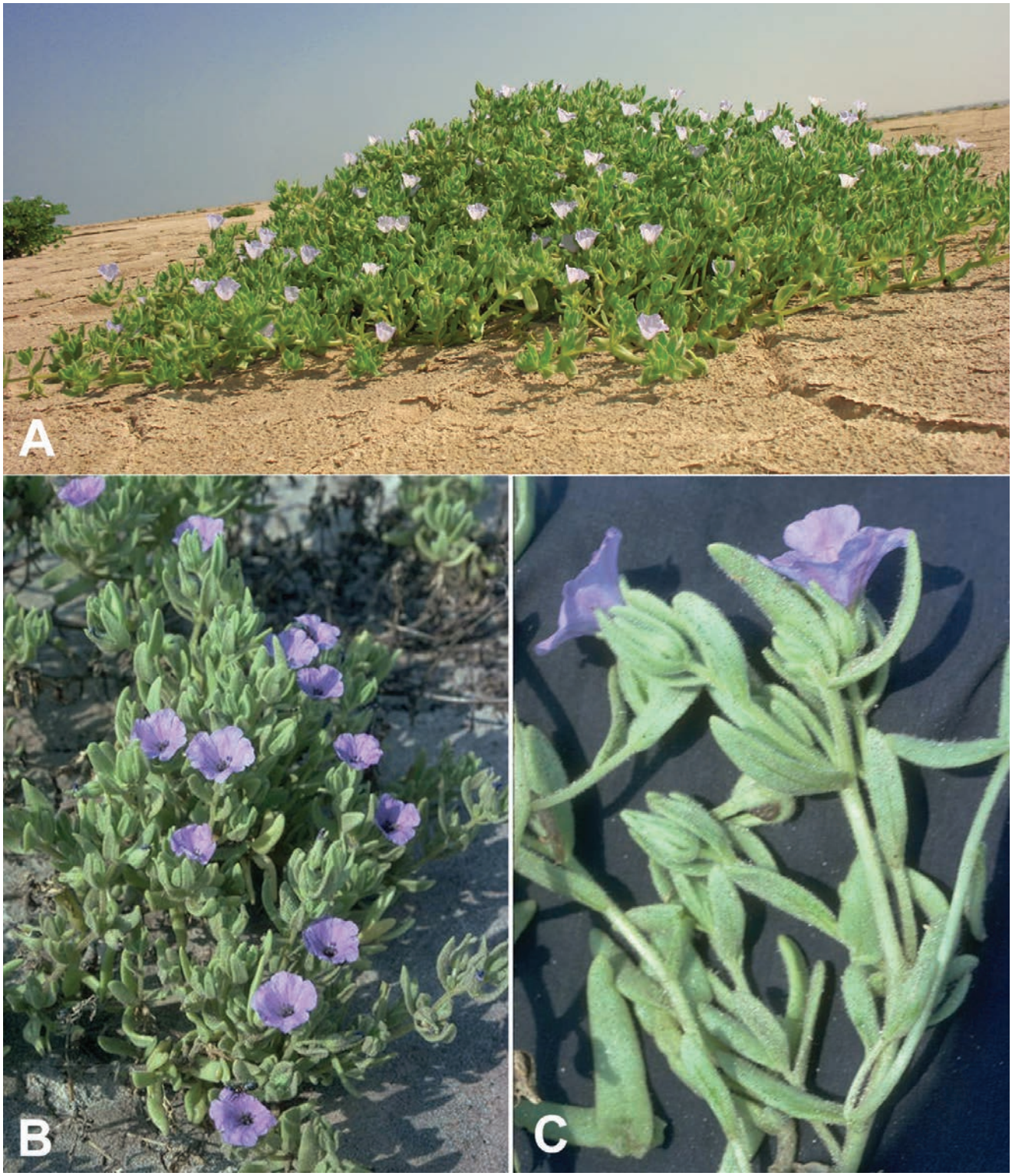


FIGURE 126. *Nolana latipes*. **A**, Prostrate shrub with lime-green herbage; **B**, Flowers are purple or violet; **C**, Oblong leaf blades, sessile base.

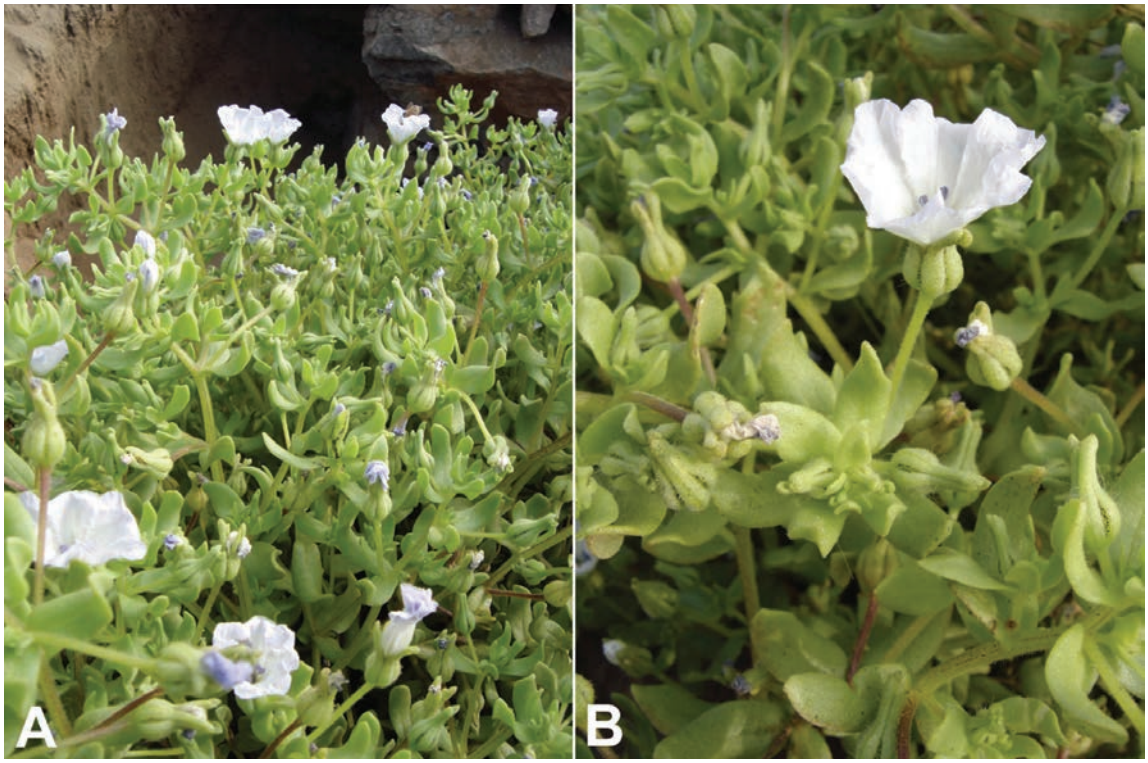


FIGURE 127. *Nolana latipes*. **A**, White-flowered individual; **B**, Closeup of white flowers and bilabiate calyces.

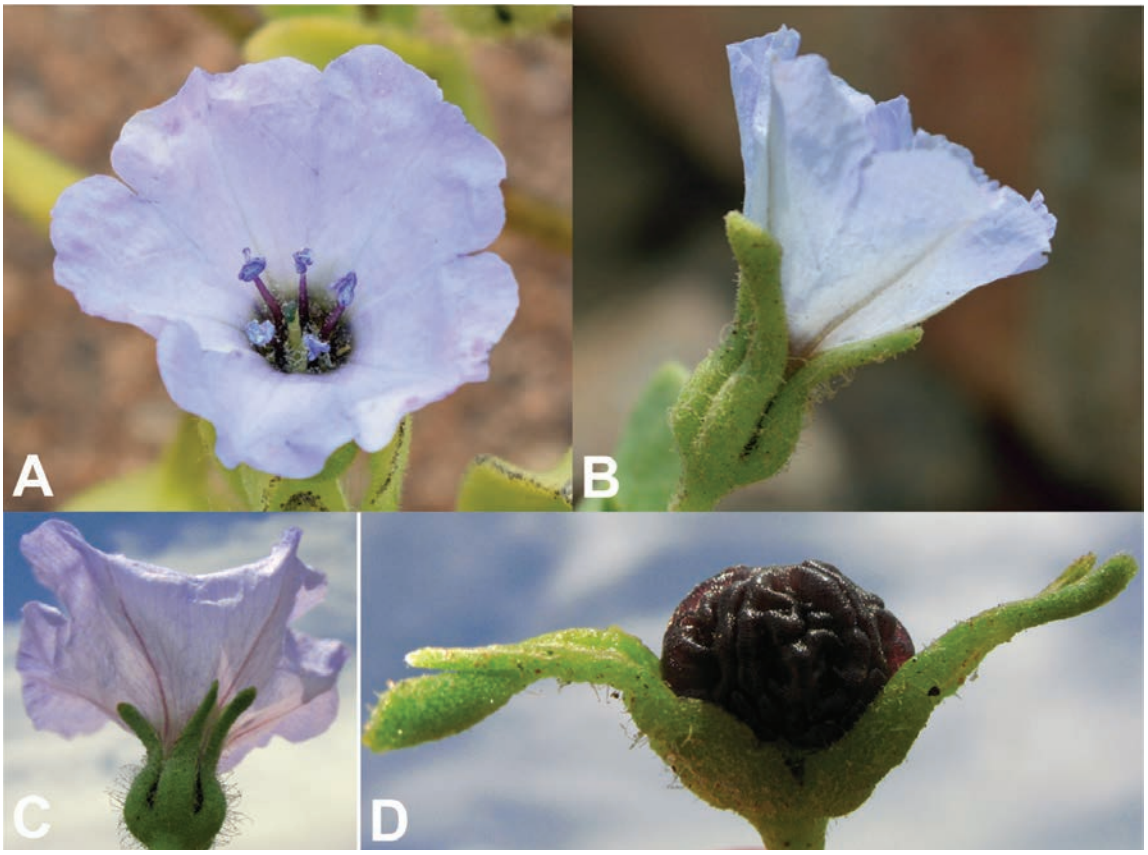


FIGURE 128. *Nolana latipes*. **A**, Light blue corolla with dark basal spot and blue anthers; **B**, Lateral view of pubescent, bilabiate calyx and flower; **C**, Densely, long pubescent on bilabiate calyx lobes; **D**, Gynoecium with ripe mericarps with deep wrinkles.

D9. ***Nolana laxa*** (Miers) I.M. Johnst., Contrib. Gray Herb. 112: 59. 1936. Fig. 129–131.

Basionym: *Dolia laxa* Miers, London J. Bot. 4: 504. 1845. TYPE: PERU. Lima: Canta, *H. Ruiz & J. Pavón s.n.* (Holotype: K [000532276]; Isotype: MA).

Digital image: Holotype of *Dolia laxa* from Royal Botanic Gardens, Kew [K000532276]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.k000532276

Annual *herbs*, erect, 25–35 mm tall; stems much-branched, ascending, 1–3 mm wide, densely pubescent with capitate-glandular trichomes. *Leaves* alternate, blades linear to lanceolate-spathulate or rhomboid, 9–20 mm long, 2–5 mm wide, apically obtuse, both adaxial and abaxial surfaces conspicuously pubescent with capitate-glandular trichomes; petioles 3–5 mm long. *Inflorescences* of solitary flowers; pedicels 5–8 mm long, densely glandular-pubescent, erect, abruptly deflexed in fruit. *Flowers* 5-merous; calyces campanulate, 4–6 mm long, 2.5–4.0 mm wide, papillose outside, glandular-pubescent inside, tube short, inconspicuous, lobes equal, 4–5 mm long, 1.0–1.8 mm wide, acute; corollas infundibularis, violet, 18–24 mm long, 8–12 mm wide, glandular-pubescent outside, lobes rounded, tube short, stamens unequal, united to tube more or less for 1/2 its length; filament widened at base, rarely pubescent; nectary disc patelliform, margin sinuous; style shorter than the longest filament, gynobasic; stigma capitate-lobate. *Mericarps* 3 (rarely 4–5), 1-seriate, globose, rugose, black, 4–5 mm long, 3.0–3.5 mm wide; seeds 4–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *laxus*, meaning flaccid, loose, and with the parts distinct and apart from one another, in an open or loose arrangement. The reference in relation to this species is obscure.

Distribution and Ecology: Peru, Department of Lima; (10–)800–1600 m.a.s.l. It is recorded from seasonally dry, rocky habitats from interior localities, 50–100 km outside of the influence of coastal fog (Fig. 129).

Nolana laxa is a rare species with a very narrow ecological and distributional range. It blooms in May and June, outside of the usual *lomas* blooming period between September to January. It most closely resembles *N. weberbaueri* and, to a lesser extent, *N. chapiensis*, two other upland or inland species recorded at higher elevations and outside of the influences of coastal fog.

Populations of these annuals can be dense and expansive, with a mass blooming when conditions are appropriate (Fig. 130A–B). *Nolana laxa* was cultivated by Dra. Roxana Freyre and included in breeding studies (Freyre et al., 2005). The difference in leaf size between field collected (Fig. 131A) and cultivated material from flowerpots is quite extraordinary (Fig. 131B). The overall size of the flowers did not vary to the degree that the leaves and calyces did in the cultivated plants. The number of mericarps is reduced to three, and they are globose, smooth, and shiny (Fig. 131A).

Johnston (1936: 59) believed that *Nolana laxa* was the most northern Peruvian species. He was not aware of the distribution of *N. humifusa* and *N. gayana*. He stated that *N. laxa* was obviously related to *N. weberbaueri* (Dept. Ica). No molecular data is currently available for the latter species.

Additional specimens examined: PERU. Lima: Prov. Carabayllo, San Benito, 800–1220 m.a.s.l., 21 February 2010, *A. Cano, H. Trinidad, P. Gonzáles, & E. Navarro 19588* (F 2295074, F 2295073); Prov. Lima, Chosica, 800 m.a.s.l., 19 June 1927, *N. Espasto s.n.* (MOL00004729); Chosica, 800 m.a.s.l., 29 May 1949, *R. Ferreyra 6112* (USM 81179); Chosica, 800–900 m.a.s.l., 28 May 1955, *R. Ferreyra 11072* (K [2 sheets], USM 81178); Huaico, entre Lurín and San Bartolo, 10 m.a.s.l., 21 May 1972, *R. Ferreyra 17962* (USM 81295); Prov. Canta, Dist. Santa Rosa de Quives, 11°41'31"S, 76°48'59"W, 1057 m.a.s.l., *P. Gonzáles 1710* (E00700810, USM 258761); Hacienda Santa Clara, June 1941, LUDEÑA (USM 12565); Chosica, [2800 ft], September 1932, *D .B. Stafford 51* (K); San Lorenzo, riahuelo de Cucucha, 1600 m.a.s.l., 1 May 1993, *G. Vilcapoma S. 2414* (USM 277761, USM 289241).

D10. ***Nolana lycioides*** I.M. Johnst., Contrib. Gray Herb. 112: 70. 1936. TYPE: PERU. Arequipa: Prov. Islay, Mollendo, 4 October 1902, 300 m, *A. Weberbauer 1517* (Holotype: B, not seen; Isotype: GH [GH00282334]). Fig. 132–135.

Digital image: Isotype of *Nolana lycioides* from Harvard University Herbaria, Cambridge [GH00282334]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282334

Homotypic synonym: *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *confinis* Mesa, Fl. Neotrop. Monogr. 26: 103. 1981.

Much-branched, s*ubshrubs;* roots 11–18 cm long, 6–7 mm wide; stems erect to ascending, 16–50 (–100) cm long, divaricately branched, pilose with glandular-capitate trichomes. *Leaves* fasciculate, blades linear-lanceolate to linear-spathulate, (3–)5–25(–30) mm long, 0.5–0.9 mm wide, apically obtuse, base attenuate, pilose with capitate-glandular trichomes, margin strongly revolute, sessile. *Inflorescences* of solitary flowers, axillary and terminal; pedicels 5–10 mm long, hirsute-glandular, recurved in fruit. *Flowers* 5-merous; calyces campanulate, 4.0–5.5 mm long, 3–4(–5) mm in diam., hirsute-glandular outside, glandular trichomes to 1 mm long, the tube 0.5–2.0 mm long, 1.5–2.5 mm in diam., lobes 5, unequal, lanceolate, 2.5–3.0 mm long, 1.0–1.2 mm wide, margins revolute, acuminate, scabrous-glandular pubescent inside and out; corollas infundibularis, blue, 13–22(–27) mm long, 11–13(–15) mm wide, lobes obtuse, subequal, tube hirsute outside, villous inside; stamens unequal, two larger 10–11 long, united to tube for 1/2 its length, three smaller 8.0–8.5 mm long, united to tube for 1/3 its length; nectary disc patelliform, sinuous, gynobasic, style 9–10 mm long. *Mericarps* 5–9, unequal, 4 large and 5 small, 1-seriate, globose, unequal, black, punctate, 1.6–2.5 mm long; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *lycium*, a thorny plant, and *-oides*, like, resembling, having the form or nature of *Lycium*. Johnston (1936) mentioned that the loosely branched habit suggests overall similarity to some members of *Lycium* (Solanaceae).

Distribution and Ecology: Peru, Departments of Ancash, Arequipa, Moquegua, and Tacna; Chile, Regions of Tarapacá and Antofagasta; 300–800(–2100) m.a.s.l.

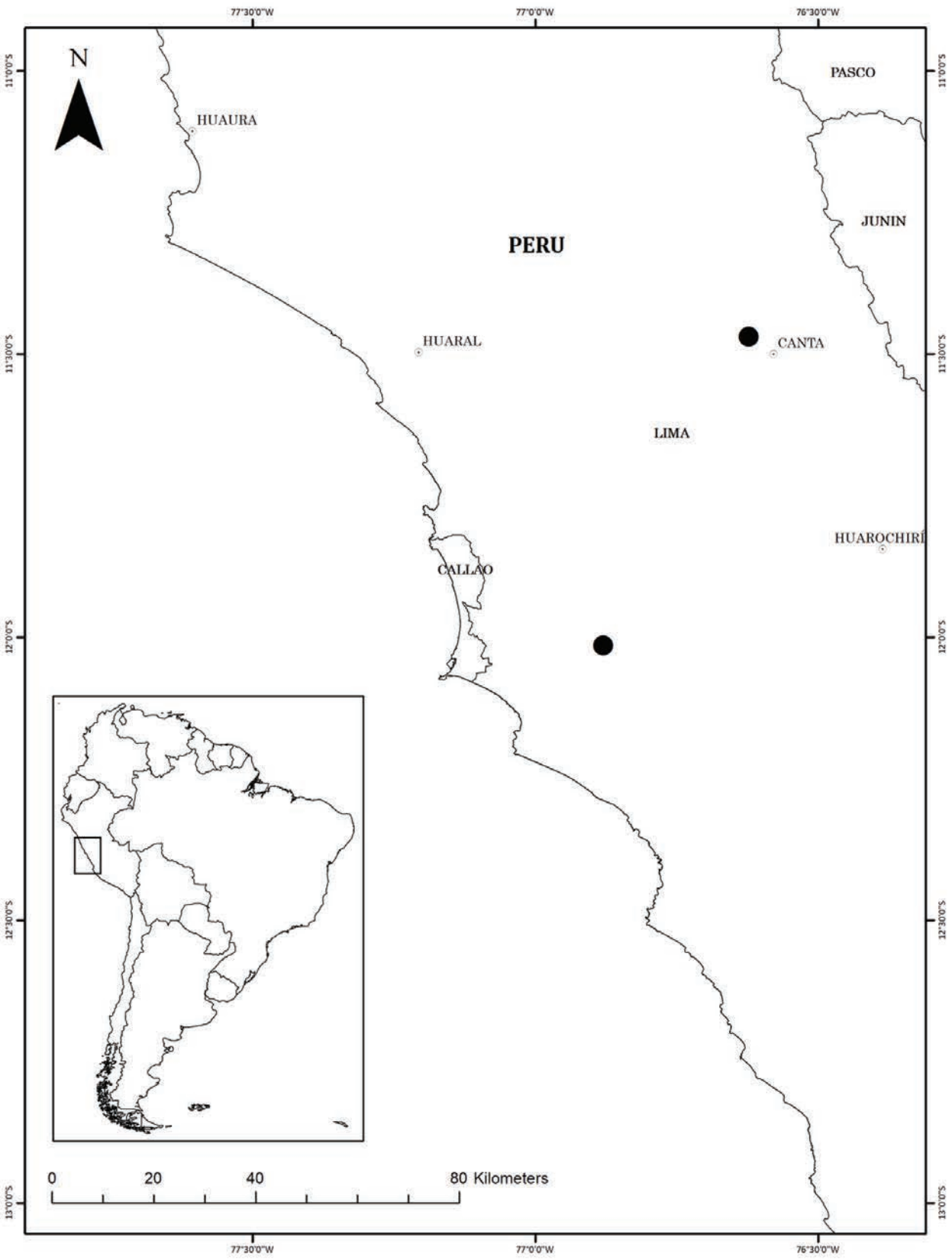


FIGURE 129. Distribution of *Nolana laxa* (Miers) I.M. Johnst.

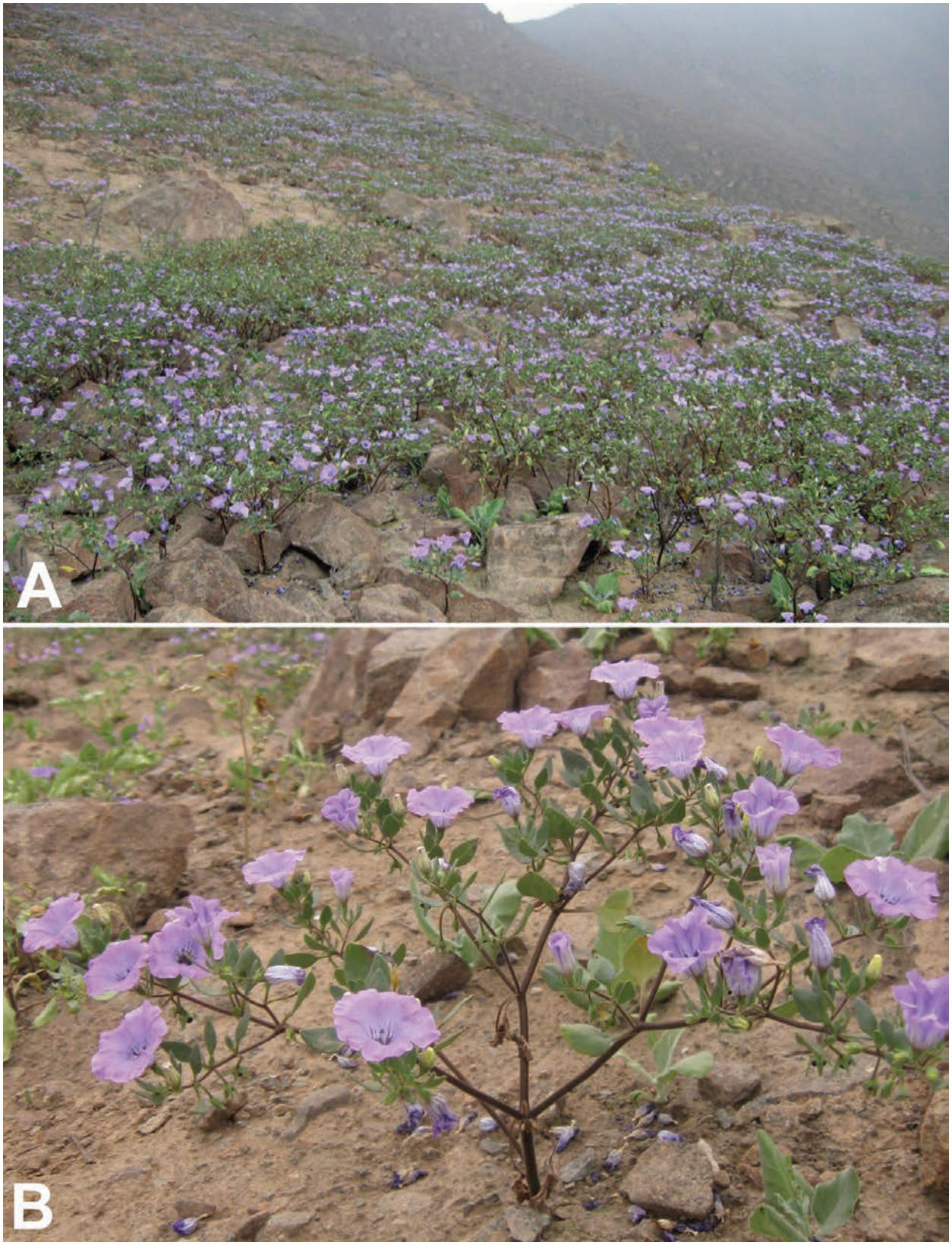


FIGURE 130. *Nolana laxa*. **A**, Population with mass blooming; **B**, Annuals branched above the base. Photographs by Asunción Cano Echeverría.

FIGURE 131. *Nolana laxa*. **A**, Field grown plant with small leaves, shiny mericarps reduced to three; **B**, Plant transplanted and grown in cultivation. Photographs by Rosanna Freyre.

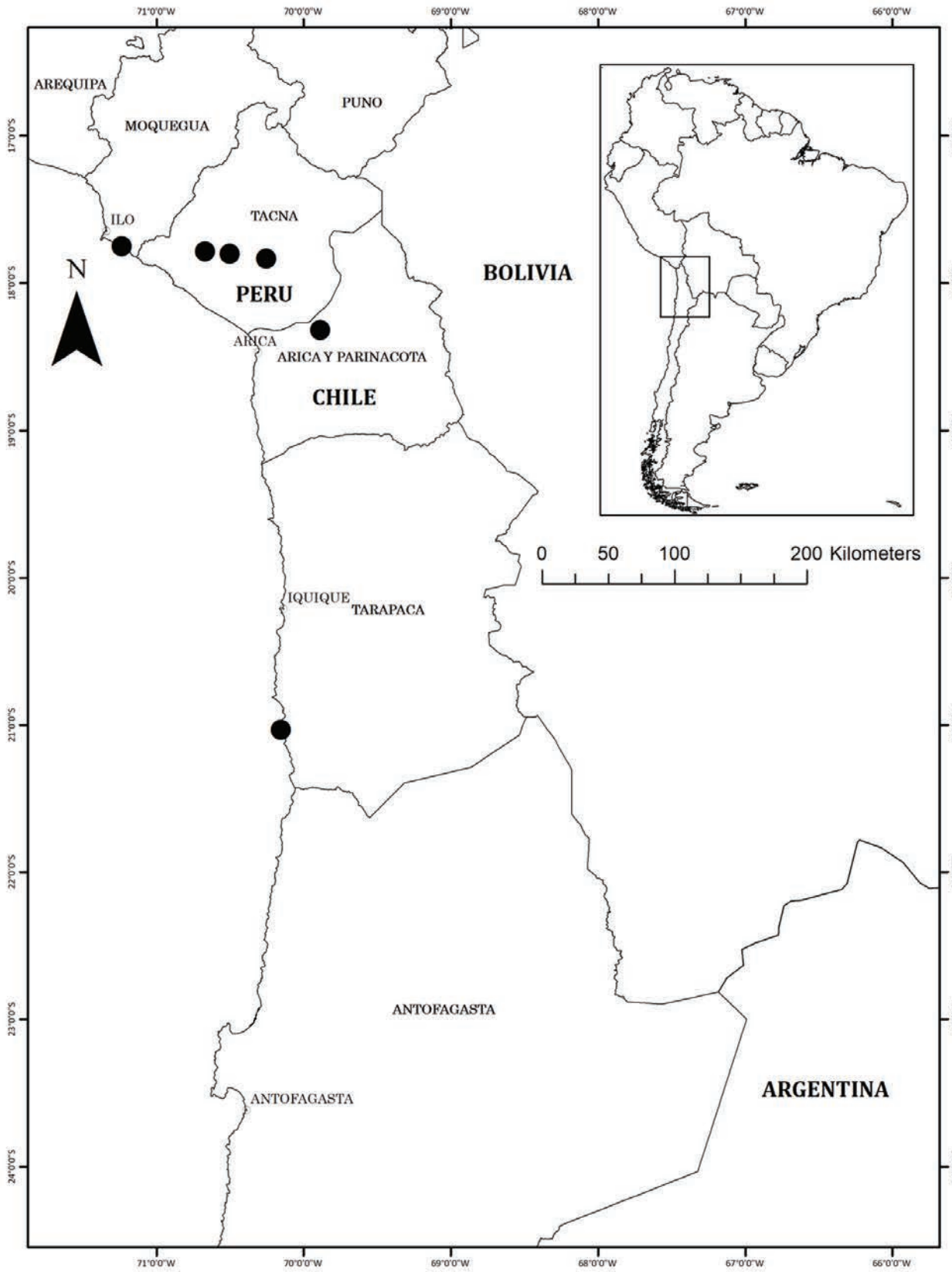


FIGURE 132. Distribution of *Nolana lycioides* I.M. Johnst.

FIGURE 133. *Nolana lycioides*. **A–B**, Woody individuals reaching over one meter tall.

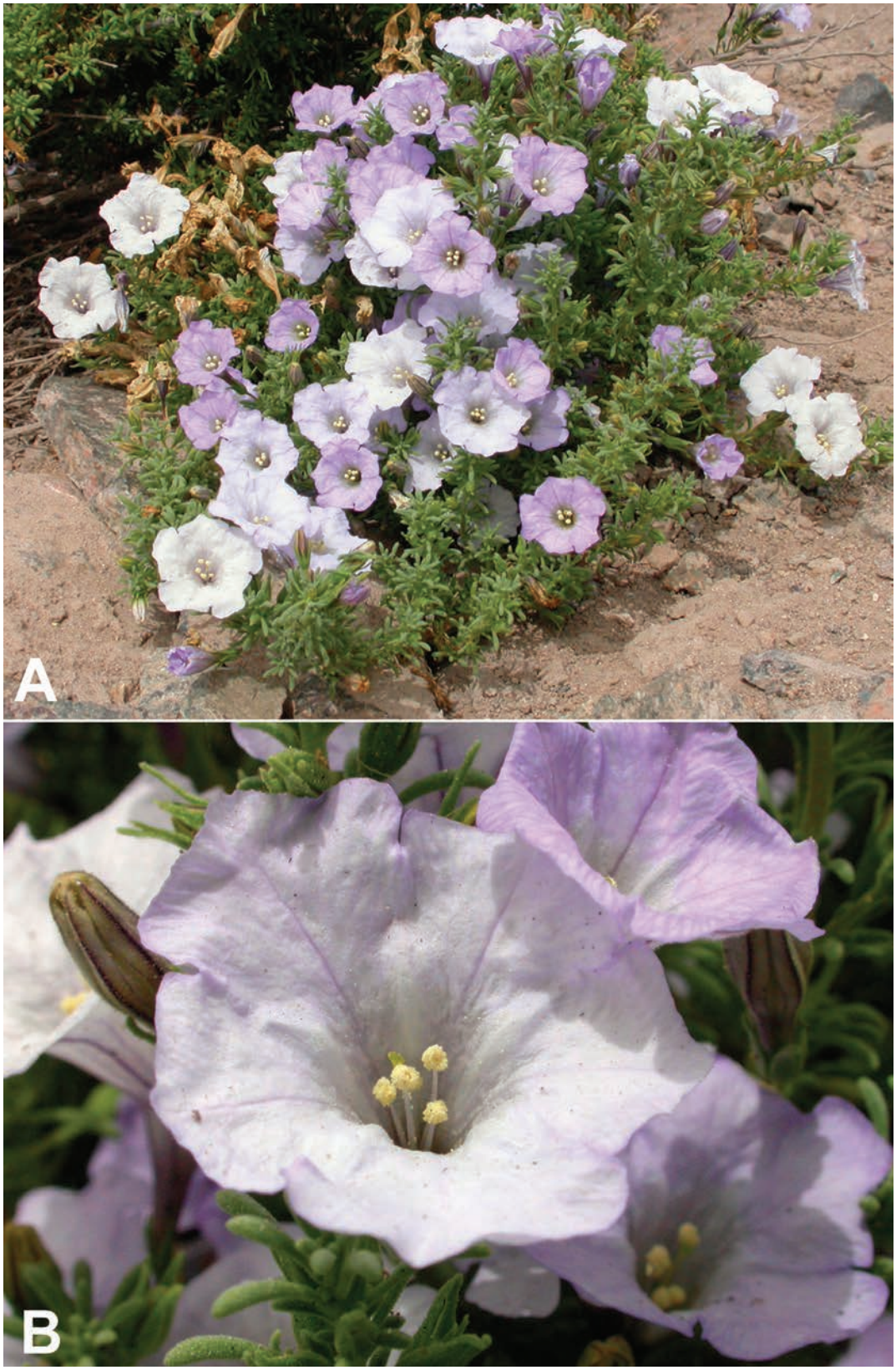


FIGURE 134. *Nolana lycioides*. **A**, Corollas are variously colored from lavender to white; **B**, Anthers have cream or yellowish pollen.

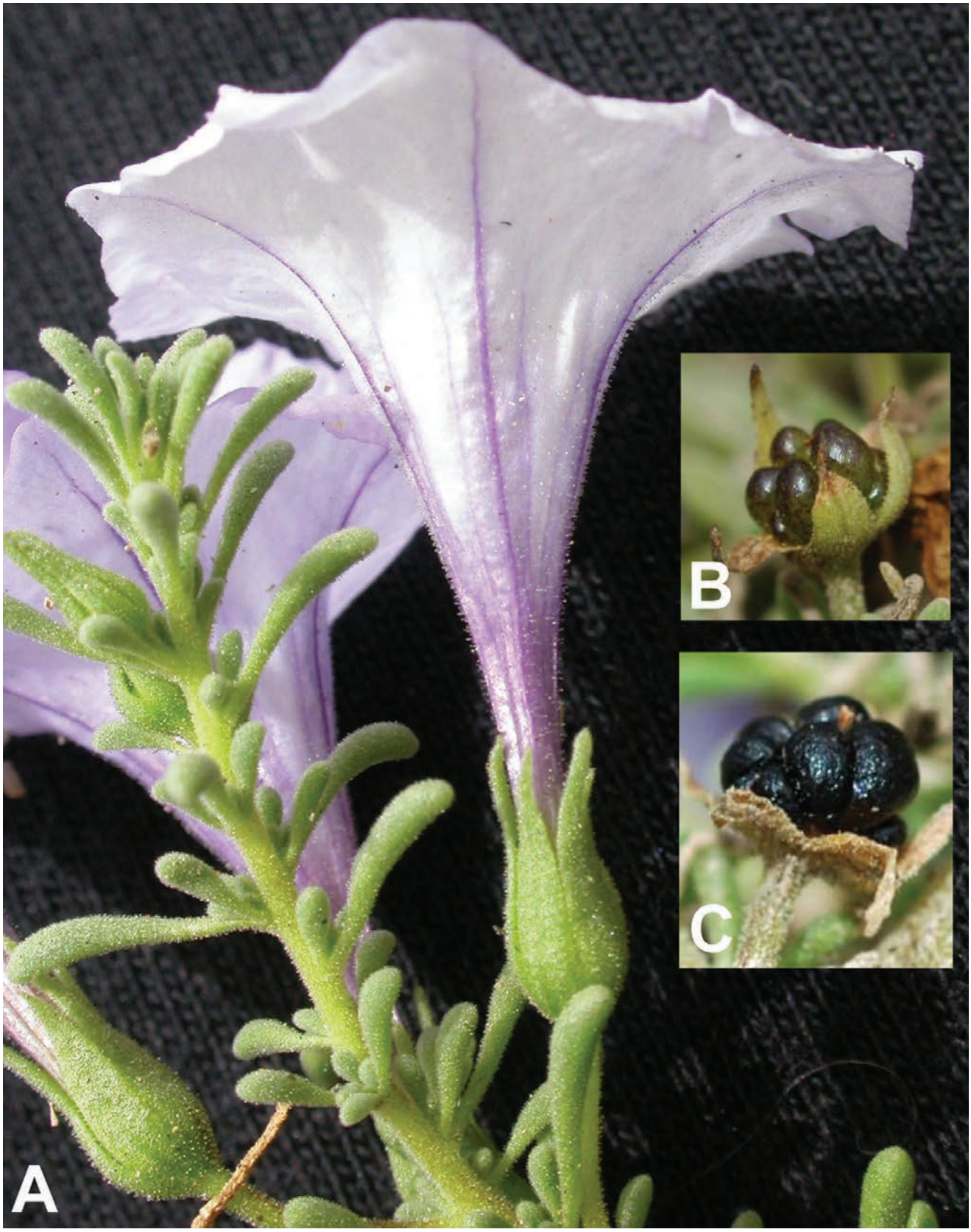


FIGURE 135. *Nolana lycioides*. **A**, Leaves and floral parts with short, capitate-glandular trichomes; **B–C**, Globose mericarps with maturing color changes.

(Fig. 132). It is recorded from rocky, near-coast habitats in Chile; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006). In Peru, it is farther inland, at higher elevations but within range of coastal fog.

Nolana lycioides is represented by a disjunct distribution in both Peru and Chile, along with *N. adansonii* and *N. gracillima*. They are decidedly woody, and individuals can reach large sizes (Fig. 133A), with stems reaching over one meter in length (Fig. 133B). The corollas are variously colored from lavender to white (Fig. 134A), and the anthers have cream or yellowish pollen (Fig. 134B). Leaves and floral parts, including the slender corollas, are covered with short, capitate-glandular trichomes (Fig. 135A). The mericarps are globose and undergo a color change as they mature to a deep black (Fig. 135B–C).

Ferreyra (1961) suggested that this species was closely related to *N. confinis*; however, the overall floral and leaf morphology allow differentiation. The data from molecular studies suggest some connection with *Nolana pallida* (Dillon et al., 2007c) and *N. volcanica* (Dillon et al., 2009; Tu et al., 2008). In Dillon et al. (2009), using the LEAFY second intron, one accession identified as *N. lycioides* (*Weigend et al. 8414*) is recovered with *N. galapagensis*. Analysis of additional material will be needed before undue emphasis can be placed upon this result.

The northern range has been extended with the addition of a collection from the Department of Ancash. It is notable that *Nolana inflata* also exhibits a similar geographic extension, suggesting biogeographical connections in the recent past.

Cesar Vargas collected material of *Nolana lycioides* and proposed the herbarium name, *N. verticillata* Vargas, based upon *C. Vargas C. 8613* (CUZ). There is no evidence that the name was ever published.

Additional specimens examined: CHILE. **Tarapacá:** Alto Punta Lobos, 21°02'S, 70°09'W, *R. Pinto s.n.* (SGO 142974). PERU. **Ancash**: Prov. Ocros, Dist. Huanchay, Huayia 4 km before a cross to Ocros on road to Cajatambo, 10°37'31"S, 77°27'29"W, 625 m.a.s.l., 8 March 2014, *P. Gonzales, M. Syfert, E. McAlister, & D. Whitmore 2968* (BM001134811). **Arequipa**: Prov. Islay, Mollendo. Quebrada Guerreros, carretera a Matarani, 16°55'S, 72°03'W, 850 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8969* (CONC, E, F 2776711, GH, HSP 005247, SGO, US 3512509); 10 km S of Mollendo, near sea level, 23 April 1939, *W. J. Eyerdam 25174* (K, USM); Mollendo, coastal flats between Mollendo and Mejia, [6–10 ft], 8 April 1939, *W. B. Gourlay 122* (E00793144, K); Al Sur de la ciudad de Mollendo, 50 m.a.s.l., 6 November 2001, 17°02'31"S, 72°00'13"W, *V. Quipuscoa S., N. Hidalgo A., D. Sotomayor M., & M. Rodríguez Z. 2808* (E, F 2293634, GH, HUT 40142, SGO, US); sur de la Mollendo, 17°02'31"S, 72°00'25"W, 50 m.a.s.l., 5 December 2002, *V. Quipuscoa S. & M. O. Dillon 2841* (HSP 000534, US 3634111); entre Matarani y Mollendo, 17°00'18"S, 72°02'36"W, 140 m.a.s.l., 21 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2913* (HSP 000545); entre Matarani and Mollendo, 17°00'18"S, 72°02'36"W, 140 m.a.s.l., 21 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2915* (HSP 000547); Mollendo, 732 m.a.s.l., 27 February 2015, *D. Ramos A. & C. Fernández A. 1839* (HSP 007995); Mollendo, 2000 ft, 15 September 1937, *D. B. Stafford 880* (BM000941273, F 1506407, K); Tambo; Lomas Chucarapi, 500–600 m.a.s.l., 12–13 November 1949, *C. Vargas C. 8613* (CUZ); Islay, road from Arequipa to Mollendo, 16°55'04"S, 72°02'57"W, 836 m.a.s.l., 22 April 2006, *M. Weigend & Ch. Schwarzer 8414* (F 2295139). **Moquegua**: Prov. Ilo, Lomas de Mostazal, 100–200 m.a.s.l., 12 October 1997, *M. Weigand & H. Förther 97/829* (F 2211294, HUT 34099, USM 137699). Prov. Mariscal Nieto Province, Moquegua, cerca de Moquegua, 800 m.a.s.l., 1 December 1959, *C. Vargas C. 13079* (CUZ). Tacna: Prov. Tacna, Lomas of Tacna, ca. 54 km N of Tacna, 6–7 km E on road to Curibaya, turn-off Pan-American Highway at KM 1238, 530–620 m.a.s.l., 20 October 1983, *M. O. Dillon & D. Dillon 3673* (CONC, E, F 1950176, GH, K, USM); **Tacna**: ca. 99 km SE of Moquegua, road E to Shintari, 17°47'S, 70°40'W, 810 m.a.s.l., 26 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8227* (CONC, E, F 2199325, GH, K, SGO, US); Lomas de Sama Grande, 500–600 m.a.s.l., 4 October 1957, *R. Ferreyra 12514* (K, USM); lomas cerca al Morro Sama, 500–600 m.a.s.l., 6 October 1957, *R. Ferreyra 12541* (USM); Formación de lomas 55 km al N de Tacna, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11646* (USM); 60 km al N de Tacna, 700 m.a.s.l., 7 October 1957, *R. Ferreyra 12640* (USM); lomas cerca al Morro Sama, 500–600 m.a.s.l., 6 October 1957, *R. Ferreyra 12548* (USM); 500–600 m.a.s.l., 4 October 1957, *R. Ferreyra 12501* (USM); La Yarada, 50 km N de Tacna, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11652* (USM); 10 km N of Tamasiri, Pan-American Highway N of Tacna, Lomas de Sama, 200 m.a.s.l., 25 November 1957, *P. C. Hutchison & J. K Wright 1846* (E00793140, F 1559988, K, US 2406447, USM).

D11. ***Nolana pallidula*** I.M. Johnst., Contrib. Gray Herb. 112: 31. 1936. TYPE: PERU. Prov. Tacna: near Tacna, ca. 650 m, August 1925, *E. Werdermann 728* (Holotype: GH [00282332]; Isotypes: B 10024850, BM [BM000021204], CONC [CONC 55627], E [E00259358], F [F 564173], G [G00383934], K [K000532282], S [S04-2773], UC [UC289206], US [US 3318610, US00507019, US 1444765, US00121960]). Fig. 14, 136–138.

Digital image: Holotype of *Nolana pallidula* from Harvard University Herbaria, Cambridge [GH00282332]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282332

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *spathulata* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 137. 1981.

Annual *herbs*, decumbent, 10–50 cm tall; stems succulent, branches 3–6 mm in diam., internodes 1–6 cm long, glabrescent. *Leaves* alternate, blades spathulate or narrowly oblanceolate, 15–40 mm long, 2–6 mm wide, succulent, glabrous, apically acute, or, rarely, obtuse, base attenuate, sclerified, sessile. *Inflorescence* of solitary flowers; pedicels 2–8 mm long. *Flowers* 5-merous; calyx

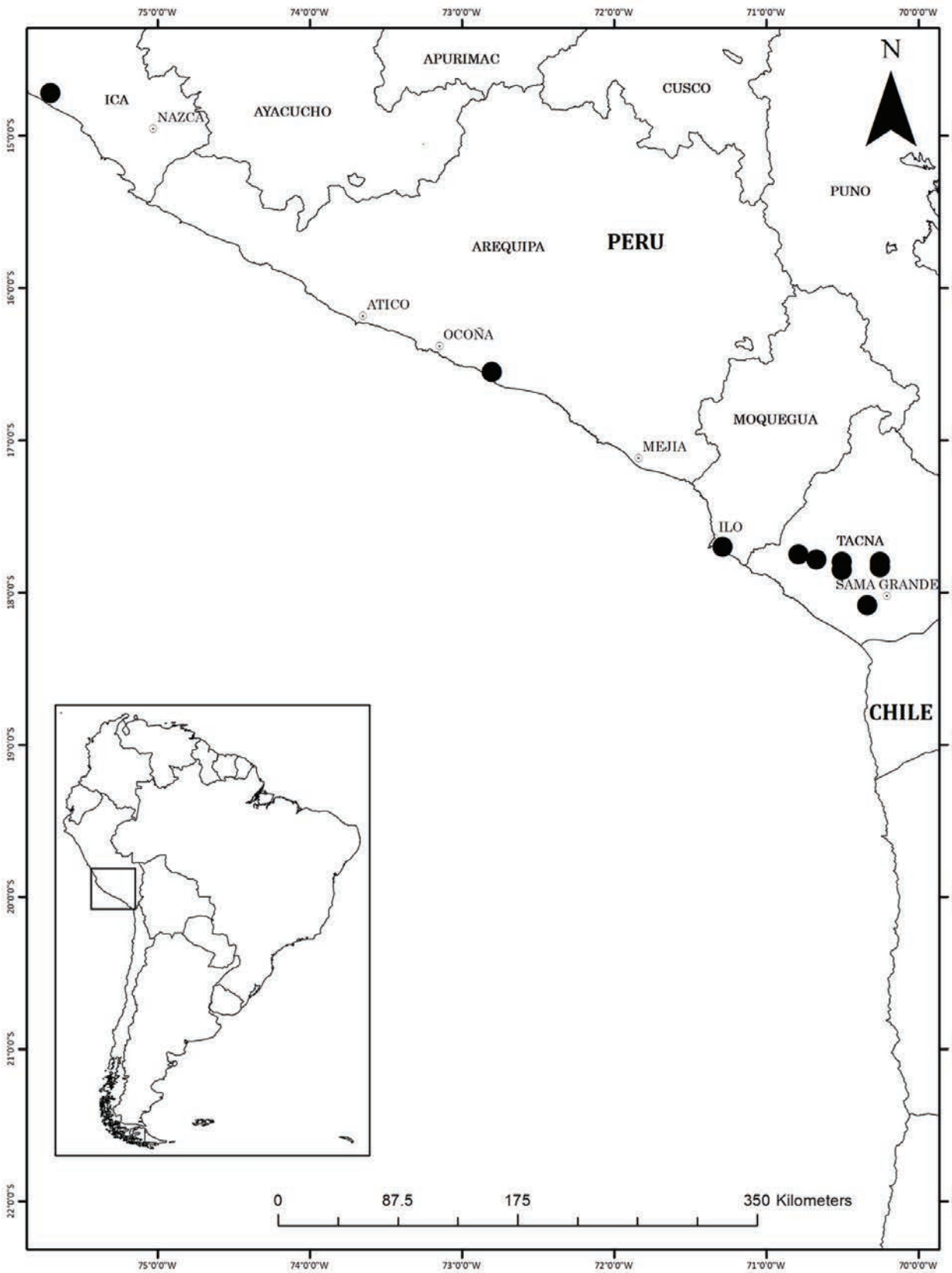


FIGURE 136. Distribution of *Nolana pallidula* I.M. Johnst.

turbinate, fleshy, 18–25 mm long, 5–7 mm in diam., more or less bifid, 5-costate; tube short, 5-lobed, interlobular region stramineous and plicate; lobes 6–10 mm long, 1.0–2.5 mm wide; corolla infundibuliform, violet, 20–30 mm long, 18–22 mm wide above, lobes obtuse, unequal, tube short, villous inside; stamens unequal, 16–18 mm long, united to tube for 1/3 its length, densely retrorse-villous; style 18–20 mm long. *Mericarps* 10–12, the 5 larger 3.5–5.5 mm long, 2–4 mm wide, the smaller 1.5–2.5 mm long, 1–2 mm wide, reniform, black, shiny, rugose; seeds 4–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *pallens*, pale, and *pallidulus*, somewhat pale, and refers to the overall aspect of the foliage.

Distribution and Ecology: Peru, Departments of Arequipa, Ica, Moquegua and Tacna, ranging > 800 km; (50–)300–600(–900) m.a.s.l. It is recorded from southern Peru in inland sites (Fig. 136).

Nolana pallidula is an annual with a spreading or decumbent habit (Fig. 137A), or more erect in some environments (Fig. 138A). The strap-shaped leaves have no obvious petioles and appear pale, gray green (Fig. 137B) or darker green (Fig. 138A–C). In the dissected corolla (Fig. 137C), the densely pubescent bases of the anther filaments have retrorse trichomes (Fig.137C) and white pollen. The corollas are blue with white throats (Fig. 138B); the bilabiate calyx lobes are illustrated in Fig. 137B. The calyx apices are expanded and laterally fused or connate to one

FIGURE 137. *Nolana pallidula*. **A**, Spreading to decumbent annuals; **B**, Strap-shaped, pale, gray-green leaves; **C**, Dissected corolla with retrorse trichomes at bases of the anther filaments and white pollen.

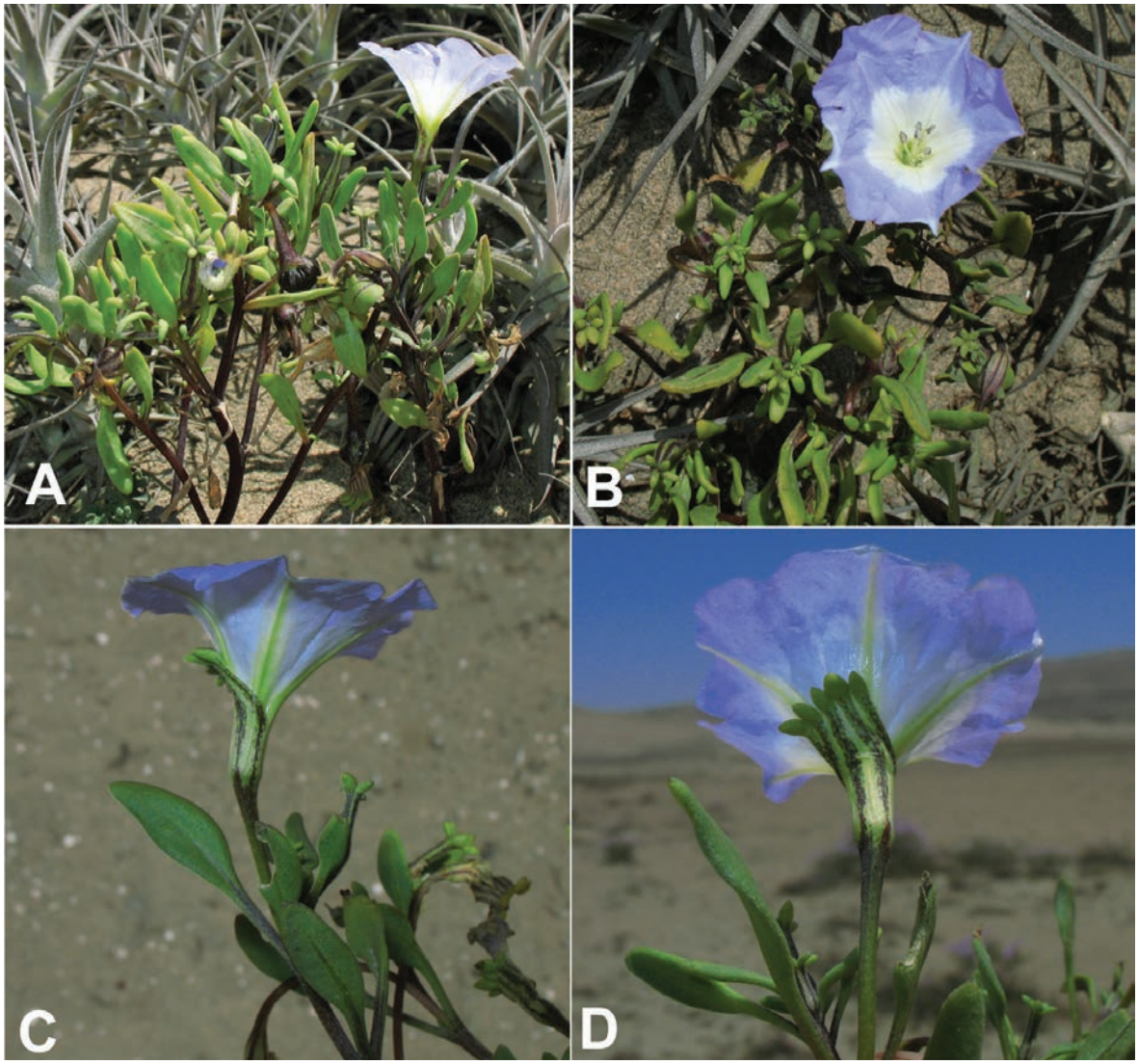


FIGURE 138. *Nolana pallidula*. **A**, Flowering plant growing with *Tillandsia* in pure sand; **B**, Slightly zygomorphic corollas with white throats; **C**, Lateral view of flower illustrating zygomorphic calyx lobes; **D**, All calyx lobes connate and to one side.

side (Fig. 138C), as in *N. spathulata*; however, the leaves are distinctive in shape and color. The anthers are obviously different between these two species. Its complete lack of leaf pubescence separates it from many other Peruvian *Nolana* species.

A few accessions from Tacna represent diminutive individuals and are here assigned to *Nolana pallidula* because of the salient characters of being entirely glabrous and having long calyx lobes. The collections in this group are *Dillon et al. 8228* (F2199326), *Dillon et al. 8229* (F 2199328), and *Dillon et al. 8237* (F 2199338). Future studies may suggest formal recognition of these populations.

Ferreyra 8876 was distributed to GH under the name *Nolana pallida*; however, that same number was applied to a collection by Ferreyra of *Nolana pallidula*.

In the Lomas of Sama Grande, it was observed that the branches bent inward during senescence, curling into a sphere, with the characteristics of a tumbleweed, uprooting and rolling over the dunes (Fig. 14).

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, Loma Formation entre Camaná y Ocoña, 300–350 m.a.s.l., 13 November 1952, *R. Ferreyra 8876* (GH, K [2 sheets], USM). **Ica**: Dist. Santiago, Lomas de Amára, 14°43'47"S, 75°41'48"W, 780 m.a.s.l., 18 November 2007, *V. Quipuscoa, M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3505* (HSP 000652). **Moquegua**: Prov. Ilo, Frente a terminal terrestre de Ilo, 50 m.a.s.l., 22 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2925* (HSP 000552); Lomas de Ilo, 17°41'26"S, 71°14'35"W, 597 m.a.s.l., 15 November 2007, *V. Quipuscoa, M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3429* (HSP 002677). **Tacna**: Prov. Tacna, ca. 21 km SE of Moquegua/Tacna border, Km 1225 S of Lima, 850–900 m.a.s.l., 16 February 1983, *M. O. Dillon, P. Matekaitis, & L. Watanabe 3388* (E, F 1919528, GH); Lomas of Tacna; ca. 54 km N of Tacna, 6–7 km E on road to Curibaya; turn-off Pan-American Highway at Km 1238,

530–620 m.a.s.l., 20 October 1983, *M. O. Dillon & D. Dillon 3666* (E, F 1950177, GH, K); Lomas of Tacna, ca. 45 km N of Tacna, ca. 3 km E of Pan-American Highway, 560 m.a.s.l., 9 November 1983, *M. O. Dillon & D. Dillon 3888* (CONC, E, F 1950506, GH, K, SGO, US); ca. 20 km WNW of Tacna on Pan-American Highway (Pampa Alto de La Alianza), Km 1260–1261, 515 m.a.s.l., 14 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4759* (CONC, E, F 2014377, GH, HUT 22943, K, SGO); Prov. Ilo, ca. 15 km SE of Ilo, 17°42'S, 71°17'W, 340 m.a.s.l., 26 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8224* (CONC, E, F 2199320, GH, SGO); ca. 84 km SE of Moquegua en route to Tacna, ca. 2 km E of Panamericana Hwy., 17°45'S, 70°47'W, 810 m.a.s.l., 26 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8226* (CONC, E, F 2199324, GH, SGO); ca. 99 km SE of Moquegua, road E to Shintari, 17°47'S, 70°40'W, 810 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8228* (F 2199326); ca. 99 km SE of Moquegua, road E to Shintari, 17°47'S, 70°40'W, 810 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8229* (F 2199328); ca. 99 km SE of Moquegua, road E to Shintari, 17°47'S, 70°40'W, 810 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8234* (F 2199330); ca. 99 km SE of Moquegua, road E to Shintari, 17°47'S, 70°40'W, 810 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8237* (E, F 2199338, GH); Tomasiri, ca. 35 km N of Tacna, ca. 116 km SE of Moquegua, 17°51'S, 70°30'W, 450 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8238* (F 2199341); Loma formation N of Tacna, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11648* (K); Lomas de Tacna, 800–900 m.a.s.l., 4 October 1957, *R. Ferreyra 12523* (GH, K); Tacna, 10 km N of Tamasiri, Pan-American Highway N of Tacna, Lomas de Sama, 200 m.a.s.l., 25 November 1957, *P. C. Hutchison 1848* (F 1559987, GH, K, UC, US 2406449); 20 km del peaje de Tacna, 17°49'56"S, 70°32'19"W, 438 m.a.s.l., 15 November 2007, *V. Quipuscoa, M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3413* (HSP 002669); Km 2.5 on road Tacna to La Yarda, Rio Caplina, ca. 200 m.a.s.l., 10 October 1997, *M. Weigend & H. Förther 97/823* (F 2211304)**. No exact locality**. Tacna, September 1864, *R. Pearce s.n.* (BM000941311).

D12. ***Nolana pearcei*** I.M. Johnst., Contrib. Gray Herb. 112: 58. 1936. TYPE: PERU. Prov. Tacna: Tacna, September 1864, *R. Pearce s.n.* (Holotype: K [000532278]; Isotype: BM [BM00021199]). Fig. 139–140.

Digital image: Holotype of *Nolana pearcei* from Royal Botanic Gardens, Kew [K000532278]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.k000532278

Homotypic synonym: *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *aplocaryoides* (Gaudich.) Mesa, Fl. Neotrop. Monogr. 26: 107. 1981.

Annual *herbs*, erect, single-stemmed, 3-branched above, 20–30 cm tall, branches villous with flagelliform trichomes. *Leaves* alternate, blades elliptic or narrowly lanceolate, 10–20 mm long, 3–6 mm wide, villous with flagelliform trichomes, margin revolute, apically acute, bases abruptly attenuate; petioles 6–10 mm long. *Inflorescences* of sessile flowers at branch apices. *Flowers* 5-merous, pedicels to ca. 1 mm long; calyces 6–8 mm long, tube cupulate, 2–3 mm in diam., lobes 1.5–2.5 mm long, linear, unequal; corollas infundibularis, violet, 20–25 mm long, puberulent outside, tube briefly pilose inside, to ca. 1.3 mm in diam., lobes 10–15 mm diam.; stamens unequal, 6–8 mm long, glabrous. *Mericarps* unknown. Chromosome number: unknown.

Etymology: The species epithet commemorates Richard Pearce (b. 1835–d. 1868), a British plant collector who traveled to South America to collect in Bolivia, Chile, and Patagonia in 1859. He visited Peru in 1862 and was the collector of the species described by Johnston (1936).

Distribution and Ecology: Peru, Department of Tacna; no details concerning its environmental preferences (Fig. 139).

Nolana pearcei has not been recollected since the type collection (Fig. 140A–B), and its relationships have not been tested. The overall habit of these annual plants suggests *Nolana laxa* or *N. rhombifolia*, but mericarps have not been recorded. Further speculation as to its closest relatives must await a more complete knowledge of its morphology. Johnston (1936: 58) commented on this new species, noting that the type consists of only the upper part of the plant and was flowering at the time of the collection. The material at the British Museum shows the root but is a poorer specimen. Johnston said it was a very distinct species and related it to *N. aplocaryoides*; however, until it is recollected, this conjecture cannot be tested.

Additional specimens examined: No additional collections of this species have been made in the field or encountered in herbarium studies.

D13. ***Nolana platyphylla*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 60. 1936. Fig. 141–142.

Basionym: *Bargemontia platyphylla* I.M. Johnst., Contrib. Gray Herb. 85: 175. 1929. TYPE: PERU. Moquegua: hills SE of Moquegua, "with other desert annuals, flowers sky-blue, leaves fleshy," 17°12'S, 70°50'W, 1500–1600 m, March 1925, *A. Weberbauer 7455* (Holotype: F [552696]; Isotypes: G [G00383559, G00383562], GH [GH00282358]; K [K000532277], B, not seen, S [S04-2774], US [US 1474516, US00121974], USM [USM 242127, USM000554]).

Digital image: Isotype of *Bargemontia platyphylla* from Harvard University Herbaria, Cambridge [GH00282358]. https://s3.amazonaws.com/huhwebimages/81951CF00D8D4CB/type/full/282358.jpg

Homotypic synonym: *Nolana laxa* (Miers) I.M. Johnst., Contr. Gray Herb. 112: 59. 1936, fide Mesa-M., 1981.

Erect, annual *herbs*, 10–15 cm tall; stems simple to branched, ascending or procumbent, internodes 20–60 mm long, villous. *Leaves* alternate, blades lanceolate to lanceolate-ovate, 20–25 mm long, 7–10 mm wide, obscurely penninerved, basally attenuate, apically acute, sparsely villous with dendritic trichomes branched distally; petioles 5–10 mm long. *Inflorescences* of solitary flowers; pedicels villous, 2–15 mm long. *Flowers* 5-merous; calyces cupulate, 8–10 mm long, villous outside, tube 2–3 mm long, 2.0–2.5 mm wide, lobes lanceolate, acuminate, ca. 7 mm long, unequal, erect; corolla infundibularis, violet, ca.10 mm long, lobes rounded, tube ca. 2 mm long and ca.

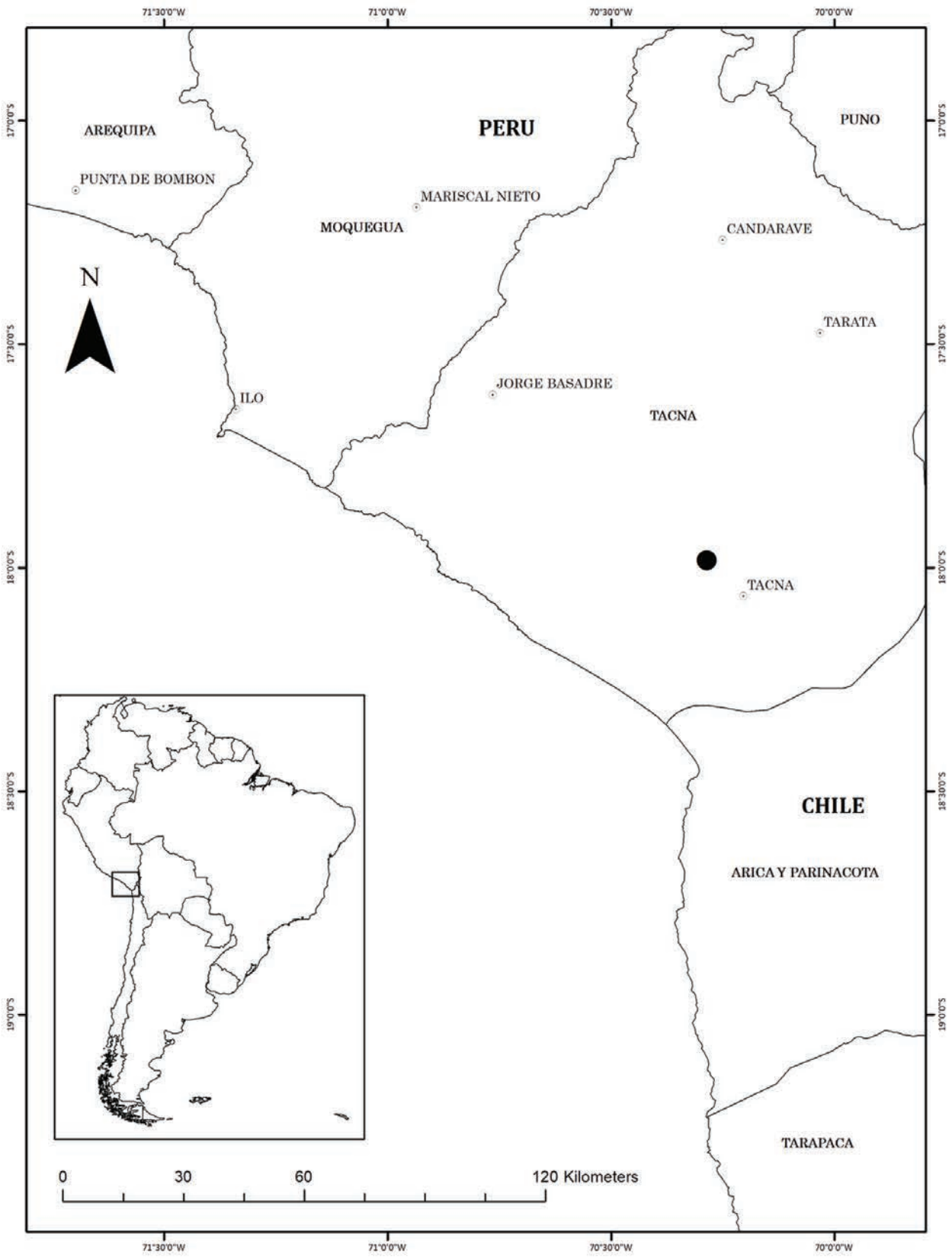


FIGURE 139. Distribution of *Nolana pearcei* I.M. Johnst.

FIGURE 140. *Nolana pearcei*. **A**, Portion of holotype sheet housed at Kew, *R. Pearce s.n.*; **B**, Enlargement with arrow drawn by Johnston to call attention to the flower on the type sheet.

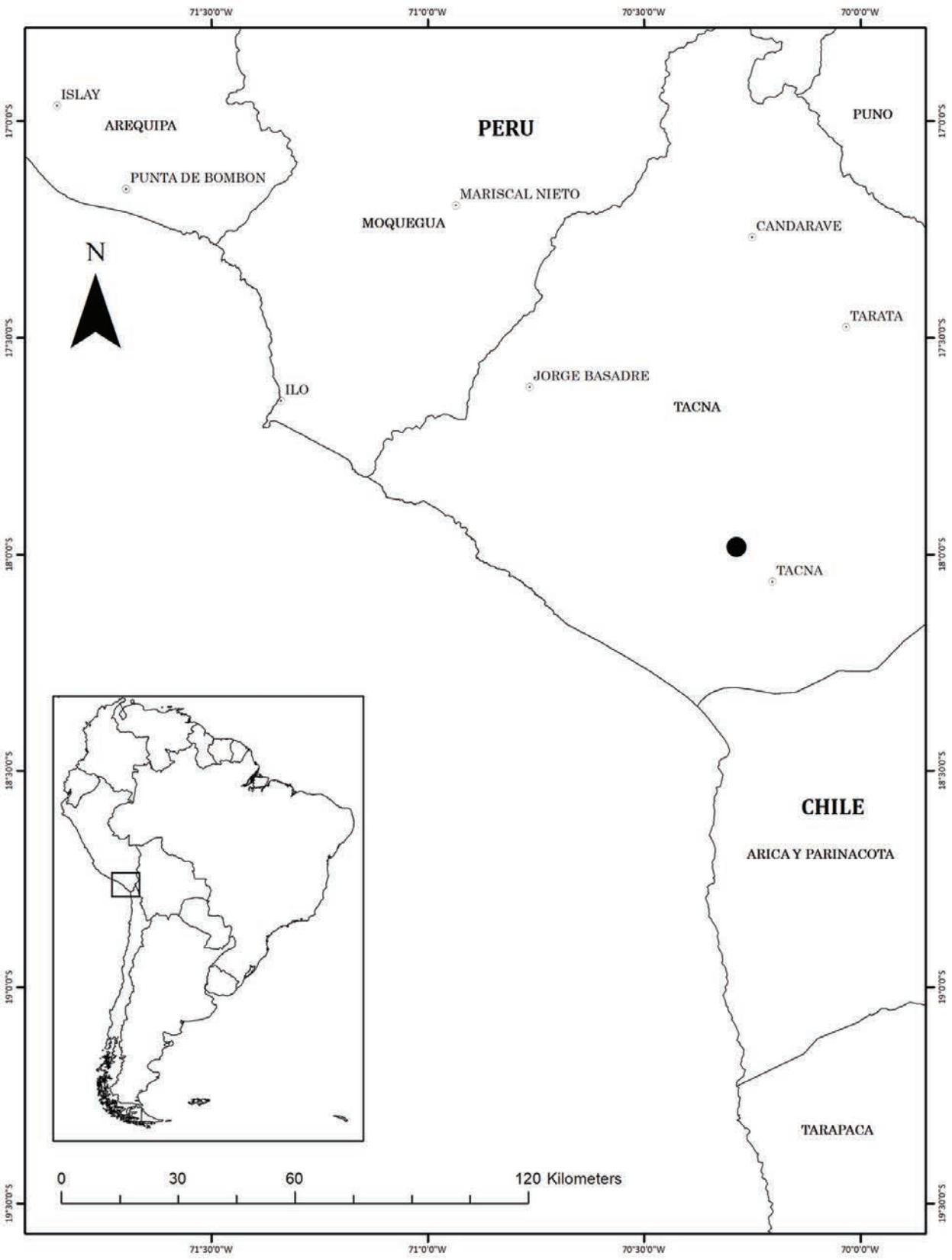


FIGURE 141. Distribution of *Nolana platyphylla* (I.M. Johnst.) I.M. Johnst.

2 mm wide; anther filaments 2.0–3.5 mm long, sparsely villous. *Mericarps* (5–)10, ovoid, ca. 2 mm in diam.; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *platy-*, and *platyphyllus*, meaning broad-leaved.

Distribution and Ecology: Peru, Department of Moquegua; 1500–1600(–2396) m.a.s.l. It is recorded from areas of the interior and away from the coastal fog, ca. 50 km from the coast (Fig. 141), but in areas that do receive seasonal rains.

Nolana platyphylla is distinctive among the Peruvian species, with lanceolate, fleshy leaves with sparse pubescence of dendritic trichomes, and white to lavender corollas that just surpass the calyx lobes (Fig. 142A–C). The species is apparently rare and is represented by only three collections over the past 100 years; I have not encountered this species in the field.

Johnston (1929: 176) stated that this species was very distinct and recognized by its broad leaves and annual herbaceous habit. He surmised that it was one of only three distinctly annual species in the genus, *Nolana aplocaryoides* from coastal Chile, and *N. gracillima*, which he only knew from southern Peru. Johnston (1936: 60) further commented that he believed *N. platyphylla* was related to *N. gracillima* but quite distinct. He remarked that the pedicels were stouter, the calyces larger and coarser, and the 5–10 mericarps were erect, obovoid and basally affixed to the low, convex gynobase. This species has not been included in any of the molecular marker studies, but I would not relate this taxon to *N. aplocaryoides* or *N. gracillima*, based on overall morphology.

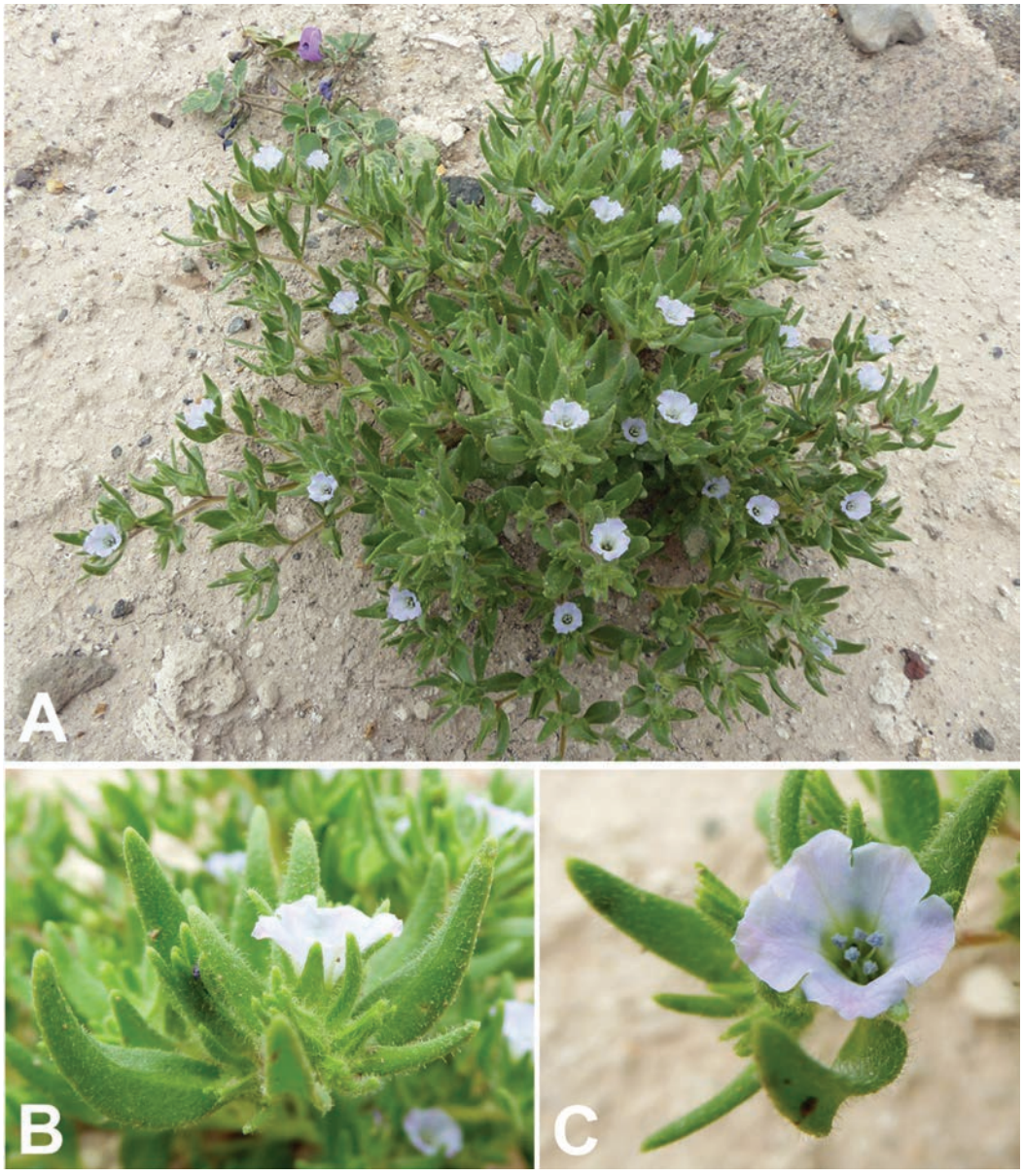


FIGURE 142. *Nolana platyphylla*. **A**, Robust annual herbs; **B**, Fleshy leaves with dendritic trichomes; **C**, White to lavender corollas just surpassing the calyx lobes. Photograph by Daniel Montesinos.

Additional specimens examined: PERU. **Moquegua**. Prov. General Sánchez Cerro, Dist. Omate, between Quinistaquillas and Omate, 16°45'41"S, 70°59'31"W, 1378 m.a.s.l., 14 March 2017, *D. Montesinos, J. de Vos, & K. Chicalla. 5077* (F 2330854, HSP); Prov. Mariscal Nieto, Torata–Omate, 46–48 km from Yacanco, 16°52'02"S, 70°54'35"W, 2396 m.a.s.l., 23 March 2012, *T. Särkinen, A. Matthews, & P. Gonzáles 4093* (BM001114856).

D14. ***Nolana plicata*** I.M. Johnst., Contrib. Gray Herb 85: 174. 1929. TYPE: PERU. Arequipa: Prov. Camaná, Atiquipa, ca. 270 m, November 1915, *A. Weberbauer 7190* (Holotype: F [549065]; Isotypes: F [F 628043], G [G00383947]). Fig. 143–146.

Digital image: Holotype of *Nolana plicata* from the Field Museum, Chicago [F 549065]. https://fm-digital-assets.fieldmuseum.org/138/059/V0075996F.jpg

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. subsp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 133. 1981.

Perennial *herbs*, prostrate to procumbent, or erect *shrubs*; stems to ca. 1 m long. Basal rosette of narrowly lanceolate *leaves*, to 10 cm long, 1–2 mm wide; cauline *leaves* alternate, blades lanceolate to narrowly ovate, strap-shaped upon drying, 10–65 mm long, ca. 13 mm wide, puberulent with capitate-glandular trichomes, margins revolute, abaxially conspicuously ribbed, shaggy-villous, sessile. *Inflorescences* of solitary flowers; pedicels 10–20 (–50) cm long, densely pubescent with capitate-glandular trichomes, recurving in fruit. *Flowers* 5-merous; calyces 10–18 mm long, tube campanulate, bilabiate, lobes to ca. 6 mm long; corollas infundibularis, 20–34 mm long, ca. 25 mm wide, polymorphic for flower color, white and blue forms; stamens unequal; filament widened at the base, pubescent or not; nectary disc patelliform; style ca. 8 mm long, gynobasic; stigma capitate-globose. *Mericarps* 3–5, pyriform to ovoid, 3–5 mm long, ca. 3 mm wide, occasionally with projections to 1.5 mm long; seeds 3–6 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *plica*, a fold, and *plicatus*, folded into pleats or furrows lengthwise, and refers to the overall form of the calyx. Johnston stated that the calyx was strongly angular with pronounced plications extending down each calyx lobe in a manner suggestive of some *Mimulus* species.

Distribution and Ecology: Peru, Departments of Arequipa and Ica; (100–)300–400(–900) m.a.s.l. It is recorded from areas with halophytic soils and gravel at some distance from the ocean, but within range of the coastal fog (Fig. 143).

Nolana plicata has long, strap-shaped, strongly revolute leaves and pronounced pubescent veins on the abaxial surface (Fig. 144). The plants are often members of sand dune communities, where only the tips of the branches are above the surface (Fig. 145A); the flowers are borne from the upper leaf axils. The opened corollas show the pubescent anther filament bases (Fig. 145B) and bluish pollen. The mericarps are connate, lustrous with five large mericarps and another much smaller five mericarps (Fig. 145C). The overall habit is strongly affected by the surroundings and can range from prostrate and covered with sand (Fig. 146A) to erect (Fig. 146B).

Johnston (1929: 175) observed that mericarps in *N. plicata* have a near plane, vertical commissural face with a pale attachment scar, and that the bases of the mericarps are strongly convex and irregularly rugose. Toward the apical end there often is a rather definite dry and bony keel. The calyx is strongly angulate with pronounced plications extending down each calyx lobe in a manner suggestive some *Mimulus* L. He speculated that *N. plicata* was most closely related to *N. coronata*, which is a glabrate plant with broader leaf blades that are more abruptly contracted into the petiole. In molecular studies, *Nolana plicata* is always recovered in a group of southern Peruvian species, and marker data suggest it is related to *N. chancoana*, *N. inflata*, and *N. weissiana* (Dillon et al., 2007c).

Additional specimens examined: PERU. **Arequipa**: Prov. Caravelí, Loma cerca de Lomas, 390 m.a.s.l., 13 November 1957, *N. Angulo E. s.n.* (HUT 2553); Lomas of Jahuay, ca. 52 km S of Nazca, near border with Dept. Ica, Km 513–515 S of Lima, 365–380 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3759* (CONC, E, F 1950171, GH, K, USM); Lomas of Jahuay, ca. 51 km NW of Chaviña, 300 m.a.s.l., 7 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3225* (F 2043423); ca. 67 km S of Nasca, 15°25'S, 74°53'W, 400 m.a.s.l., 20 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8197* (F 2198748); Lomas de Jahuay, enter Nazca y Chala (KM 524), 300–400 m.a.s.l., 17 October 1946, *R. Ferreyra 1391* (USM 81244); Atiquipa, cerca de Chala entre Nazca y Chala, 100–200 m.a.s.l., *R. Ferreyra 1509* (K, US 1998567, USM 81247); 300–400 m.a.s.l., 8 November 1947, 8 November 1947, *R. Ferreyra 2512* (US 1998575, USM 81245); Lomas de Jahuay, 300–400 m.a.s.l., 2 May 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 8663* (USM 75183); Lomas de Jahuay, Nazca and Chala, 400 m.a.s.l., 9 November 1952, *R. Ferreyra 8799* (F 1488844, K, USM 81255); Lomas de Jahuay, 300–400 m.a.s.l., 9 October 1955, *R. Ferreyra 11431* (USM 81251); Lomas de Jahuay, 400–500 m.a.s.l., 11 October 1955, *R. Ferreyra 11487* (USM 81249); Lomas de Jahuay, 300–400 m.a.s.l., 3 December 1955, *R. Ferreyra 11758* (USM 81252); Lomas de Atiquipa, Los Cerrillos, entre Chala y Nazca, 650–700 m.a.s.l., 23 September 1958, *R. Ferreyra 13448* (USM 81245); Lomas de Jahuay, 250–350 m.a.s.l., 25 October 1976, *R. Ferreyra 18684* (USM 81253); Lomas de Jahuay, 300–400 m.a.s.l., 28 April 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19779* (USM 49023); Lomas de Jahuay, 300–400 m.a.s.l., 2 March 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19852* (USM 50472); Lomas de Jahuay, 300–400 m.a.s.l., 5 September 1984, *R. Ferreyra & M. Ono 20312* (USM 55729); Lomas de Atiquipa, 600 m.a.s.l., 17 November 1986, *R. Ferreyra 20720* (USM 72660); hilltop between Jahuay and San Juan, ca. 15 km coast side of Pan American Hwy, 1 November 1984, *M. Ono & T. Masuzawa s.n.* (MAK 229697); Dist. Lomas, Lomas de Jahuay, 15°24'25"S, 74°53'15"W, 372 m.a.s.l., 19

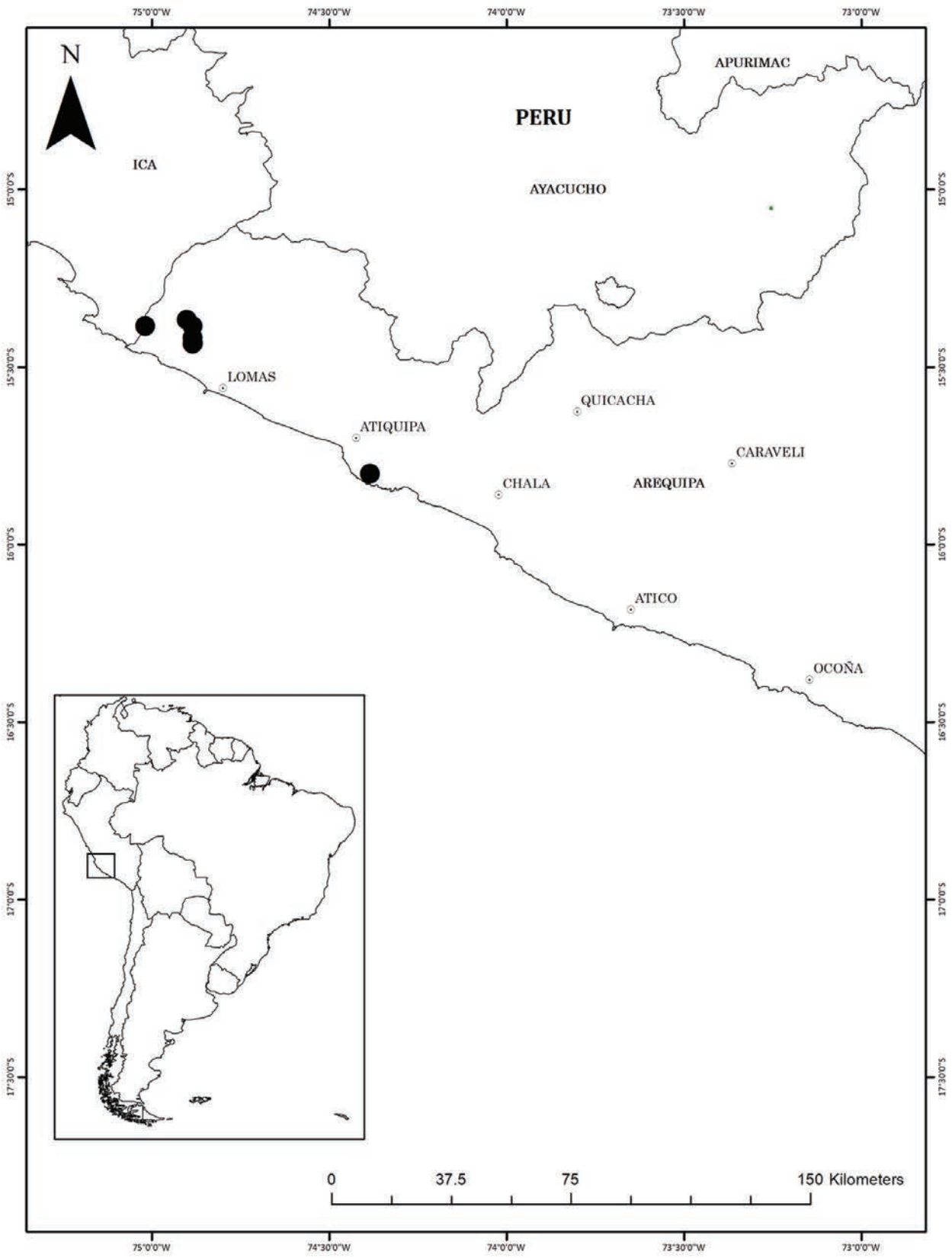


FIGURE 143. Distribution of *Nolana plicata* I.M. Johnst.

FIGURE 144. *Nolana plicata*. Basal rosette of strap-shaped leaves with three flowering branches.

November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3527* (HSP 000665); Alto Grande, Km 520 de la Panamericana Sur, 15°26'01"S, 74°52'02"W, 321 m.a.s.l., 19 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3532* (HSP 000670); Dist. Lomas, ca. Km 523 de la carretera Panamericana, 15°25'55"S, 74°53'00"W, 362 m.a.s.l., 26 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6603* (HSP 8801, HUT 60423); Dist. Lomas, Panamericana Sur Km 521, entre Lomas y Marcona, 15°25'03"S, 74°53'24"W, 386 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez, S. Huamani Q., & M. Bedoya C. 7647* (HSP 011858); Chaviña, 200 m.a.s.l., 16 March 1957, *W. Rauh & G. Hirsch P469* (F 1572610); Jahuay ["Haway"], 17 November 1957, *O. Tovar S. 2735* (USM 54280). **Ica**: Prov. Nazca, SE of Marcona, along Hwy 109, near Km 40, 350 m.a.s.l., 19 February 1994, *E. F. Anderson, J. McAuliffe, K.& F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7868* (F 2143990); SE of Marcona, along Hwy 109, near KM 40, 19 February 1994, 360 m.a.s.l., *E. F. Anderson J. McAuliffe, K. & F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7871* (F 2143991); Marcona, Sur de Nazca Km. 518, 15°23'S, 74°53'W, 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8782* (F 2276724, US 3512503); Lomas cerca Marcona, 900 m.a.s.l., 22 September 1958, *R. Ferreyra 13375* (USM 81254); Lomas de San Nicolás, 800–900 m.a.s.l., 22 September 1958, *R. Ferreyra 13387* (USM 81243); Lomas de San Nicolás, 800 m.a.s.l., 22 September 1958, *R. Ferreyra 13391* (USM 81246); Punta de Los Ingleses, al N de San Nicolás, 400–450 m.a.s.l., 22 September 1958, *R. Ferreyra 13409* (USM 81250); Lomas de Marcona, 500 m.a.s.l., *P. Gonzales 4024* (USM, not seen); Marcona, Lomas San Fernando, 15°06'43"S, 75°18'03"W, 794 m.a.s.l., 30 October 2012, *B. Klitgaard, J. P. Cardenas, A. Cooper, O. Whaley, & J. Moat KPP9* (USM 263943).

D15. ***Nolana rhombifolia*** Marti. & Quez., Bol. Soc. Biol. Concepción 48: 91. 1974. TYPE: CHILE. Arica & Parinacota: Prov. Arica, Camino al Portezuelo de Chapiquina, Quebrada Cardones, frente al Cordon de Huanune, 18°28'S, 69°50'W, 1850 m, 24 March 1961, *M. Ricardi, C. Marticorena, & O. Matthei 37* (Holotype: CONC [40606]). Fig. 147–150.

Digital image: No digital image for *Nolana rhombifolia* is available via the internet; the image published here (Fig. 148) was provided by Museo Nacional de Historia Natural, Santiago, Chile.

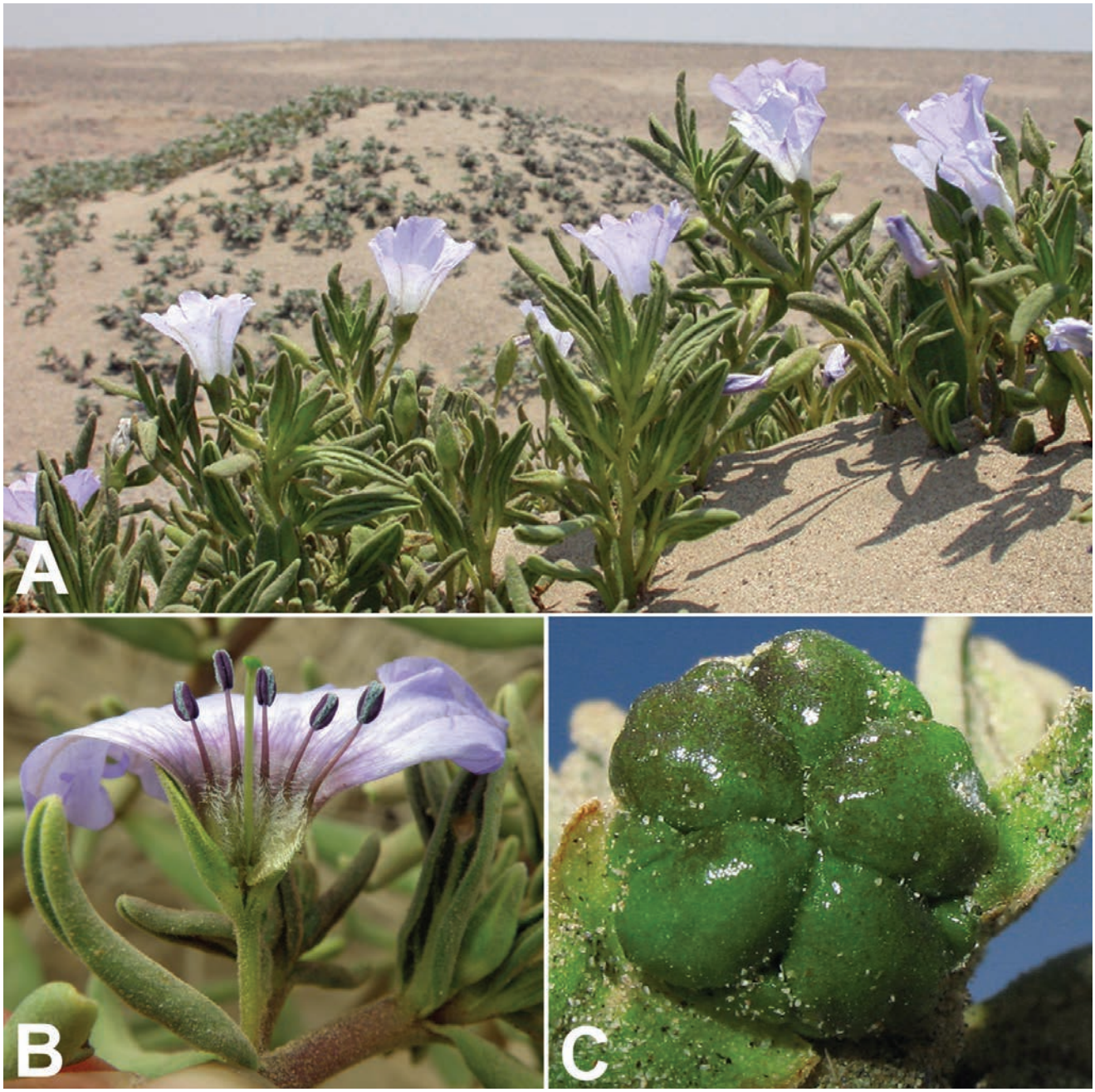


FIGURE 145. *Nolana plicata*. **A**, Sand dunes with branch tips at the surface; **B**, Open corollas with pubescent anther filament bases and bluish pollen. Photograph by Paul Gonzáles Arce; **C**, Connate mericarps.

Homotypic synonym: *Nolana laxa* (Miers) I.M. Johnst., Contr. Gray Herb. 112 : 59. 1936, fide Mesa-M. (1981).

Erect, annual *herbs*, 12–28 cm tall, branched above the midpoint, pubescent with short-stalked, capitate-glandular trichomes; branchlets densely pubescent with long-stalked, capitate-glandular trichomes; roots simple, 5–10 cm long. *Leaves* alternate, blades lance-ovate to rhomboid, (6–)15–20 mm long, (2–)7–12 mm wide, margins plain, abaxial and adaxial surfaces with capitate-glandular trichomes; petioles 5–15 mm long, densely pubescent with capitate-glandular trichomes. *Inflorescences* of solitary flowers, subsessile; pedicels 1–2 mm long. *Flowers* 5-merous; calyces campanulate, 4–6 mm long, ca. 2 mm wide, densely pubescent with capitate-glandular trichomes, lobes linear, unequal, 3.5–5.0 mm long; corollas narrowly infundibularis, violet to whitish-blue, 18–24 mm long, 9–11 mm wide, outer surface pubescent with capitate-glandular trichomes, inner surface glabrous except for region of anther insertion, 5-lobed, lobes triangular, ca. 2 mm long; stamens unequal,

FIGURE 146. *Nolana plicata*. **A**, Prostrate habit; **B**, Erect habit growing with *Tillandsia*. Photograph by Paul Gonzáles Arce.

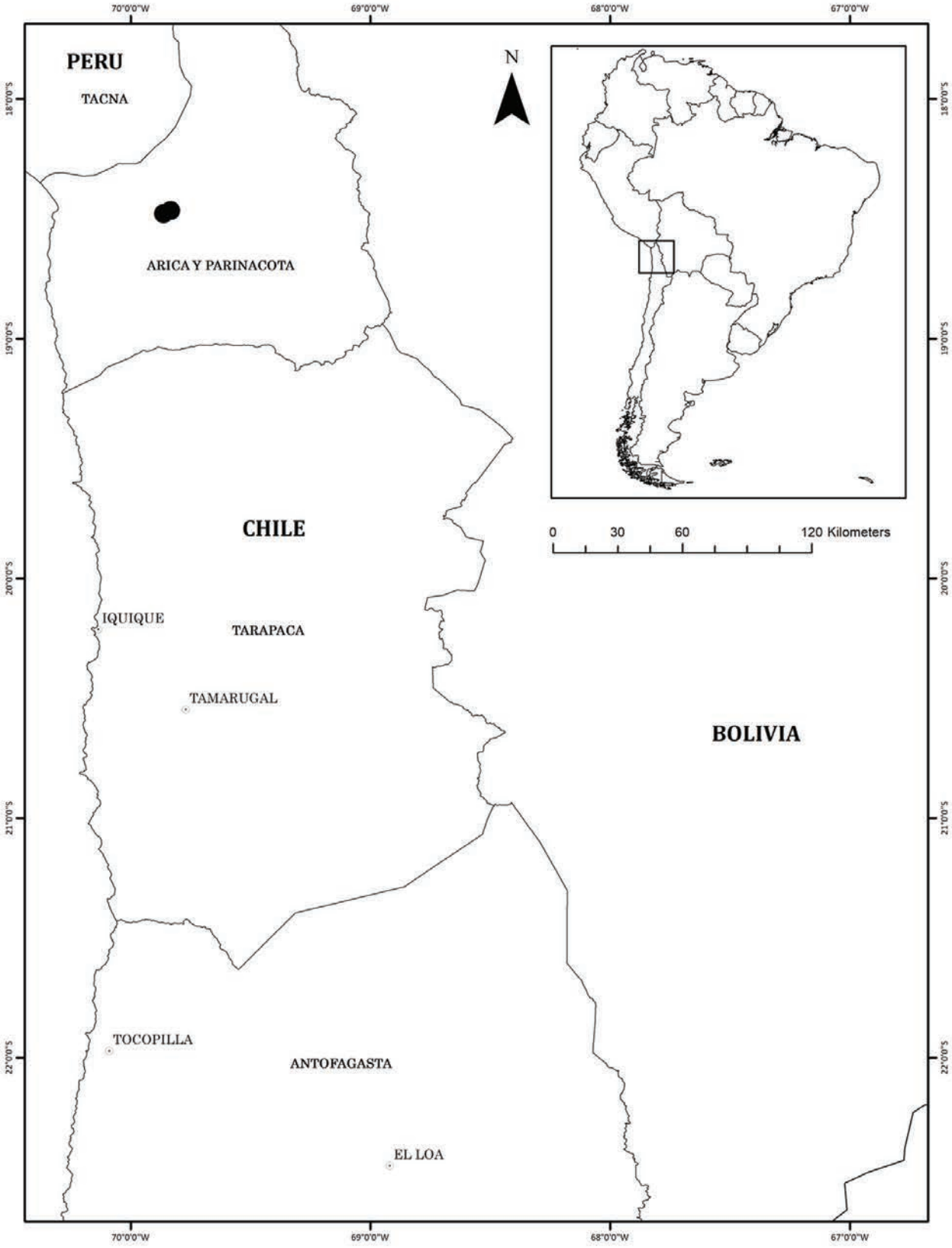


FIGURE 147. Distribution of *Nolana rhombifolia* Marti. & Quez.

FIGURE 148. Holotype of *Nolana rhombifolia* Marti. & Quez. housed at CONC. No digital image is available via the internet.

the 2 larger, 13.0–18.5 mm long, the 3 shorter, 10.0–10.5 mm long; styles 6.5–10.5 mm long; receptacles 0.8–1.7 mm in diam. *Mericarps* 5, 1-seriate, piriform, black, ca. 1.5 mm in diam., attached basally; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *rhombos*, or the Latin, *rhombicus*, and refers to the leaf blades often exhibited in this species.

Distribution and Ecology: Chile, Region of Arica & Parinacota; 1800–1900 m.a.s.l. It is recorded from rocky, alluvial fans at higher elevations, far inland from coastal fog (Fig. 147): Desértico Tropical Costero Interior (Luebert and Pliscoff, 2006).

Nolana rhombifolia is a distinctive annual species with a single, unbranched stem (Fig. 149A), only branching at the apices. However, when given sufficient available moisture at germination, the development of the plant can lead to a very different vegetative aspect, as exhibited in some individuals (Fig. 149B). The distinctive rhomboid leaves and elongate corollas (Fig. 150A–B) are very similar to Peruvian species, such as *N. chapiensis*, *N. laxa*, and *N. weberbaueri*. When plants are water stressed, the leaf size, especially the leaf width, is reduced. This results in some specimens looking quite unlike the type collections.

One collection, *Eggli et al. 2834*, is unusual and is considered a water-stressed individual. Repeated here is the label data from *Eggli et al. 2834*, "Probably perennial shrublets to 70 cm with solitary main stem and richly branched crown; green, appressed to corolla; corolla tube basally narrow, whitish, above flaring funnel-shaped, pale blue with violet-lilac hue; petals ascending, like upper part of tube, without differently colored mouth; seeds typically three per mericarp. Material with small leaves and flowers collected from a drought-stressed specimen." It is noteworthy that one of the community associates of *Nolana rhombifolia* and *N. chapiensis* is the cactus, *Browningia candelaris*.

Additional specimens examined: CHILE. **Arica & Parinacota**: Prov. Arica, ca. 60 km E of the Panamericana on Ruta 11 towards Putre, just below Planta Quiborad, 1800 m.a.s.l., *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2834* (B, CONC 138463, SGO 146043); along Rt. 11 from Arica to Tamboquemado, 7 November 1995, *K. Gengler 63* (SGO 137325); Lecho Rio San José, 18°31'12"S, 70°11'14"W, 19 June 2015, *J. Gonzáles, J. Molina, & L. Lázaro s.n.* (CONC 185307); Rio San José, 18°31'06"S, 70°11'24"W, 19 June 2015, *J. Gonzáles, J. Molina, & L. Lázaro s.n.* (CONC 185312); Ruta Ch 11 Quiborax Km 57, 18°28'46"S, 69°51'44"W, 1831 m.a.s.l., 17 April 2011, *B. Knapton 83* (SGO); Ruta Ch 11 Quiborax Km 57, 18°28'46"S, 69°51'44"W, 1831 m.a.s.l., 29 April 2011, *B. Knapton 88* (SGO); Camino Arica–Putre, Km 54.5, 18°26'08"S, 60°55'53"W, 1484 m.a.s.l., 24 May 2011, *A. Moreira M., M. Muñoz S., & V. Morales 1568* (CONC 183398); Camino de Poconchile a Zapahuira, frente a los cerros de Huanune, 1900 m.a.s.l., 3 May 1972, *M. Ricardi, E. Weldt, & M. Quezada 50* (CONC 40607); camino Arica–Putre, cerros un poco más arriba de Molinos, 18°24'57"S, 69°58'13"W, 1200 m.a.s.l., 17 April 2011, *S. Teillier & A. Buben 6587* (CONC 173780).

D16. ***Nolana samaensis*** M.O. Dillon & Quip., Harv. Pap. Bot. 28(1): 9. 2023. TYPE: PERU. Tacna: Prov. Tacna, Dist. Sama, Lomas de Sama, 17°58'23"S, 70°46'12"W, 503 m, 19 Noviembre 2021, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., & J. Muñuico M. 8029* (Holotype: HSP [12378]; Isotypes: HSP [12379], F 2330852, HUT, USM). Fig. 151–153.

Subshrubs to ca. 30 cm tall; stems intricately branched, erect to decumbent, ca. 20 cm long, internodes to 1 cm long, densely villous with capitate-glandular trichomes. *Leaves* alternate, fasciculate, blades oblanceolate or obovate, 4–7 mm long, 1.0–1.5 mm wide, pilose, succulent, base attenuate, apex rounded to obtuse, sessile or subsessile. *Inflorescences* of solitary flowers in leaf axils; pedicel cylindrical, densely pubescent, 1–2 mm long. *Flowers* 5-merous; calyx narrowly campanulate, 5.0–6.6 mm long, 4–5(–6) mm wide at anthesis, densely pilose, 5-lobed, tube 1.0–1.5 mm long, 1.0–1.5 mm in diam., lobes oblong-lanceolate, unequal, 4–5 mm long, 1.0–1.2 mm wide, apex acute; corolla zygomorphic, infundibuliform, 10–15 mm wide at anthesis, 9–11(–13) mm long, light lavender or lilac, throat with dark purple ring, externally pilose, trichomes uniseriate, internally glabrous; stamens 5, included, filaments inserted on lower third of corolla, unequal, (5–)7–8 mm long, glabrous at bases; anther thecae purple, ca. 0.5 mm long, ca. 0.5 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 1.0–1.2 mm wide, basal nectary ca. 1 mm wide, carpels 5, style included, 6–7 mm long, stigma bilobed, purple, ca. 0.3 mm long. *Mericarps* 6–8(–9), 2-seriate, polyhedrons, black, rugose-punctate, 1.0–2.5 mm long, 2–4 large, 4 or 5 small, included within expanding calyx; seeds 1–5 per mericarp. Chromosome number: unknown.

Etymology: The specific epithet is from the latinisation of the geographic locality of the type collection, Sama, in the Department of Tacna.

Distribution and Ecology: Peru, Department of Tacna; 100–600(–810) m.a.s.l.; restricted to sandy soils and inland localities within 10 km of the ocean (Fig. 151).

Nolana samaensis is distinguished by a combination of characters not seen in other species; erect subshrubs (Fig. 153A) with small, densely pubescent leaves less than 10 mm long and ca. 1.5 mm wide. The shape, size and pubescence of the calyx lobes in *N. samaensis* are distinctive among other southern Peruvian congeners (Fig. 153B). Two species recorded from the Department of Tacna, *N. confinis* and *N. lycioides*, are shrubby and have similar sized leaves but very different pubescence. Their calyx lobes are long attenuate and densely lanuginous or have short, capitate-glandular trichomes. *Nolana hoxeyi* and *N. gracillima* both have leaves up to 25 cm long; *N. gracillima* lacks leaf pubescence, while *N. hoxeyi* has densely strigose leaves.

Additional specimens examined: No additional collections of this species have been encountered in the field or in herbarium studies.

FIGURE 149. *Nolana rhombifolia*. **A**, Annual habit with rapid flowering after rains; **B**, Annual habit when excess moisture at germination leads to a much more robust vegetative aspect. Photographs by Barbara Knapton.

FIGURE 150. *Nolana rhombifolia*. **A**, Frontal view of flowers; **B**, Lateral view of flowers with distinctive corollas. Photographs by Barbara Knapton.

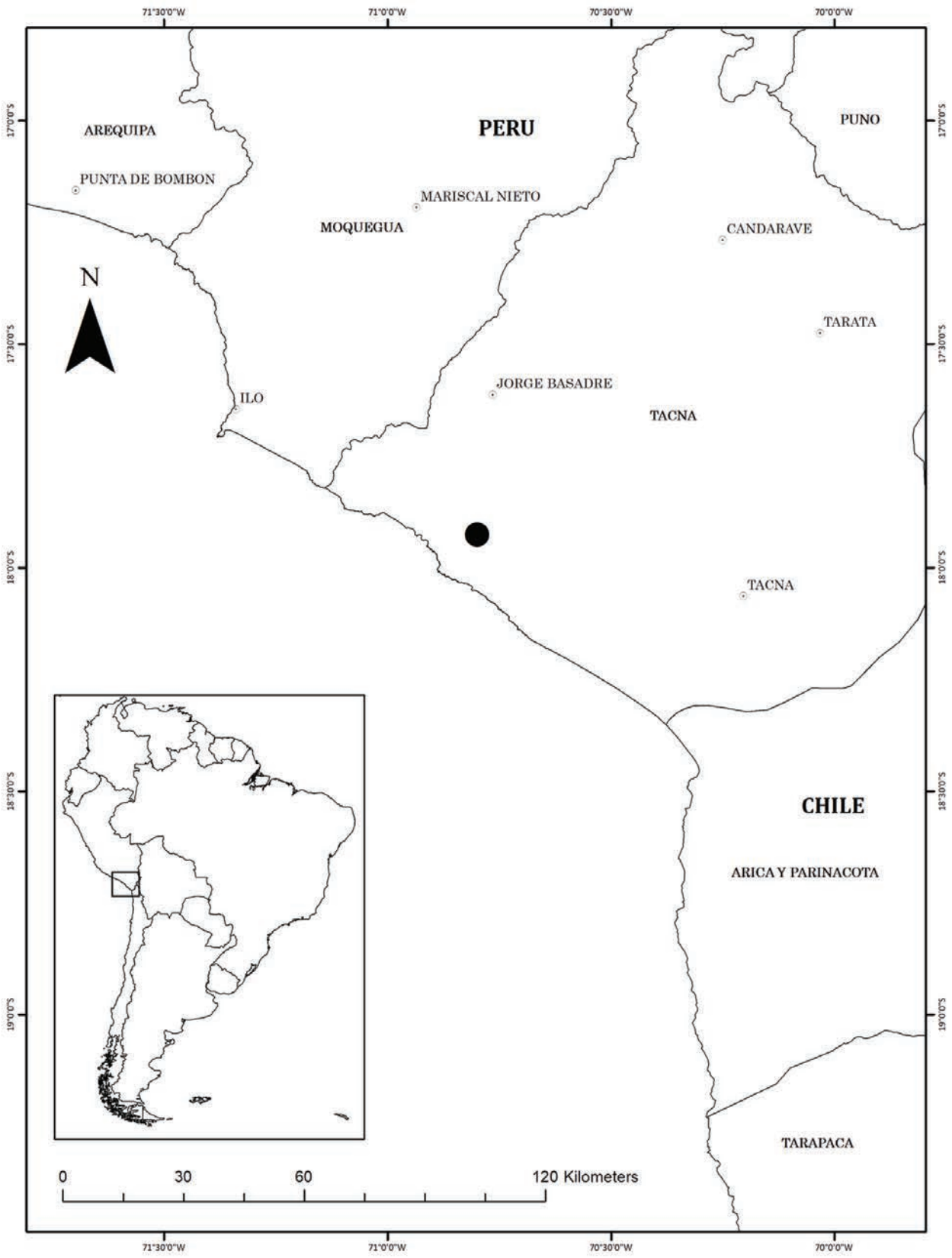


FIGURE 151. Distribution of *Nolana samaensis* M.O. Dillon & Quip.

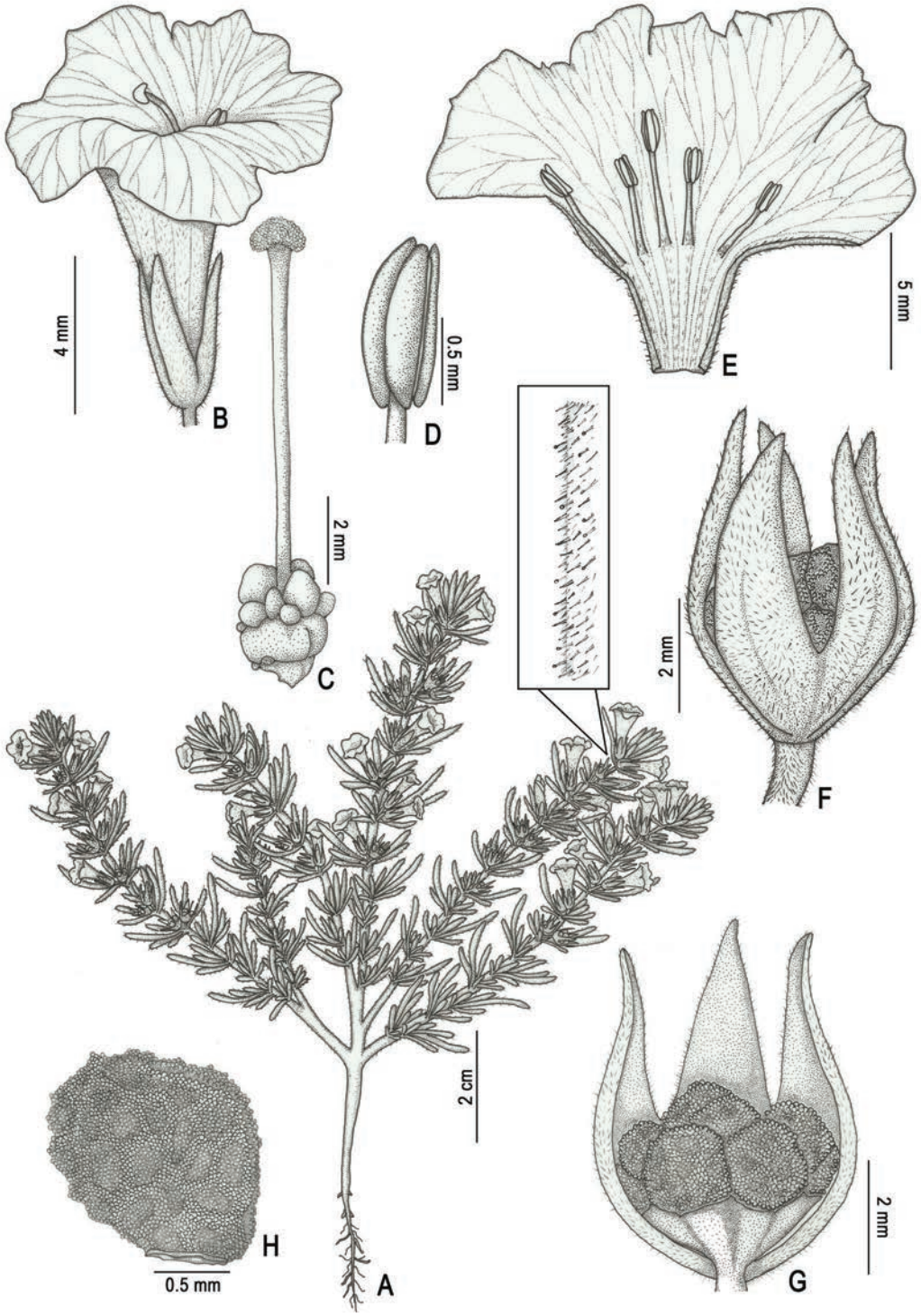


FIGURE 152. Illustration of *Nolana samaensis*. **A**, Habit with enlargement of surface pubescence; **B**, Flower; **C**, Ovary and style; **D**, Anther; **E**, Dissected corolla; **F**, Calyx; **G**, Dissected calyx with mericarps; **H**, Mericarp. Drawn by Maricruz Bedoya Cuno.

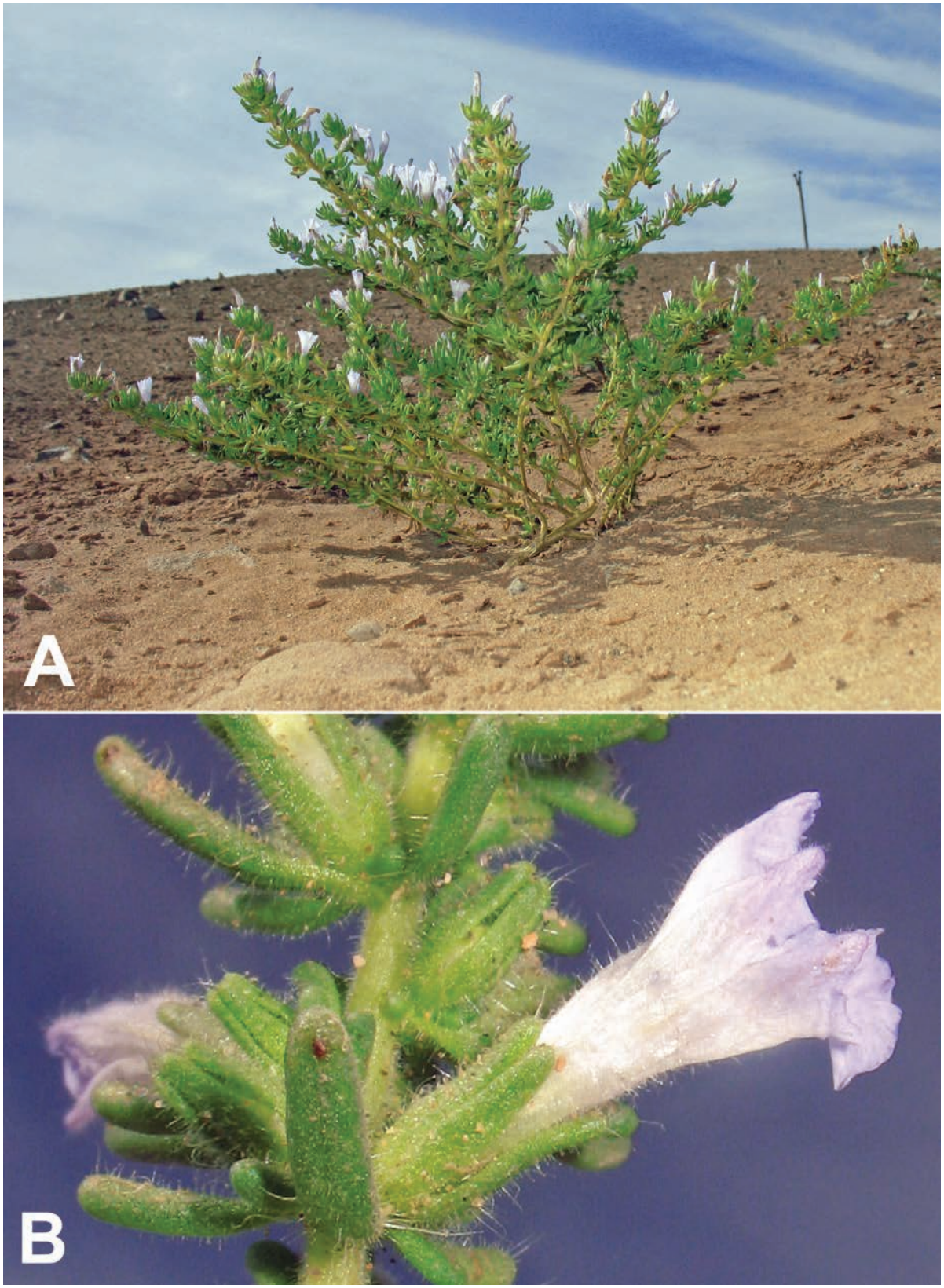


FIGURE 153. *Nolana samaensis*. **A**, Perennial habit of flowering plant; **B**, Closeup of flowering branch illustrating pubescence on leaves, calyces, and corollas.

D17. ***Nolana scaposa*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 5. 1955. TYPE: PERU. Arequipa: Prov. Camaná, *R. Ferreyra 2538* (Holotype: USM [242140, USM000573]). Fig. 154–155.

Digital image: Holotype for *Nolana scaposa* from Herbario San Marcos, Lima [USM 242140]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000573

Annual *herbs*, scapose, 10–35 mm tall, hirsute. Basal *leaves* rosulate, blades spathulate to oval or orbicular, 12–90 mm long, 10–28 mm wide, apically obtuse, base attenuate, hirsute; petioles 14–50 mm long, 1.0–1.8 mm wide; cauline flowering stems erect to ascending, bracts ovate to oval, ca. 1 cm long, ca. 1 cm wide, sessile. *Inflorescences* cymose; pedicels 1–2 mm long, hirsute. *Flowers* 5-merous; calyces campanulate, 7–9 mm long, 3.5–4.5 in diam., densely hirsute, tube short, 5-lobed, unequal, the two larger lobes spathulate 6.5–7.5 mm long, 1.4–2.2 mm wide, obtuse, three smaller lobes, lanceolate, 4.8–6.0 mm long, 1.2–1.8 mm wide; corollas infundibularis, lilac to violet, 16–21 mm long, 7–9 mm wide distally, 5-lobed, lobes obtuse, tube villous inside; stamens unequal, united to 1/2 their length, two longer, 12–13 mm long, 3 smaller, 10–11 mm long; nectary disc patelliform, margin sinuous; styles 13–14 mm long. *Mericarps* 23–24, piriform, black, muricate, the larger 14, 0.9–1.2 mm long, 0.8–1.0 mm wide, the smaller to ca. 0.6 mm long, ca. 0.4 mm wide; seeds 1 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *skapos*, or the Latin, *scapus*, referring to a stem or scape. In this instance, the reference is to the long pedicels of the inflorescences that are unique to the genus.

Distribution and Ecology: Peru, Department of Arequipa, ranging over 200 km; 20–250 m.a.s.l. (Fig. 154). It is recorded from desert habitats in pure sand.

Nolana scaposa is distinctive among all congeners with its scapose habit, long-petiolate, hirsute pubescent basal leaves (Fig. 155A–B), and multi-flowered cymose inflorescences (Fig. 155C). The 23–24 mericarps that are ca. 1 mm in diameter are also unique in the genus. With its unusual morphology, it's relationships are not obvious. Molecular analyses (Dillon et al., 2008, 2009; Tu et al., 2008) always find it recovered within a strictly Peruvian group, but never exhibiting close sister-species relationships with another taxon.

Two collections with the same collector number at Kew were distributed by Ramón Ferreyra as isotypes (*Ferreyra 11699*); however, it is doubtful that these are isotypes, since the holotype is published as *R. Ferreyra 2538* (USM 242140).

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, 9–16 km S of Camaná, 400 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L Martell 8209* (F 2198772); a 3 km del Peaje de Camaná, Quebrada El Toro, 16°38'S, 72°37'W, 144–250 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8940* (F 2276705, US 3512539); a 3 km del Peaje de Camaná, Quebrada El Toro, 16°38'S, 72°37'W, 144–250 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8943* (F 2276706, HSP 005228, US 3512540); Lomas de Camaná, 100 m.a.s.l., 2 December 1955, *R. Ferreyra 11699* (K [2 sheets], USM 81279); Lomas de Camaná, 200–250 m.a.s.l., 7 October 1957, *R. Ferreyra 12628* (USM 81277); Dist. Quilca, Quebrada del Toro, 16°36'39"S, 72°37'46"W, 400 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2895* (HSP 000338); Lomas de Camaná, 600–700 m.a.s.l., 30 October 1966, *C. Vargas C. 18175* (CUZ); Prov. Caravelí, ca. 5 km S of Camaná, ca. 1 km E of ocean, 16°39'S, 72°40'W, 10 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8207* (F 2198774); Prov. Caravelí, ca. 9 km S of Camaná on road to interior, 16°39'S, 72°38'W, 80 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8209* (F 2198772).

D18. ***Nolana spathulata*** Ruiz & Pav., Fl. Peruv. 2: 7, tab. 113a. 1799. TYPE: PERU. Arequipa: Prov. Camaná, "Pongo et Atiquipa", *J. Tafalla s.n.* [*435*] (Lectotype designated by Dillon and Quipuscoa, 2023: MA [815133]; Isolectotypes: B [B W03449], BC, F [F 843636, F 845155], FI [FI132659], G [G00383935, G00383937, FM neg. 23244], MA [MA815132, MA815134, MA815135, MA817982], MPU [MPU012112]). Fig. 156–161.

Digital image: Lectotype for *Nolana spathulata* from Royal Botanic Garden, Madrid [MA815133]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.ma815133

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. subsp. *spathulata* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 136. 1981; *Nolana bipartita* Ruiz & Pav., Fl. Peruv. 2: 7, t. 113a. 1799, herbarium name.

Heterotypic synonym: *Nolana guentheri* I.M. Johnst., Contrib. Gray Herb. 112: 55. 1936. TYPE: PERU. Arequipa: Islay, Cachendo, al Este de Mollendo, 1000 m.a.s.l., 15 October 1923, *E. K. F. Günther & O. Buchtien 113* (Holotype: HBG [522236]; Isotypes: GH [GH00282356]; HBG [HBG522237]).

Annual to short-lived perennial *herbs*, suffruticose, 10–75 cm tall, erect, hirsute, branched, stems 5–12 cm long, 1–5 mm in diam., internodes 3–7 cm long, densely pubescent with glandular, flagelliform trichomes. *Leaves* alternate, blades ovate to elliptic, cordiform or spathulate-reniform, 10–60 mm long, 8–38 mm wide, hirsute with capitate-glandular trichomes, apically obtuse, basally truncate, cordate or reniform; petioles 6–25 mm long, 1.5–2.0 mm wide, vellose to hirsute-glandular. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 14–30 mm long, hirsute-glandular. *Flowers* 5-merous; calyces campanulate, 10–18 mm long, 4–7 mm in diam., pubescent with capitate-glandular trichomes outside, tube 3–4 mm long, ca. 5 mm wide, fusiform, 5-costate, zygomorphic, 2-cleft, 4- to 5-dentate, lobes spathulate, acute, 3.2–6.0 mm long, 2.5–6.0 mm wide; pedicels 5–25 mm long; corollas rotatus to briefly infundibularis, 20–25(–30) mm long, 15–18(–30) mm wide, pale lavender to blue, inconspicuously lobed, tube short, villous inside; stamens unequal, united 1/2 their

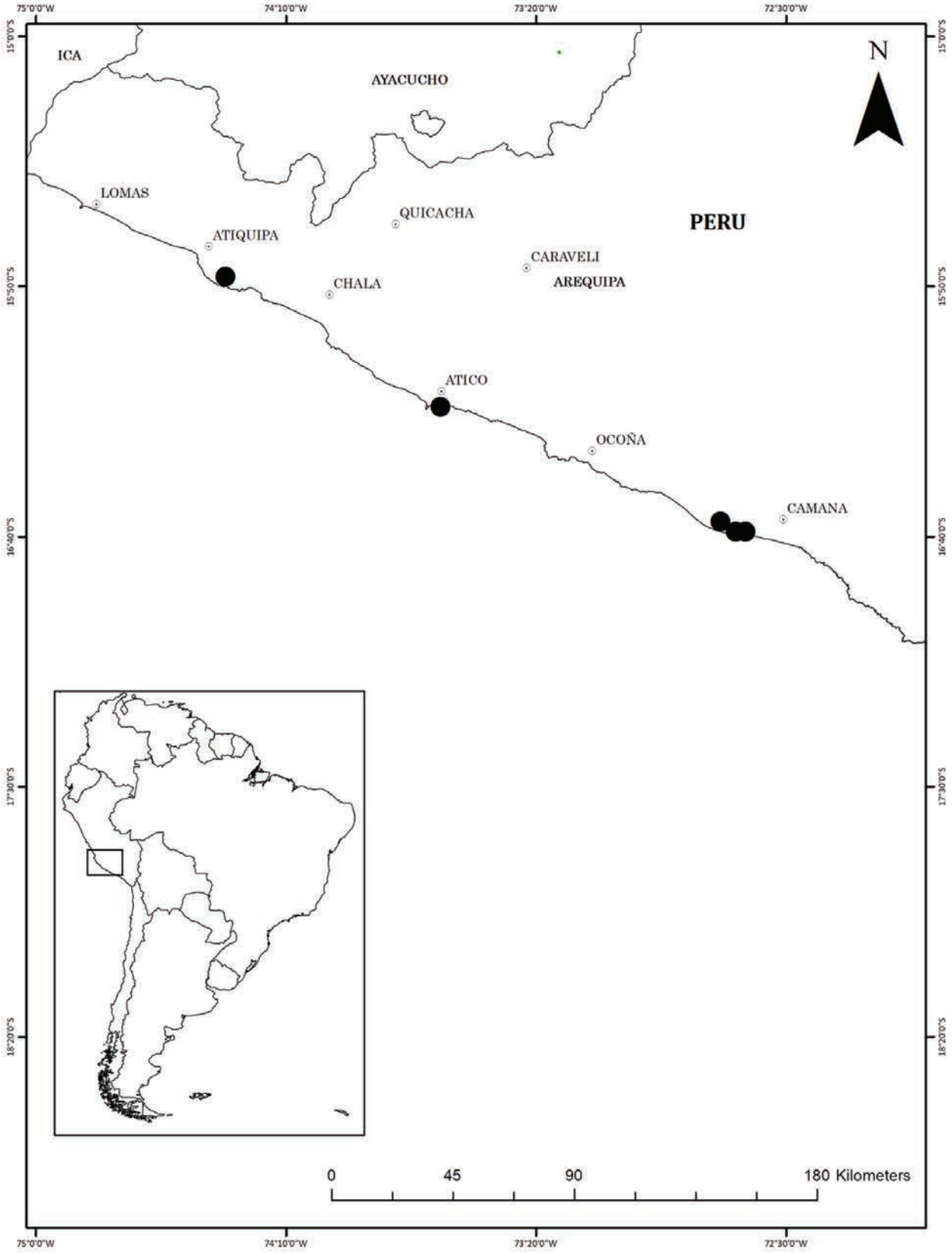


FIGURE 154. Distribution of *Nolana scaposa* Ferreyra.

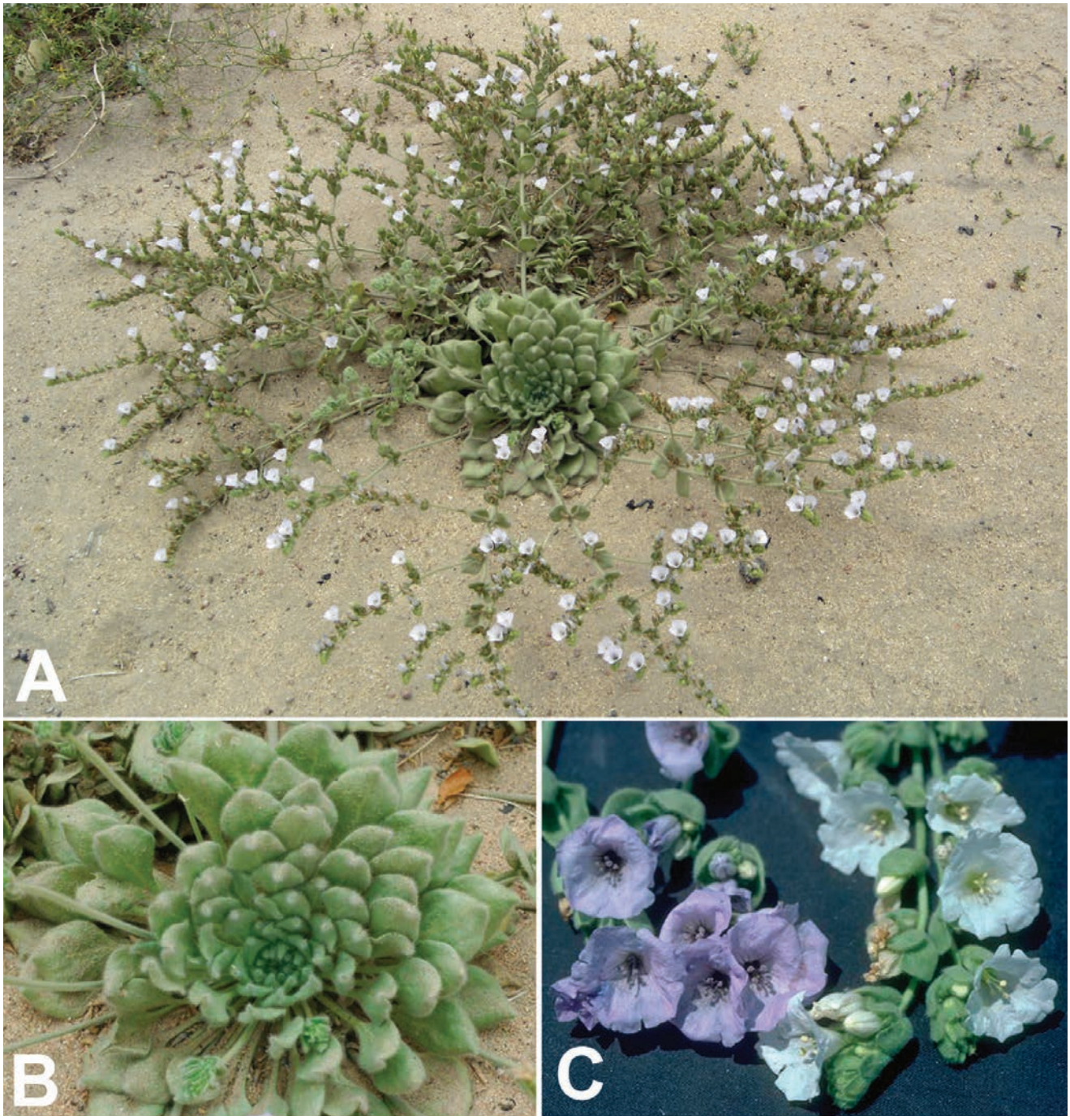


FIGURE 155. *Nolana scaposa*. **A**, Scapose habit; **B**, Long-petiolate, pubescent basal leaves; **C**, Multi-flowered cymose inflorescences.

length, 2 larger 16–17 mm long, 3 smaller 12–13 mm long; filaments widened at the base, pubescent; style 11–12 mm long; anthers lilac; nectary disc patelliform; style ca. 8 mm long; gynobasic; stigmas capitate-globose. *Mericarps* 5(–6), rarely more, 1-seriate, unequal, reniform, black, 4.2–8.0 mm long, 3–6 mm wide; seeds 5–7 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *spathulatus*, meaning a broad, rounded upper part tapering gradually downward, and refers to the greatly expanded apices of the calyx lobes.

Distribution and Ecology: Peru, Departments of Arequipa, Ica, Lima, Moquegua, and Tacna, ranging >950 km; sea level to 1000 m.a.s.l. It is recorded from near-shore and interior localities (Fig. 156).

Illustration: Fig. 157. Illustration of *Nolana spathulata* from the Royal Botanical Expedition to the Viceroyalty of Peru, plate 113. H. Ruiz-López & J. Pavón (1777–1816). Drawn by Francisco Pulgar (1799).

Nolana spathulata is a distinctive annual herb with showy flowers. Individual size can vary from large, when excessive available moisture from a runoff pool allows for such growth

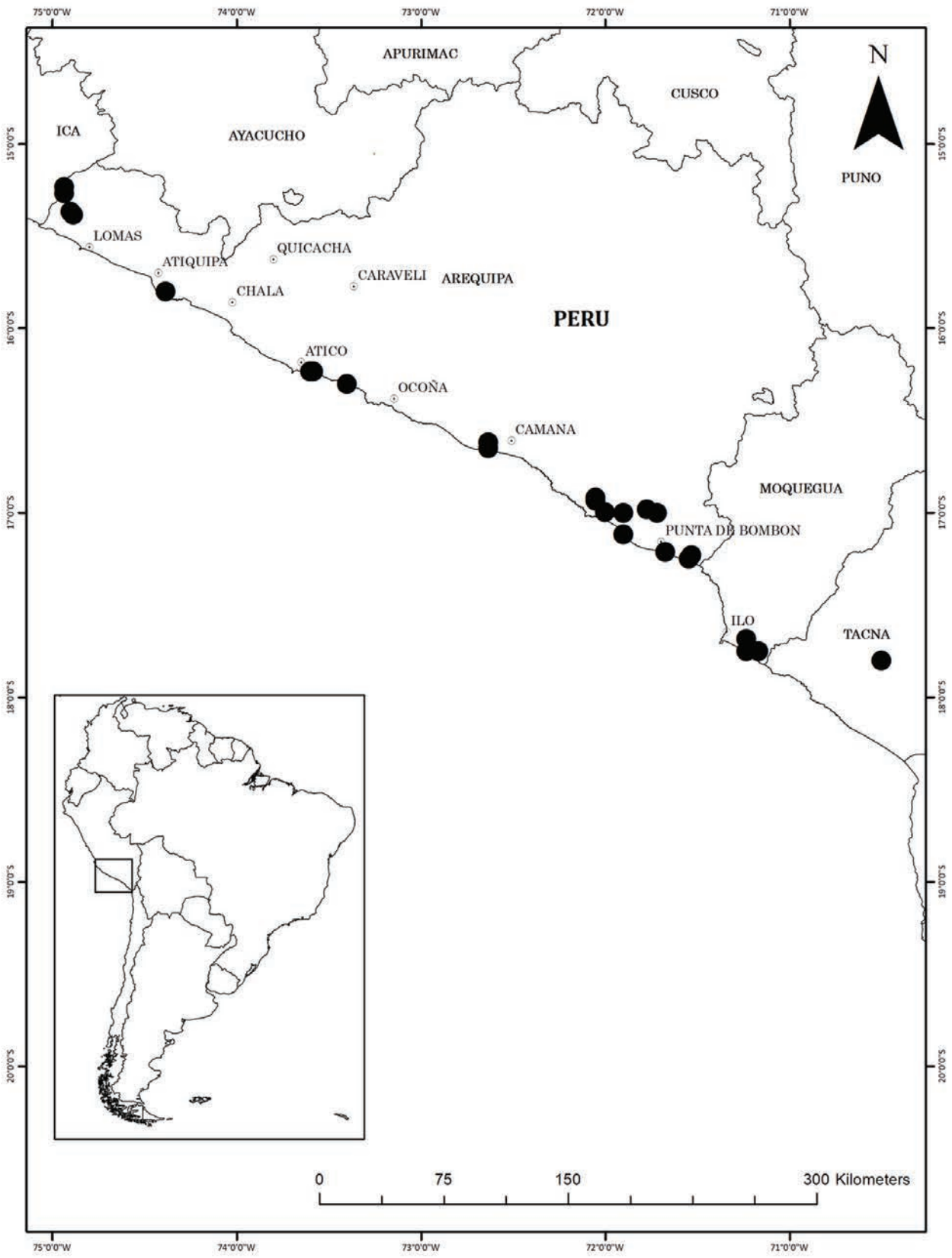


FIGURE 156. Distribution of *Nolana spathulata* Ruiz & Pav.

FIGURE 157. Illustration of *Nolana spathulata* for the Royal Botanical Expedition to the Viceroyalty of Peru, plate 113. H. Ruiz & J. Pavón (1777–1816). Drawn by Francisco Pulgar (1799).

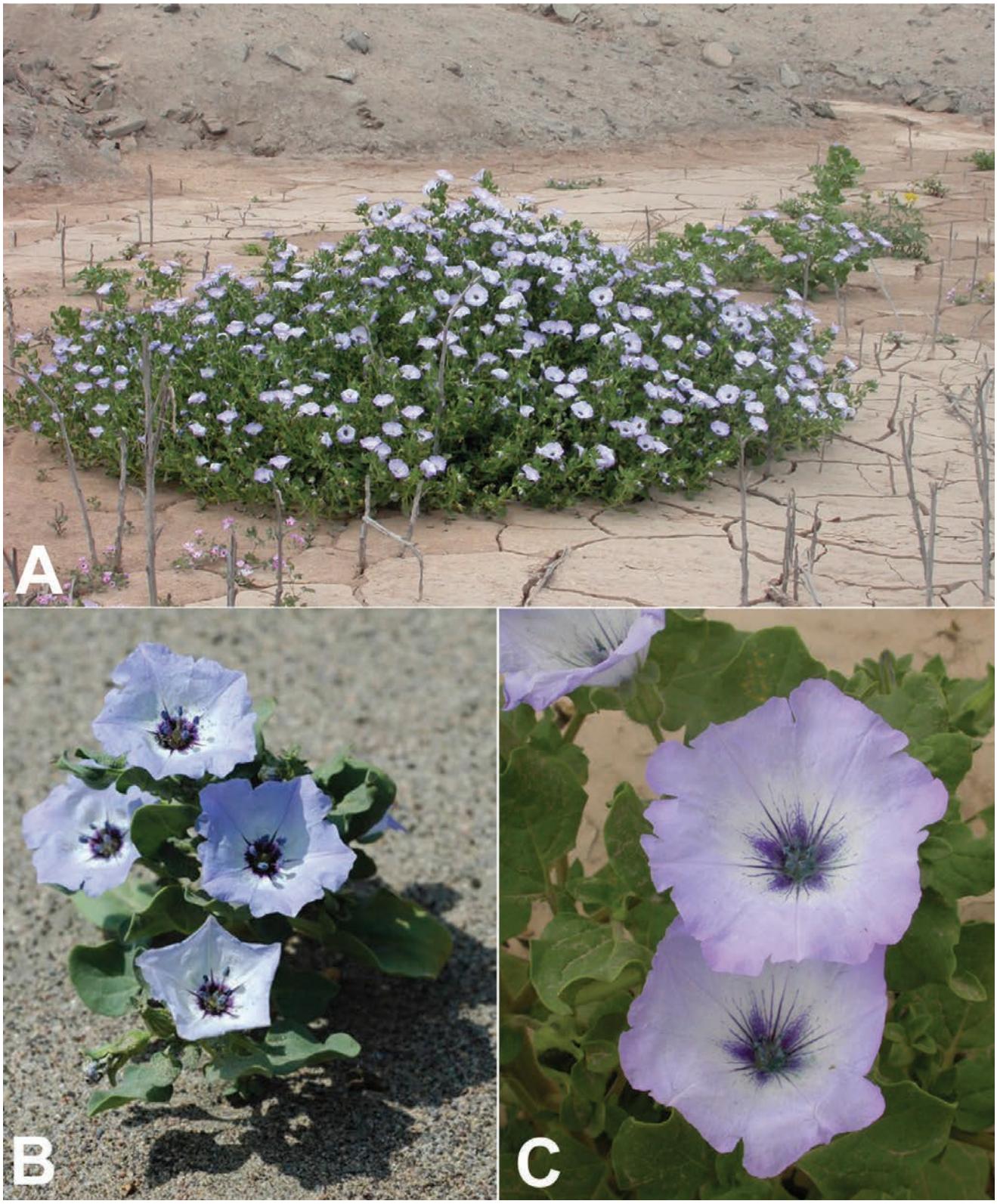


FIGURE 158. *Nolana spathulata*. **A**, Large growth habit with excessive available moisture; **B**, Small habit as individual germinates and flowers when only a few centimeters tall; **C**, Corollas with purple guides in throat.

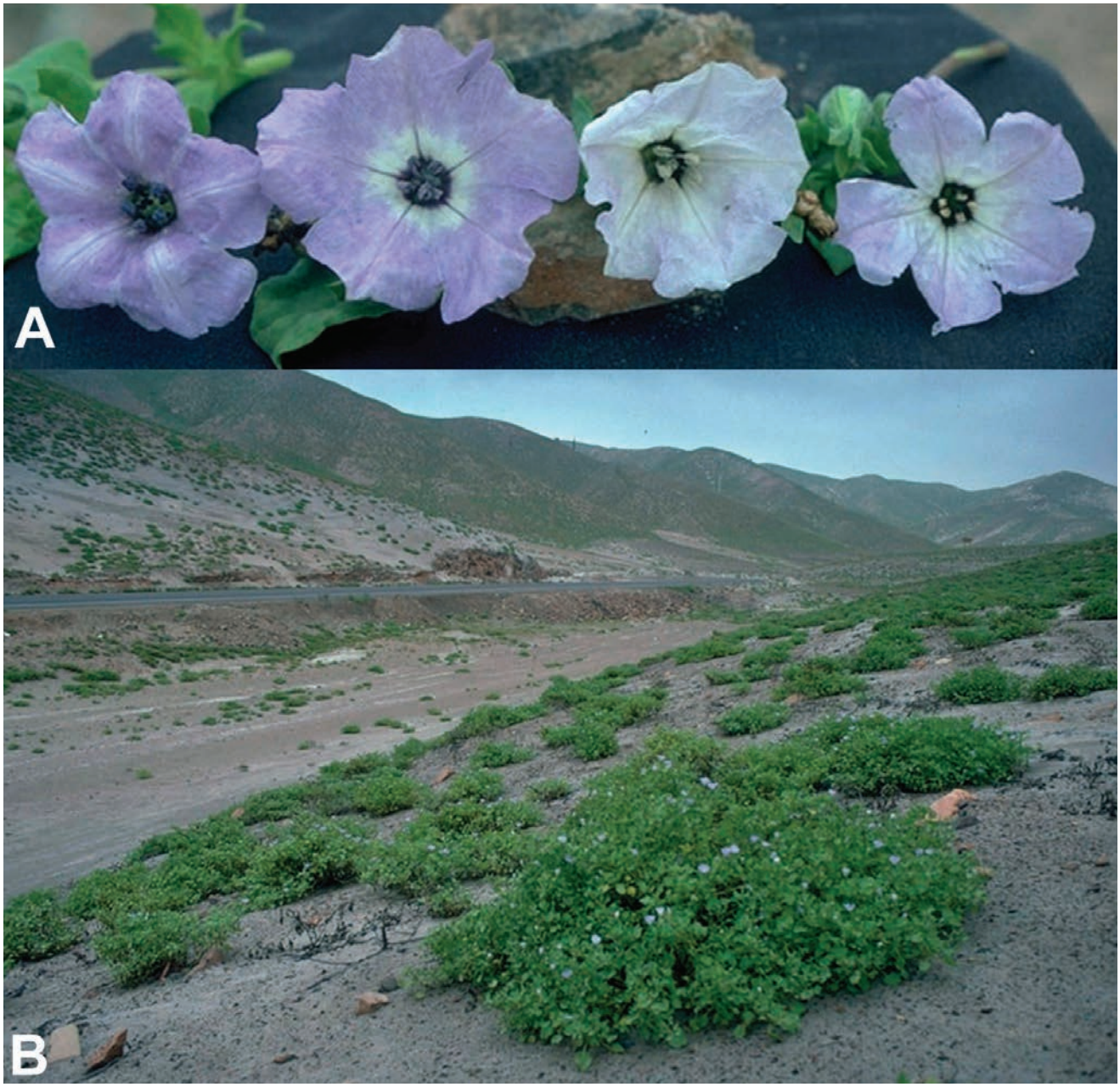


FIGURE 159. *Nolana spathulata*. **A**, Corollas are variable in size and color, all with dark purple guides at the base of the throat. **B**, Population at the Lomas of Cachendo, Peru, 1998.

(Fig. 158A); or, under appropriate conditions, an individual can germinate and flower when only a few centimeters tall (Fig. 158B). The corollas are variable in size and color, but always have dark purple guides at the base of the corollas (Fig. 158B–C). Within the large population at the Lomas of Cachendo, there is a range of corolla shapes and coloration patterns (Fig. 159A). I visited this population in 1983, 1998, 2005, and 2021. While there has been increased disturbance due to mining activities, the number of plants remains large (Fig. 159B). The plants growing in this region agree with *N. spathulata* in all diagnostic characters, with ovate to elliptic leaf blades (2–6 cm wide) with truncate to cordiform bases (Fig. 157), calyces with expanded apices (Fig. 160A–B), and large, showy corollas to ca. 40 mm wide (Fig. 158B–C). The calyx is unequally cleft with three and two lobes becoming obvious as the mericarps mature (Fig. 160D) and the calyx splits (Fig. 160E). It can be compared to *N. arenicola*, the other Peruvian species with elongate calyx lobes that are expanded at the apex, but it is distinguished from *N. arenicola*, which has narrowly elliptic leaves. It is also distinguished from *N. pallidula*, which has glabrous, narrowly spathulate to oblanceolate leaf blades (Fig. 161A) and a different floral morphology (Fig. 161B).

Dahlgren (1940, pg. 185) and Tepe (2018) have discussed

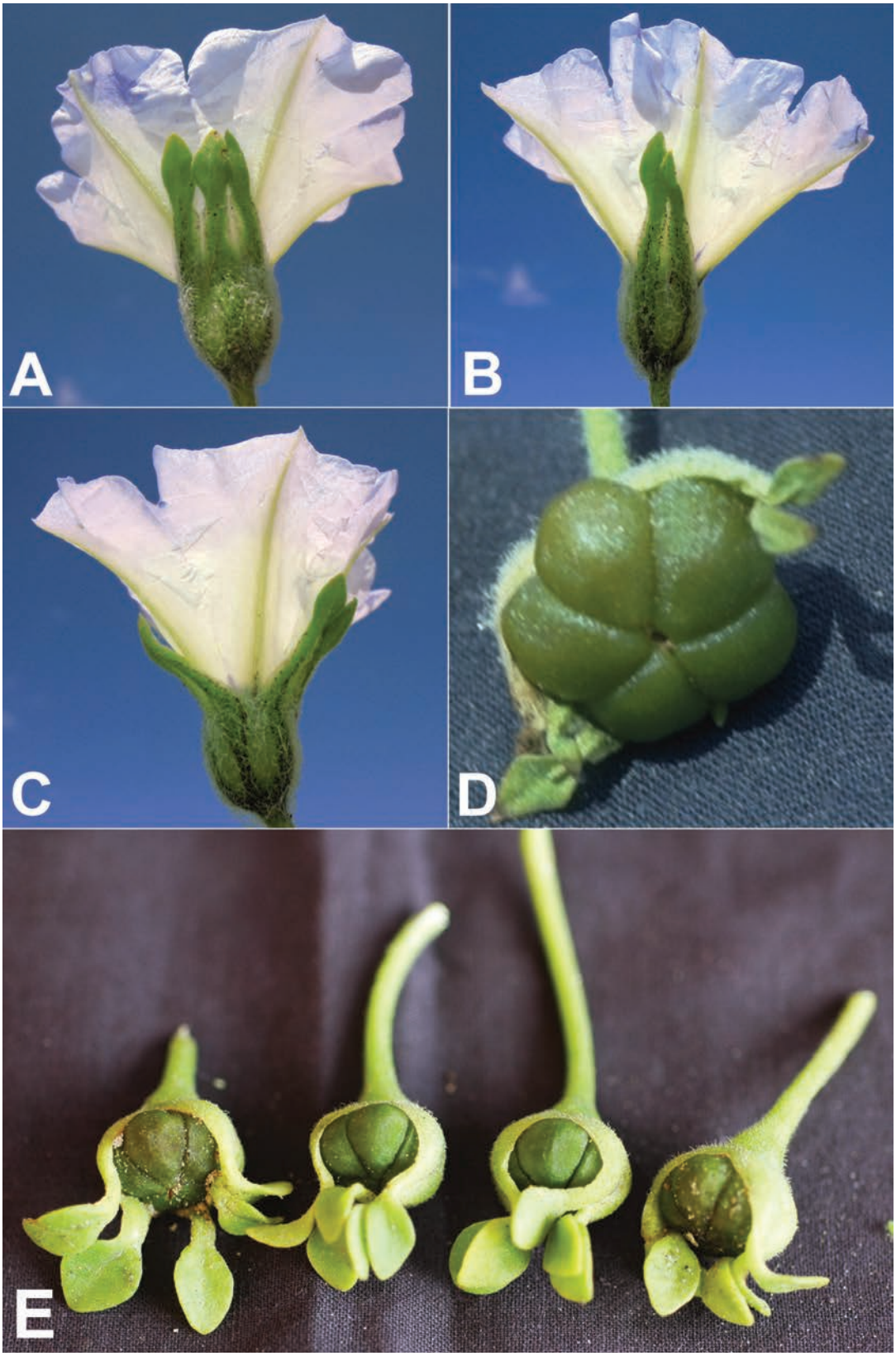


FIGURE 160. *Nolana spathulata*. **A–C**, Flowers with bilabiate calyx lobes, **D**, Five connate mericarps; **E**, Calyces opening with apically expanded unequal lobes.

FIGURE 161. *Nolana spathulata* compared with *N. pallidula*. **A1**, *Nolana spathulata*; **A2**, *N. pallidula*; **B1**, *N. spathulata* dissected corolla; **B2**, *N. pallidula* dissected corolla.

Tafalla, who collected with and for Ruiz and Pavón; he joined them on 14 November 1784. The Institut Botanic de Barcelona (BC) contains a few duplicate collections from the Royal Spanish Expeditions to Latin America (Ibáñez et al., 2006). The information cited in the checklist is as follows: *Nolana spathulata* [m. Pavón] "*Habitat in Peruvia collibus ad camana provintiam in Pongo et Atiquipa arenosis locis, nude Zuanes Tafalla nobis iconesis et descriptiones misit*." [m. Colmeiro] Revision label: *Nolana spathulata* Ruiz & Pav. [m. Llerd] 2/1/1941 BC- Ruiz & Pav. 558.

Nolana guentheri was described from an interior site near Cachendo, NW of El Fiscal at ca. 1000 m.a.s.l. From the inspection of material annotated by Johnston, this species resembles a rather pubescent form of *N. spathulata*, but with the leaf shape, expanded calyx apices, and mericarp number and size all agreeing with the more common and widespread *N. spathulata*. Although Johnston (1936) suggested that *N. guentheri* might be related to *N. humifusa*, molecular data and overall morphology suggest these two are not closely related. The type of *N. guentheri* was placed under *N. prostrata* (= *N. humifusa*) by Bruns (1929), but the type mostly closely resembles *N. spathulata*.

A sheet of *Nolana spathulata* housed at HUT (*Weigend & Förther 97/755*, HUT 34151), has a label that corresponds to *Weigend & Förther 97/754*, as it has the small field label attached to the stem of the actual specimen (*Weigend & Förther 97/754*). The Field Museum sheet of *Weigend & Förther 97/754* represents *N. inflata*.

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, ca. 9 km S of Camaná on road to interior, 16°39'S, 72°38'W, 80 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8208* (F 2198773); ca. 13 km S of Camaná on road to interior, 16°37'S, 72°38'W, 200 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8211* (F 2198770, F 2199318); Ocoña, N de Ocoña, ca. Km 767, 16°26'S, 73°08'W, 300 m.a.s.l., 12 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8761* (F 2276719, HSP 005096, US 3512517); Ocoña, N de Ocoña, ca. Km 767, 16°16'S, 73°28'W, 300 m.a.s.l., 12 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V. , M. Corrales M., & G. Castillo P. 8762* (F 2276720, HSP 005097, US 3512516); 3 km del Peaje de Camaná, Quebrada El Toro, 16°38'S, 72°37'W, 144–250 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8948* (F 2276707, HSP 005233, US 3512541); Lomas de Camaná, Camaná and Arequipa, Km 161–162, 400–500 m.a.s.l., R. *Ferreyra 2560* (US 1998580, USM 81274); Lomas de Camaná, 500–600 m.a.s.l., 10 November 1952, *R. Ferreyra 8823* (USM 81271); El Arenal, cerca de Ocoña, 100 m.a.s.l., 23 October 1976, *R. Ferreyra 18638* (USM 81276). Prov. Caravelí, Nasca–Chala, 14 February 1958, *D. S. Correll & E. E. Smith P172* (US 2340533); Lomas of Jahuay, ca. 51 km NW of Chaviña, 300 m.a.s.l., 7 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3219* (CONC, E, F 2016607, F 2043424, GH, NY, SGO, US 3470033); Lomas of Jahuay, 365–380 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3757* (F 1940844); Lomas de Jahuay, 30 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3767* (CONC, E, F 1950164, GH, K); Lomas of Atico, ca. 8 km S of Atico along Pan-American Highway, KM 706–707 S of Lima, 40 m.a.s.l., 3 November 1983, *M. O. Dillon & D. Dillon 3837* (CONC, E, F 1950514, GH, K, SGO, US, USM); ca. 23 km S of Atico, 16°18'S, 73°24'W, 0 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8204* (E, F 2198755, GH, SGO, US); Ocoña, N de Ocoña, Km 787, 16°16'S, 73°28'W, 300 m.a.s.l., 12 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8763* (F 2276721, HSP 005098, HUSA 6265, US 3512515); Chala, al S de Chala, 15°52'S, 74°13'W, 180 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8875* (F 2276736, HSP 005177, US 3512500); Chala, al S de Chala, 15°52'S, 74°13'W, 230 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8877* (F 2276738, HSP 005179, US 3512502); Cháparra, 6 km al E de Panamericana Sur, camino a Cháparra, 15°52'S, 74°07'W, 400–600 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8907* (F 2276698, US 3512532); Lomas de Atico, 300–400 m.a.s.l., 17 October 1946, *R. Ferreyra 1386* (US 2051318, USM 81269); Lomas de Atico, 150–200 m.a.s.l., 13 November 1949, *R. Ferreyra 6460* (USM 81259); Lomas de Jahuay, 300-400 m.a.s.l., 28 April 1983, *R. Ferreyra 8595* (USM 49034); Lomas de Jahuay, 300–400 m.a.s.l., 2 May 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 8634* (USM 81292); Lomas de Atico, 50–100 m.a.s.l., 3 December 1955, *R. Ferreyra 11719* (USM 81273); Lomas de Jahuay, 300–400 m.a.s.l., 3 December 1955, *R. Ferreyra 11755* (USM 81262); Lomas de Cápac, 200–260 m.a.s.l., 10 October 1956, *R. Ferreyra 11937* (USM 81269); Lomas de Cháparra, cerca de Chala, 200–250 m.a.s.l., 14 October 1956, *R. Ferreyra 11959* (USM 81264); Lomas de Atico, 100–150 m.a.s.l., 8 December 1956, *R. Ferreyra 12016* (USM 81261); Lomas de Jahuay, 300–400 m.a.s.l., 3 October 1957, *R. Ferreyra 12486* (USM 81266); Lomas de Jahuay, 300–400 m.a.s.l., 20 December 1959, *R. Ferreyra 14021* (USM 81267); arriba de Mollendo, 800–900 m.a.s.l., 24 October 1976, *R. Ferreyra 18668* (USM 81299); Lomas de Jahuay, 300–400 m.a.s.l., 28 April 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19774* (USM 45712); Lomas de Jahuay, 300–400 m.a.s.l., 28 April 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19781* (USM 49022); Cachendo, *E. K. F. Günther & O. Buchtien 110* (HBG 522241), *123* (HBG 522240), *E. K. F. Günther & O. Buchtien 115* (HBG 522243, HBG 522242); Lomas de Cápac, Panamericana Hwy Km 652 S of Lima, 6 km S of Chala, 200 m.a.s.l., 13 September 1957, *P. C. Hutchison 1287* (F 1559939, K, US 2404054, USM 81263); ca. 4 km NW of Cerro de Arena between Atico and Ocoña, 14 January 1963, *H. M. Iltis, C. M. Iltis, D. Ugent, & V. Ugent 1543* (GH, US 2558196); 4 km NW of Cerro de Arena, Atico–Ocoña, 14 January 1963, roadside of Agua Salada, between Tanaka and Atiquipa, ca. 550 km S of Lima, 28 September 1985, *M. Ono, T. Masuzawa, & N.*

Kawakubo s.n. (MAK 229690); Quebrada del Jahuay, entre los km 809–810 de Panamericana Sur, 20–100 m.a.s.l., 17 July 1996, *J. Roque 265* (HUT 40885, HUT 58202); 11 km S of Atico, Km 712 Pan-Americana Sur, 4 October 1997, ca. 50 m.a.s.l., *M. Weigend & H. Förther 97/755* (F 2211305). Prov. Islay, sand flats between Mollendo and Mejía, 6–10 ft, 8 April 1939, *W. B. Gourlay 131* (E00793135); Lomas de Cachendo, ca. 1050 m.a.s.l., 9 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3284* (CONC, E, F 1950169, GH, SGO, US); Lomas de Cachendo; ca. 84 km S of Arequipa and ca. 25 km S of La Joya (Km 1028), 900 m.a.s.l., 9 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3286* (F 1950168); Lomas of Mollendo, ca. 9 km NW of Mollendo, 100 m.a.s.l., 20 November 1983, *M. O. Dillon & D. Dillon 3919* (F 1941145); ca. 14 km N of Matarani, 16°56'S, 72°03'W, 730 m.a.s.l., 23 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8218* (E, F 2198761, GH); Lomas de Cachendo, ca. 106 km N of Moquegua, 17°00'S, 71°43'W, 430 m.a.s.l., 1 March 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8239* (F 2199339); Cocachacra, Lomas de Cachendo, 16°59'S, 70°46'W, 1000 m.a.s.l., 20 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9014* (F 2276621, GH, HSP 005284, US 3512555); 10 km S of Mollendo, sea level, 23 April 1939, *W. J. Eyerdam 25153* (K), *25154* (K); Lomas de Cachendo, 1 May 1983, 900–1000 m.a.s.l., *R. Ferreyra, E. Cerrate, & M. Chanco 8652* (USM 75176); Jahuay, entre Nazca and Chala, 400 m.a.s.l., 9 November 1952, *R. Ferreyra 8805* (USM 81272); Lomas de Mollendo, Quebrada de Guerreros, 800–900 m.a.s.l., 7 October 1957, *R. Ferreyra 12622* (USM 81270); Mollendo, 24 October 1976, 150–200 m.a.s.l., *R. Ferreyra 18647* (USM); Lomas de Cachendo, 900–1000 m.a.s.l., 1 May 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19828* (USM 75869); Lomas de Cachendo, 16°59'13"S, 71°46'46"W, 861 m.a.s.l., 19 September 2014, *A. Pauca T., C. Fernandez, & P. Jimenez M. 497* (HSP 007875); Lomas de Yuta, a 1 km de Matarani, 16°57'23"S, 72°04'07"W, 521 m.a.s.l., 16 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3455* (HSP 000627); Dist. Mollendo, a 9 km de la Carretera Panamericana (El Fiscal), 24 April 2019, *M. Quispe T. 195* (HSP 12014); cima del Cerro Yuta, 16°56'26"S, 72°4'32"W, 879 m.a.s.l., 4 November 2012, *V. Quipuscoa S., C. Tejada P., J. Quispe T., & J. Cárdenas R. 5119* (HSP 003858); Dist. Punta de Bombón, ca. Km 157 carretera costañera Punta de Bombón–Ilo, 17°12'41"S, 71°40'22"W, 7 m.a.s.l., 28 October 2017, *V. Quipuscoa S., D. Rodríguez P., M. Balvin A., & M. Bedoya C. 6231* (HSP 8767); Dist. Punta de Bombón, Lomas de Jesús, 17°13'43"S, 71°31'51"W, 259 m.a.s.l., 29 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., M. Bedoya C., C. Sanz N., & M. Flores M. 6306* (HSP 011332); parte alto Lomas de Cachendo, 16°58'53"S, 71°46'21"W, 961 m.a.s.l., 31 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., M. Bedoya C., C. Sanz N., & M. Flores M. 6352* (HSP 011350, HUT 60405); Lomas de Mollendo, 16°59'45" S, 72°00'00"W, 306 m.a.s.l., 2 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6391* (HSP 6391); Lomas de Jesús, 17°14'50"S, 71°32'43"W, 267 m.a.s.l., 6 January 2018, *V. Quipuscoa S., M. O. Dillon, & C. Tejada P. 6858* (HSP 12035); Mollendo, 732 m.a.s.l., 27 February 2015, *D. Ramos A. & C. Fernández A. 1837* (HSP 007993); Mollendo, 26 July 1937, 200 ft, *D. B. Stafford 840* (BM000941271, K); Cachendo, 1 November 1937, 3000 ft, *D. B. Stafford 1024* (BM000941270, K); Lomas de Tambo, 9 April 1959, 900–1000 m.a.s.l., *C. Vargas C. 12656* (CUZ, USM 80817); Lomas de Tambo, 800 m.a.s.l., 1 December 1959, *C. Vargas C. 13085* (USM 80816); 8 km S of Mollendo, 28 September 1938, 3 m.a.s.l., *C. R. Worth & J. L. Morrison 15735* (K). **Ica**. Prov. Nazca: Marcona, Km 489, cruz para Marcona, 15°15'S, 74°56'W, 580 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8772* (F 227622, US 3512514); Marcona, sur de Nazca, Km 518, 15°23'S, 74°55'W, 420 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8780* (F 2276723, US 3512507); Lomas de Marcona, 900 m.a.s.l., 22 September 1958, *R. Ferreyra 13378* (USM 81265); Chaviña, 200 m.a.s.l., 16 March 1957, *W. Rauh & G. Hirsch P468* (F 1572608); 12 km de Nazca, 25 July 1944, *C. A. Ridoutt s.n.* (USM 14661). **Lima**: Prov. Chancay, Lomas de Chancay, Pasamayo, 7 October 1980, 200–250 m.a.s.l., *M. Ono & Masuy s.n.* (USM 35847). **Moquegua**: Prov. Mariscal Nieto, Lomas of Ilo; ca. 20 km E of Ilo, 620 m.a.s.l., 12 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3315* (CONC, E, F 1950166, F 2043419, GH, SGO, US); Lomas of Ilo, ca. 79 km SW of Moquegua and just SW of Ilo, 260–460 m.a.s.l., 18 October 1983, *M. O. Dillon & D. Dillon 3645* (E, F 1950180, GH, K); Ilo: ca. 16 km SE of Ilo, 17°41'S, 71°14'W, 25 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8222* (F 2199321); Lomas of Ilo (Mostazal), 6 October 1957, 600–650 m.a.s.l., *R. Ferreyra 12570a* (K, USM 80808); Lomas de Ilo, 17°41'26"S, 71°14'35"W, 597 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3427* (HSP 002675); Lomas de Ilo, 17°41'26"S, 71°14'35"W, 597 m.a.s.l., 15 November 2007, *V. Quipuscoa, M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3430* (HSP 002678); Lomas de Ilo, 17°41'50"S, 71°15'09"W, 566 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3434* (HSP 002682); Lomas de Mostazal, 10 km S of Ilo, 100–200 m.a.s.l., 12 October 1997, *M. Weigend & H. Förther 97/839* (F 2211303, HUT 34230); Lomas de Mostazal, ca. 10 km S of Ilo, 100–200 m.a.s.l., 12 October 1997, *M. Weigend & H. Förther 97/840* (F 2211311, K). **Tacna**: Prov. Tacna, 29–32 km WNW of Tacna on Pan-Americana Highway (Pampa de Sama), Km 1241–1247, 17°48'S, 70°30'W, 550–630 m.a.s.l., 14 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4784* (BM, CONC, E,F 1980810, GH, HUT 22763, US 3470030, USM

74851); Lomas of Tacna; ca. 45 km N of Tacna, ca. 3 km E of Pan-American Highway, 560 m.a.s.l., 9 November 1983, *M. O. Dillon & D. Dillon 3894* (CONC, E, F 1950505, GH); Tacna, ca. 99 km SE of Moquegua, 17°37'S, 70°40'W, 810 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8233* (F 2199334); Dist. Inclán, Sama Grande, 17°47'43"S, 70°38'06"W, 574 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3415* (HSP 002668); Lomas de Sama, 700–800 m.a.s.l., 1 May 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 8638* (USM 75169); Lomas de Morro Sama, 500–600 m.a.s.l., 6 October 1957, *R. Ferreyra 12546* (GH, USM 80807); Lomas de Sama Grande, ca. 40 km NW of Tacna, 700–900 m.a.s.l., 10 October 1997, *W. Weigand & H. Förther 97/811* (F 2211296, HUT 34153); Near Tacna, ca. 800 m.a.s.l., August 1925, *E. Werdermann 723* (B, BM000941364, CONC 55629, E00273875, F 564168, GH, K, US 3318609, US 1444763).

D19. ***Nolana weberbaueri*** I.M. Johnst., Contrib. Gray Herb. 112: 58. 1936. TYPE: PERU. Ica: Prov. Pisco, District Huancáno, western Andean slopes east of the port of Pisco, between Huauyanga and Pampano [13°33'S, 75°30'W], 1000–1200 m, steep rocky places, annual herb with somewhat fleshy leaves, flowers "rot-lilia", May 1910, *A. Weberbauer 5385* (Holotype: GH [00282366]; Isotypes: F [F 627943], B, US [US 1473528, US00121964]). Fig. 162–164.

Digital image: Holotype of *Nolana weberbaueri* from Harvard University Herbaria, Cambridge [GH00 282366]. https://s3.amazonaws.com/huhwebimages/4A10005AB61C468/type/full/282366.jpg

Homotypic synonym: *Nolana laxa* (Miers) I.M. Johnst., Contr. Gray Herb. 112: 59. 1936, fide Mesa-M. (1981).

Annual *herbs*, erect, 10–20(–50) cm tall, pilose with capitate-glandular trichomes; stems 2–3(–5) mm in diam., laxly dichotomous branching above, internodes 1–3 cm long, purplish. *Leaves* alternate to subopposite, blades ovate or deltoid-ovate to lanceolate, 7–15 mm long, 4–10 mm wide, apically obtuse, basally rounded or obtuse, densely pubescent with capitate-glandular trichomes; petioles 5–20 mm long, upper leaves sessile. *Inflorescences* of solitary flowers; pedicels 4–10 mm long. *Flowers* 5-merous; calyces cupulate, 5–7 mm long, tube ca. 2 mm in diam., lobes lanceolate, unequal, 4–5 mm long; corolla infundibuliform, reddish-violet, 15–18 mm long, ca. 12 mm wide, outer puberulent pubescent; inner nectar guides distinct, tube 2–3 mm long, 1–2 mm wide, villous inside, lobes rounded; stamens unequal, linear, glabrous, 4–5 mm long; pollen blue. *Mericarps* 4–6, globose, black, 2–3 mm in diam., tuberculate-rugose; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Augusto Weberbauer (b. 1871–d. 1948), a Polish- or German-born naturalist, botanist and university professor, who systematically explored Peru in search of new plant species. His collections are the types for many Peruvian species; he sold several thousand duplicates to the Field Museum in the 1920s and 1930s.

Distribution and Ecology: Peru, Departments of Ayacucho and Ica; 1000–1200 m.a.s.l. It is recorded from sandy soils in upper elevation sites distant from the coast (Fig. 162). These habitats are dominated by rocky slopes with scattered shrubs and annual grasses, that are sustained by winter fog from the coast and/or, more commonly, seasonal rains from the adjacent Andes.

Nolana weberbaueri is part of a complex of species, including *N. laxa* to the north and *N. chapiensis* and *N. rhombifolia* to the south. It is a rare species, represented by only a few collections. The recent collection by *Quipuscoa et al. 7617* from Ayachucho was from an area that had recently received rain, and the runoff had formed a small pond or *pozo*. The plant in Fig. 163A was collected from within the drying pond and was more robust, with branching stems reaching ca. 50 cm long, with ovate, petiolate lower leaves. The corollas expand above the unequal calyx lobes (Fig 163B), and they are densely pubescent with capitate-glandular trichomes (Fig. 163C). The individual in the type collection is more diminutive in stature, 10–20 cm tall.

I. M. Johnston (1936) commented on this taxon and suggested its affinities were with *N. laxa*, another species of the western cordilleran slopes of central Peru and nearly 100 km inland. A collection by Paul Gonzáles Arce (*#1629*) from Ica displays an enlarged root, ca. 12 mm in diameter, but is still simply a robust annual and was likely collected from an area with substantial available moisture.

Additional specimens examined: PERU. **Ayacucho**: Prov. Lucanas, Dist. Sancos, ca. a San Luis, carretera a Coracora, 15°17'28"S, 74°18'15"W, 703 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7617* (HSP 12043). **Ica**: Prov. Chincha, Cerro Lindo, 13°04'28"S, 75°59'32"W, 900–2496 m.a.s.l., 27 September 2011, *P. Gonzáles 1629* (USM 255392); Prov. Pisco, La Bolívar, 1048 m.a.s.l., 3 March 2014, *E. Mendivil, S. Novoa, M. Fernández, M. Zablith, & K Bravo 008* (MOL), 1161 m.a.s.l., *E. Mendivil, S. Novoa, M. Fernández, M. Zablith, & K Bravo 010* (USM 280099).

D20. ***Nolana weissiana*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 9. 1955. TYPE: PERU. Arequipa: Lomas de Cháparra, cerca a Chala, 450 m, 30 April 1950, *R. Ferreyra 7232* (Holotype: USM [242146, USM000582]; Isotypes: GH [GH00282365], US [US 2028332, US00121965]). Fig. 165–168.

Digital image: Holotype of *Nolana weissiana* from Herbario San Marcos, Lima [USM 242146]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000582

Perennial *herbs*, suffrutescent, with basal rosette; taproot to ca. 15 cm long; stems erect to decumbent, 10–45 cm long, 1.2–3.0 mm in diam., densely arachnoid-tomentose. Basal *leaves* rosulate, blades spathulate to lanceolate or rhomboid, 20–150 mm long, 11–85 mm wide, densely pubescent, capitate-glandular, and non-glandular, flagelliform trichomes, apically obtuse, basally attenuate to truncate, margins undulate, abaxial nerves prominent; petioles 15–40

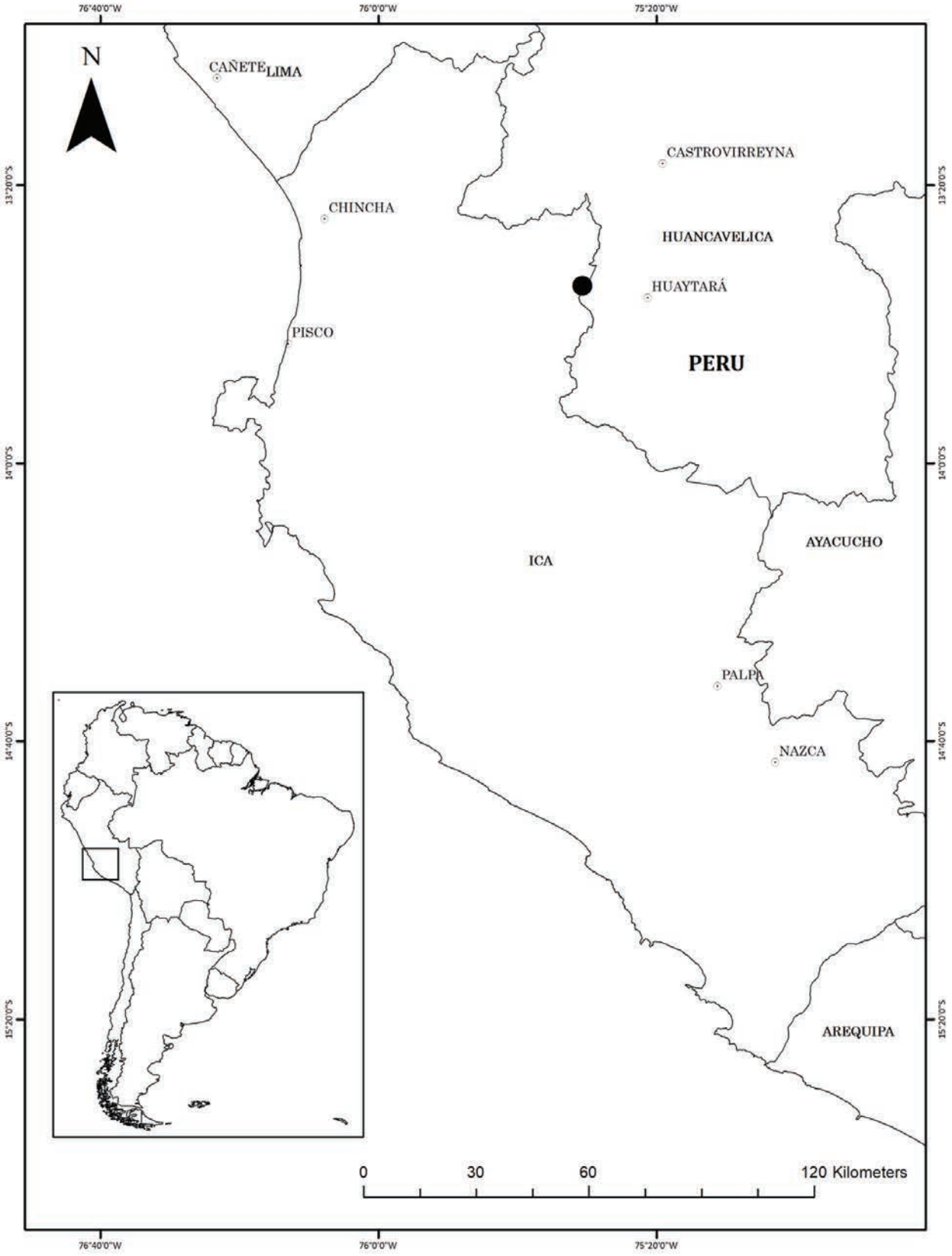


FIGURE 162. Distribution of *Nolana weberbaueri* I.M. Johnst.

FIGURE 163. *Nolana weberbaueri*. **A**, Robust plant in pond, or *pozo*, drying out. **B**, Leaves ovate, corollas expand above the calyx, **C**, Pubescent calyx with capitate-glandular trichomes. Photographs by Victor Quipuscoa Silvestre.

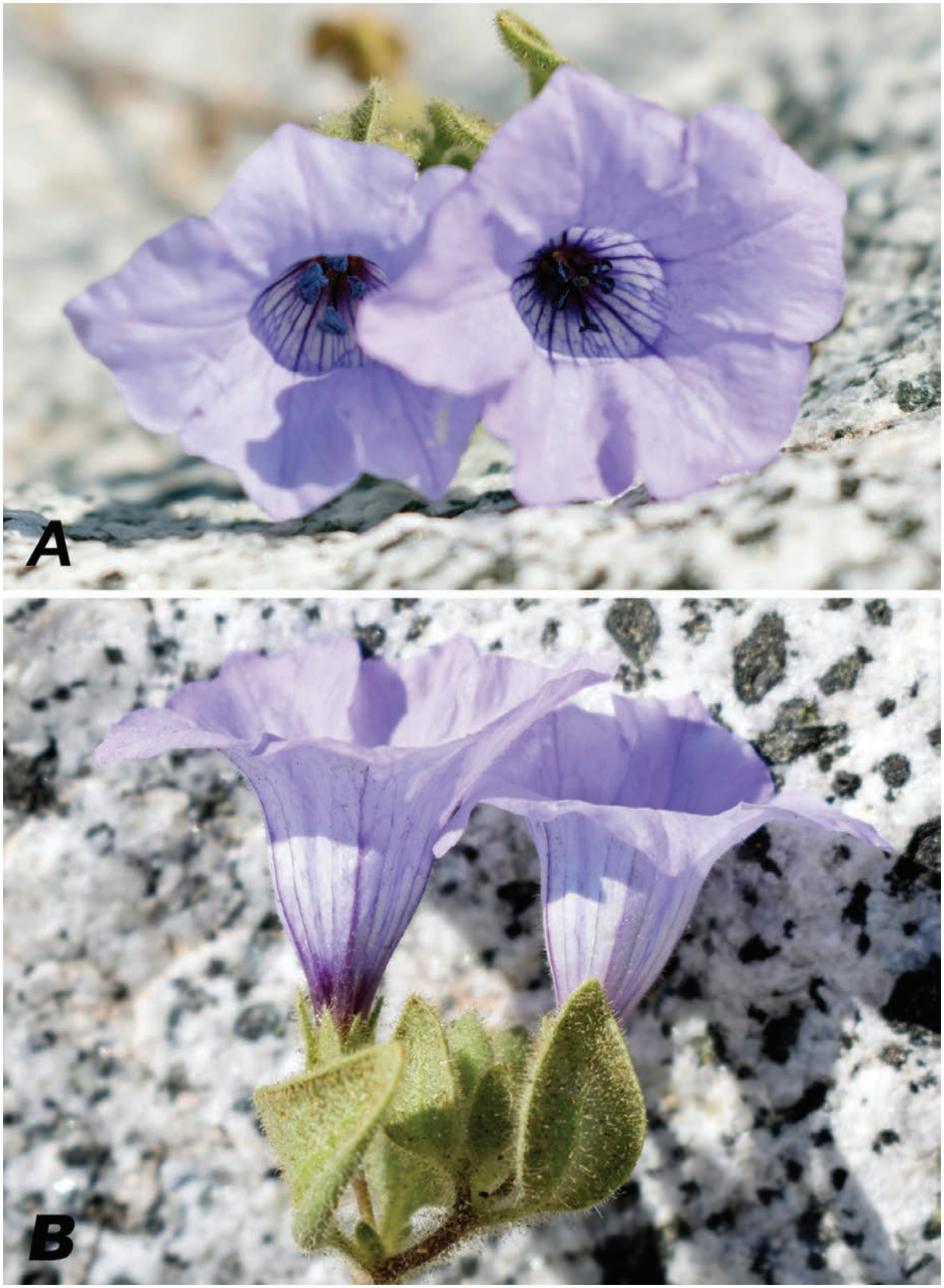


FIGURE 164. *Nolana weberbaueri*. **A**, Frontal view of corollas with purple guides at base of throat; **B**, Apical, densely pubescent leaves and flowers. Photographs by Victor Quipuscoa Silvestre.

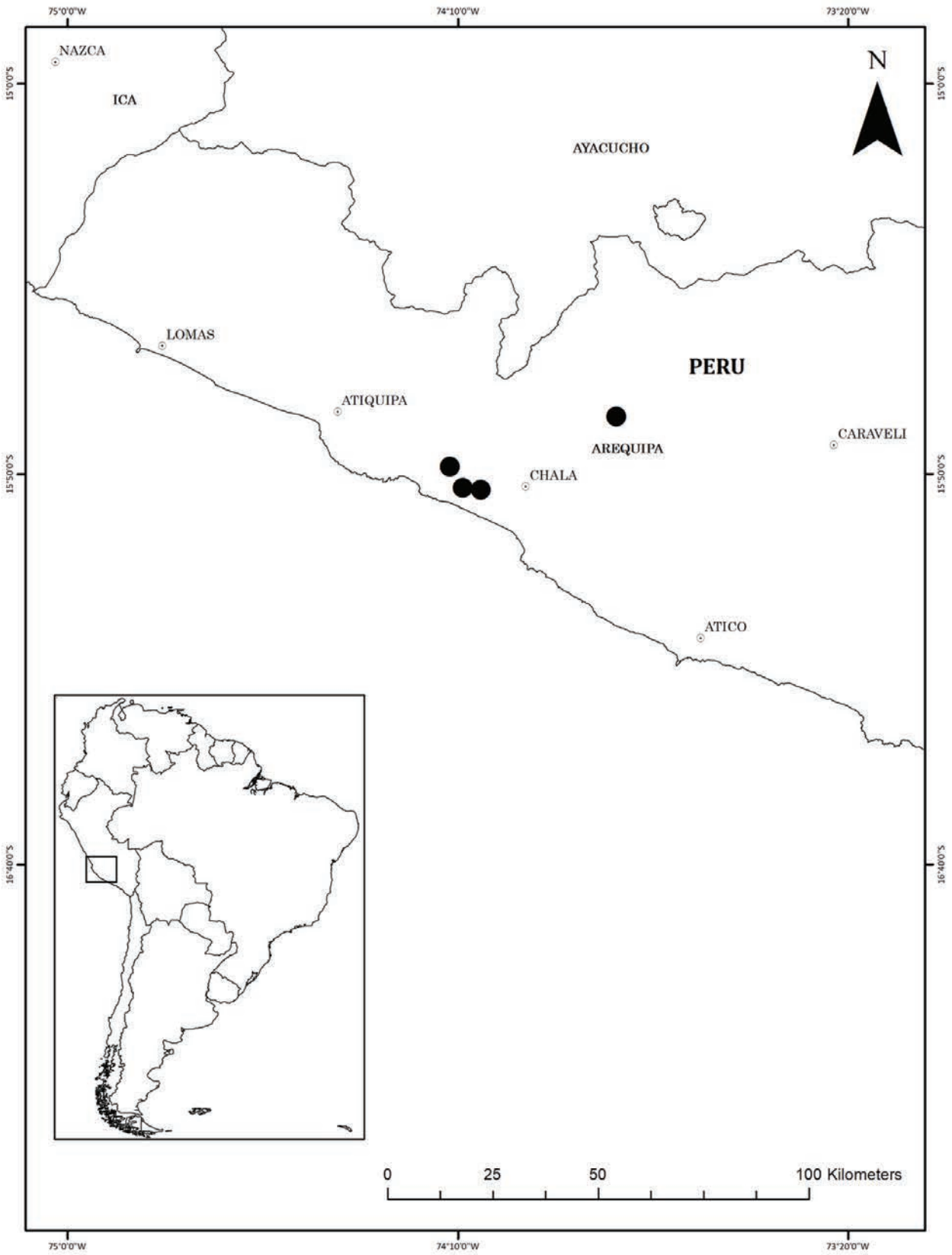


FIGURE 165. Distribution of *Nolana weissiana* Ferreyra.

FIGURE 166. *Nolana weissiana*. Basal rosettes and specialized prostrate stems forming many-flowered inflorescences.

mm long; flowering stems prostrate to ascending, cauline leaves alternate, blades ovate, ca. 30 mm long, 20–25 mm wide, apically obtuse, basally attenuate to cordate, arachnoid-tomentose, gradually smaller toward apex; petioles ca. 20 mm long, ca. 3 mm wide. *Inflorescences* weakly cymose, flowers terminal and axillary; pedicels 2–10 mm long. *Flowers* 5-merous; calyces 9–11 mm long, 5.0–6.5 mm in diam., globose-campanulate, densely arachnoid pubescent outside, tube 5.0–5.5 mm long, lobes 5, triangular, 3.5–6.0 mm long, 2.2–4.0 mm wide at base, acute, pubescent dorsally; corollas infundibularis, regular to weakly zygomorphic, 19–22 long, 16–30 mm wide, violet to deep purple; stamens, unequal, united to tube for 1/2 its length, 2 larger 10–11 mm long, 3 smaller 8.5–9.0 mm long; style 7–10 mm long. *Mericarps* 9–10, 5 larger, reniform, 3–4 mm long, 2–3 mm wide, 4–5-smaller ovoid, ca. 1mm in diam.; seeds 2–8. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Pedro Weiss Harvey (b. 1893–d. 1985), a medical doctor and anthropologist at the Universidad Nacional Mayor de San Marcos, Lima, and is considered to be the first to study human pathology in Peru.

Distribution and Ecology: Peru, Departments of Arequipa and Ayacucho; 200–500(–1375) m.a.s.l. (Fig. 165). It is recorded from interior sites over 50 km from the ocean.

Nolana weissiana has basal rosettes and specialized prostrate stems that form inflorescences with many flowers (Fig. 166). The type locality has individuals growing on the slopes at Cháparra (Fig. 167A). The basal rosette of leaves is comparable to those in *N. inflata* (Fig. 167B). Ferreyra (1955) distinguished these two by the differences in pubescence, calyx shape, corolla color, and mericarp size; however, this material shares so many characters with *N. inflata*, it is only tentatively recognized, and it is recovered with that species in molecular studies (Dillon et al., 2009). The flowers are invariably purple with deep blue guides at the base of the throats (Fig. 168A). The gynoecium is composed of five principal mericarps and five minor mericarps (Fig. 168B). The lateral view of the gynoecium illustrates the position of the mericarps and the green receptacle (Fig. 168C).

In his monograph of Peruvian species, Ferreyra (1961: 32) cited *Ferreyra 7322* (USM) as the holotype; this was obviously a *lapsus calami*, since an examination of all types shows it to be *Ferreyra 7232* (GH, USM, US).

Additional specimens examined: PERU. **Arequipa**: Prov. Caravelí, a 6 km al E de Panamericana Sur, camino a Cháparra, 15˚52'S, 74˚07'W, 400–600 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8898* (F 2276697, HSP 005193, US 3512531); Lomas de Cháparra, 200–300 m.a.s.l., 19 October 1946, *R. Ferreyra 1457* (US 2051319); Lomas de Cápac, cerca de Chala, 200–260 m.a.s.l., 10 October 1956, *R. Ferreyra 11931* (K, USM 81286); entre Nazca y Chala, 300–400 m.a.s.l., 18 October 1946, *R. Ferreyra 1418* (USM 81287); Lomas near Chala, 260–400 m.a.s.l., 10 October 1955, *R. Ferreyra 11458* (K, USM 81289); Lomas de Cháparra, sur de Chala, 300–400 m.a.s.l., 5 September 1984, *R. Ferreyra & M. Ono 20323* (USM

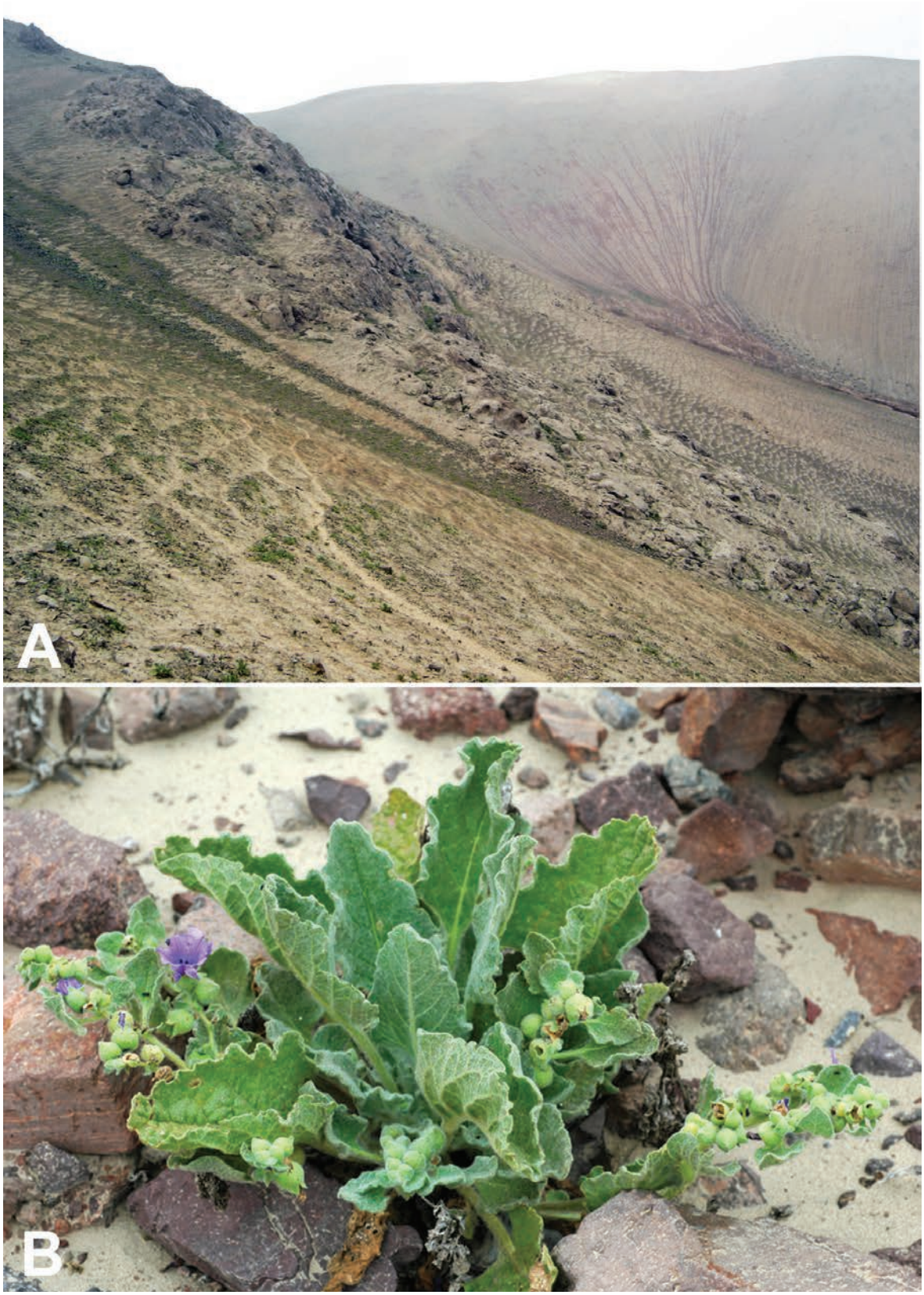


FIGURE 167. *Nolana weissiana*. **A**, Slopes at the type locality at Lomas de Cháparra, Peru; **B**, Basal rosette comparable to *N. inflata*.

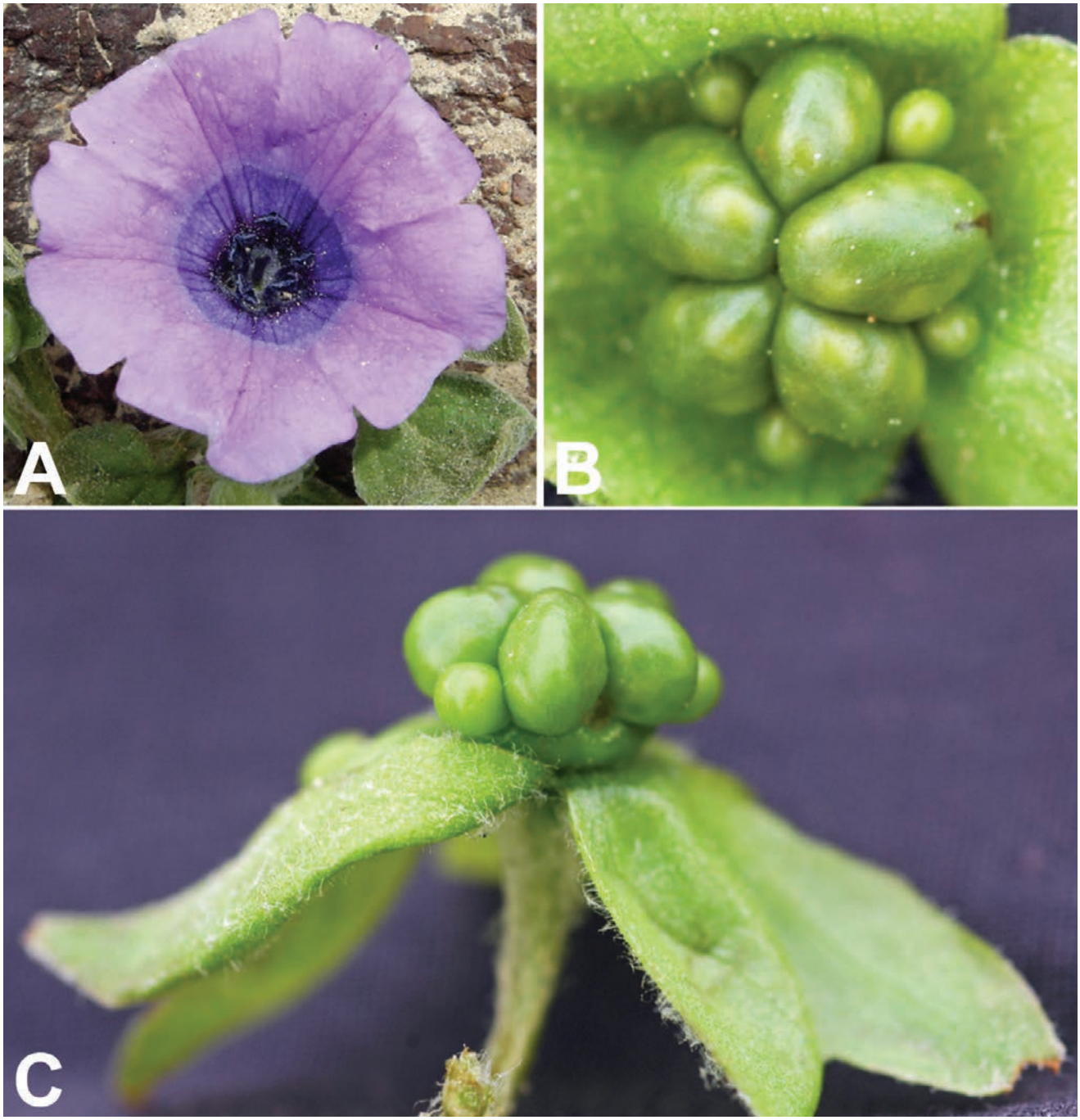


FIGURE 168. *Nolana weissiana*. **A**, Corolla invariably purple with deep blue guides at the base of throats; **B**, Gynoecium with five principal mericarps, five minor mericarps; **C**, lateral view of the gynoecium.

81289*);* Lomas de Cápac, 225 m.a.s.l., 14 September 1957, *P. C. Hutchison 1316* (F 1559927, US 2406366, USM 81289); Dist. Cháparra, Lomas de Cápac, 15°51'48"S, 74°11'30"W, 197 m.a.s.l., 20 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3591* (HSP 002522); Dist. Cháparra, 15°51'43"S, 74°09'20"W, 504 m.a.s.l., 29 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., M. Bedoya C., & W. Ancalla C. 6717* (HSP 12032); Dist. Cháparra, cerca a Arasqui Km 49, 15°42'36"S, 73°49'40"W, 1374 m.a.s.l., 30 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., M. Bedoya C., & W. Ancalla C. 6725* (HSP 8821). **Ayacucho**: Prov. Parinacochas, Dist. Pullo, desvío a Palca, entre San Luis y Carrizal, camino a Coracora, 15°14'22"S, 74°13'57"W, 905 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7644* (HSP 10558).

D21. ***Nolana willeana*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 12: 42. 1961. TYPE: PERU. Ica: Prov. Santiago, Lomas de Amará, cerca a desembocadura del Río Ica, July 1956, 700 m, *M. E. Köie s.n.* (Holotype: USM [242147, USM000585]; Isotype: C). Fig. 169–172.

Digital image: Holotype of *Nolana willeana* from Herbario San Marcos, Lima [USM 242147]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000585

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 134. 1981.

Spreading perennial *herbs* to ca. 30 cm tall; stems erect to decumbent, branched, canescent, lanuginose, branches 2–3 mm in diam. Basal *leaves* rosulate, blades spathulate to oblong, 18–32 mm long, 5–10 mm wide, subsessile, apically obtuse, base attenuate, uninerved, canescent, densely lanuginose; cauline leaves alternate, blades ovate to elliptic, ca. 15 mm long, ca. 10 mm wide, thick, succulent, canescent. *Inflorescences* of solitary flowers; pedicels 12–16 mm long. *Flowers* 5-merous; calyces globose, 14–18 mm long, 7–9 mm wide, trilobed, lobes triangular, 8–10 mm long, 4–5 mm wide, acute; corolla infundibuliform, lavender, regular, 30–33 mm long, 25–30 mm wide, 5-lobed, lobes obtuse, tube short, tomentose inside; stamens unequal 13–15 mm long; nectary disc patelliform; style 15–16 mm long. *Mericarps* 15–19, 2-seriate, reniform, black, five 4–5 mm long, 2.5–4.0 mm wide, ten 2.0–3.8 mm long, 1.4–3.0 mm wide; seeds ca. 3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Johannes (Juan) Eduard Wille (b. 1892–d. 1959), a German-born and trained entomologist who moved to Peru in 1929, when he was contracted by the Ministerio de Agriculture. He became the Head of the Entomology Department in the Estación Experimental Agrícola, Escuela Nacional de Agricultura, La Molina.

Distribution and Ecology: Peru, Department of Ica; 700–780 m.a.s.l. (Fig. 169). The species is only recorded from the Lomas de Amará growing in pure sand. For a full discussion of this area, see Whaley et al., 2019.

Nolana willeana has a small distribution of a few hectares. When visiting the site in 2007, only a few dozen individuals were interspersed in a community of desert shrubs (Fig. 170). The stems have densely pubescent, canescent or gray, succulent leaves, and the fruiting peduncles are recurved or nodding (Fig. 171A). Stems arise from a central basal rosette of strap-shaped leaves, not unlike the cauline leaves, but with obvious petioles (Fig. 171B). The calyx is globose and distinctive, with only three triangular lobes (Fig. 172A). The corollas are lavender, and, while the anther thecae are lavender, the pollen is white (Fig. 172B). When the calyx and corolla are removed, the orange nectary is visible, as are the gynoecium and style (Fig. 172C). The lateral view of the gynoecium shows the five major mericarps and a second series of minor mericarps (Fig. 172D).

Ferreyra (1961) related *N. willeana* to *N. tomentella* but noted that its leaves and calyx were quite different. This species was included in molecular studies (Dillon et al., 2009), and marker data suggest that it is related to *N. inflata* and *N. weissiana*, two species with similar calyx shapes and fruit morphology. While suitable material for molecular analysis of *Nolana insularis* is not currently available, its overall morphology suggests that it is related to *N. willeana*. Leaf shape, pubescence, and the unusual, three-lobed, globose calyx all point to the close relationship between these two taxa. Type material was collected by Dr. Mogens Engell Køie (also spelled Köie) (b. 1911–d. 2000), a Danish ecologist and soil expert, who spent 18 months working for UNESCO in Peru in 1956–1957, where he investigated coastal desert vegetation. In 2015, a search by the curators at the Natural History Museum of Denmark (C), where his primary set of collections is deposited, turned up one duplicate of the type collection. The staff at Copenhagen (C) did find one other collection of *Nolana inflata*, *Køie s.n.*, collected in July 1956 from N. of Puerto Chala.

Additional specimens examined: PERU. **Ica**: Prov. Santiago, Lomas de Amára, 14°43'47"S, 75°41'48"W, 780 m.a.s.l., 18 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3493* (HUSA), *3499* (HUSA).

Clade E

E1. ***Nolana clivicola*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 73. 1936. Fig. 173–175.

Basionym: *Bargemontia clivicola* I.M. Johnst., Contrib. Gray Herb. 85: 158. 1929. TYPE: CHILE. Antofagasta: Prov. Tocopilla, Tocopilla, steep hillside ca. 6 km N of port and about opposite Caleta Duendes, 18 October 1925, *I. M. Johnston 6307* (Holotype: GH [00282353]).

Digital image: Holotype of *Bargemontia clivicola* Harvard University Herbaria, Cambridge [GH00282353]. https://s3.amazonaws.com/huhwebimages/D2796EF99E7F4E5/type/full/282353.jpg

Homotypic synonym: *Nolana peruviana* (Gaudich.) I.M. Johnst. ssp. *divaricata* (Lindl.) Mesa, Fl. Neotrop. Monogr. 26: 82. 1981.

Erect *shrubs* to ca. 1 m tall; stems much-branched, erect. *Leaves* alternate to fasciculate, blades narrowly spathulate to linear, 7–10 mm long, 1.0–1.5 mm wide, densely pubescent with capitate-glandular trichomes, abaxial surface concave, apically rounded, bases truncate, epetiolate. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 4–9 mm long. *Flowers* 5-merous; calyces 10–12 mm long, tube 2–3 mm long, lobes linear, ca. 8 mm long, ca. 1 mm wide; corollas narrowly tubular-campanulate, 12–14 mm long, limb 3–4 mm wide, tube 3–4 mm long, ca. 1 mm wide, minutely pubescent within; anther filaments glabrous, ca. 4 mm long; style ca. 10 mm long. *Mericarps* 5, ovoid, basally affixed; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is derived from the Latin, *clivus* or *clivi*, referring to the sloping side of a hill, and *-cola*, dweller or exists only, in this case, on steep hillsides.

Distribution and Ecology: Chile, Region of Antofagasta; 30–250(–800) m.a.s.l. (Fig. 173). It is recorded from environments in near-coast habitats; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

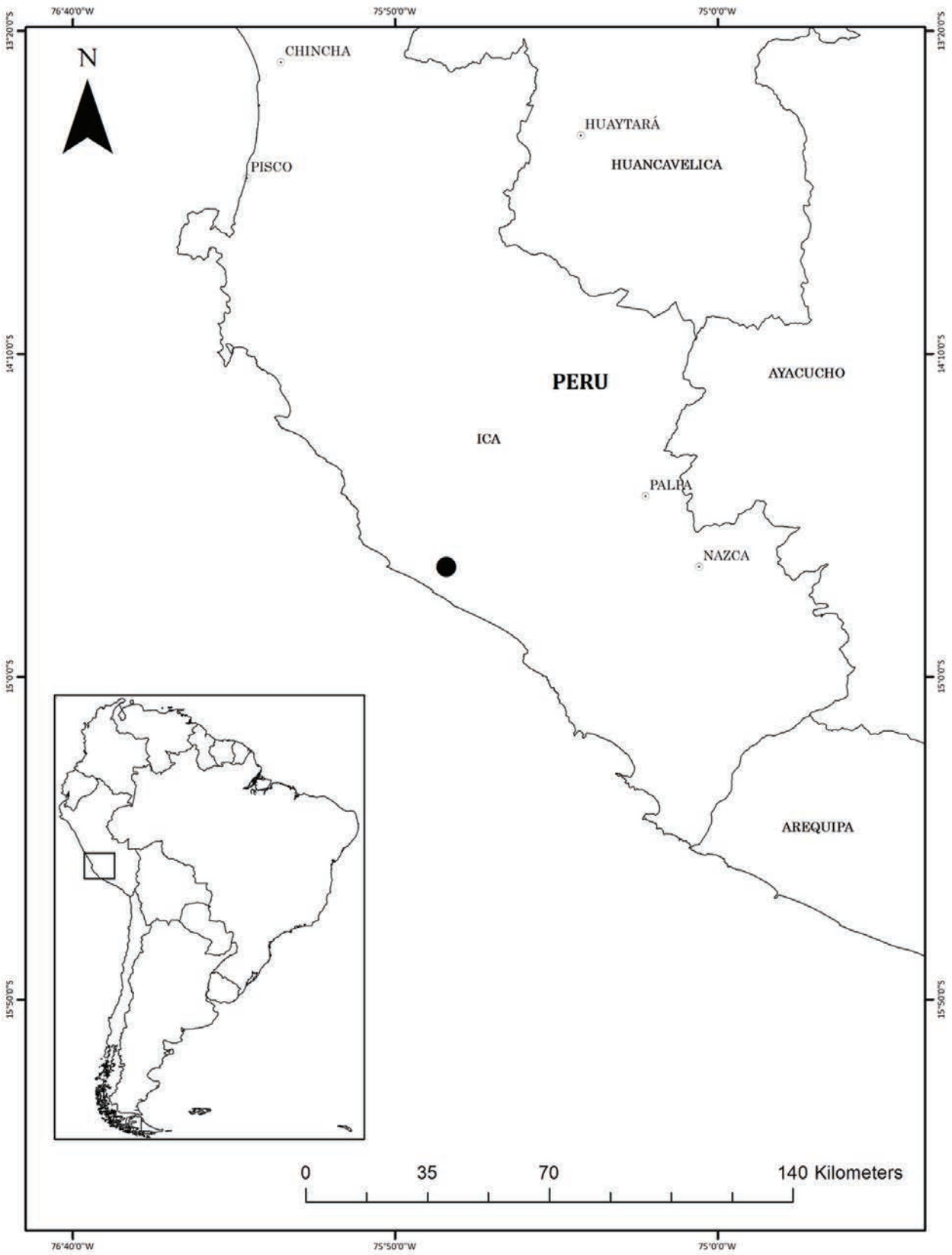


FIGURE 169. Distribution of *Nolana willeana* Ferreyra.

FIGURE 170. *Nolana willeana*. Photograph of M. O. Dillon and an individual plant buried in sand at Lomas de Amará, Peru.

Illustration: Fig. 174. Illustration of *Nolana clivicola* as *Dolia salsoloides*. Plate 113. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from I. M. Johnston (1944).

Nolana clivicola is decidedly shrubby, with individuals reaching two meters tall in rocky habitats (Fig. 175A); flowers are visited by moths that may be potential pollinators (Fig. 175B). The leaves and calyces are densely pubescent with capitate-glandular trichomes (Fig. 175C), and the corollas and anther thecae are pale lavender with white pollen (Fig. 175D).

In the dried state, *Nolana clivicola* is identified with difficulty; the collections referred to here have linear leaves with minute erect trichomes and elongate calyces (10–12 mm long) with linear lobes cut nearly to the base of the flower. Initially, I confused *N. clivicola* with *N. inconspicua*, a species that also has longer, rather succulent calyx lobes, and infundibularis corollas that clearly surpass the calyx; the leaves are wider and densely pubescent with long, capitate-glandular trichomes. Several accessions originally assigned to *N. inconspicua* have been move to *N. clivicola*, a consequence of a greater understanding of the parameters of each species.

Johnston (1929: 85) considered *Nolana clivicola* to be related to *N. foliosa*, a species recorded from over 90 kms from the coast and over 300 km to the north. The stems, leaves, pedicels and calyces in *N. clivicola* are all covered with short erect gland-tipped trichomes, which, though copious, are inconspicuous. The type was originally collected with *I. M. Johnston 3603* on 18 October 1925 and was separated later and assigned a number at that time; hence, the large gap in collection numbers (i.e., *3603* to *6307*).

Johnston (1936) considered the Gaudichaud plate 113, labeled as *Dolia salsoloides* Lindl., to be *Nolana ramosissima*; however, it is more likely that Gaudichaud encountered material now described as *N. clivicola* from Cobija (*Gaudichaud 4*, F and GH). The four sheets at the Field Museum are ex-P, but a search of material at Paris has not provided any corresponding material. One collection at Paris, labeled as *Gaudichaud 4*, corresponds to a collection made on Isla San Lorenzo, Peru, and is a type of *Geranium limae* R. Kunth.

In the Webb (FI) herbarium, two sheets labeled "*Gaudichaud 1839, Cobija*" correspond to *N. clivicola*. The fact that Gaudichaud visited Cobija in 1836, and not 1839, suggests a transcription error. Details of the calyx and corollas do not match material treated as *N. salsoloides*

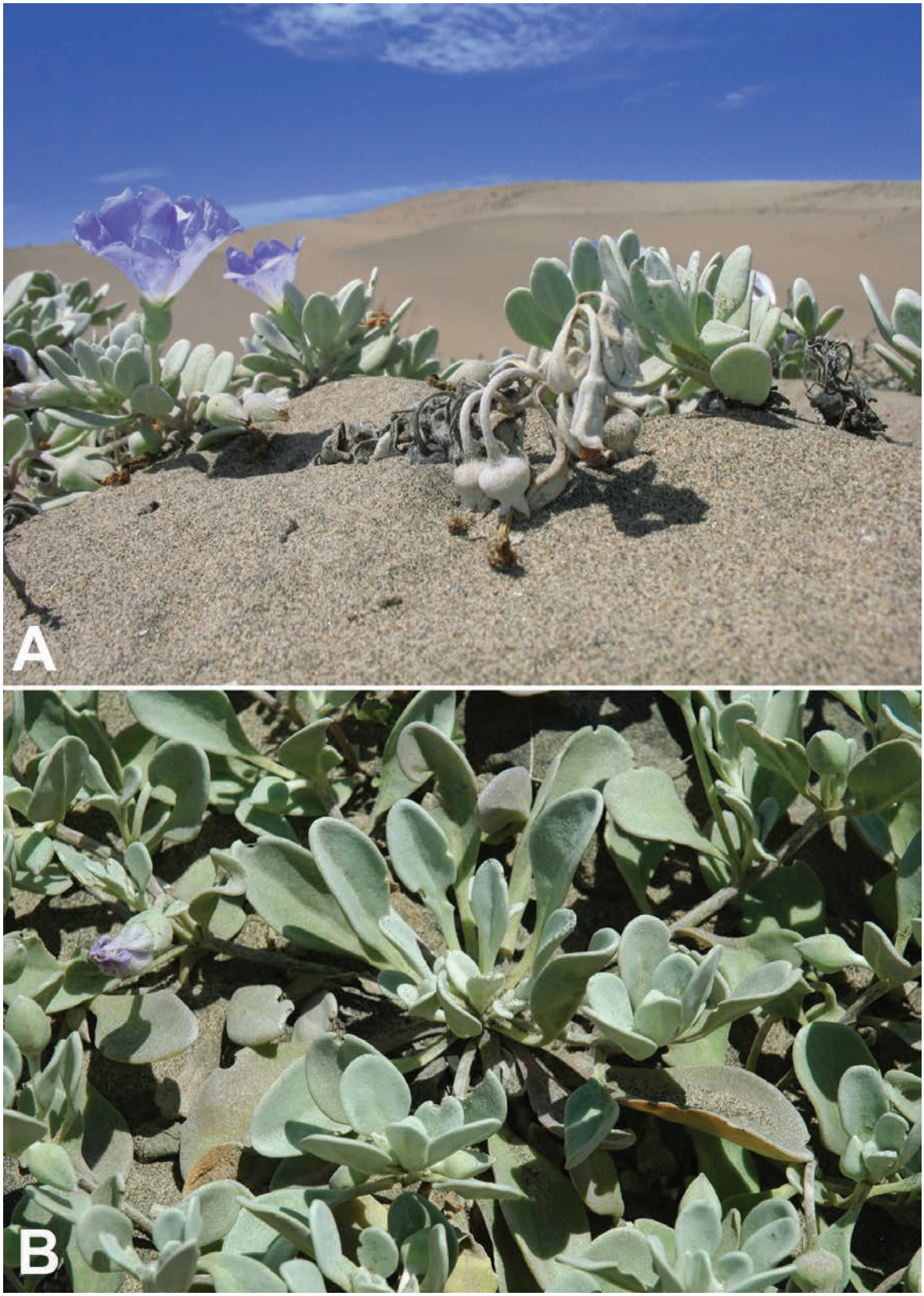


FIGURE 171. *Nolana willeana*. **A**, Stems submerged in sand with fruiting peduncles displaying the recurving or nodding in fruit; **B**, Central basal rosette of strap-shaped leaves.

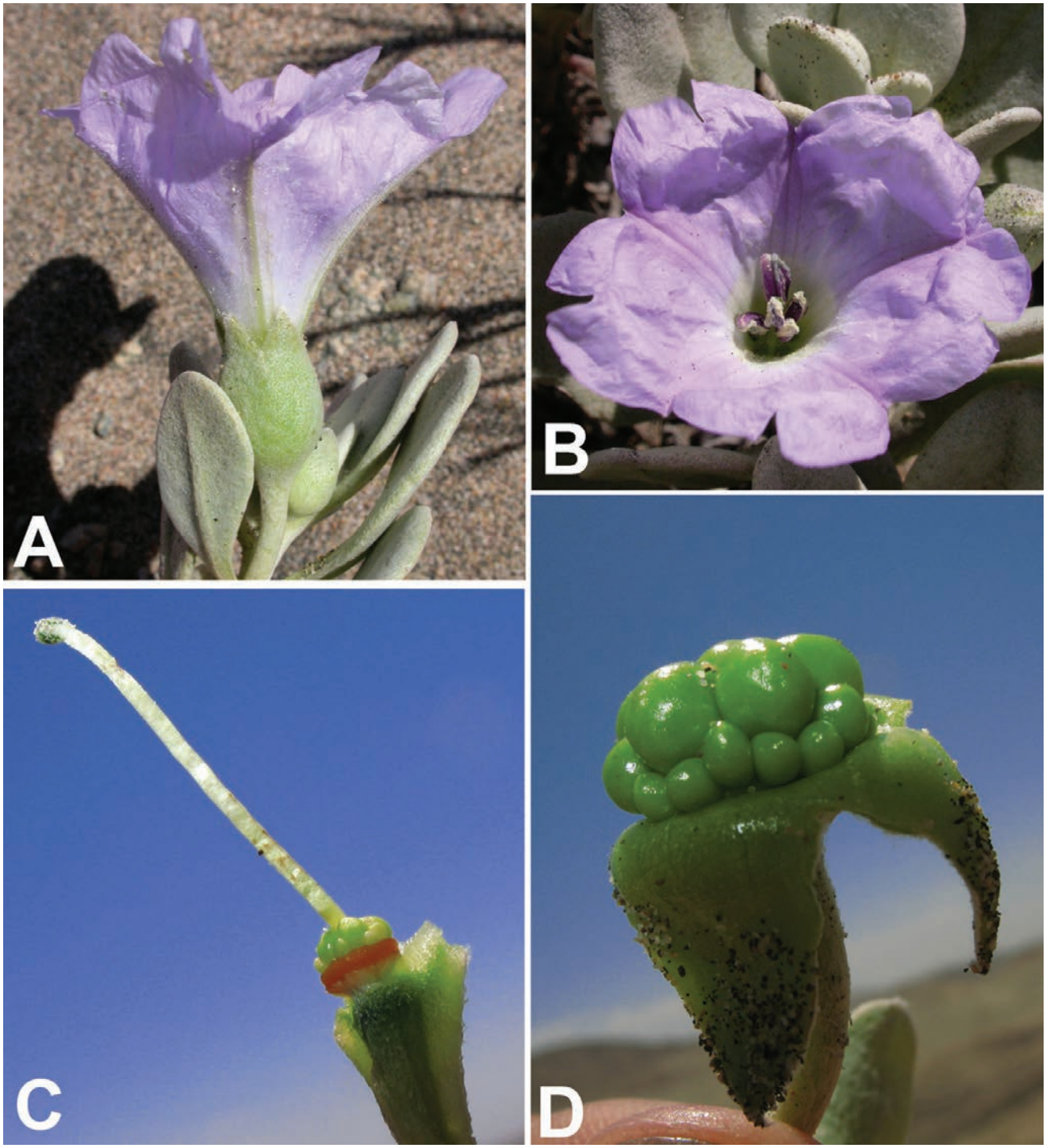


FIGURE 172. *Nolana willeana*. **A**, Globose calyx with three lobes. **B**, Lavender corollas, lavender anther thecae, white pollen; **C**, Corolla are removed exposing orange nectary, gynoecium, and style; **D**, Lateral view of the gynoecium with major and minor mericarps.

or *N. ramosissima*, as suggested by I. M. Johnston, but do match that of his *N. clivicola*. Although apparently glabrous to the naked eye, the plant has leaves and branchlets that have short, inconspicuous, simple gland-tipped hairs.

E. Perry s.n. (CONC 4387) is placed here with some doubts; it is a poor collection, and, while it does have the characteristic pubescence of capitate-glandular trichomes, the leaves are generally very short. *Schlegel 7736* was listed under *N. tocopillensis* by Mesa-M. (1997), but its leaves and pubescence are more characteristic of *Nolana clivicola*.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Tocopilla, Tocopilla, Quebrada 2–3 km N of Tocopilla, 22°05'S, 70°11'W, 150–250 m.a.s.l., 18 October 1988, *M. O. Dillon & D. Dillon 5713* (CONC, E, F 2014367, GH, SGO);

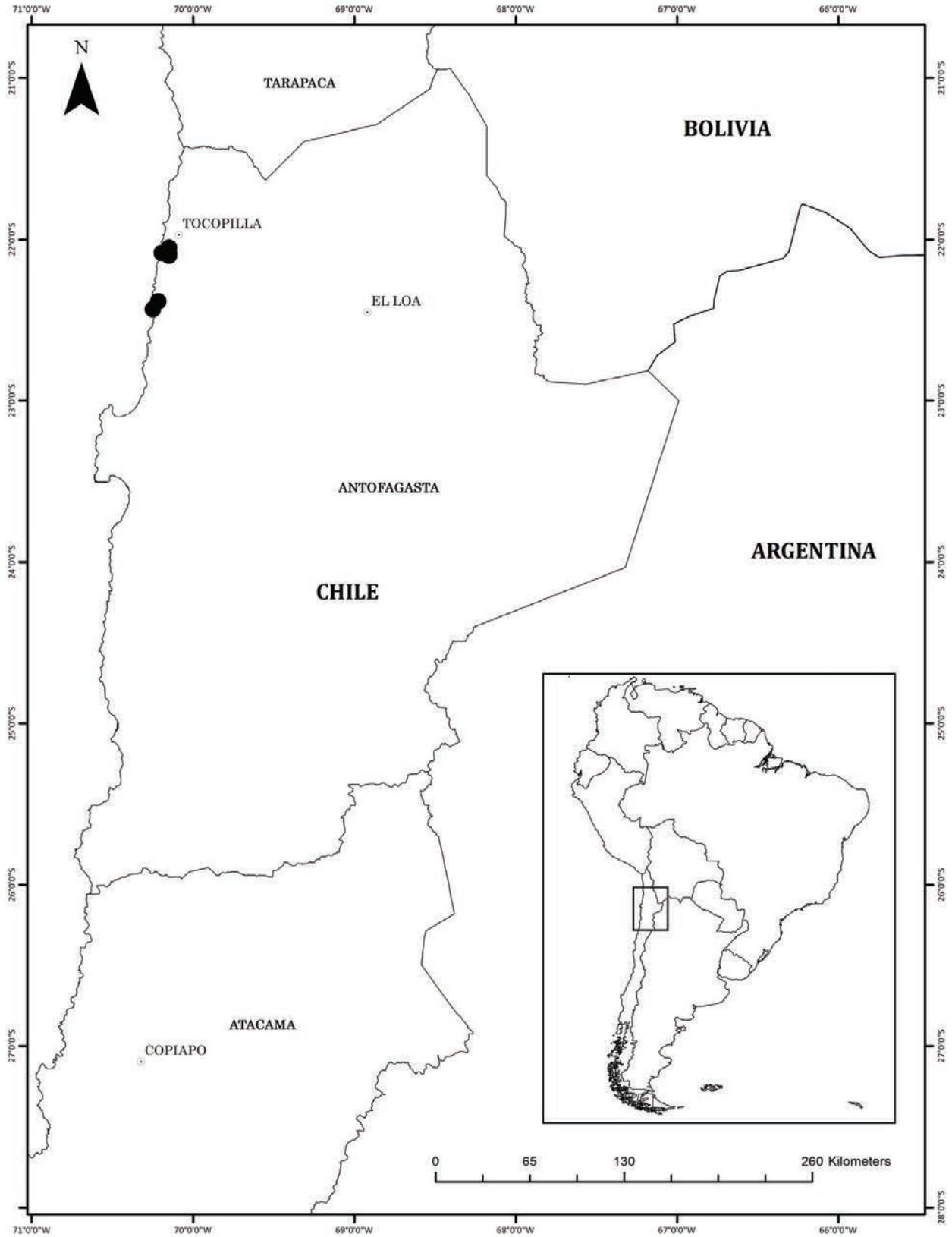


FIGURE 173. Distribution of *Nolana clivicola* (I.M. Johnst.) I.M. Johnst.

FIGURE 174. Illustration of *Nolana clivicola* as *Dolia salsoloides*. Plate 113. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

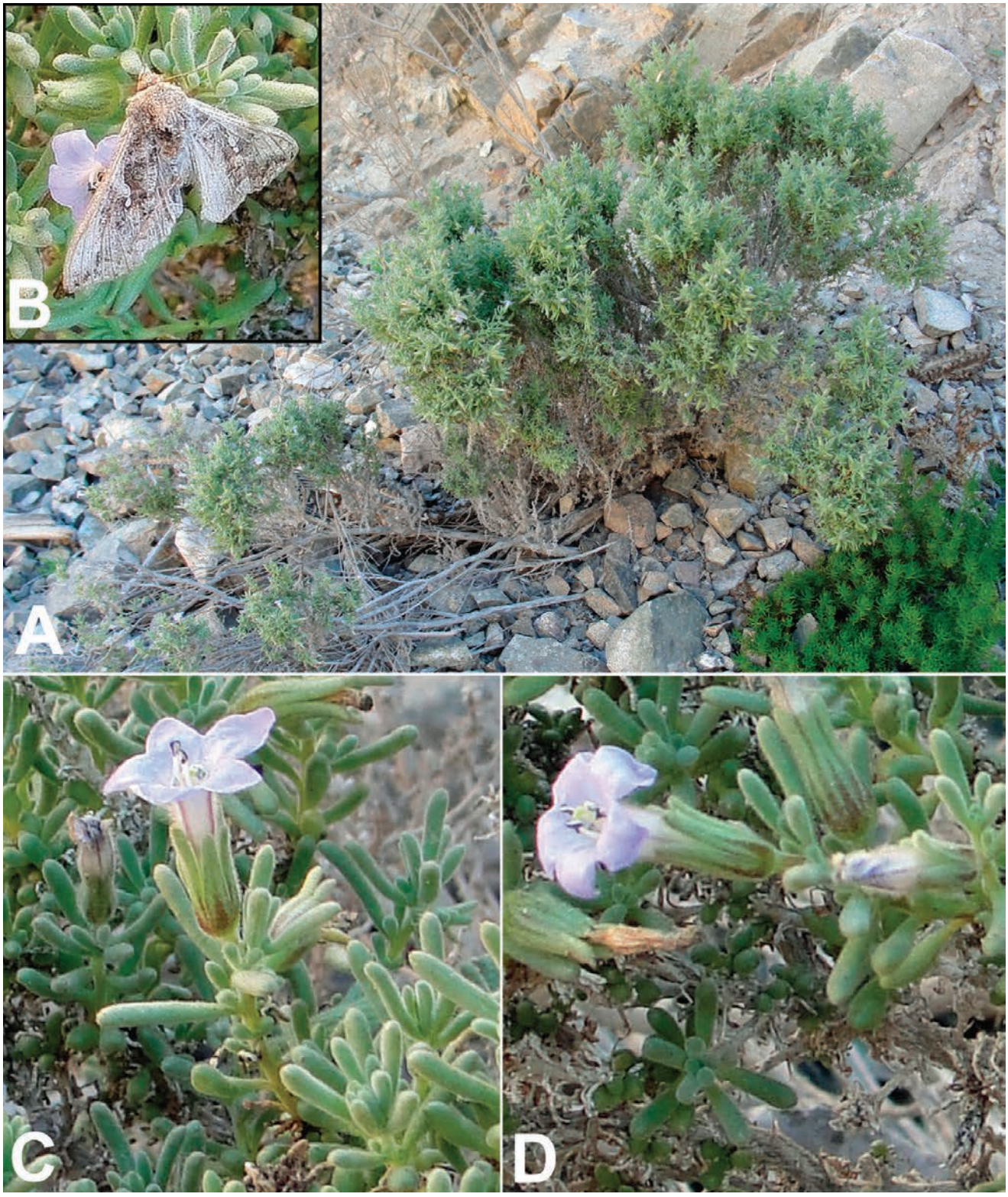


FIGURE 175. *Nolana clivicola*. **A**, Shrubs two meters tall in rocky habitats; **B**, Flowers visited by moths as potential pollinators; **C**, Leaves and calyces densely pubescent with capitate-glandular trichomes; **D**, Corollas and anther thecae are pale lavender, pollen white. Photographs by Mauricio Gonzales.

Quebrada 2–3 km N of Tocopilla, 22°05'S, 70°11'W, 150–250 m.a.s.l., 18 October 1988, *M. O. Dillon & D. Dillon 5721* (CONC, E, F 2045834, GH, SGO); Cerro Rosario, *M. R. Espinosa s.n.* (SGO 143262); Quebrada de Los Barriles, *M. R. Espinosa s.n.* (SGO 143276, SGO 143278); Quebrada que baja al sur a Barriles, *M. R. Espinosa s.n.* (SGO 139544); Quebrada Barriles, *M. R. Espinosa s.n.* (SGO 139536); 1–3 July 1836, Cobija, 1836, *C. Gaudichaud 4* (F 1000371, F 1000373, F 679044, F 679045); Tocopilla, 27 October 1930, *F. Jaffuel 1016* (GH); Tocopilla, 27 October 1930, *F. Jaffuel 1023* (GH); Tocopilla, 27 October 1930, *F. Jaffuel 1031* (GH); Tocopilla, September 1931, *F. Jaffuel 2503* (GH), *2513* (CONC 73264, GH); Quebrada La Carmelita, *C. Jiles 5347* (CONC 103606), *5358* (CONC 103553); Quebrada Chapacase, 22°01'24"S, 70°10'02"W, 700–800 m.a.s.l., 22 October 2009, *F. Luebert & A. Moreira M. 2990* (SGO 158972); camino de Tocopilla a Antofagasta, Caleta Buena, 22°26'S, 70°15'W, 30 m.a.s.l., 27 September 1996, *O. Matthei 490* (CONC 137094, SGO 152822); Quebrada Barriles, *E. Perry s.n.* (CONC 4387); Camino a Mina Mantos de La Luna, *M. Quezada & E. Ruiz 16* (CONC 121070; Cobija, 29 September 1954, *M. Ricardi 3032* (CONC 18265); Mina Indiana, 21°57'S, 70°10'W, 300 m.a.s.l., 27 October 1985, *F. Schlegel 7736* (CONC 115604).

E2. ***Nolana foliosa*** (Phil.) I.M. Johnst., Contrib. Gray Herb. 112: 77. 1936. Fig. 176–177.

Basionym: *Dolia foliosa* Phil., Anal. Mus. Nac. Bot. 2, Cat. Pl. Itin. Tarapacá 2: 68. 1891. TYPE: CHILE. Tarapacá: entre Mocha et Guaviña, February 1885, *F. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55164, SGO000004352]).

Digital image: Lectotype for *Dolia foliosa* from Museo Nacional de Historia Natural, Santiago [SGO 055164]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004352

Homotypic synonym: *Bargemontia foliosa* (Phil.) I.M. Johnst., Contr. Gray Herb. 85: 111. 1929.

Paratype: CHILE. Tarapacá: Tarapacá, February 1888, *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [42694, SGO00000).

Robust annual *herbs* 4–50 cm tall. *Leaves* alternate, blades linear, 6–15 mm long, 2–3 cm wide, terete, very sparsely pubescent with simple trichomes, epetiolate, apically rounded. *Inflorescences* of solitary flowers, sessile. *Flowers* 5-merous, axillary, sessile; calyces ca. 8 mm long, lobes lanceolate, apically attenuate; corollas infundibularis, 10–11 mm long, light lavender or blue with weak purple guides in the mouth of the throat; stamens white. *Mericarps* 2 (–3), round, black, nitid; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *folium*, leaf, and *foliosus*, leafy.

Distribution and Ecology: Chile, Region Tarapacá; 1800–2200 m.a.s.l. (Fig. 176). It is recorded from environments over 90 km from the coast; Desértico Tropical Costero Interior (Luebert and Pliscoff, 2006).

Nolana foliosa is a rare species of the interior of northern Chile, recorded from between Mocha (19°48'S, 69°16'W) and Guaviña (Huaviña, 19°48'S, 69°13'W). It most closely resembles *N. tarapacana* but differs in its smaller leaves and overall habit (Fig. 177A–B). Given that *N. foliosa* typically develops only two mericarps and has a leaf morphology nearly identical to that of *N. tarapacana*, these two species may prove to be conspecific. Mesa-M. (1981: 120) considered *N. foliosa* as a synonym of *N. tarapacana*.

The collections at US and K are here cited as isolectotypes, but it is possible that they represent paratypes distributed by SGO with labels that do not identify the collector, only the general locality, "Tarapacá." Another collection was made by *C. Rahmer s.n.* (SGO 42694) from the same locality, given as Mocha–Guaviña, and in the same expedition with *F. Philippi s.n.*, but in March of 1885.

I. M. Johnston (1936: 78) remarked that material examined by him suggested affinities with *N. confinis* and *N. tocopillensis*, since all have regularly dichotomous branching, but the corollas in *N. foliosa* are smaller, the leaves are less densely fasciculate, and the stems less evidently nodose than in those species. He noted that some of the glabrescent forms of *N. confinis* seem to approach *N. foliosa* rather closely, and that both *N. foliosa* and *N. confinis* are species of the interior.

Additional specimens examined: CHILE. **Tarapacá**: Tarapacá, Com. R. A. Philippi 2/1888, *R. A. Philippi s.n.* (SGO, K000532196).

E3. ***Nolana gracillima*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 59. 1936. Fig. 178–180.

Basionym: *Bargemontia gracillima* I.M. Johnst. Contr. Gray Herb. 85: 176. 1929. TYPE: PERU. Moquegua: 1500–1600 m, March 1925, *A. Weberbauer 7457* (Holotype: F [552698, F neg. 56677]; Isotypes: G [G00383963, G00383967], GH [GH00282373], K [K000532280], US [US 1474543, US00121972, US 1778492, US00053390]).

Digital image: Isotype of *Bargemontia gracillima* from Harvard University Herbaria, Cambridge [GH00 282373]. https://s3.amazonaws.com/huhwebimages/E50A5344150E4EE/type/full/282373.jpg

Homotypic synonym: *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *confinis* Mesa, Fl. Neotrop. Monogr. 26: 103. 1981.

Erect annual *herbs*, 8–15 cm tall; stems subterete, branched, ascending, pilose to glabrescent. *Leaves* alternate, blades linear, 8–25 mm long, 0.8–1.5 mm wide, apically obtuse, subsessile, glabrous to sparsely pubescent. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 5–13 mm long, glabrous to sparsely pilose with capitate-glandular trichomes. *Flowers* 5-merous; calyx 5.0–5.5(–6.0) mm long, 3–4 mm wide at anthesis, glabrous to glabrescent; tube short, cylindrical, 2.5–3.5 mm long, 1.0–1.5 mm wide; lobes subulate, acute, erect or unequally curved; corollas infundibularis, 9–12 mm long, 7–9 mm at anthesis, violet, distal portion of the tube with darker purple

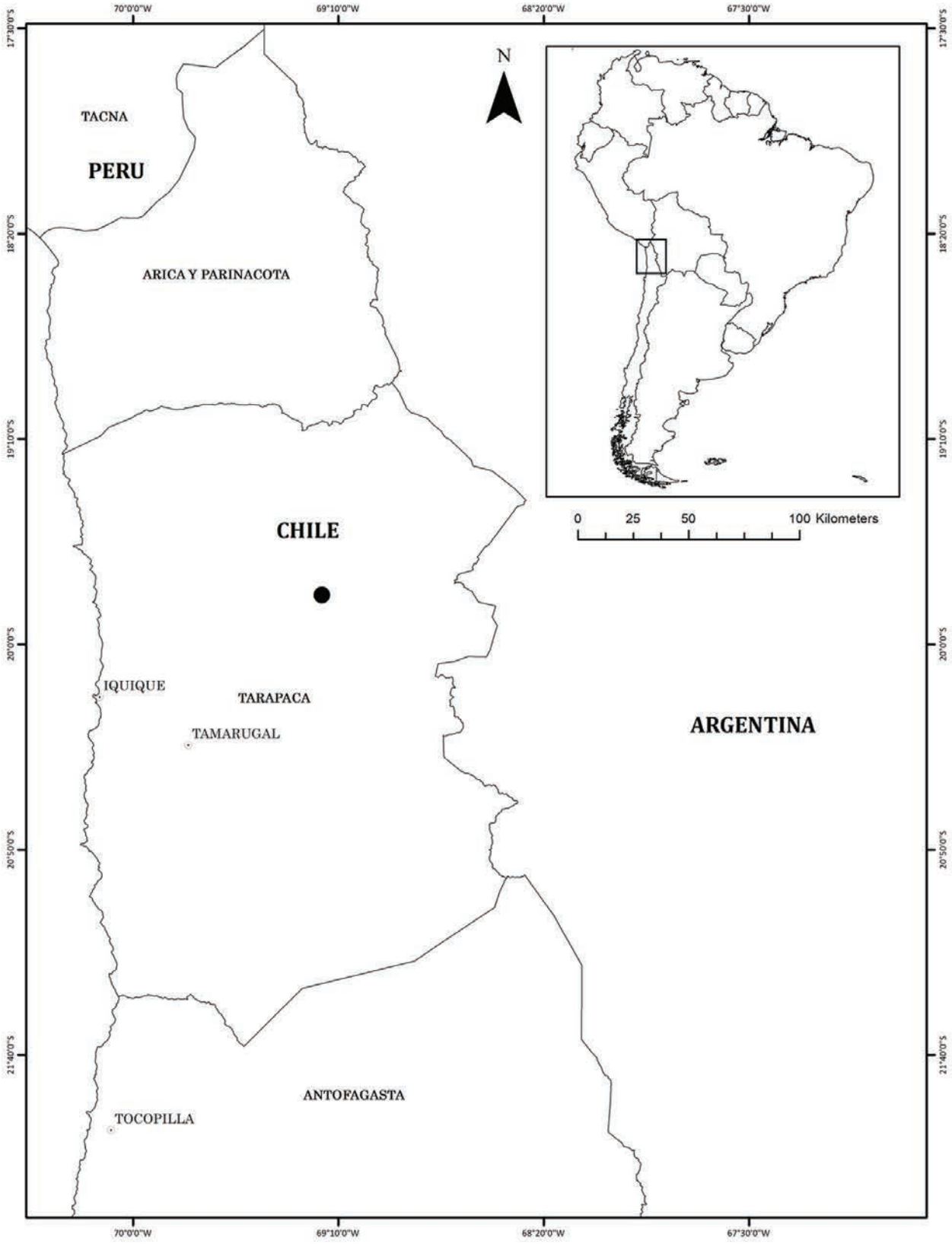


FIGURE 176. Distribution of *Nolana foliosa* (Phil.) I.M. Johnst.

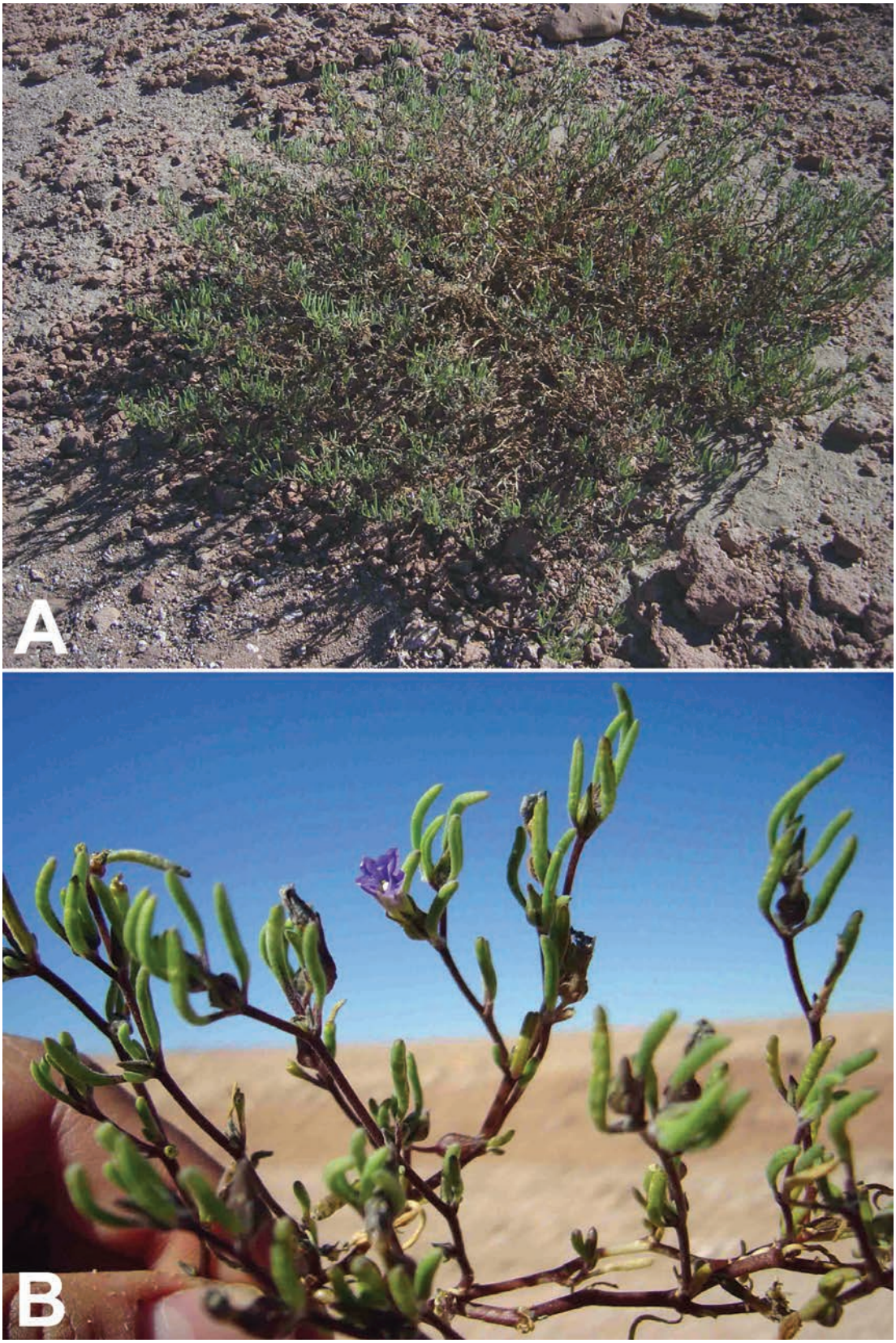


FIGURE 177. *Nolana foliosa*. **A**, Spreading perennials; **B**, Stems purplish, leaves linear, and flowers sessile. Photograph by María Teresa Eyzaguirre.

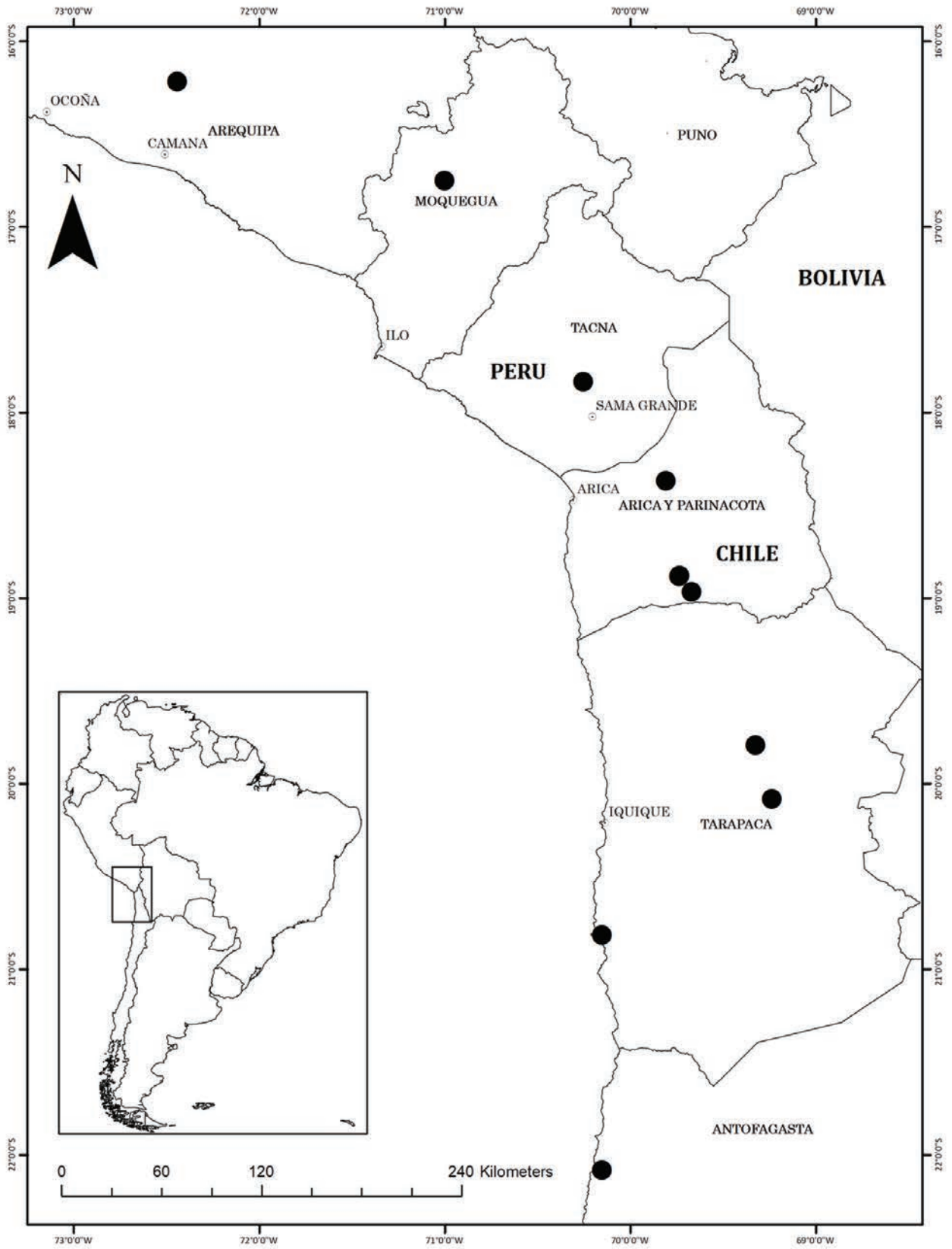


FIGURE 178. Distribution of *Nolana gracillima* (I.M. Johnst.) I.M. Johnst.

FIGURE 179. *Nolana gracillima*. **A**, Small, much-branched annuals; **B**, Flowers purple to blue with a dark spot at base of the throat. Photographs by Victor Quipuscoa Silvestre.

FIGURE 180. *Nolana gracillima*. **A**, Habit with erect stems, branching above; **B**, Corollas lavender or purple with dark guides; **C**, Flowers borne on short peduncles, mericarps three to five. Photographs by Victor Quipuscoa Silvestre.

band at the mouth, pubescent outside; tube ca. 3.5 mm long, villous inside; lobes ovate, 2.0–2.5 mm long; filaments ca. 3.5 mm long. *Mericarps* 4–5, 1-seriate, ovoid, (1.0–) 1.5–2.0 mm long, black, rugose; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is derived from the Latin, *gracilis*, referring to thin or slender linear leaves and overall delicate habit.

Distribution and Ecology: Chile, Regions of Arica & Parinacota, Tarapacá and Antofagasta; Peru, Departments of Arequipa, Moquegua and Tacna; (550–)1000–2700(–3100) m.a.s.l. (Fig. 178). It is most frequently recorded from high elevation sites, distant from coastal fog; Desértico Tropical Costero Interior (Luebert and Pliscoff, 2006).

Nolana gracillima is a small annual, much-branched (Fig. 179A) with purple to blue flowers (Fig. 179B). Some individuals are unusual in that they possess erect stems that only branch distally above 10 cm (Fig. 180A). The flowers are invariably lavender or purple, with dark guides, and are borne on short peduncles (Fig. 180B). The number of mericarps is variable, from as many as five to as few as two; however, the usual number is five (Fig. 180C). It most closely resembles *N. spergularioides*, from which it is distinguished by its glabrous flowers on obvious pedicels, rather than the sessile flowers in the leaf axils.

Two Chilean species, *N. tarapacana* and *N. foliosa,* have an overall morphology that approaches that of *N. gracillima* and *N. spergularioides*. More detailed molecular studies will be necessary before further speculation about putative relationships. Johnston (1929: 176) suggested that *N. gracillima* was most closely related to *N. platyphylla*, but the leaf and floral morphology are very different. After seeing authentic material of both, I would not infer a close relationship between *N. gracillima* and *N. platyphylla*; however, the latter species has not been included in any molecular analyses.

This taxon has not been observed in the field in Chile, but the label data for Chilean collections by Urs Eggli are quite complete: *Eggli et al. 2792*–"Annuals, stemlets and taproot thick and somewhat succulent; stemlets dark green, divaricately erect; leaves medium grass-green, succulent and appearing terete but with enrolled margins and thus underside with a longitudinal groove; pedicels pale brown; calyx pale greenish-brown; corolla tube basally whitish, above bluish, limb funnel-shaped, medium pale to rich blue with paler throat, sometimes throat first darker blue, center paler". *Eggli et al. 2760*–"Only 1 seedling found. Leaves succulent, flat, medium green; flower tube outside pale green, limb spreading, pale blue with violet hue, *throat darker* with paler centre."

Quipuscoa et al. 6728 was initially identified as *Nolana gracillima*; however, it did not completely agree with *N. gracillima* from localities at lower elevations farther to the south. It is here treated as *N. spergularioides* pending further data. A series of *Nolana* collections needs to be evaluated in light of recent discoveries; these are from Region Antofagasta, Prov. Tocopilla, camino a Mina Mantos de La Luna, *M. Quezada & E. Ruiz 17*, and *M. Quezada & E. Ruiz 19*.

Additional specimens examined: CHILE. **Arica & Parinacota**: Parinacota, camino a Tignamar, Quebrada Vizcachani, 3100 m.a.s.l., 8 May 2000, *E. Belmonte 20-102* (CONC 151108); Arica, 33 km From Panamericana toward Codpa, 18°53'S, 69°44'W, 2050 m.a.s.l., 1 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2792* (B, CONC 138606, SGO 145842); Ruta Ch 11 Quiborax Km 57, 18°28'46"S, 69°51'44"W, 1831 m.a.s.l., 17 April 2011, *B. Knapton 81* (SGO); Ruta Ch 11 Quiborax Km 57, 18°28'46"S, 69°51'44"W, 1831 m.a.s.l., 29 April 2011, *B. Knapton 90* (SGO); Arica, ruta A-31, Km 54, 18°45'13"S, 69°47'34"W, 1948 m.a.s.l., 8 July 2011, *G. Rojas s.n.* (SGO 160917); Putaralla, valley of the Río Camarones, 18°58'S, 69°40'W, 2000 m.a.s.l., 14 April 1927, *C. Troll 3300* (B). **Tarapacá:** Prov. Iquique, 52 km E of Huara towards Chusmisa (=28 km from turnoff to Tarapacá, 6 km below turnoff to Mocha), 19°48'S, 69°19'W, 2550 m.a.s.l., 26 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2760* (B); Mamiña, 20°05'S, 69°14'W, 2700 m.a.s.l., *H. Larraín 97-661* (CONC 144592); Frente Pozo Almonte y Huara, orillas Carretera Panamericana, April 1972, *C. Muñoz S. 76* (SGO 135337). **Antofagasta:** 20 km al Norte de Tocopilla, camino costero, 16 October 1991, *A. Brinck s.n.* (SGO 122819); Quebrada Honda, 18°19'S, 69°53'W, 2100 m.a.s.l., *M. Ricardi 3360* (CONC 19308); Prov. Tocopilla, Quebrada Chacaya, 22°59'S; 70°20'W, *M. Ricardi 5518* (CONC 43016); Tocopilla, Quebrada Mamilla, *F. Schlegel 7693* (CONC 115627). PERU. **Arequipa**: Prov. Condesuyos, Cerros de Arequipa, 2300–2400 m.a.s.l., 24 April 1961, *R. Ferreyra 14275* (USM); conjunción quebradas Chuquibamba y Majes, 1000 m.a.s.l., 26 April 1967, *C. Vargas C. 19559* (CUZ). **Moquegua**: Prov. General Sánchez Cerro, Dist. Omate; abajo de Omate, camino a Quinistaquillas, 16°45'03"S, 71°00'01"W, 1450 m.a.s.l., 20 March 2008, *V. Quipuscoa S. 3646* (HSP 002691), 16°45'00"S, 70°59'59"W, 1467 m.a.s.l., 22 March 2008, *V. Quipuscoa S. 3693* (HSP 002690). Prov. Mariscal Nieto, Torata–Omate, 46–48 km from Yacanco, 16°52'02"S, 70°54'35"W, 2396 m.a.s.l., 23 March 2012, *T. Särkinen, A. Matthews & P. Gonzáles 4094* (BM001114833); entre Arequipa–Moquegua, 800 m.a.s.l., 1 December 1959, *C. Vargas C. 13084* (USM); entre Arequipa–Moquegua, Lecho Río Seco, 1200 m.a.s.l., *C. Vargas C. 12644* (CUZ, USM); road from Omate to Moquegua, 31 km after bridge over Rio Tambo, 16°54'45"S, 70°54'29"W, 2548 m.a.s.l., *M. Weigend, F. Cáceres H., & C. Schwarzer 8396* (F 2295136, F 228721). **Tacna**: Prov. Tacna, 29–32 km WNW of Tacna on Pan-American Highway (Pampa de Sama), Km 1241–1247, 17°50'S; 70°15'W, 550–630 m.a.s.l., 14 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4773* (F 1980832); Tacna, September 1864, *R. Pearce* (BM000941269, K)

E4. ***Nolana spergularioides*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 8. 1955. TYPE: PERU. Arequipa: Prov. Caravelí, Lomas de Camaná, *W. Rauh 558* (holotype: USM [242141, USM000574]). Fig. 181–183.

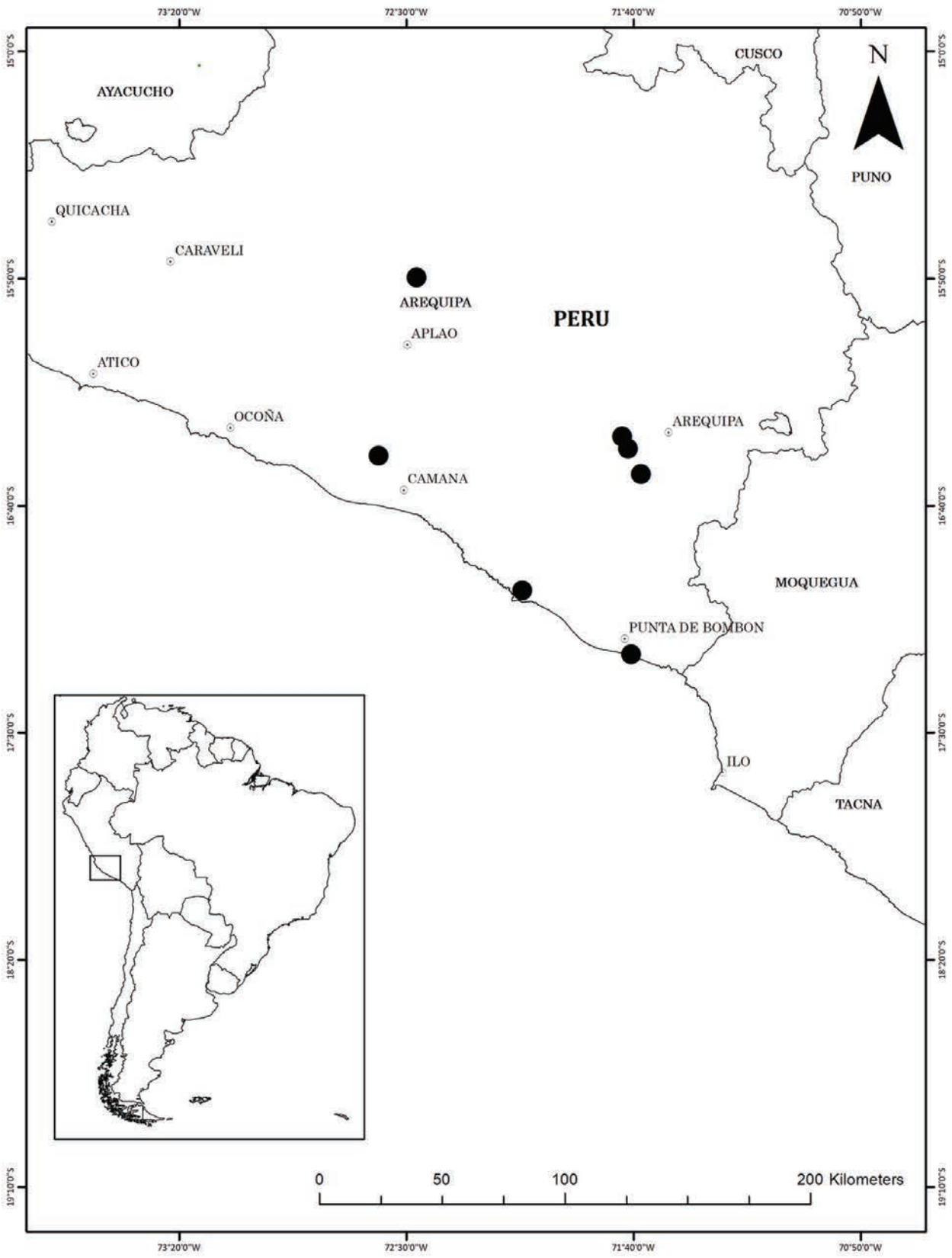


FIGURE 181. Distribution of *Nolana spergularioides* Ferreyra.

FIGURE 182. *Nolana spergularioides*. **A**, Robust annual; **B–C**, Corollas weakly zygomorphic, lavender with dark central band in the throat. Photographs by Victor Quipuscoa Silvestre.

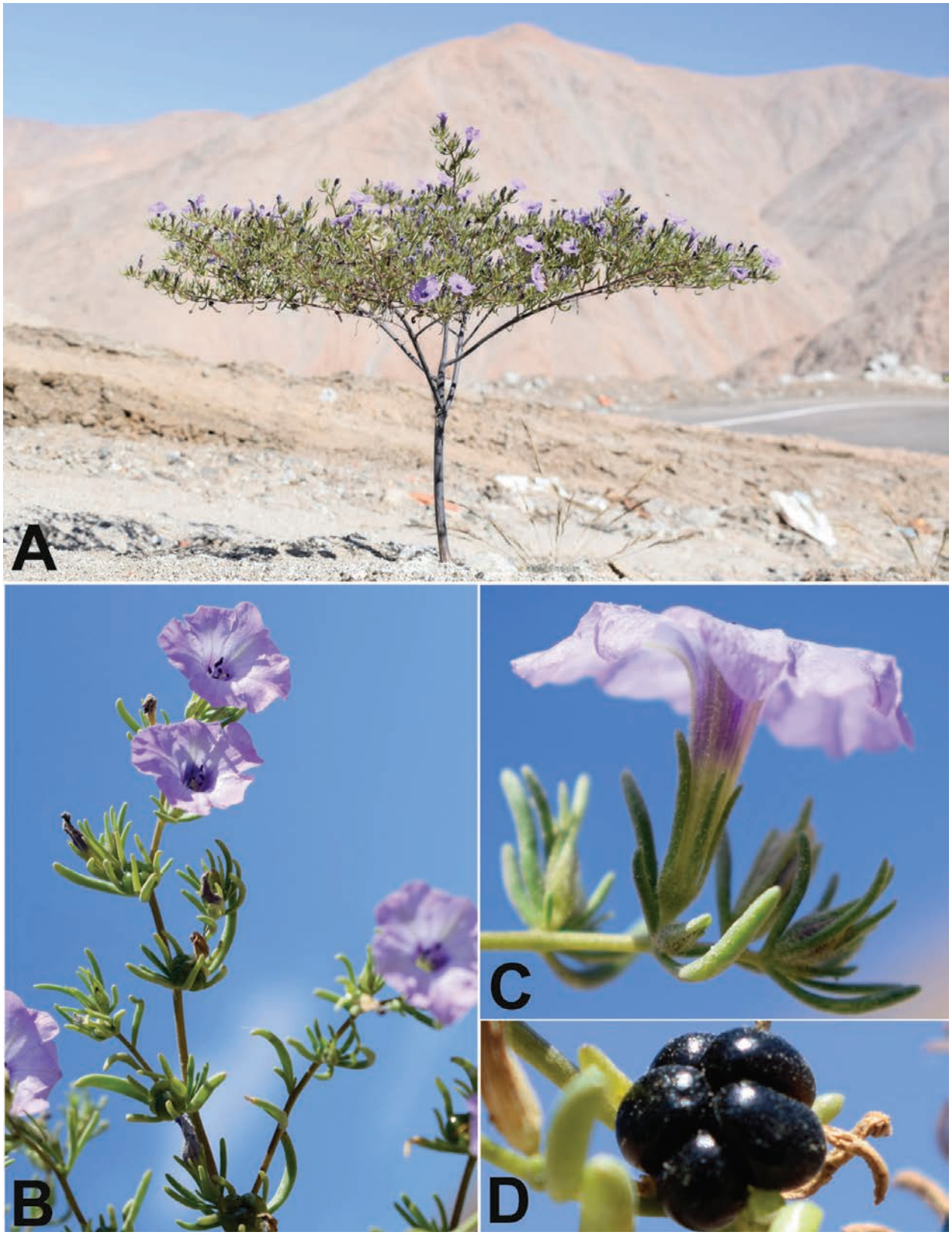


FIGURE 183. *Nolana spergularioides*. **A**, Annual with single stem and much-branched above; **B–C**, Flowers sessile, calyx lobes deeply cut nearly to the base; **D**, Gynoecium of only two to five mericarps. Photographs by Victor Quipuscoa Silvestre.

Digital image: Holotype of *Nolana spergularioides* from Herbario San Marcos, Lima [USM 242141]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000574

Homotypic synonym: *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *confinis* Mesa, Fl. Neotrop. Monogr. 26: 103. 1981.

Annual to perennial *herbs* decumbent to erect, lanuginose; stems 1–2 mm in diam. *Leaves* alternate, blades linear, 10–20 mm long, 0.8–1.0 mm wide, lanuginose with short, curly glandular-capitate trichomes, apically acuminate, basally acuminate, margins revolute, uninerved. *Inflorescences* of solitary flowers, sessile, axillary. *Flowers* 5-merous; calyces cylindrical or tubular, sessile, 8–9 mm long, 3.0–3.5 mm in diam., lanuginose, tube 3.8–4.0 mm long, 0.8–1.2 mm wide at base, acuminate; corolla infundibularis, violet, 13–15 mm long, 8–9 mm wide above, lobes unequal, margins ciliolate, 2 lobes with more cilia, tube short, villous inside; stamens unequal, united to tube for 1/2 its length, two 8.5–9.0 mm long, three 7.8–8.0 mm long; style 9–10 mm long. *Mericarps* usually 2, rarely 5, black, shiny, 2.5–3.0 mm in diam.; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet suggests a resemblance to *Spergularia*, a genus that possesses slender, succulent leaves, as in *Spergularia maritima* (All.) Chiov. (Caryophyllaceae).

Distribution and Ecology: Peru, Departments of Arequipa and Ica; (300–)1500–2000(–2600) m.a.s.l. (Fig. 181). It is a plant of sandy soils, principally from Arequipa, but one collection is recorded from Ica; the entire distribution is no more than 100 sq. km.

Nolana spergularioides is a robust annual that can persist if moisture is available (Fig. 182A). Its habit can vary from small shrubs (Fig. 182A) or, more rarely, as a single stem, with apical branching (Fig. 183A). The flowers are sessile in the upper leaf axils with zygomorphic, lavender corollas that have one larger lobe and a dark, central band at the mouth of the limb (Fig. 183B). When he described *N. spergularioides*, Johnston compared it to *N. gracillima*; however, he stated that it differs in having lanuginose pubescence, sessile flowers in the upper leaf axils (Fig. 183C), and a gynecium with only two or, more rarely, five mericarps (Fig. 183D). *Nolana foliosa* of northern Chile superficially resembles *N. spergularioides*, having very similar leaves, sessile flowers in the leaf axils, and, commonly, only two mericarps; their relationship should be investigated.

Additional specimens examined: PERU. **Arequipa**: Prov. Arequipa, Dist. Cerro Colorado, carretera hacia Uchumayo, 16°24'48"S, 71°42'19"W, 2007 m.a.s.l., 16 April 2012, *C. Fernández A, C. Talavera D., C. Tejada B., M. Espinoza R., & C. Luque F. 0007* (HSP 003189); Dist. Uchumayo, 2 km carretera hacia Uchumayo, 16°27'26"S, 71°41'06"W, 2300 m.a.s.l., 16 March 2008, *V. Quipuscoa S. & K. Durand V. 3644* (HSP 000364); Dist. Aplao, arriba de Aplao, carretera a Viraco, 15°49'45"S, 72°27'36"W, 1201 m.a.s.l., 31 May 2017, *V. Quipuscoa S., I. Treviño Z., M. Balvin A., S. Huamani Q., M. Bedoya C., & G. Rosado A. 5841* (HSP 8753, HUT 60421); Dist. Uchumayo, Batolito de la Caldera, 16°33'01"S, 71°38'15"W, 2562 m.a.s.l., 2 August 2017, *V. Quipuscoa S., D. Ramos A., D. Rodríguez P., M. Balvin A., & G. Rosado A. 6008* (HSP 12021); Dist. Cerro Colorado, 5 km al SW de la Pascana Herbazal, 16°19'44"S, 71°41'40"W, 2534 m.a.s.l., 2 May 2015, *C. Tejada P., P. Jiménez M., A. Pauca P., & E. Mamani T. 788* (HSP 006036). Prov. Camaná, Km 934 Panamericana Sur, Camaná–Tambillo, 1500 m.a.s.l., 5 October 1997, *M. Weigend & H. Förther 97/766* (F 2211297, HUT 34189). Prov. Caravelí, Dist. Huanuhuanu, ca. de Mollehuaca, 15°36'54"S, 74°0'25"W, 1604 m.a.s.l., 1 May 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7694* (HSP 010549); arriba de Mollehuaca, 15°36'37"S, 73°59'23"W, 1768 m.a.s.l., 1 May 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7710* (HSP 010551). Dist. Huanuhuanu, Entre Mollehuaca y Huanuhuanu, 15°36'28"S, 73°59'05"W, 1790 m.a.s.l., 1 May 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7716* (HSP 010552). Dist. Quicacha, arriba de Arasqui, entre Arasqui y Tiruque, 15°41'12"S, 73°49'00"W, 1473 m.a.s.l., 2 May 2018, *V. Quipuscoa S., M. Balvin A., S. Huamani Q., & M. Bedoya C. 7782* (HSP 010550). Prov. Islay, Dist. Islay, Abajo del Cerro San Andrés, 16°58'40"S, 72°04'23"W, 300 m.a.s.l., 25 November 2012, *V. Quipuscoa S. & C. Tejada P. 5253* (HSP 004065). Dist. Quicacha, arriba de Arasqui Km 49, 15°42'36"S, 73°49'40"W, 1374 m.a.s.l., 30 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., M. Bedoya C., & W. Ancalla C. 6728* (HSP 12033); arriba de Arasqui Km 53, 15°40'55"S, 73°48'54"W, 1511 m.a.s.l., 30 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., M. Bedoya C., & W. Ancalla C. 6735* (F 2325078, HSP 12034): **Ica**: Prov. Nazca, Km 16 on road Nazca–Puquio, 1100 m.a.s.l., 2 October 1977, *M. Weigand & H. Förther 97/639* (F 2211313, HUT 34128).

E5. ***Nolana tarapacana*** (Phil.) I.M. Johnst., Contrib. Gray Herb. 112: 61. 1936. Fig. 184–185.

Basionym: *Dolia tarapacana* Phil., Cat. Pl. Itin. Tarapacá 68: 1891. TYPE: CHILE. Tarapacá: March 1885, Pica [20°29'S, 69°19'W], March 1885, *F. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [055176, SGO000004359]; Isolectotype: SGO [SGO 042691, SGO000004360]). **Paratype**: CHILE. Tarapacá: Tarapacá, February 1888, *R. A. Philippi s.n.* (paratype: K [K000532196]).

Digital image: Lectotype of *Dolia tarapacana* from Museo Nacional de Historia Natural, Santiago [SGO 055176]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004359

Erect to spreading *annuals* or short-lived perennial *herbs*; ca. 25 cm tall, 50 cm diam.; stems much-branched, pubescent with capitate-glandular trichomes. *Leaves* alternate to fasciculate, blades linear-spathulate, (7–)10–20(–30) mm long, ca. 2 mm wide, densely pubescent with capitate-glandular trichomes, epetiolate, apically acute, basally truncate, prominent adaxial furrow. *Inflorescences* of solitary flowers, axillary; pedicels 5–10 mm long, recurved in fruit. *Flowers* 5-merous; calyces tubular, 8–10 mm long, densely pubescent with capitate-glandular trichomes,

FIGURE 184. Distribution of *Nolana tarapacana* (Phil.) I.M. Johnst.

FIGURE 185. *Nolana tarapacana*. **A**, Densely branched, leafy annuals; **B**, Leaves densely set with short, capitate-glandular trichomes; **C**, Corollas with a purple band in the throat. Photographs by Marcelo Rosas.

throat 3–4 mm long, lobes linear 5–7 mm long, ca. 1 mm wide, unequal, apically acute; corollas infundibularis, 7–8 mm long, violet, slightly longer than calyx lobes; stamens unequal; filaments rarely pubescent; nectary patelliform, lobed; style gynobasic. *Mericarps* (2–)3–5, two large, obovoid, ca. 3 mm long, ca. 2 mm wide, slight reticulate pattern, nitid, attached laterally; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet refers to the geographic region of the type locality, Province of Tarapacá, much of which was a province of Peru but was annexed by Chile in 1883 at the close of the War of the Pacific.

Distribution and Ecology: Chile, Regions of Arica & Parinacota and Tarapacá; 1000–2600 m.a.s.l. (Fig. 184). It is recorded from a very few collections from interior localities, far from coastal fog.

Nolana tarapacana is a densely branched, leafy annual with a large taproot (Fig. 185A). The leaves are densely set and the pubescence is short capitate-glandular (Fig. 185). The corollas have a deep purple band at the mouth of the limb (Fig. 185C), like those found in many Peruvian species. A preponderance of characters suggests that it is related to *Nolana gracillima*. It is especially difficult to discriminate *Nolana tarapacana* from *N. gracillima* when they are dried; the number of mericarps is variable.

I had originally classified *Gengler 63* and *Eggli et al. 2834* as *N. tarapacana*; however, after examining many collections, these are assigned here to *N. rhombifolia* on the strength of overall morphology and mericarp size. The Kew sheet collected by *R. A. Philippi* from Tarapacá is best treated as a paratype (K000532196), given that it was collected by the father, not the son, who had collected the lectotype.

Additional specimens examined: CHILE. **Arica & Parinacota**: Cuesta El Aguila, 1800 m.a.s.l., *E. Belmonte 96-346* (CONC 135408); Camino Azapa–Lluta, *J. Castillo L. 177-74* (CONC 92459); Prov. Arica, Pampa El Muerto, 1550 m.a.s.l., *A. Hoffmann 8934* (CONC 106083); Pampa Hilaricos, 14 April 1972, *C. Muñoz S. 77* (SGO 135338). **Tarapacá**: Alto de Tambillo, crece en Altos de Pica, en sectores pedregosos y arenosos, 2620 m.a.s.l., 16 September 1975, *G. Dalannais 48* (SGO 116761); Altos de Pica, 2600 m.a.s.l., 16 September 1975, *G. Dalannais 49* (SGO 116760); Camino a Mamiña pasando Duplijsa Km 60 [Quebrada Guataguata], 20°05'00"S, 69°16'44"W, 26 April 2008, *M. Muñoz S. & A. Moreira M. 4912* (SGO 157242); Km 25 despues del cruce a Mamiña, 20°16'36"S, 69°14'52"W, 2290 m.a.s.l., 26 April 2008, *M. Muñoz S. & A. Moreira M. 4916* (SGO 157247); Pica, Quebrada Quisma, camino al salar de Huasco, 20°25'S, 69°08'W, 2750 m.a.s.l., *S. Teillier 4803* (CONC 150917); Pozo Almonte, Quebrada Cahuisa, acceso por camino a la mina Quebrada Blanca, 20°49'S, 69°04'W, *S. Teillier 4798* (CONC 150841); NE de Pica, Propiedades mineras Chacarilla Oeste, Chacarilla Este, Challacollo–Sipuca y Pucana, 2600 m.a.s.l., 4–7 July 2000, *S. Teillier s.n.* (F 2324241). Prov. Iquique. Trayecto entre Quebrada de Guasquiña y Chusmiza, 19°45'S, 69°18'W, *C. Villagrán, L.F. Hinojosa, & C. Lattore 9040* (CONC 142999); Pampa del Tamarugal, 5 km antes de la junta camino a Guatacondo, 1200 m.a.s.l., *M. Ricardi, E. Weldt, & M. Quezada 19* (CONC 43006); Camino de Huara a Cancosa, entre Pachica y Poroma, 19°53'S, 69°15'W, 2000 m.a.s.l., 2 April 1961, *M. Ricardi, C. Marticorena, & O. Matthei 355* (CONC 36178); Pica, 20°29'S, 69°20'W, 1400 m.a.s.l., September 1925, *E. Werdermann 741* (B, BM000941365, CONC 56091, E00130943, F 564186, GH [2 sheets], K, US 3312684, US 1444767).

Clade F

F1. ***Nolana adansonii*** (Roem. & Schult.) I.M. Johnst., Contrib. Gray Herb. 112: 47. 1936. Fig. 186–190.

Basionym: *Tula adansonii* Roem. & Schult., Syst. veg. 4: 355. 1819. TYPE: PERU. Moquegua: [beach S of Ilo], 29 August 1710, "Soldanella facie, flore infundibuli forma", *L.É. Feuillée s.n.* (based upon polynomial and illustration, Jour. Observ. 3: 15. 1725, tab. 44).

Digital image: No digital image for the types of *Nolana adansonii* is available via the internet.

Heterotypic synonym: *Sorema cordata* Rémy, Ann. Sci. Nat. Ser. 3, 6: 351. 1846. TYPE: PERU. Arequipa: Islay, 1833, *A. d'Orbigny* [*1850*] (Holotype: P [0060 5842]; Isotype: G [G00383956], F neg. 23239). *Nolana cordata* (Rémy) Dunal, Prodr. 13: 13. 1852; *Nolana amplexicaulis* Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 7. 1955. TYPE: PERU. Arequipa: Caravelí, Lomas de Cápac [Capacc], cerca a Chala, *R. Ferreyra 11747* (Holotype: USM [15721, USM 242128, USM000555]; Isotypes: K [K000532267, K000532268]).

Annual *herbs*, 10–100 cm tall; stems erect, glandular, branches 6–15 cm long, 1–2 mm wide, glandular, purple. *Leaves* alternate, blades cordiform, rarely reniform, to lanceolate or elliptic, 5–12 mm long, 4–13 mm wide, margin ciliolate with stiff, non-glandular trichomes, apically obtuse, bases amplexicaulis, auriculate or, at times, completely fused and connate around the stem, pubescent with salt glands; petioles 4–14 mm long, base stipuliform, auriculate or connate, amplexicaulis, pubescent-glandular with salt glands. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 1–4 mm long; calyces campanulate, 5–8 mm long, 5–6 mm in diam., glandular outside, pubescent inside, trichomes erect, 0.2–0.4 mm long, tube campanulate, 3–5 mm long, 2.8–3.2 mm in diam., lobes equal, acute, long-ciliolate, 1.8–2.2 mm long, 1.2–1.8 mm wide; corolla narrowly infundibularis, blue with dark veins or a spot basally, 21–26 mm long, 5–7 mm wide, lobes unequal, 2 acute, 3 obtuse; stamens unequal, two larger 16–17 mm long, three smaller 13–14 mm long, united to tube for 1/2 its length; style 14–15 mm long; receptacle 3.5–4.0 mm in diam. Mericarps 15–20, 3-seriate, gynobasic receptacle, globose, 1–2 mm diam., black; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Michel Adanson (b. 1727–d. 1806), a French naturalist and botanist of Scottish descent; in 1763, he authored *Familles naturelles des plantes*.

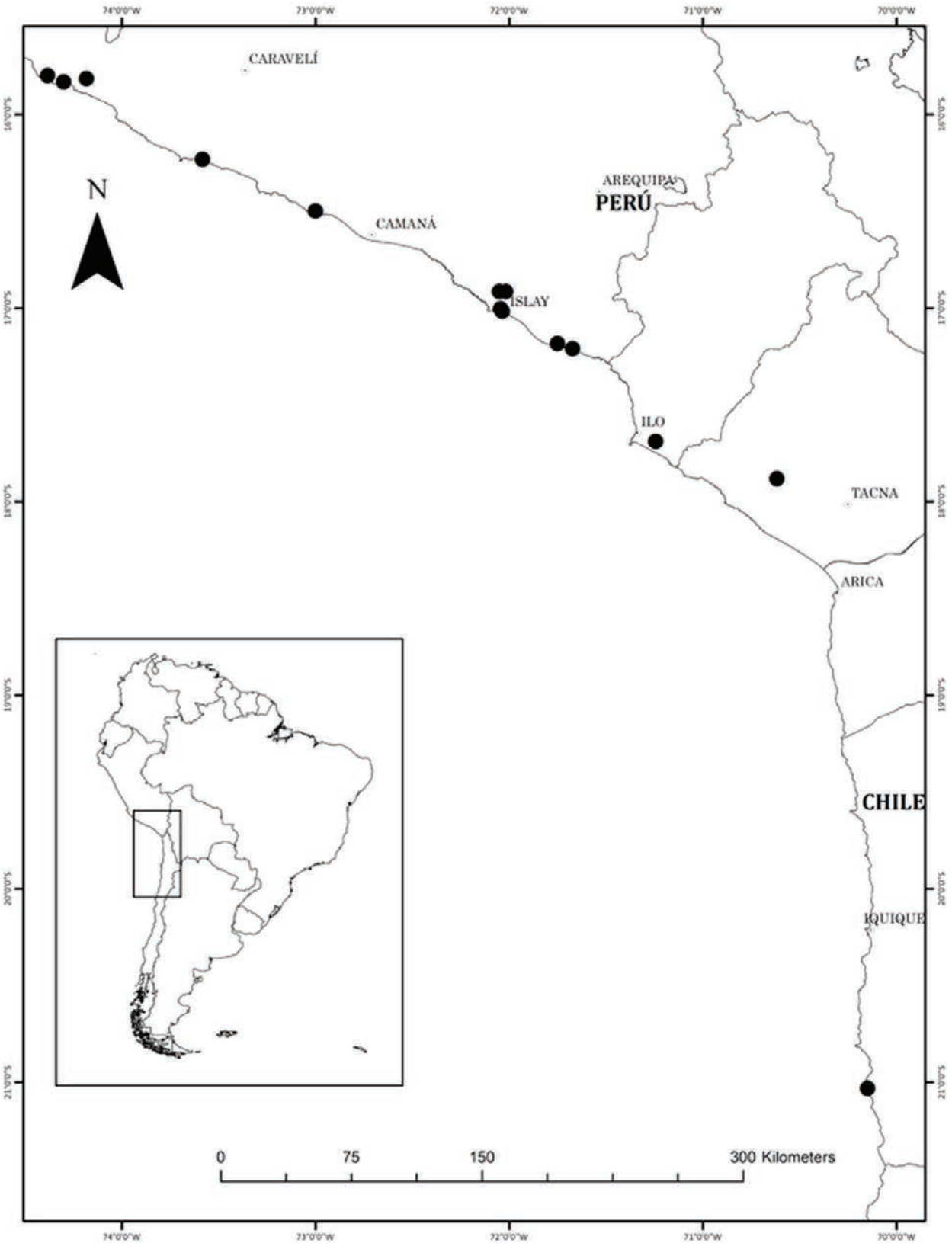


FIGURE 186. Distribution of *Nolana adansonii* (Feuillée ex Roem. & Schult.) I.M. Johnst.

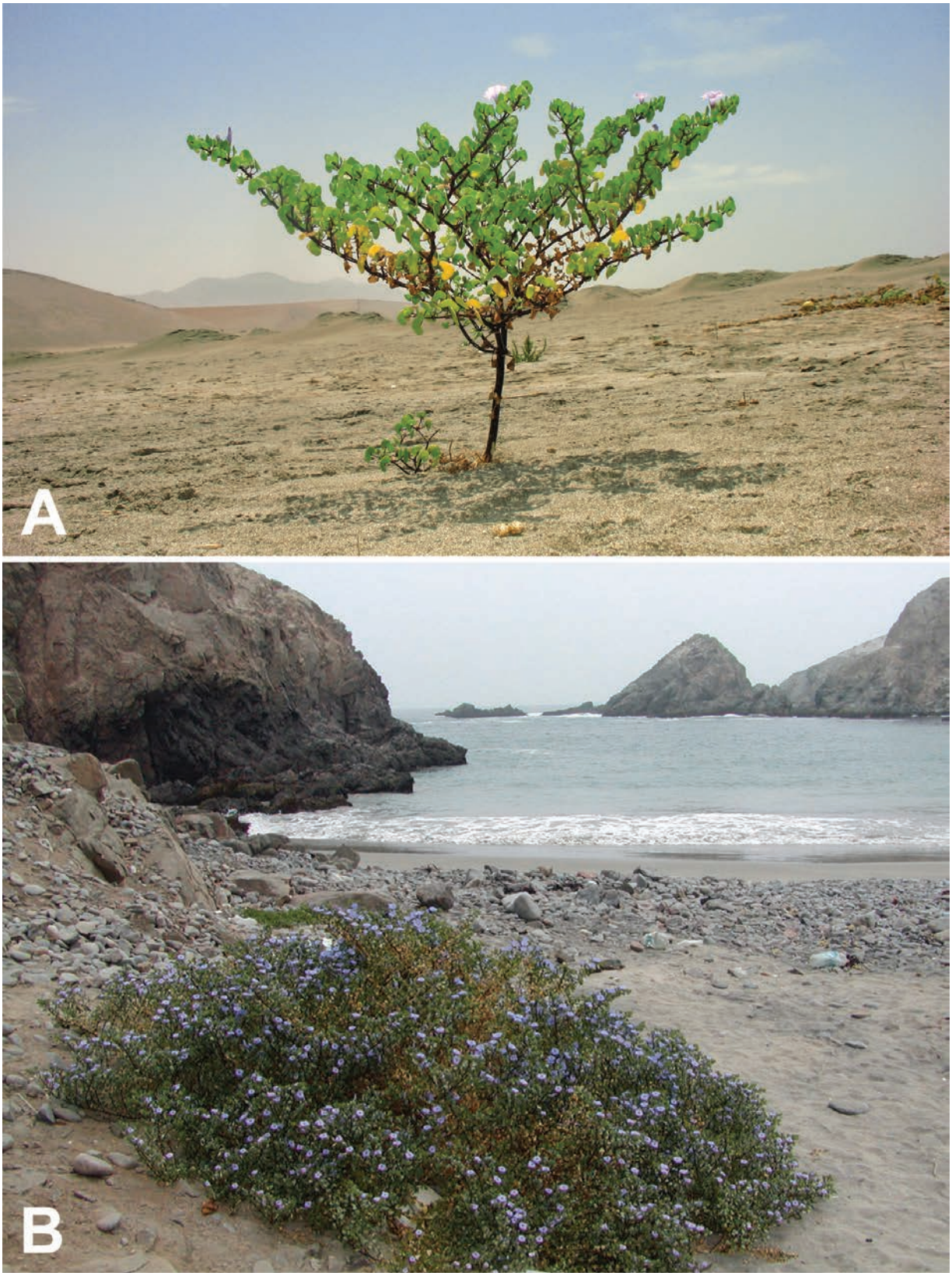


FIGURE 187. *Nolana adansonii*. **A**, Annual habit; **B**, Large, spreading plants with unlimited moisture. Photographs by Victor Quipuscoa Silvestre.

FIGURE 188. *Nolana adansonii*. **A**, Intricately branched annuals; **B**, Leaf blades cordate to reniform, petiolate; **C**, Flowers and leaves erect. Photographs by Victor Quipuscoa Silvestre.

FIGURE 189. *Nolana adansonii*. A, Leaves and flowers oriented to intercept winds; **B**, Salt glands identified as the dark brown spots on the leaf surfaces, elongate trichomes prevalent on the calyx. Photographs by Victor Quipuscoa Silvestre.

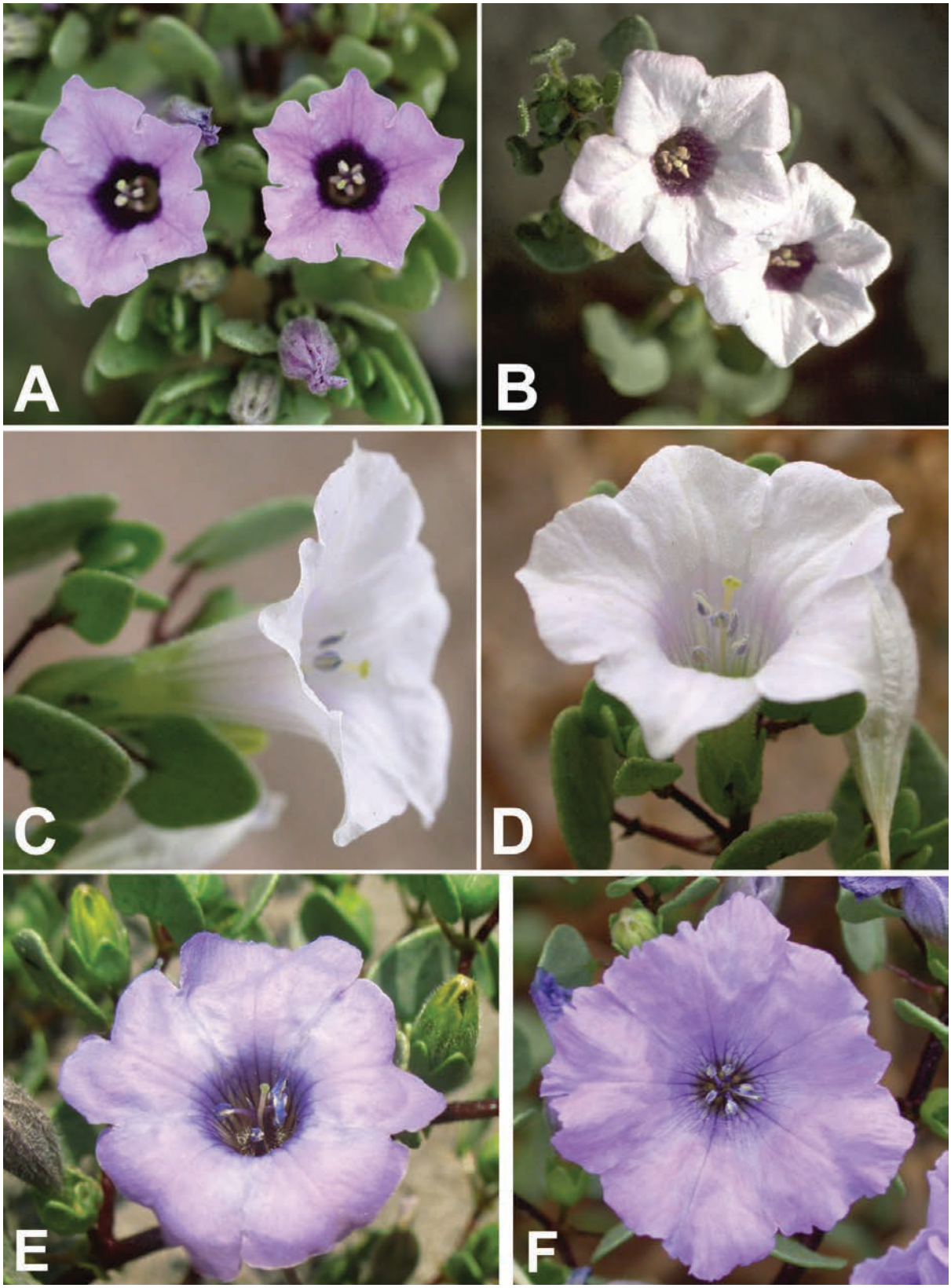


FIGURE 190. *Nolana adansonii* corollas. **A,** Corollas pink to lavender with a dark throat (*Dillon et al. 8913*); **B,** Corollas white with a dark throat (*Dillon & Dillon 3917*).; **C–D**, Corolla white with light pink throats; **E,** Corolla 5-lobed; **F,** Corolla 5-lobed but appearing square (*Dillon et al. 8984*).

Distribution and Ecology: Peru, Departments of Arequipa, Ayacucho, Moquegua, Tacna; disjunct populations, Chile, Region of Tarapacá; sea level to 850 m.a.s.l. (Fig. 186). It is recorded from a wide range of environments; Matorral Desertico Tropical Costera (Luebert and Pliscoff, 2006).

Nolana adansonii is typically an annual (Fig. 187A), and, given sufficient moisture, individuals can become large, spreading plants (Fig. 187B). The plants are intricately branched (Fig. 188A) and easily recognized by their cordate to reniform leaf blades (Fig. 188B). Flowering branch apices illustrate the orientation of the flowers and leaves (Fig. 188C). The leaves are oriented vertically; this likely plays a role in intercepting moisture in saturated environments (Fig. 189A). The leaf surfaces appear shiny and oily to the touch due to the hydrated salt glands on the surfaces. The glands can be identified as dark brown spots on the leaf surfaces; elongate trichomes are prevalent on the calyx (Fig. 189B). The corollas vary in size, shape, and color (Fig. 190A–F). In general, there are dark purple guides at the base of the corolla throat (Fig. 190A–B). The shape and size of the corolla lobes is variable and should be studied in more detail (Fig. 190D–F).

Nolana adansonii was first collected by Louis Éconches Feuillée near Ilo (Peru, Dept. Moquegua) in 1710 and later described as a polynomial "*Soldanella facie, flore infundibuli forma*," Jour. Observ. Phys. 2: 15. 1725. Adanson (1763) proposed the generic name, *Tula*, based upon the polynomial description published by Feuillée (1725). Roemer and Schultes (1819) provided a specific epithet and cited the plate (tab. 44) published by Feuillée (Hist. Pl. Medicinal 63, tab. 44, 1725). Plate 44 was an engraving by Jacques Philippe Le Bas, after a sketch by Louis Feuillée in 1725.

Ferreyra (1961) described *N. amplexicaulis* and related it to *N. adansonii*. He distinguished this new species from *N. adansonii* as having a reduced habit and unusual lanceolate leaves. After examining a large number of collections from throughout its range, as well as the type material, these two species are clearly conspecific.

Additional specimens examined: CHILE. **Tarapacá**: cerros E de Palo Buque, 22 km S Iquique, 225 m.a.s.l., 9 October 2015, *H. Larraín s.n.* (SGO 169085); Alto Punta Lobos, 21°02'S, 70°09'W, 55–250 m.a.s.l., 1 November 1997, *R. Pinto s.n.* (SGO 142966); Alto Punta Lobos, 21°02'S, 70°09'W, 800 m.a.s.l., 17 January 1998, *R. Pinto s.n.* (SGO 142965). PERU. **Arequipa**: Prov. Caravelí, Atico y Ocoña, 14 November 1957, *N. Angulo E. s.n.* (HUT 2570); Lomas of Atico, ca. 48 km SE of Chala, 100 m.a.s.l., 8 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3263* (E, F 1934759, US 3470032); ca. 7 km N of Chala, 15°50'S, 74°18'W, 110 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8199* (F 2198750); entre Atico and Camaná, 16°10'S, 73°40'W, 50 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, S. Leiva, V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8913* (F 2276699, HSP 005199, US 3512533); entre Atico and Camaná, 16°13'S, 73°42'W, 30 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8918* (F 2276702, HSP 005205, US 3512536); Lomas de Atiquipa, 3 December 1955, *R. Ferreyra 11751* (USM); Atico, 50–100 m.a.s.l., 19 December 1959, *R. Ferreyra 13932* (USM 80832); Atico, *R. Ferreyra 17806* (USM); Lomas de Atiquipa, 19 December 1959, *R. Ferreyra 13951* (USM); Lomas de Atico, 50–100 m.a.s.l., 15 November 1966, *R. Ferreyra 17086* (USM); Pan-American Highway Km 648 S of Lima, 2 km S of Chala, Lomas de Cápac, 150 m.a.s.l., 14 September 1957, *P. C. Hutchison 1314* (F 1559926, K, UC, US 2404063, USM); W of Ocoña, Km 778, 800 m.a.s.l., 14 January 1963, *H. M., Iltis, C. M. Iltis, D. Ugent, & V. Ugent 1555* (US 2558197); Atico, 300 m.a.s.l., 24 March 1970, *A. López M. s.n.* (HUT-7378); Pan-American Hwy, 7.9 km N de Puente Sta. Rosa, 9 September 2001, *M. McMahon & L. Hufford 546* (F 2243065); Atiquipa, 400–600 m.a.s.l., 5 November 1953, *C. Vargas C. 10943* (CUZ, USM); Lomas de Atico, 400–450 m.a.s.l., 31 October 1966, *C. Vargas C. 18233* (CUZ, USM); Lomas de Atiquipa, 400–500 m.a.s.l., 1 November 1966, *C. Vargas C. 18252* (CUZ); Lomas de Atico, 600 m.a.s.l., 31 October 1966, *C. Vargas C. 18211* (CUZ); Lomas de Chala, 400–500 m.a.s.l., 31 October 1966, *C. Vargas C. 18239* (CUZ). Prov. Camaná, ca. 5 km N of Ocoña, ca. 775 S of Lima, 270 m.a.s.l., 2 December 1964, *P. C. Hutchison & J. K. Wright 7255* (F 1642071, UC, USM); between Camaná and Ocoña, 24 October 1980, *T. Masuzawa s.n.* (MAK 197077); Lomas de Ocoña, 31 October 1966, *C. Vargas C. 18208* (CUZ); Lomas de Camaná, 31 October 1966, *C. Vargas C. 18299* (CUZ). Prov. Islay, ca. 4 km N of Mejía, ca. 15 m.a.s.l., 26 October 1983, *M. O. Dillon & D. Dillon 3744* (F 1940847, HUT 20289, USM); Lomas of Mollendo, ca. 9 km NW of Mollendo, ca. 100 m.a.s.l., 26 October 1983, *M. O. Dillon & D. Dillon 3917* (F 1941146); Alrededores de Catarindo, 17°01'S, 72°02'W, 5–10 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva, V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8974* (F 2276713, GH, HSP 005252, US 3512528); Sur de Mollendo, 17°01'S, 72°00'W, 100 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8984* (CONC, E, F 2276718, GH, HSP 005258, US 3512523); Carretera Costanera, ca. 10 km al Sur de Punta Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8993* (F 2276601, GH, US 3514026); Cocachacra, El Fiscal, 16°59'S, 71°44'W, 630 m.a.s.l., 20 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9018a* (CONC, E, F 2276622, GH, HSP 005288, SGO, US 3512556); 7 km N of Rio Tambo, 550 m.a.s.l., 19 August 1957, *H. Ellenberg 2712* (U 096207); 10 km S of Mollendo, sea level, 23 April 1939, *W. J. Eyerdam 25156* (GH, K); arriba de Mejía, 10–20 m.a.s.l., 12 November 1949, *R. Ferreyra 6387* (F 1442801, GH, USM); Valle del Tambo, Hacienda Chucarapi, 500–600 m.a.s.l., 29 November 1955, *R. Ferreyra 11584* (K [2 sheets], USM); Mollendo, 100–200 m.a.s.l., 7 October 1957, *R. Ferreyra*

12589 (USM); Mollendo, 150–200 m.a.s.l., 24 October 1976, *R. Ferreyra 18651* (USM); coastal flats between Mollendo and Mejia, 6–10 ft, 8 April 1939, *W. Balfour Gourlay 123* (E00793130, K, US 2142198); Mejía, 10 m.a.s.l., 6 November 1923, *E. K. F. Günther & O. Buchtien 109* (CONC 109131, GH); Mollendo, February 1919, *E. K. F. Günther s.n.* (US 1134918); Mollendo, 1 January 1903, *A. W. Hill 342* (K); south of Mollendo, 15 m.a.s.l., 17 November 1935, *Y. E. J. Mexia 4182* (GH), *7773* (B, GH, K, US 1705289); alrededores del INDEHI-UNSA, Catarindo, 20 m.a.s.l., 20 November 2002, *V. Quipuscoa S., N. Hidalgo A., D. Sotomayor M., & M. Rodríguez Z. 2829* (HUT 40143); a 1 km Sur de Mejía, 17°06'20"S, 71°54'19"W, 10 m.a.s.l., 4 December 2002, *V. Quipuscoa S. & M. O. Dillon 2835* (HUT 40144, US 3634121); alrededores del INDEHI-UNSA, Catarindo, 17°01'02"S, 72°02'06"W, 0–20 m.a.s.l., 5 December 2002, *V. Quipuscoa S. & M. O. Dillon 2843* (HSP 000535, HUT 40145); entre Matarani y Mollendo, 17°00'18"S, 72°02'36"W, 140 m.a.s.l., 21 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2914* (HSP 000546); Dist. Punta de Bombón, ca. Km 157 Carretera Costanera, 17°12'41"S, 71°40'22"W, 7 m.a.s.l., 28 October 2017, *V. Quipuscoa, M. O. Dillon, M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6242* (HSP 011306); Mollendo, sea level–500 ft, August–September 1932, *D. B. Stafford 29* (BM000941267, K); 10 km S of Mollendo, 28 September 1938, *C. R. Worth & J. L. Morrison 15725* (GH, K); Lomas Mollendo–Matarani, 100–300 m.a.s.l., 11 August 1949, *C. Vargas C. 8463* (CUZ, GH); Las Lagunillas S. of Mollendo, 80 m.a.s.l., 14 October 1997, *M. Weigend & H. Förther 97/866* (F 2211301, HUT 34152); 10 km S of Mollendo, 28 September 1938, *C. R. Worth & J. L. Morrison 15725* (F 1488328, K). **Ayacucho**: Prov. Lucanas, Dist. Santa Lucia, ca. al limite con Bella Union, carretera a Huanca, 15°08'42"S, 74°30'01"W, 661 m.a.s.l., 28 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez, S. Huamani Q., & M. Bedoya C. 7575* (HSP 011333); Dist. Sacos, entre San Luis y Carrizales, carretera a Coracora, 15°15'58"S, 74°15'43"W, 841 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez, S. Huamani Q., & M. Bedoya C. 7633* (HSP 011850, HUT 60414). **Moquegua**: Prov. Ilo, N of Ilo, [100 ft], 23 September 1937, *D. B. Stafford 921* (BM000941264, K). **Tacna**: Prov. Tacna, 25 km N de Tacna, 600 m.a.s.l., 6 October 1957, *R. Ferreyra 12535* (USM); Tacna, September 1864, *R. Pearce s.n.* (BM000941266); Lomas de Sama, 500 m.a.s.l., 7 August 1967, *C. Vargas C. 19932* (CUZ).

F2. ***Nolana aenigma*** M.O. Dillon, S. Leiva, & Quip., Arnaldoa 14(2): 172. 2007. TYPE: PERU. La Libertad: Prov. Trujillo, Dist. Trujillo, Km 580, Cerro Cabezón, 10 February 1998, *S. Leiva G., M. O. Dillon, A. Sagástegui A., & V. Quipuscoa S. 2165* (Holotype: HAO, destroyed; Lectotype designated by Dillon and Quipuscoa, 2023: HUT [031950]; Isolectotype: F 2329912). Fig. 191–194.

Digital image: No image is currently available via the internet; the lectotype image of *Nolana aenigma* (Fig. 192) was provided by Herbario Universidad Nacional de Trujillo, Trujillo [HUT031950].

Succulent, annual *herbs*; stems erect, ca. 40 cm long, much-branched, glabrous. *Leaves* alternate, blades cordate, reniform to ovate, 15–25 mm long, 15–25 mm wide, glabrous, succulent, apically obtuse to rounded, basally obtuse to cordate; petioles 10–15 mm long. *Inflorescences* of solitary flowers in upper leaf axils, pedicels stout, glabrous, 1.5–2.0 cm long. *Flowers* 5-merous; calyx campanulate, 4.0–4.5 mm wide at anthesis, glabrous, 5-lobed, lobes lanceolate, equal, 4.5–5.0 mm long, 2.0–2.5 mm wide, apices acute, penicillate; corollas infundibularis, ca. 12 mm wide, ca. 8 mm long, purple to lavender, throat deep purple, internally glabrous, externally pubescent along the nerves, trichomes uniseriate; stamens 5, included, filaments inserted on lower third of corolla, equal, 4.0–4.5 mm long, pilose at the bases; anther thecae ca. 1.5 mm long, ca. 1.5 mm wide, purple, glabrous; ovary glabrous, ca. 1 mm long, 1.0–1.5 mm wide, basal nectary ca. 2 mm wide, 5 carpels, style included, 4.5–5.0 mm long, stigma lateral, green, ca. 1.5 mm long. *Mericarps* 5, immature; seeds unknown. Chromosome number: unknown.

Etymology: The specific epithet is from the Latin, *aenigma*, a mystery, puzzling or inexplicable occurrence or situation.

Distribution and Ecology: Peru, Department La Libertad; 300–400 m.a.s.l. (Fig. 191). It is recorded from the type locality at the base of Cerro Cabezón ca. 20 km north of Trujillo. Collected within a dense, flourishing population of *Nolana humifusa*, that was covering the lower slopes of Cerro Cabezón during this period of intense influence of the ongoing 1998 El Niño phenomenon.

Nolana aenigma is unusual among the species in northern Peru, especially its erect habit with basal branching, and short corollas that barely surpass the calyx lobes (Fig. 193). Only *Nolana adansonii* approaches *N. aenigma* in possessing an erect habit; however, the former is easily distinguished by its purple stems, 10–15 small mericarps, and a distribution restricted to southern Peru and northern Chile. The cordate to reniform leaf blades (Fig. 193B, 194B) superficially resemble those in *Nolana paradoxa* from central and southern Chile; however, that species has an essentially prostrate habit, much larger flowers, and 15–20 mericarps. This species has not been included in the molecular studies.

During field studies in the El Niño year of 1998, I only encountered one individual of this species in the field, despite repeated efforts to locate additional material at the type locality. Subsequent years have not produced expansive flowering in northern Peru, and the next El Niño event may present an opportunity to re-encounter this distinct species.

Additional specimens examined: This species has not been encountered since the type was collected.

F3. ***Nolana arequipensis*** M.O. Dillon & Quip., Arnaldoa 14(2): 175. 2007. TYPE: PERU. Arequipa: Prov. Caravelí, Dist. Bella Unión, Sur de Nazca entre Km 518 y Km 590, 15°26'S, 74°52"W, 80–310 m, 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8790* (Holotype: HUSA; Isotypes: F 2319992, HSP 005113, US, USM). Fig. 195–197.

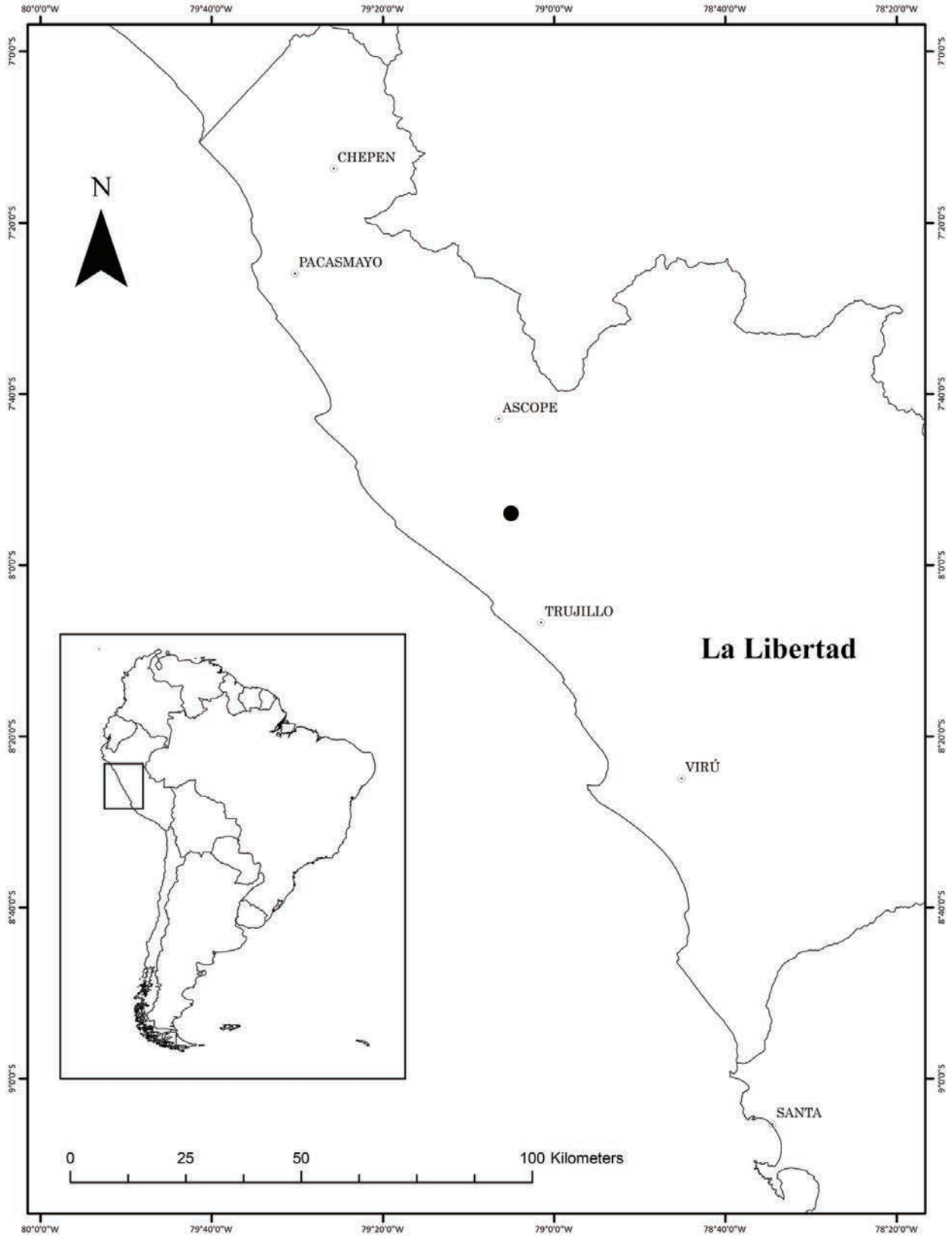


FIGURE 191. Distribution of *Nolana aenigma* M.O. Dillon, S. Leiva, & Quip.

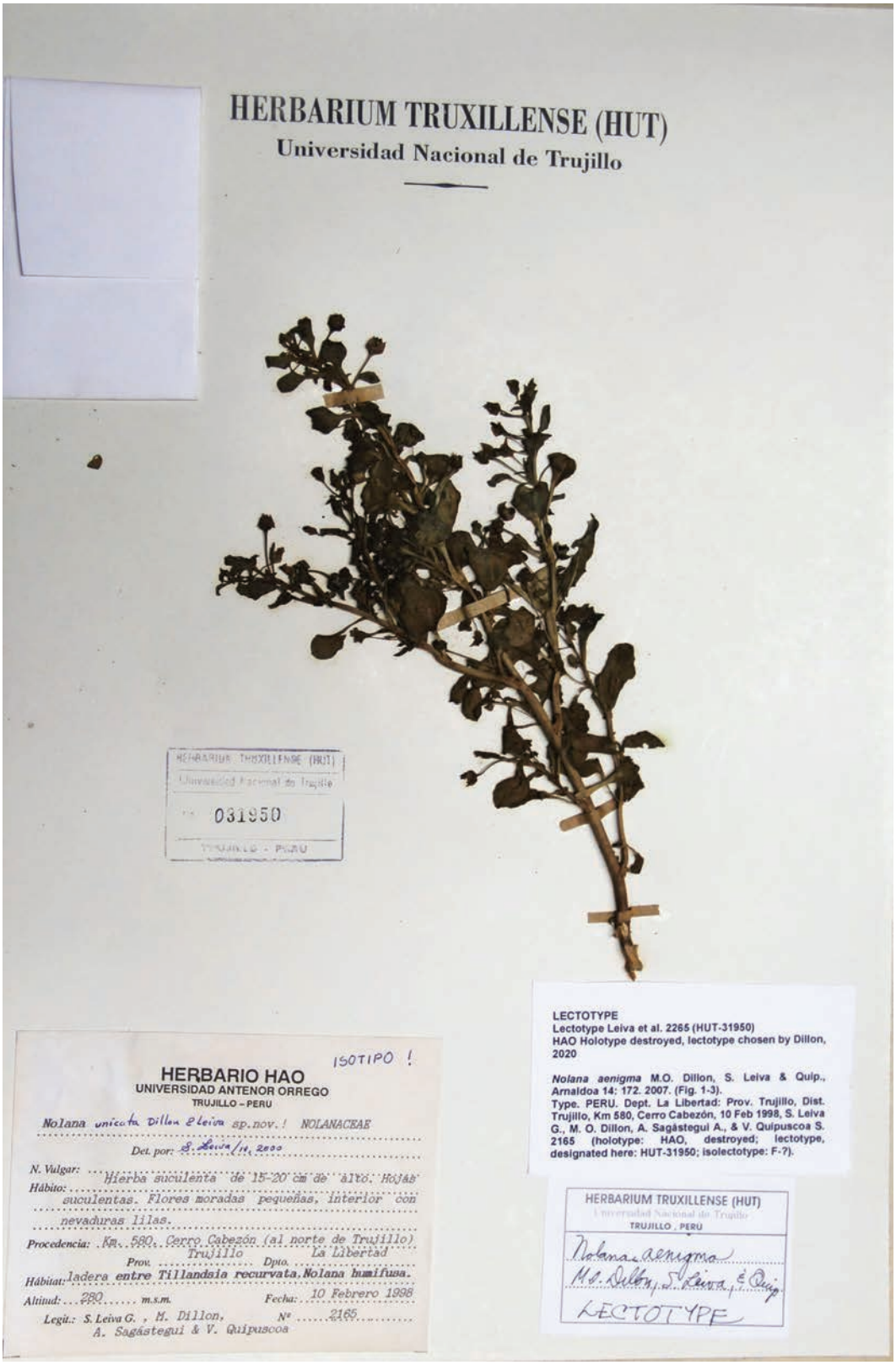


FIGURE 192. Lectotype of *Nolana aenigma* M.O. Dillon, S. Leiva, & Quip. housed at HUT. No digital image is available via the internet.

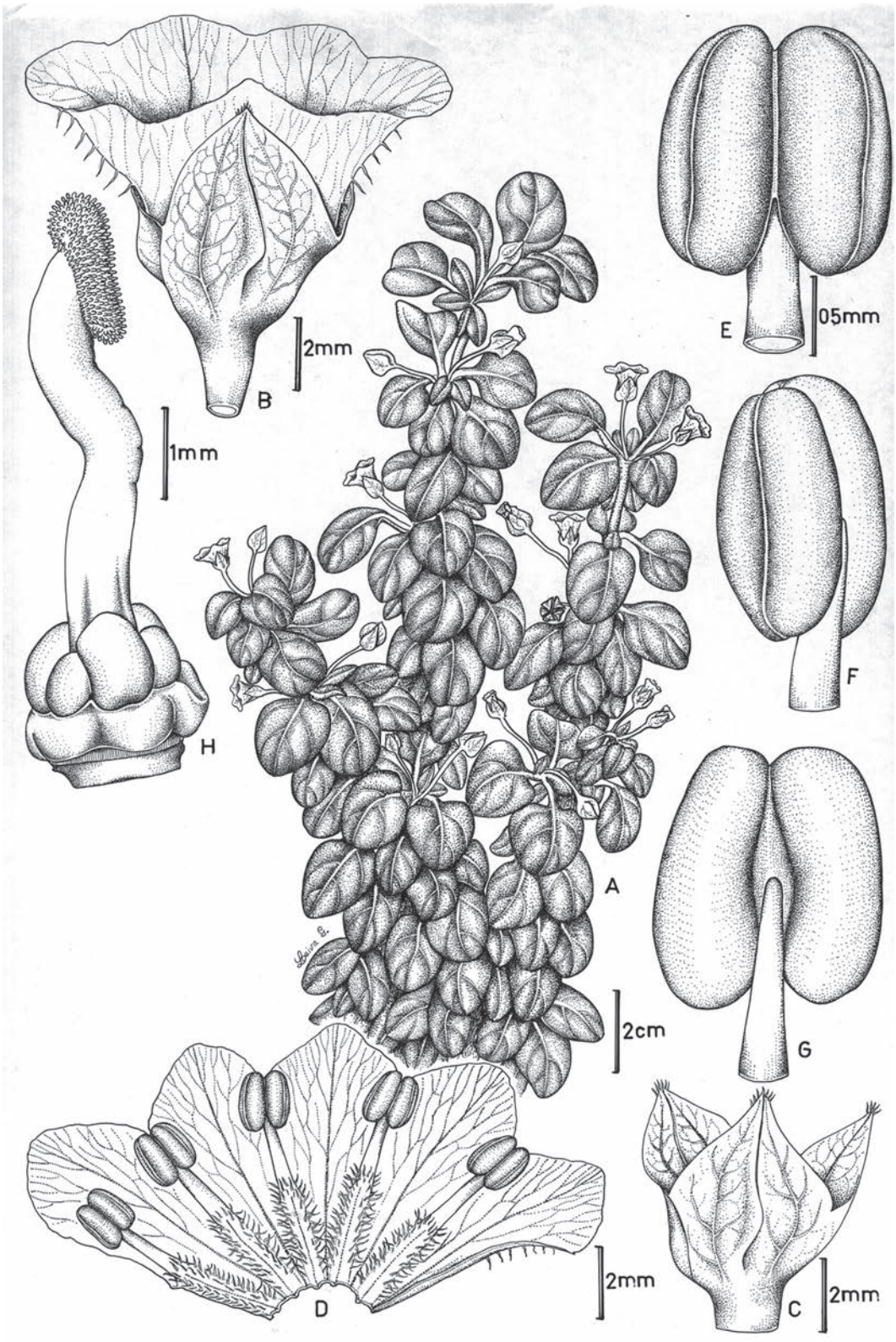


FIGURE 193. Illustration of *Nolana aenigma*. **A**, Flowering branch; **B**, Flower; **C**, Calyx; **D**, Dissected corolla; **E**, Anther thecae dorsal view; **F**, Anther thecae lateral view; **G**, Anther thecae ventral view; **H**, Gynoecium. Drawn by Segundo Leiva Gonzáles.

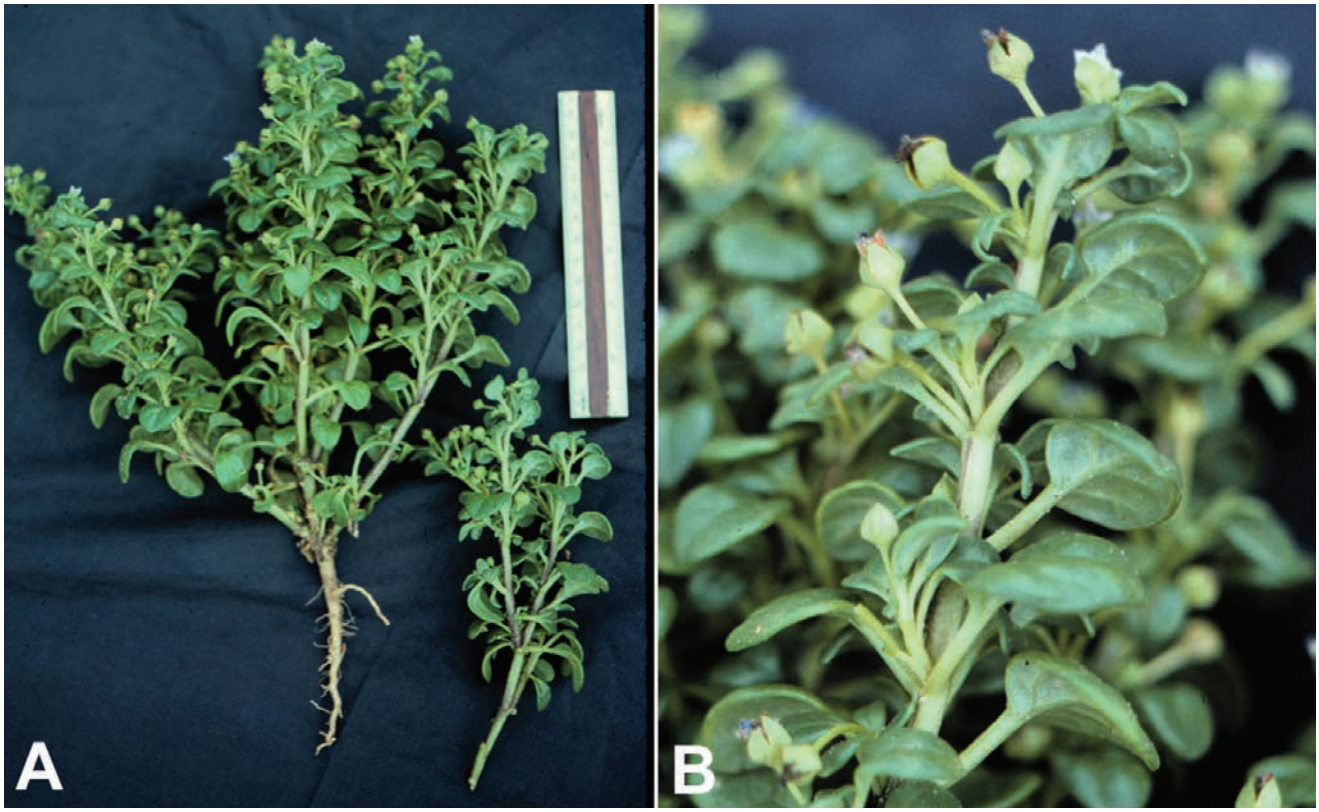


FIGURE 194. *Nolana aenigma*. **A**, Erect, multibranched annual herb; **B**, Closeup of flowering branch showing petiolate leaves and long peduncles. Photograph of *Leiva et al. 2165* (HAO).

Digital image: Isotype of *Nolana arequipensis* from The Field Museum, Chicago [F 2319992]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.f0361464f?loggedin=true

Succulent, perennial *herbs*; stems prostrate, 25–50 cm long, much-branched, glabrous. *Leaves* alternate to subopposite, blades obovate to oblanceolate, 10–20 mm long, 2–4 mm wide, glabrous, succulent, terete, apically obtuse, basally cuneate; petioles 1–3 mm long or sessile. *Inflorescences* of solitary flowers in upper leaf axils, pedicels filiform, glabrous, 5–10 mm long. *Flowers* 5-merous; calyces cylindrical, 2–3 mm wide at anthesis, glabrous, tube ca. 5 mm long; bilabiate, lobes deltoid, equal, 1–2 mm long, 1–2 mm wide; corollas hypocrateriformis to tubular, 6–12 mm wide, white, internally light purple, veined, glabrous, externally glabrous, tube 7–12 mm long, ca. 2 mm wide, 5-lobed, lobes acute, 5–8 mm long, 2–4 mm wide; stamens 5, filaments inserted on lower third of corolla, unequal, three 2–3 mm long, two 3.5–4.5 mm long, pilose at the base; anther thecae 1.0–1.5 mm long, 0.8–1.2 mm wide, white, glabrous; ovary glabrous, ca. 0.8 mm long, ca. 1 mm wide, basal nectary ca. 1.5 mm wide, 2 carpels, style included, ca. 8 mm long, stigma capitate, green, ca. 0.5 mm in diam. *Mericarps* 2, equal, strongly united, included within the expanding calyx, ca. 6 mm long, ca. 5 mm wide; seeds 4–6 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is the latinisation of the geographic locality of the type, Department of Arequipa.

Distribution and Ecology: Peru, Departments of Arequipa and Ica; (0–)100–500(–900) m.a.s.l. (Fig. 195). It is recorded from sandy soils over a range of 150 km.

Nolana arequipensis is a prostrate, much-branched perennial herb (Fig. 197A) with succulent, glabrous leaves and white to pale lavender corollas (Fig. 197B). The calyces are cylindrical with essentially one unequal lobe (Fig. 197C), and the number of connate mericarps is reduced to only two (Fig. 197D). It most closely resembles *N. thinophila*, and several collections were previous classified under that species. *N. thinophila* has larger purple corollas, often with five mericarps, and occurs near the ocean (>20 m). The overall habit and leaf morphology of *N. arequipensis* suggests that it is related to *N. thinophila*, since they share similar terete, succulent leaves and prostrate stems. Utilizing the GBSSI waxy marker (Dillon et al., 2007c), *N. arequipensis* is shown to be related to, but not the sister species of, *N. thinophila*. It is recovered in a well-supported clade with several other southern Peruvian taxa, including *N. confinis, N. johnstonii, N. pallida, N. lycioides, N. cerrateana, N. pilosa, N. volcanica,* and *N. thinophila*.

Unusual morphotypes that have been observed in the region of the type locality may represent the products of hybridization. The molecular data also suggest that some hybridization and/or introgression may have occurred, given that one clone of *N. arequipensis* (*Dillon et al. 8790*, clone 1) is recovered in a clade containing *N. gayana* (Dillon et al., 2007c). The other clones of *N. arequipensis* group together and are sister taxa.

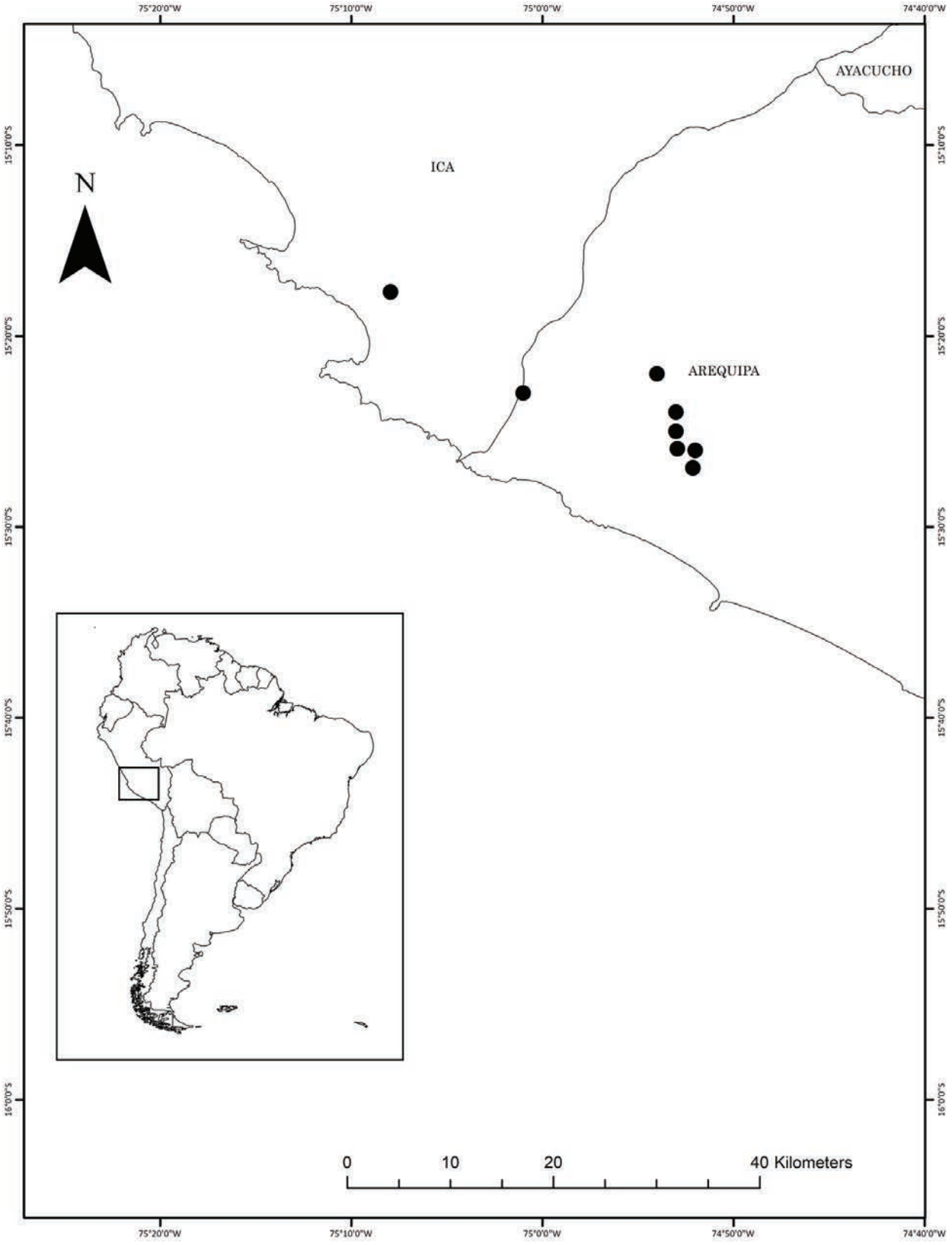


FIGURE 195. Distribution of *Nolana arequipensis* M.O. Dillon & Quip.

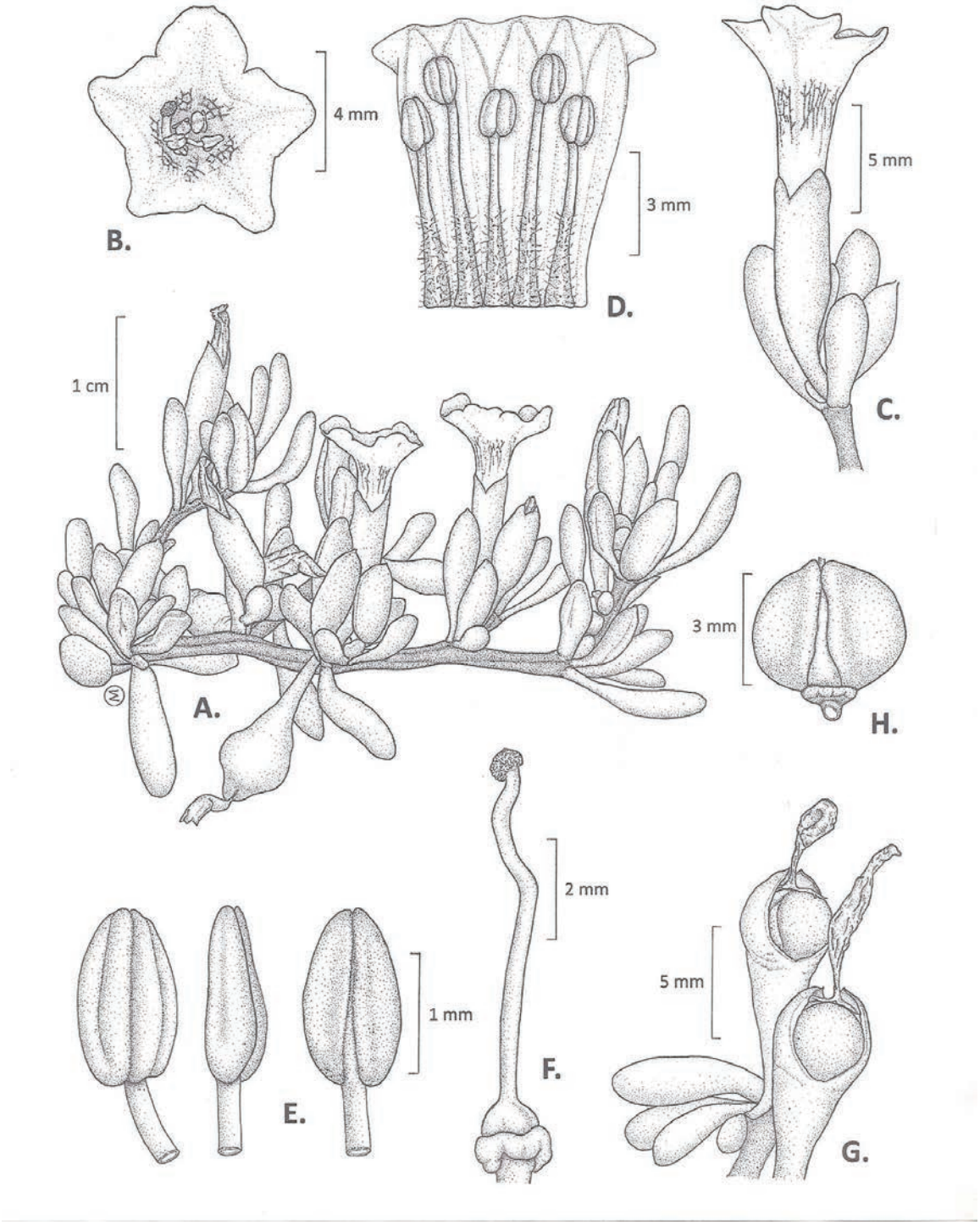


FIGURE 196. Illustration of *Nolana arequipensis*. **A**, Flowering and fruiting branch; **B**, Frontal view of corolla; **C**, Lateral view of flower; **D**, Dissected corolla exposing anthers; **E**, Anthers in ventral, lateral, and dorsal views; **F**, Gynoecium, style, and stigma; **G**, Ripe mericarps; **H,** Mericarp in lateral view. Drawn by Edgardo Ortiz Valencia.

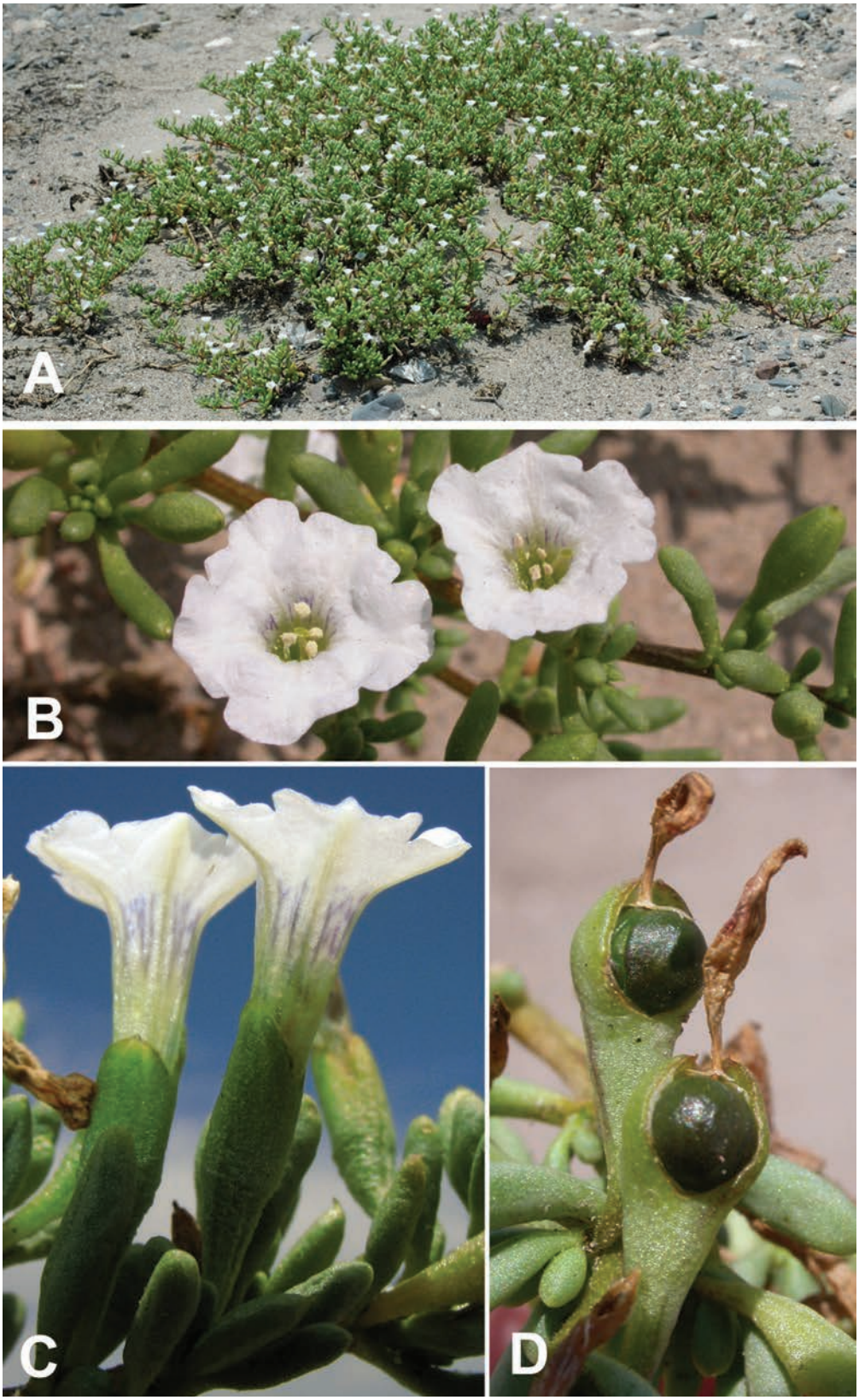


FIGURE 197. *Nolana arequipensis*. **A**, Spreading habit; **B**, Lateral view of branch apex with leaves and flowers; **C**, Closeup of corolla displaying zygomorphic lobes; **D**, Mericarps.

The highly reduced gynoecium composed of only two large, fused mericarps (Fig. 196G, 197D) is not common among Peruvian *Nolana*. It is notable that the *Nolana* species which do occur sympatrically, such as *N. spathulata* and *N. plicata*, are more distantly related and are in a clade with *N. chancoana*, *N. weissiana* and *N. inflata*. Further sampling and analysis are needed to understand the relationships within these southern Peruvian species.

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, Lomas of Ocoña, ca. 285 m.a.s.l., 4 November 1983, *M. O. Dillon & D. Dillon 3861* (F 1941207); between Ocoña and Camaná, 300–350 m.a.s.l., 13 November 1949, *R. Ferreyra 6454* (MOL, US 1998709); between Camaná and Ocoña, ca. 50 km north of Camaná, 300–350 m.a.s.l., 13 November 1952, *R. Ferreyra 8872* (F 1488883, USM 277473); Lomas of Camaná, 30–50 m.a.s.l., 2 December 1955, *R. Ferreyra 11694* (GH, USM 81234); Lomas de Ocoña, 250–300 m.a.s.l., 3 December 1955, *R. Ferreyra 11711* (USM 81241); Camaná, sea level, 14 January 1963, *H. H. & C. M. Iltis 1525* (US 2814960); Alto Grande, Km 520 de la Panamericana Sur, 15°26'01"S, 74°52'02"W, 321 m.a.s.l., 19 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3529* (HUSA, HUT, HSP 000667, USM); Alto Grande, Km 520 de la Panamericana Sur, 15°26'01"S, 74°52'02"W, 321 m.a.s.l., 19 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3535* (HSP 000673); Dist. Mariscal Cáceres, Lomas de Chira, 16°29'59"S, 72°55'51"W, 129 m.a.s.l., 6 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6545* (HSP 12029); 3 km N of Camaná, 0 m.a.s.l., 7 May 1977, *J. Solomon 2800* (USM 53183); ca. 680 km S of Lima, 12 January 1975, *Z. Zimny s.n.* (K); Prov. Caravelí, Lomas of Jahuay, ca. 33 WNW of Chaviña, ca. 300 m.a.s.l., 7 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3240* (CONC, E, F 2043421, GH, SGO, US); Lomas of Jahuay, ca. 300 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3768* (F 1950163, GH, US); ca. 31 km S of Atico, 110–140 m.a.s.l., 4 November 1983, *M. O. Dillon & D. Dillon 3851* (CONC, E, F 1950509, GH, SGO); ca. 67 km S of Nazca, 15°25'S, 74°53'W, 400 m.a.s.l., 20 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8196* (CONC, E, F 2198747, GH, SGO); ca. 77 km S of Chala, 5 km N of Atico, 16°13'S, 73°40'W, 60 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8201* (E, F 2198752, GH, US); ca. 5 km S of Camaná, ca. 1 km E of ocean, 16°39'S, 74°40'W, 10 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8206* (F 2198775); Lomas de Jahuay, entre Nazca and Chala, 400–450 m.a.s.l., 11 October 1955, *R. Ferreyra 11493* (USM 81249); Lomas de Jahuay, entre Nazca and Chala, 400–450 m.a.s.l., 11 October 1955, *R. Ferreyra 11496* (USM 81236); Lomas de Cápac, near Chala, 100–150 m.a.s.l., 3 December 1955, *R. Ferreyra 11743* (K, USM); Lomas de Atiquipa, 100–150 m.a.s.l., 3 December 1955, *R. Ferreyra 11749* (USM 81233); Lomas de Atico, 100 m.a.s.l., 8 December 1956, *R. Ferreyra 11999* (USM 81237); Lomas of Jahuay, entre Nazca and Cala, 300–400 m.a.s.l., 20 December 1959, *R. Ferreyra 14018* (USM 81238); Lomas de Jahuay, 300–400 m.a.s.l., 2 May 1983, *R. Ferreyra, E. Cerrate, & M. Chanco 19862* (USM 50464); Lomas de Jahuay, between Nazca and Chala, 150 m.a.s.l., 15 September 1957, *P. C. Hutchison 1323* (F 1559931, GH, K, US 2406369, USM 81235); Tres Hermanos, near Jahuay, ca. 15 km toward coast from Panamericana Hwy, 5 October 1984, *N. Ohga s.n.* (MAK 225311); hilltop between Jahuay and San Juan, 18 October 1984, *S. Oka s.n.* (MAK 229699); Entre Puerto Lomas y Museo Sacaco, 15°26'55"S, 74°52'07"W, 238 m.a.s.l., 26 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6589* (HSP 8799, HUT 60424); Dist. Lomas, ca. Km 523 de carretera Panamericana, 15°25'55"S, 74°52'56"W, 362 m.a.s.l., 26 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6604* (HSP 12031); Dist. Atico, Panamericana Sur Km 716 al sur de Atico, 16°14'31"S, 73°34'23"W, 35 m.a.s.l., 3 December 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6851* (HSP 010544); Dist. Lomas, Panamericana Sur Km 521, entre Lomas y Marcona, 15°25'03"S, 74°53'24"W, 386 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez, S. Huamani Q., & M. Bedoya C. 7649* (HSP 011859, HUT6 0402); Km 705 S of Lima, between Chala and Camaná, 100 m.a.s.l., April 1973, *A. Richardson 2104* (HUA 7221, HUA0001157, USM 81303); Lomas de Atico, 400–500 m.a.s.l., 31 October 1966, *C. Vargas C. 18228* (CUZ 21435, USM 81239). **Ica.** Prov. Nazca, SE of Marcona, along Hwy 109, near KM 40, 15°23'15"S, 75°01'54"W, 350 m.a.s.l., 19 February 1994, *E. F. Anderson, J. McAuliffe, K. & F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7869* (ASU0045336, F 2143989); Bella Unión, Sur de Nazca entre Km 518 y Km 590, 80–310 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8793* (BM, F 2319995, HSP 005115, HUSA 6224, HUT, US, USM); Lomas de San Nicolás, 800–900 m.a.s.l., 22 September 1958, *R. Ferreyra s.n.* (USM 13385); Marcona, Lomas San Fernando, 15°04'59"S, 75°17'58"W, 857 m.a.s.l., 30 October 2012, *B. Klitgaard, J. P. Cardenas, A. Cooper, O. Whaley, & J. Moat KPP6* (USM 263940); arriba de San Juan de Marcona, ca. Km 28, 15°17'42"S, 75°07'57"W, 366 m.a.s.l., 26 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6595* (HSP 12030).

F4. ***Nolana aticoana*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 13. 1955. TYPE: PERU. Arequipa: Prov. Caravelí, Lomas de Atico, *R. Ferreyra 2524* (Holotype: USM [015726, USM000556]). Fig. 198–200.

Digital image: Holotype for *Nolana aticoana* from Herbario San Marcos, Lima [USM 015726]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000556

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 133. 1981.

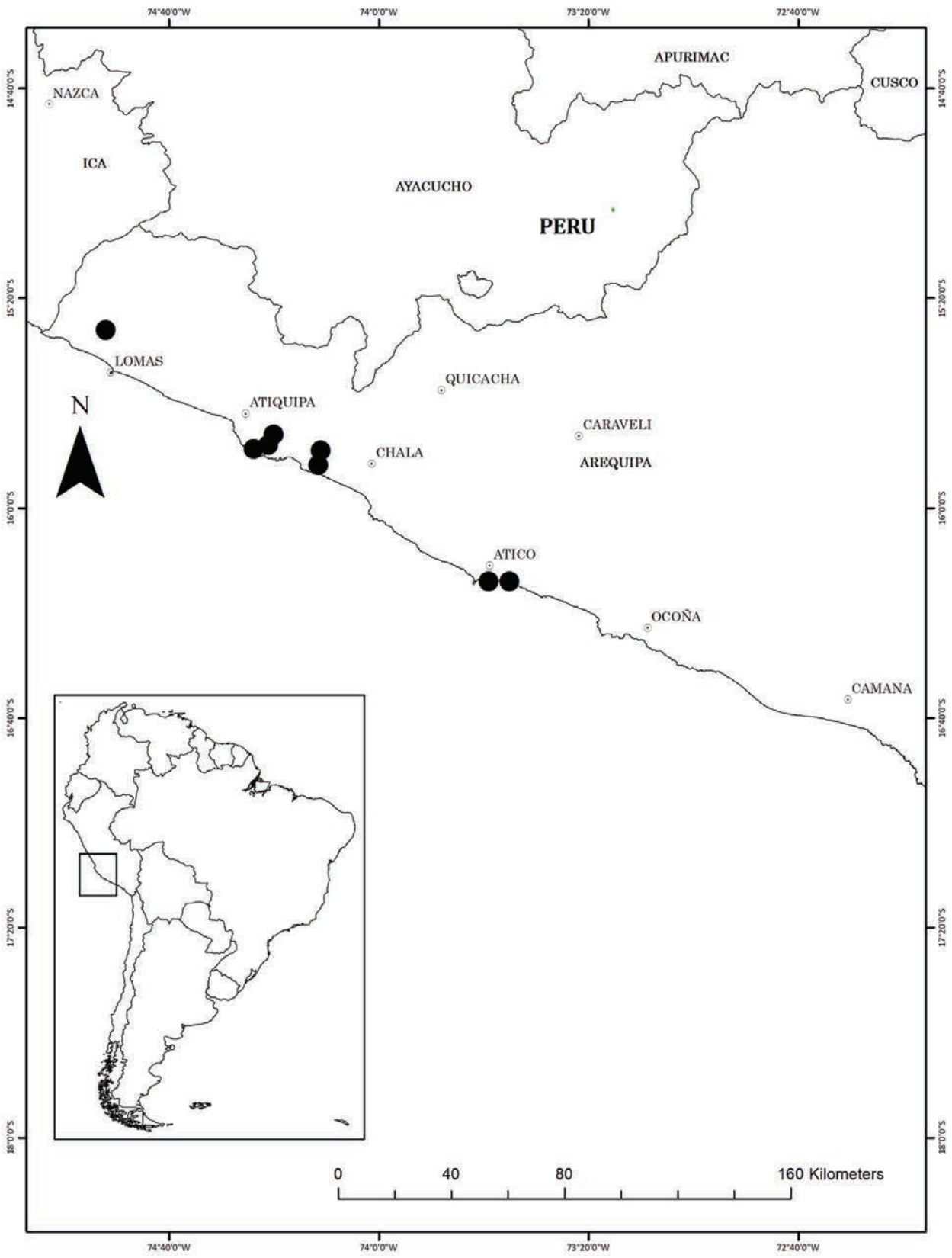


FIGURE 198. Distribution of *Nolana aticoana* Ferreyra.

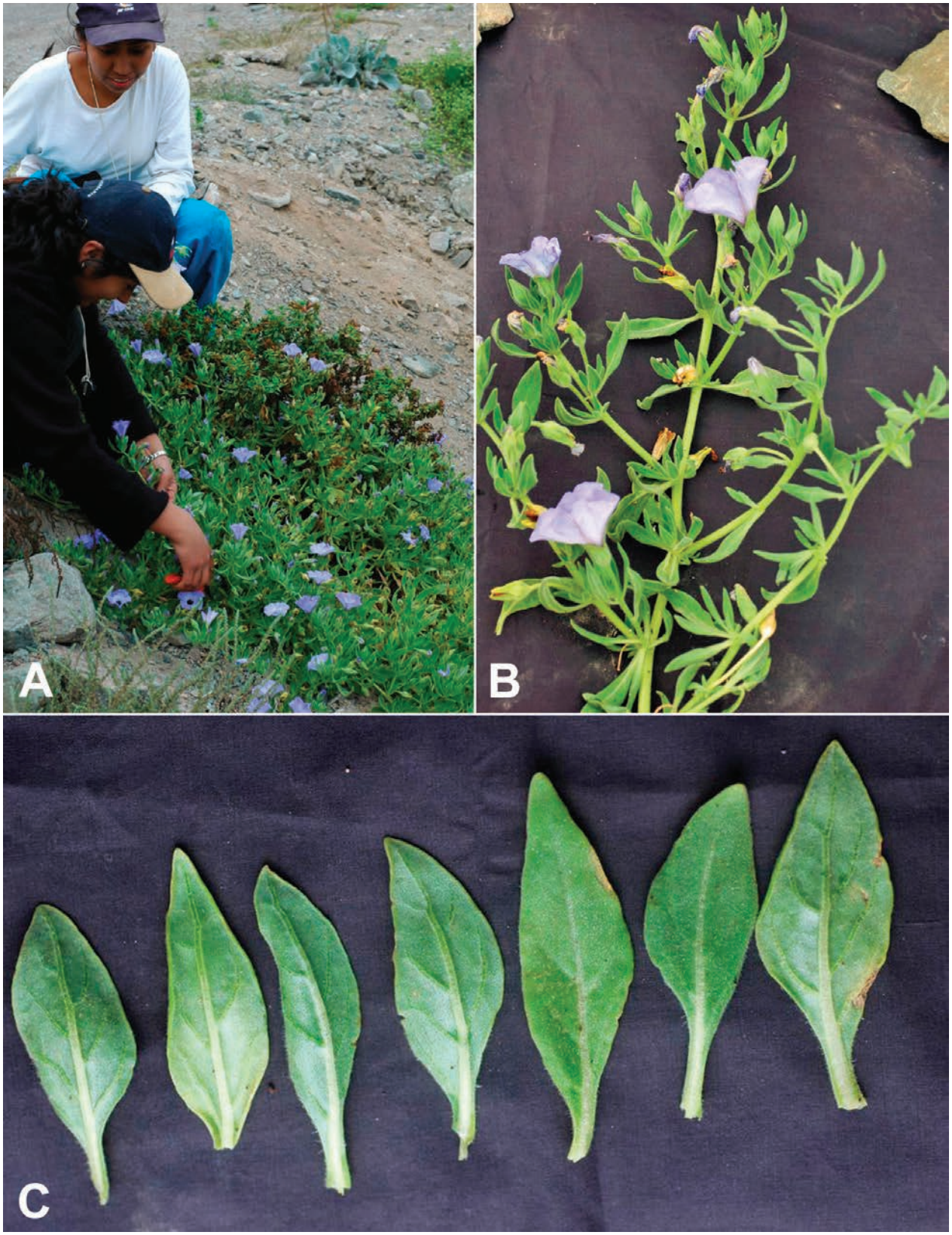


FIGURE 199. *Nolana aticoana*. **A**, Large spreading annuals; **B**, Long internodes, pedicels, and bilabiate calyces; **C**, Selection of leaves.

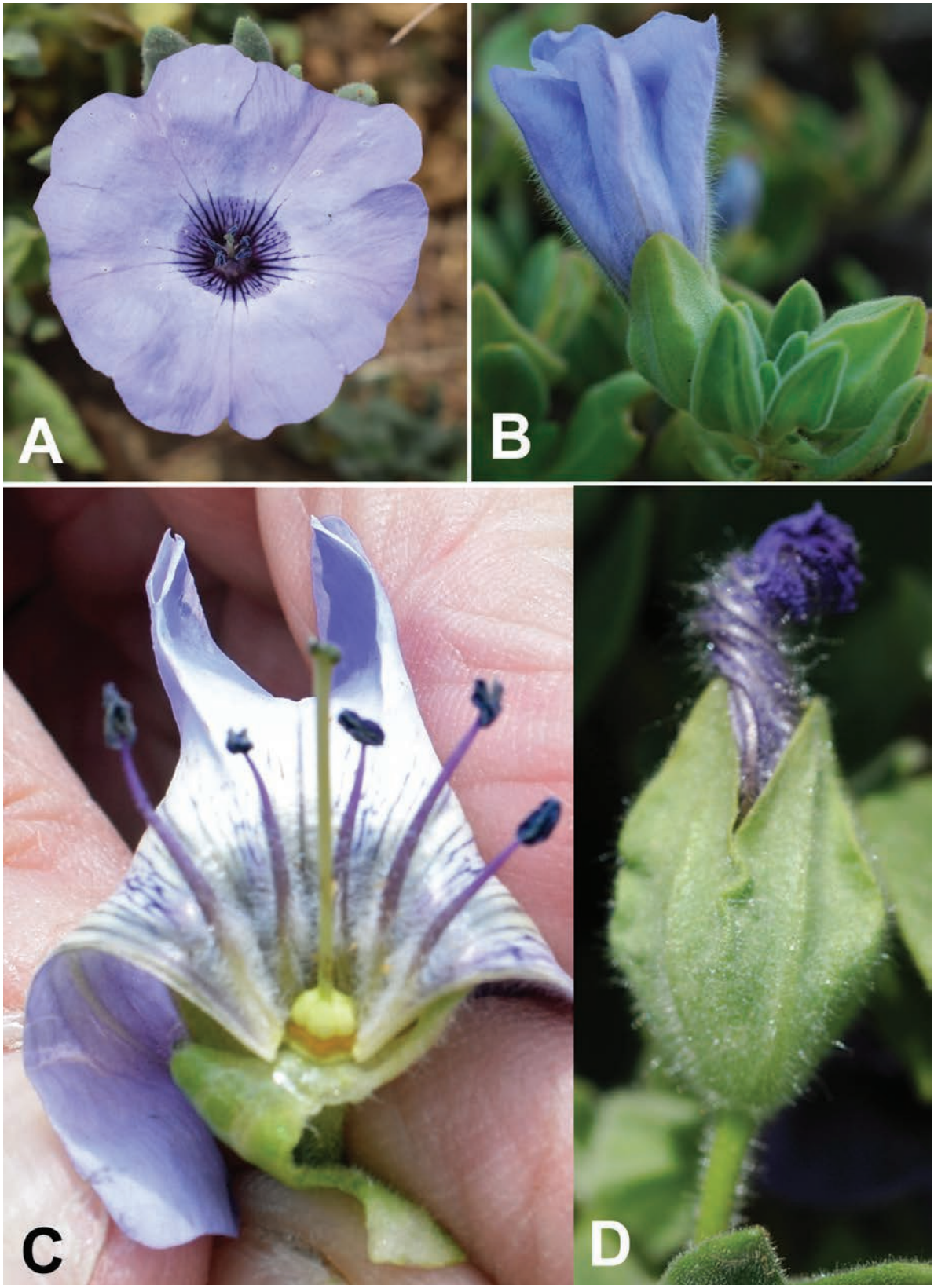


FIGURE 200. *Nolana aticoana*. **A**, Frontal views of corolla with dark purple guides and spot at base of throat; **B**, Connate calyx lobes; **C**, Dissected corolla with gynoecium on top of the orange nectary; **D**, Calyces covered with capitate-glandular trichomes.

Sprawling, perennial *herbs*, 20–75 cm tall; stems 4–10 mm in diam., villous with erect trichomes. *Leaves* alternate, blades lanceolate, rarely ovate-elliptic, 40–70 mm long, 15–30 mm wide, acute or obtuse, base attenuate, penninerved, midnerve prominent, densely pubescent with capitate-glandular trichomes, apically acuminate; petioles to 1 cm long or sessile. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 7–60 mm long, villous with capitate-glandular trichomes. *Flowers* 5-merous; calyces 15–26 mm long, 5–20 mm in diam., campanulate, hirsute, bilabiate, tube 7–14 mm long, lobes triangular 8–12 mm long, 3.8–10.0 mm wide, acute; corollas infundibularis, blue, 28–50 mm long, 25–60 mm wide, lobes inconspicuous, obtuse, tube short, densely pubescent-glandular inside, pubescent outside; stamens blue, unequal 2 larger 15–20 mm long, united to tube for 1/3 its length, 3 smaller 14–18 mm long, filaments villous. *Mericarps* 3–4, 1-seriate, rarely 4 larger and 1 small, inconspicuous, reniform, 5–11 mm long, 4–9 mm wide, black, shiny; seeds 5–10(–13) per mericarp. Chromosome number: not know

Etymology: The species epithet is the latinisation of the geographic locality of the type, Lomas of Atico in Province Caravelí, Department of Arequipa, Peru.

Distribution and Ecology: Peru, Department of Arequipa; (50–)200–600(–1900) m.a.s.l. (Fig. 198). It is frequent on rocky slopes and in areas that receive coastal fog.

Nolana aticoana is a robust, sprawling annual with showy flowers (Fig. 199A–B). It is distinguished by long pedicels, bilabiate calyces (Fig. 199B), and variable, elliptic leaves without pronounced petioles (Fig. 199C). The corollas are typically blue to purple with dark purple guides (Fig. 200A) and bilabiate calyces (Fig. 200B). The dissected corolla reveals the position and pubescence of the anther filaments and the gynoecium that sits on top of the orange nectary (Fig. 200C). The calyces, like the leaves, are covered with capitate-glandular trichomes (Fig. 200D). It has large, reniform mericarps that can reach ca. 10 mm in diameter, and as many as 13 seeds, as represented by pores on the face.

Nolana aticoana occurs sympatrically with *N. coronata* in the region of Atiquipa. Some plants have morphological variation in leaf shape and pubescence, which suggests putative interactions between these two species.

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, Quebrada El Toro, arriba de Camaná, 16°34'S, 72°37'W, 680 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8957* (F 2276709, HSP 005239, US 3512518). Prov. Caravelí: Lomas of Atico, ca. 8 km S of Atico along Pan-Americana Hwy, Km 706–707 S of Lima, 2 November 1983, *M. O. Dillon & D. Dillon 3838* (CONC, E, F 1950160, GH, K); ca. 11 km S of Atico, 16°16'S, 73°31'W, 50 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8202* (F 2198753); N de Atiquipa, Km 593, 15°49'S, 74°23'W, 270 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8806* (F 2276729, HSP 005126, US 3512465); N de Atiquipa, Km 593, 15°46'23"S, 74°20'57"W, 380 m.a.s.l., 14 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P 8811* (F 2276730, HSP 005127, US 3512464); Atiquipa, a 2 km E del Cementerio de la Comunidad de Atiquipa, 15°46'16"S, 70°50'24"W, 394 m.a.s.l., 14 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8816* (F 2276732, US 3512495); Chala, al S de Santa Rosa, 15°49'13"S, 74°20'17"W, 283–300 m.a.s.l., 14 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8873* (F 2276779, HSP 005175, US 3512498); al S de Chala, 15°52'S, 74°11'W, 230 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8876* (F 2276737, HSP 005178, US 3512501); entre Atico y Camana, 16°15'S, 73°32'W, 80 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8928* (F 2276703, HSP 005213, US 3512537); Lomas de Atiquipa, between Nazca and Chala, 250–300 m.a.s.l., 14 November 1949, *R. Ferreyra 6474* (US 1998716, USM 80829); Atiquipa, entre Nazca y Chala, 200–250 m.a.s.l., 13 November 1952, *R. Ferreyra 8903* (USM 80827); Lomas de Okopa [Ocopa] , cerca Atiquipa, 300–400 m.a.s.l., 11 October 1955, *R. Ferreyra 11483* (USM 80826); Lomas de Atico, entre Chala y Camaná, 50–100 m.a.s.l., 10 October 1956, *R. Ferreyra 11943* (K, USM 80825); Lomas de Atico, 100–150 m.a.s.l., 8 December 1956, *R. Ferreyra 12003* (USM 80831); Lomas de Atiquipa, Taimara, 500–600 m.a.s.l., 27 November 1958, *R. Ferreyra 13488* (USM 84701); Lomas entre Chala y Yauca, Km. 630, 200 m.a.s.l., March 1953, *J. P. Hjerting 1135* (USM 80828); coastal cliff of Atico between Chala and Camaná, 28 September 1985, *M. Ono et al.* (MAK 229686); Dist. Samuel Pastor, Quebrada El Toro, 16°36'39"S, 72°37'46"W, 400 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2893* (HUSA 4349); Atiquipa, entre Silaca y Ocopa, 15°49'06"S, 74°23'32"W, 203 m.a.s.l., 20 August 2006, *V. Quipuscoa S., M. Laura Q., & Y. Cano B. 3380* (HSP 000614); Silaca, Km 590 de la Panamericana Sur, 15°48'42"S, 74°23'48"W, 291 m.a.s.l., 19 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3559* (HSP 000690); Dist. Cháparra, Lomas de Cápac, 15°51'48"S, 74°11'30"W, 197 m.a.s.l., 20 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3587* (HSP 002525); ca. a Santa Rosa, 15°48'17"S, 74°21'53"W, 207 m.a.s.l., 27 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6633* (HSP 011447, HUT 60404); cerca la plaza de Atiquipa, 15°47'47"S, 74°21'52"W, 305 m.a.s.l., 28 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6636* (HSP 011449, HUT 60413); Dist. Atico, Panamericana Sur Km 716 al sur de Atico, 16°15'05"S, 73°31'06"W, 251 m.a.s.l., 2 December 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6802* (HSP 010545); Km 722 Panamericana Sur, 16°16'09"S, 73°30'13"W, 57 m.a.s.l., 3

December 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6854* (HSP 8830, HUT 60422); ca. al desvío a Atiquipa, 15°48'16"S, 74°22'01"W, 276 m.a.s.l., 30 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez, S. Huamani Q., & M. Bedoya C. 7658* (HSP 011364); Dist. Quicacha, arriba de Tierras Blancas, carretera a Sóndor, 15°36'11"S, 73°46'51"W, 1900 m.a.s.l., 3 May 2018, *V. Quipuscoa S., M. Balvin A., M. Bedoya C., & J. Muñuico M. 7823* (HSP 010546); Lomas de Atiquipa, Km 591 PanAmerican Sur, 150–750 m.a.s.l., 17 October 1997, *M. Weigend & H. Förther 97/923* (F 2211295).

F5. ***Nolana bombonensis*** Quip. & M.O. Dillon, Arnaldoa 25(2): 244. 2018. TYPE: PERU. Arequipa: Prov. Islay, Dist. Punta de Bombón, Lomas de Alto La Punta, 17°09'37"S, 71°46'36"W, 168 m, 31 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., M. Bedoya C., C. Sanz N., & M. Flores M. 6338* (Holotype: HSP [007821]; Isotypes: F [F 2322991], HUT [HUT 60419], USM [USM 301275]). Fig. 201–204.

Digital image: No image is currently available via the internet; the holotype image of *Nolana bombonensis* (Fig. 202) was provided by Herbario Sur Peruano, Arequipa [HSP 007821].

Sprawling, cinereous, suffrutescent *subshrubs*, to ca. 1.5 m in diam., 25–50 cm tall; stems intricately branched, prostrate to decumbent or spreading, stems to ca. 50 cm long, much-branched, densely lanuginous or arachnoid-tomentose. *Leaves* alternate, blades oblong, 5–8(–11) mm long, 1.0–2.5 mm wide, densely lanuginous pubescent, succulent, apically rounded, bases cuneate, margins revolute, abaxially canaliculate, sessile. *Inflorescences* of solitary flowers in upper leaf axils; pedicels cylindrical, densely pubescent, 2–7(–10) mm long. *Flowers* 5-merous; calyces narrowly campanulate, 3–4 mm wide at anthesis, densely lanuginous, 5-lobed, tube ca. 3 mm long, 3–5 mm in diam., lobes oblong-lanceolate, unequal, 4.0–5.5 mm long, 1.5–2.0 mm wide, apices obtuse or rounded; corollas zygomorphic, infundibuliform, 15–20 mm wide at anthesis, 15–20(–22) mm long, light lavender or lilac, throat clear, externally and internally glabrous, trichomes uniseriate; stamens 5, included, filaments inserted on lower third of corolla, unequal, 8–14 mm long, pilose at the bases; anther thecae purple, ca.1.2 mm long, ca. 1 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 1.2–1.5 mm wide, basal nectary ca. 1 mm wide, carpels 5, style included, (4–)7–11 mm long, stigma lateral, green, ca. 0.5 mm long. *Mericarps* 5, 1-seriate, polyhedrons, brown to black, rugose, 2.0–2.5 mm long, included within the expanding calyx; seeds 3–4 per mericarp. Chromosome number: unknown.

Etymology: The specific epithet is derived from the geographic area of Punta de Bombón, near the town of Cocachacra in the southern Department of Arequipa.

Distribution and Ecology: Peru, Department of Arequipa; 0–200 m.a.s.l. (Fig. 201). It is restricted to sandy sites, most commonly from near-ocean localities near sea level, and, if more inland, never above 200 m.a.s.l.

Nolana bombonensis is distinctive among its congeners in Peru with its dense mats with gray, arachnoid-tomentose pubescence and light lavender corollas. The spreading perennial, prostrate habit is evident along the beach south of Punta de Bombón (Fig. 203A-1, B); at that locality it is sympatric with several *Nolana* species, including *N. thinophila* (Fig. 203A-2). The corollas are a very light lavender with only faint guides, and dark purple anther thecae (Fig. 204A). Branches, leaves, and calyces all have densely lanuginous to arachnoid pubescence (Fig. 204B); there are invariably five mericarps with smooth surfaces (Fig. 204C).

This species is apparently an endemic restricted to a small, environmentally distinct habitat, and is sympatric at some localities with other *Nolana* species, such as *N. adansonii*, *N. pilosa*, *N. spathulata*, and *N. thinophila*. When this plant was first encountered in 2003, it was mistaken for *N. volcanica*, a species originally described from above Mollendo in the Lomas of Yuta (Quipuscoa et al., 2016). When detailed sampling more clearly defined the range of the phenotypic variation in *N. volcanica*, the population at Punta de Bombón was deemed distinct.

The growth form is not unique among *Nolana*, but the gray character of the dense arachnoid pubescence is not common in Peruvian species. There are pubescent taxa found in Chile with curly trichomes, including *Nolana diffusa*, *N. tocopillensis*, and *N. sedifolia*; these species are very different in their floral and vegetative morphology and have no close relationship with any Peruvian species (Dillon et al., 2009).

Nolana bombonensis was initially confused with *Nolana volcanica,* the latter species was based upon a collection by Ms. Dora B. Stafford (holotype: K000532281) from a locality ca. 40 km north of the Río Tambo (Ferreyra, 1960). That collection was from the quebrada above Mollendo at ca. 600 m.a.s.l. from habitats of "sand and volcanic ash" in the Lomas of Yuta. Collections of *N. volcanica* throughout its range and over a period of years revealed that the density of the pubescence is variable. The floral morphology and corolla coloration pattern in *Nolana volcanica* is significantly different from *N. bombonensis*. In contrast to *N. bombonensis*, *N. volcanica* is a spreading perennial that appears green; the flowers have attenuate calyx lobes and shorter, pale blue corollas with a dark purple band and nectar guides within the throat.

Additional specimens examined: PERU. **Arequipa**: Prov. Islay, Punta de Bombón, Carretera Costanera, ca. 10 km S de Punta de Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8989* (F 2276597, GH, HSP 005261, HUSA, US 3512521); Punta de Bombón, Carretera Costanera, ca. 10 km S de Punta de Bombón, 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz, M. Zapata C., M. Corrales M., & G. Castillo P. 8995* (F 2276603, HSP 005265, HUSA, US 3514028); ca. Km 153 carretera Punta de Bombón–Ilo, 17°11'58"S, 71°42'09"W, 7

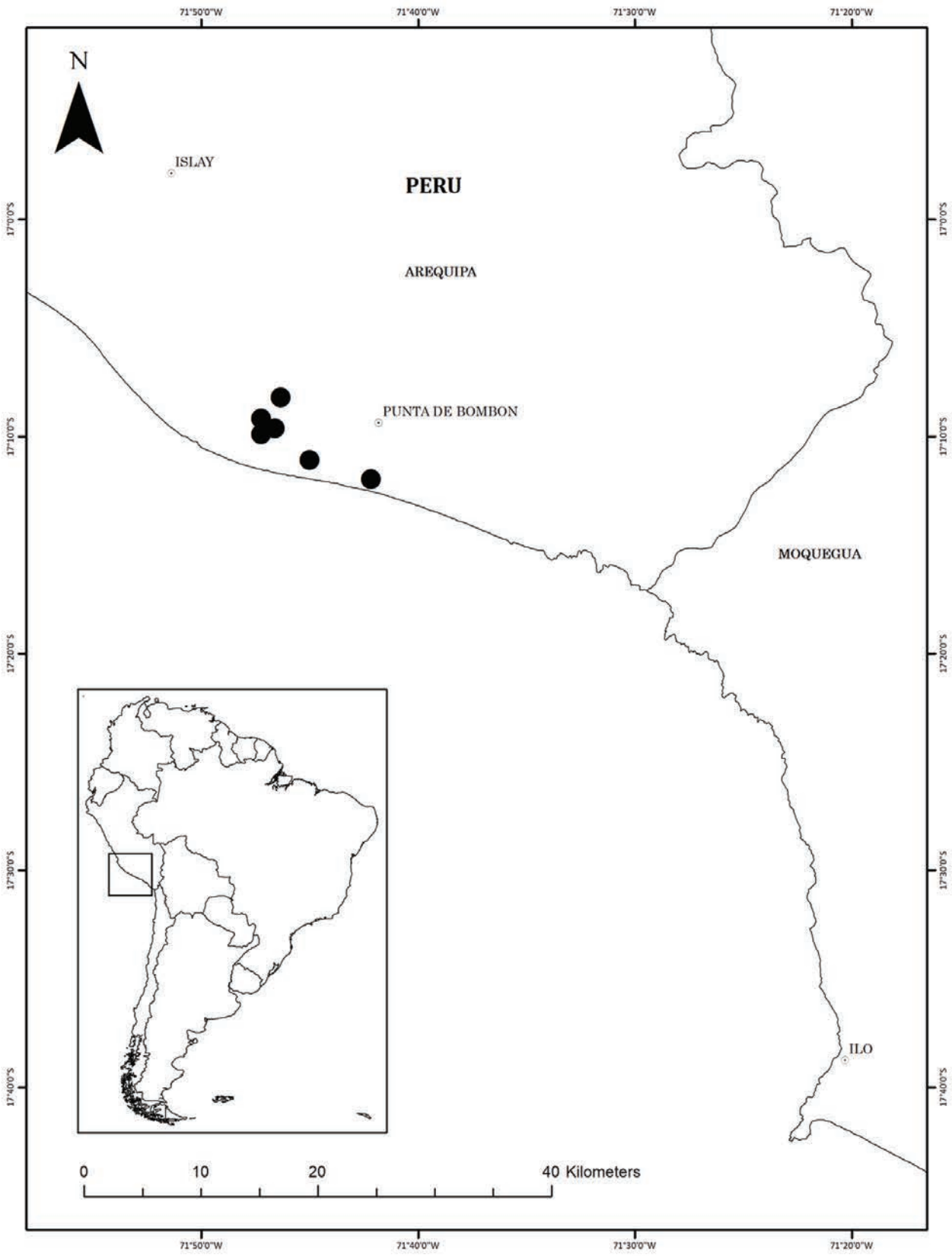


FIGURE 201. Distribution of *Nolana bombonensis* Quip. & M.O. Dillon.

FIGURE 202. Holotype of *Nolana bombonensis* housed at HSP. No digital image is available via the internet.

FIGURE 203. *Nolana* recorded from the beaches at Punta de Bombón, Peru. **A1**, *N. bombonensis* and **A2**, *N. pilosa*; **B,** Individual of *N. bombonensis* growing in sand near the ocean with Massiel Nataly Corrales Medina. Photographs by Victor Quipuscoa Silvestre.

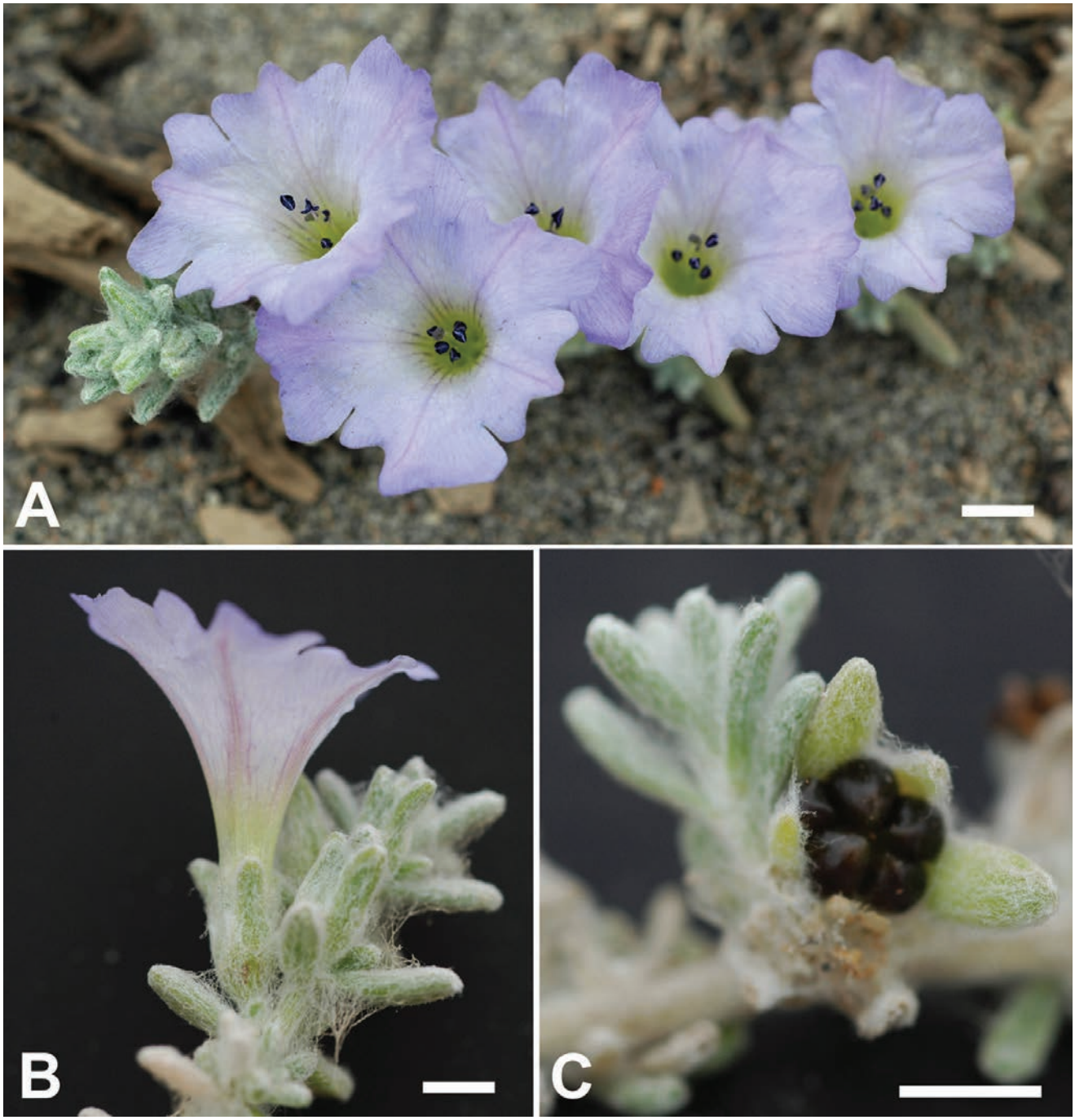


FIGURE 204. *Nolana bombonensis*. **A**, Flowering branch, scale bar = 5 mm (*Dillon et al. 8989*); **B**, Flowering stem with corolla, scale bar = 8 mm; **C**, Mericarps, scale bar = 5 mm.

m.a.s.l., 28 October 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6226* (HSP 011301, HUT 60403); Dist. Punta de Bombón, ca. Km 157 carretera costañera Punta de Bombón–Ilo, 17°12'41"S, 71°40'22"W, 7 m.a.s.l., 28 October 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & M. Bedoya C. 6229* (HSP 10547); Dist. Punta de Bombón, Lomas de Alto La Punta, 17°09'39"S, 71°46'36"W, 168 m.a.s.l., 31 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., M. Bedoya C., C. Sanz N., & M. Flores M. 6335* (HSP 011345, HUT 60410); ca. 200 m al S de La Pampilla, 17°09'10"S, 71°47'13"W, 50 m.a.s.l., 13 January 2018, *V. Quipuscoa S. & M. Balvin A. 6861* (HSP 12038); Alto La Punta, 17°09'53"S, 71°47'01"W, 122 m.a.s.l., 13 January 2018, *V. Quipuscoa S. & M. Balvin A. 6863* (HSP 12040).

F6. ***Nolana callae*** Quip. & M.O. Dillon, Arnaldoa 25(2): 246. 2018. TYPE: PERU. Arequipa: Prov. Islay, Dist. Punta de Bombón, Lomas de Jesús, ca. Km 172 carretera costanera, entre Corío y Yerba Buena, 17°14'39"S, 71°32'47"W, 265 m, 06 enero 2018, *V. Quipuscoa S., M. O. Dillon, & C. Tejada P. 6857* (Holotype, HSP [007823]; Isotypes, F [F 2322992], HSP [HSP 007824], HUT [HUT 60420], USM [USM 301277]). Fig. 205–206.

Digital image: Isotype of *Nolana callae* from Herbarium Sur Peruana, Arequipa [HSP 007823]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.hsp010

Suffruticose *perennials*, 0.7–1.2 m in diam.; stems decumbent to repent, much-branched, lanuginose to glabrescent, young branches greenish-purple, pubescence of non-glandular trichomes. *Leaves* alternate, blades elliptic to lanceolate, 15–30(–40) mm long, 5–12(–15) mm wide, sericeous, succulent, apically acute, basally attenuate, slightly revolute; petioles 3–7(–10) mm long, basally swollen, 2–4 mm wide, sclerified, slightly ribbed. *Inflorescences* of solitary flowers in upper leaf axles; pedicels 5–30(–35) mm long, lanuginous. *Flowers* 5-merous; calyx campanulate 4–7(–8) mm wide, densely lanuginous, 5-lobed, tube 1.5–2.0 mm long, 3–5 mm in diam., lobes narrowly deltoid to linear, unequal, 5–10 (–12) mm long, 1.0–2.5(–3.0) mm wide, apices acute to obtuse; corollas zygomorphic, infundibuliform, 15–23 mm wide at anthesis, 17–23(–25) mm long, lavender, inner throat purple, externally and internally glabrous; stamens 5, included, filaments 11–15(–17) mm long, 2 long, 3 short, bases pilose; anther thecae purple, 2.0–2.5 mm long, ca. 1 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 1.2–1.5 mm wide; nectary basal, orange, ca. 1 mm wide, carpels 5, styles included, 6–9 mm long, stigma lateral, green, ca. 0.5 mm long. *Mericarps* 5, 1-seriate, polyhedrons, black, lightly rugose to smooth, 4–3 mm long, 2–3 mm in diam., equal, included within maturing calyx; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The specific epithet is in honor of Abraham Calla Paredes, Professor of Botany at the National University of San Agustin de Arequipa for, for his dedication to the teaching of algae and for our shared friendship for many years.

Distribution and Ecology: Peru, Department of Arequipa; 100–900 m.a.s.l. (Fig. 205). It is restricted to dry, rocky slopes at the lower part of the Lomas de Jesus, recorded from the type locality, along with *Nolana adansonii*, *N. bombonensis*, and *N. spathulata*. It was discovered in disturbed roadside localities and likely, with continued exploration, it is anticipated that the distribution may be extended upslope.

Nolana callae is a low shrublet that has a narrow distribution (Fig. 206A). The light purple corollas with dark purple guides are not unlike other species in southern Peru (Fig. 206B). The mericarps are shiny and there are invariably five (Fig. 206C). It resembles *N. cerrateana*, a species from farther north near Camaná, Arequipa, and it also shares similarities with *N. intonsa* from northern Chile. These species also have a prominent dark band in the throat and nectar guides in the corolla.

This species was included in the molecular studies under the name *N. volcanica* (*Quipuscoa et al. 2930*), and its relationships were with other southern Peruvian species. Utilizing a variety of DNA markers, *N. volcanica* was recovered with congeners, and GBSSI sequences (Dillon et al., 2007c) found *N. lycioides* to be its sister taxon; LEAFY second intron marker (Tu et al., 2008) recovered it in a clade with *N. cerrateana*, *N. intonsa* (Chile), and *N. lycioides*. A variety of chloroplast markers recovered it in an unresolved clade with over a dozen other species from Arequipa (Dillon et al., 2009). It is morphologically similar to *N. cerrateana*, sharing habit and lanuginous leaves; however, *N. cerrateana* has longer pedicels (to ca. 50 mm long), more fasciculate leaves, calyces with purple coloration, and 10–14 mericarps.

Additional specimens examined: PERU. **Arequipa**: Prov. Islay, Dist. Punta de Bombón. Punta de Bombón, 17°15'S, 71°33'W, 27 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2930* (HSP 000600, HUSA); Punta de Bombón, 17°15'S, 71°33'W, 27 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2933* (F 2330874, HSP 000603, HUSA 4114); Dist. Punta de Bombón, Lomas de Jesús, 17°14'41"S, 71°32'46"W, 267 m.a.s.l., 29 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6309* (HSP 12023, F 2325077); Dist. Punta de Bombón, ca. Km 170 carretera costañera Punta de Bombón–Ilo, 17°14'42"S, 71°32'46"W, 119 m.a.s.l., 28 October 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & M. Bedoya C. 6255* (HSP 10548); Lomas de Jesús, 17°14'50"S, 71°32'43"W, 6 January 2018, *V. Quipuscoa S., M. O. Dillon, & C. Tejada P. 6859* (F 2330855, HSP 12036); Quebrada de Yuta, 16°56'47"S, 72°04'22"W, 858 m.a.s.l., 13 January 2018, *V. Quipuscoa S. & M. Balvin A. 6860* (HSP 12037).

F7. ***Nolana cerrateana*** Ferreyra, Publ. Mus. Nat. Hist. Ser. B. 10: 11. 1955. TYPE: PERU. Arequipa: Prov. Camaná, entre Camaná y Arequipa, Km 161–162, 450–500 m, 10 November 1947, *R. Ferreyra 2558* (Holotype: USM [242130, USM000557]; Isotypes: G [G00383955], GH [GH00282352, GH00282354], K [K000532265], MOL [MOL 00548, MOL0004732], UC [UC 042490, UC104 2498], US [US 1998579, US00121957]). Fig. 207–210.

Digital image: Holotype of *Nolana cerrateana* from Herbario San Marcos, Lima [USM 242130]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000557

Homotypic synonym: *Nolana crassulifolia* Poepp. subsp. *revoluta* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 94. 1981.

Suffrutescent *shrubs*, decumbent, much-branched, branches ascending, 6.5–14.0 cm long, lanuginous, flexulose. *Leaves* alternate to fasciculate, blades lanceolate, 11–26 mm long, 2.0–5.5 mm wide, apically acute, basally attenuate, densely villous, margins revolute, subsessile. *Inflorescences* of solitary flowers, terminal and axillary; pedicel conspicuous, 20–50 mm long, ascending, pubescent. *Flowers* 5-merous; calyces 9–15 mm long, 6–10 mm wide, globose to campanulate, pubescent outside, lanuginous, tube 3–7 mm long with purplish striations, lobes 5, 4–7(–10) mm

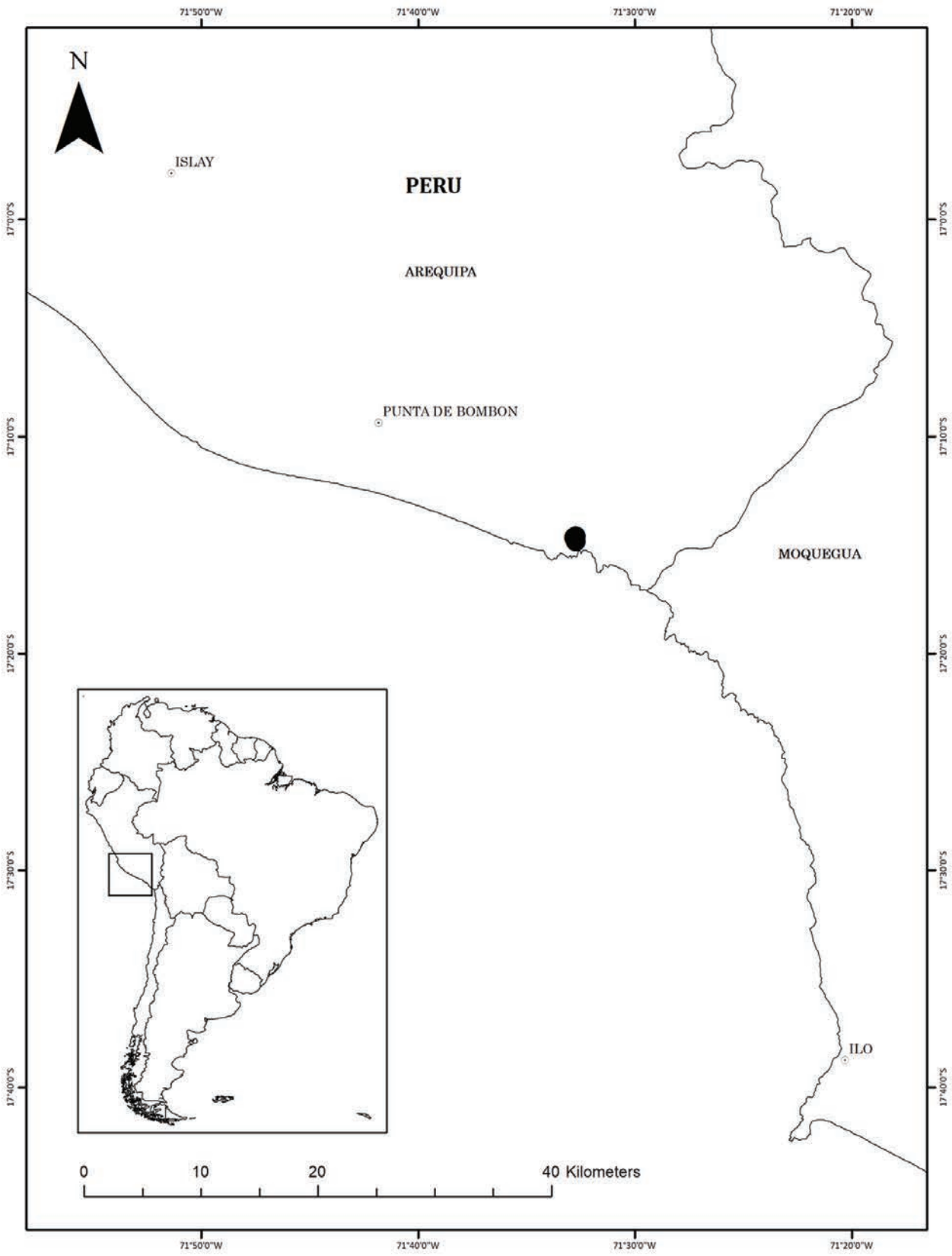


FIGURE 205. Distribution of *Nolana callae* Quip. & M.O. Dillon.

FIGURE 206. *Nolana callae*. **A**, Flowering individual with Cristian Tejeda-Perez; **B**, Corollas, scale bar = 5 mm; **C**, Mericarps, scale bar = 10 mm (*Quipuscoa et al. 6857*).

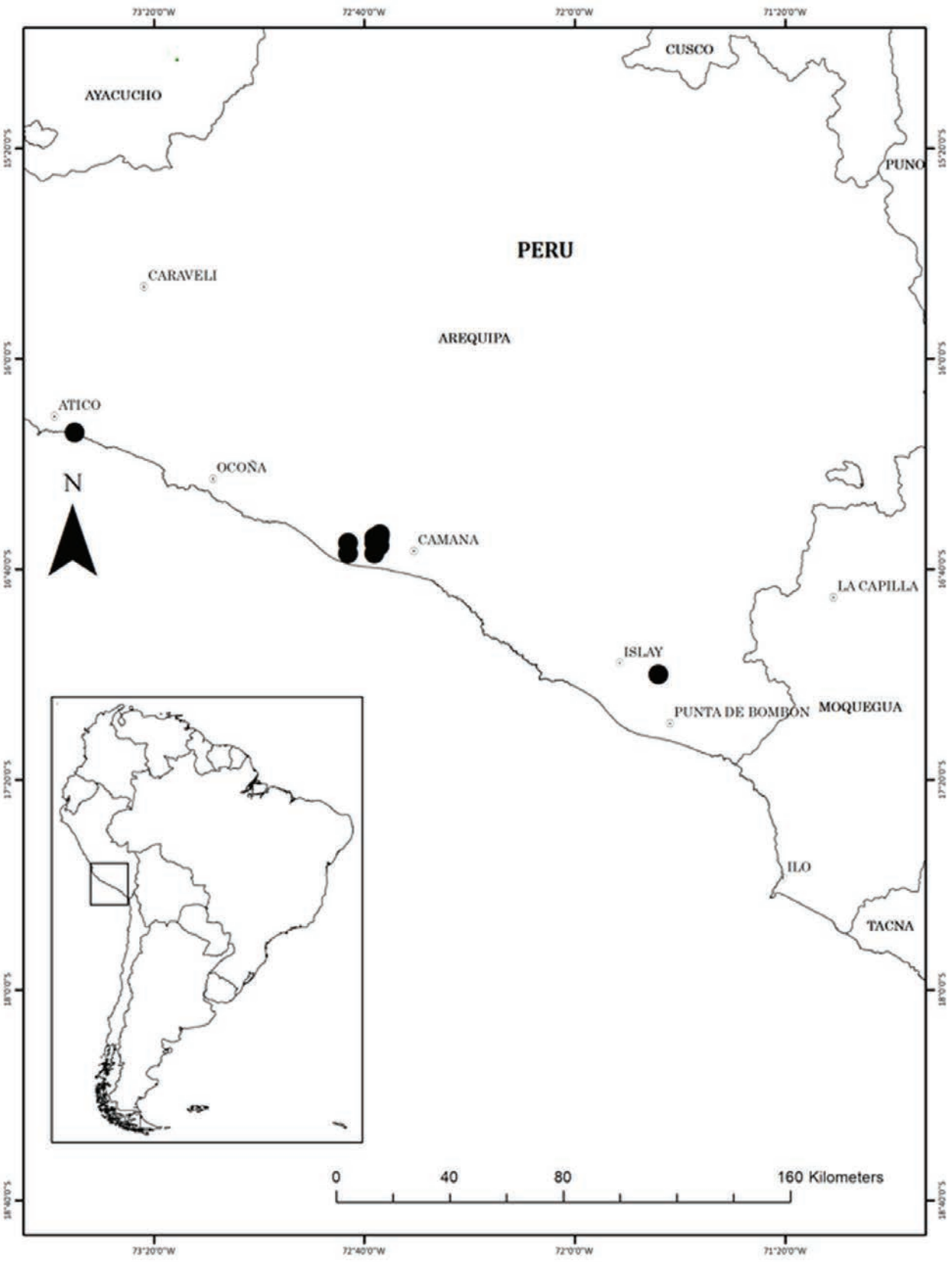


FIGURE 207. Distribution of *Nolana cerrateana* Ferreyra.

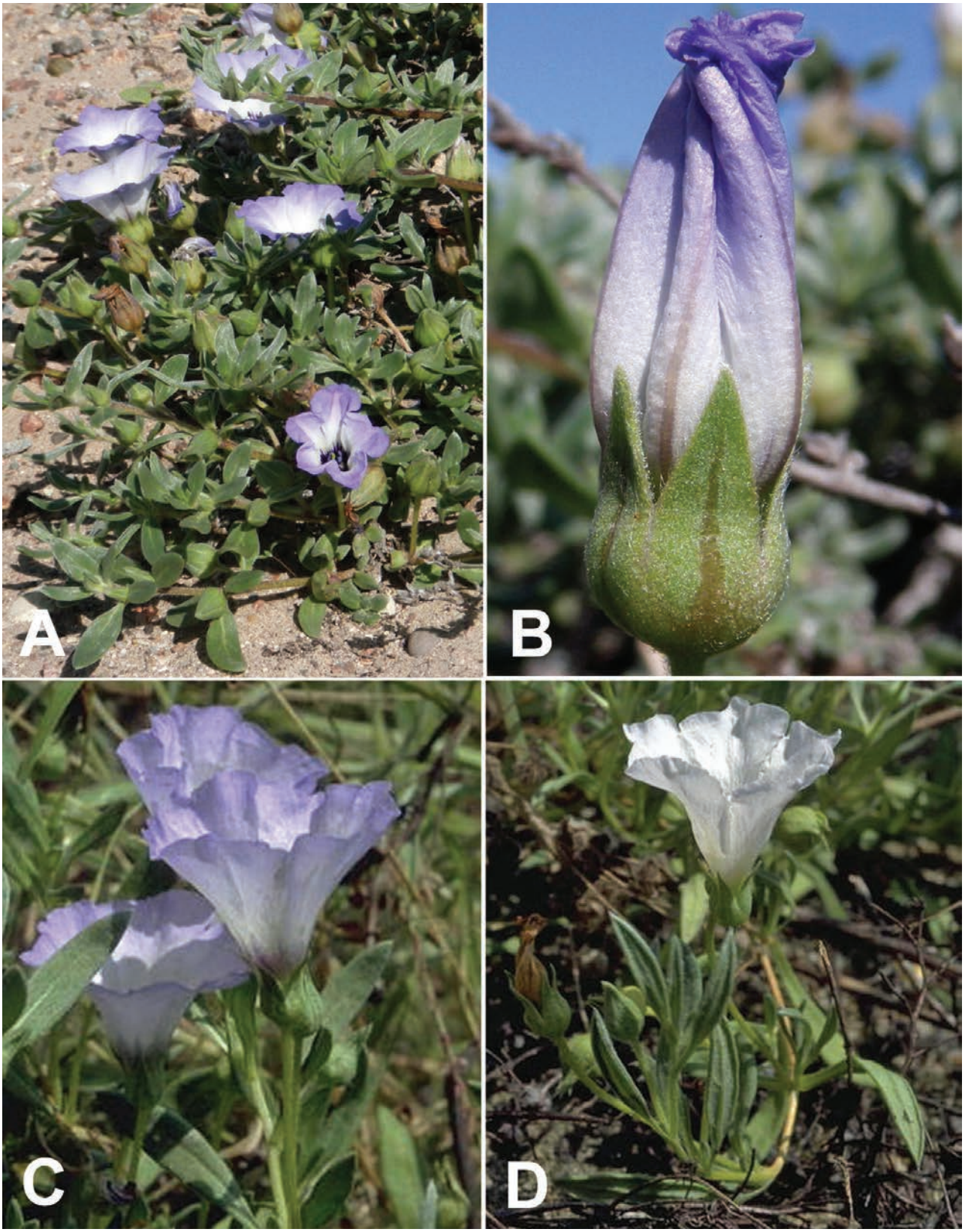


FIGURE 208. *Nolana cerrateana*. **A,** Much-branched low perennials; **B**, Lateral view of flower with globose to campanulate calyces, note purple striations at each lobe; **C**, Corolla violet to lavender; **D,** Corolla white. Photographs by Maxim S. Nuraliev.

FIGURE 209. *Nolana cerrateana*. **A–B**, Corollas with a dark band and purple guides in the throat; **C**, Closeup of the throat and blue anther thecae, green capitate style in the center. Photographs by Maxim S. Nuraliev.

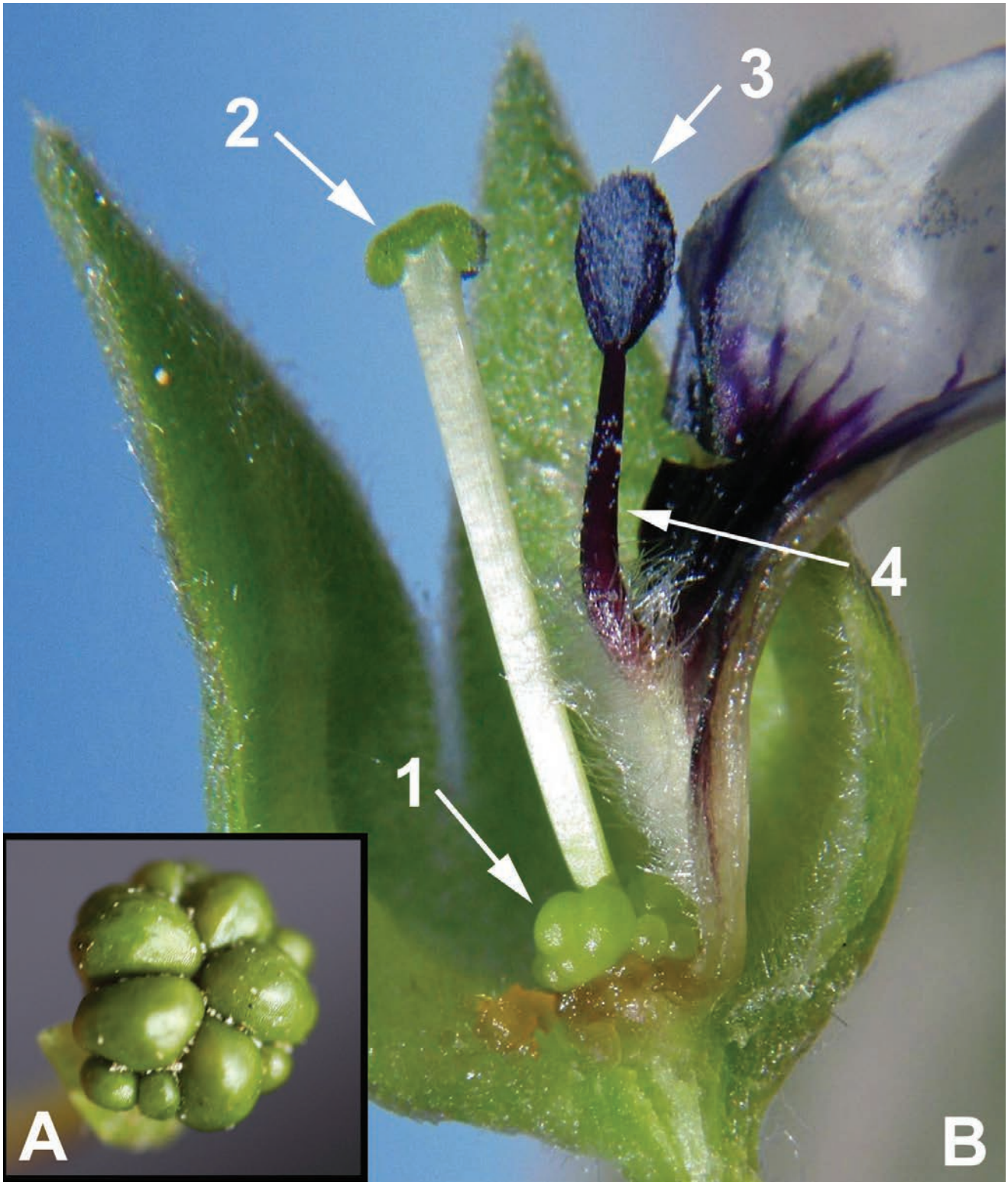


FIGURE 210. *Nolana cerrateana*. **A**, Major mericarps connate, surrounded by as many as ten minor mericarps; **B1**, Flower dissection with gynoecium; **B2**, Green, bilobed stigma; **B3**, Blue anther thecae; **B4**, Densely pubescent anther filaments. Photographs by Maxim S. Nuraliev.

long, 1.8–3.5 mm wide, acuminate; corolla infundibularis, violet to lavender, prominent dark band and nectar guides in the lighter throat, 17–24 mm long, 12–20 mm wide at mouth, 5-lobed, lobes inconspicuous, rounded; stamens unequal, 2 larger 11–14 mm long, 3 smaller 9–11 mm long; pollen blue; nectary 6.0–6.5 mm in diam., style 7.0–8.5 mm long; gynobasic. *Mericarps* 10–14, 2-seriate, reniform, five 3.5–4.8 mm long, 3.0–3.5 mm wide, 5–9 outer series 2.8–3.0 mm long, 1.8–2.0 mm wide; seeds 5–6 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dra. Emma Cerrate Valenzuela (b. 1920–d. 2016), a botanist, curator, and "Professora" in biological sciences at the Universidad Nacional Mayor de San Marcos. Between 1985 and 1988, she was Directora of the Herbario San Marcos (USM) and the Museo de Historia Natural "Javier Prado".

Distribution and Ecology: Peru, Department of Arequipa; (50–)400–980(–1000) m.a.s.l. (Fig. 207). A collection from Atico expands the range ca. 100 km to the north, and a collection from the Lomas de Quilca, ca. 20 km to the southeast. It is most frequently recorded from sandy, alluvial soils.

Nolana cerrateana is a low, much-branched shrublet distinguished by its strongly revolute, villous leaves (Fig. 208A) and flowers with globose to campanulate calyces to one centimeter wide and with purple striations at each lobe (Fig. 208B). Corollas vary from violet to lavender on pedicels up to 50 mm long (Fig. 208C), or the corollas can be nearly white (Fig. 208D). Regardless of color, the corollas have a lighter throat and a prominent dark band and purple guides in the proximal portion of the corolla (Fig. 209A–C). Five major mericarps are surrounded by as many as 10 minor mericarps (Fig. 210A). The dissection in Figure 210B illustrates the position of the gynoecium (Fig. 210B-1) in relation to the densely pubescent anther filaments (Fig. 210B-4). The style (Fig. 210B-2) is in proximity of the anther thecae (Fig. 210B-3).

It was concluded from molecular studies that *Nolana cerrateana* is related to other southern Peruvian taxa; however, it was not well-resolved (Dillon et al., 2007c; Tu et al., 2008). In Dillon et al. (2009), various clones from *Quipuscoa et al. 2890* are recovered with different taxa, including *N. aticoana*, *N. johnstonii*, *N. intonsa,* and *N. pallida*.

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, Lomas of Camaná, ca. 32 km SE of Camaná, ca. 1000 m.a.s.l., 5 November 1983, *M. O. Dillon & D. Dillon 3862* (CONC, E, F 1950507, GH, K, USM); ca. 13 km S of Camaná on road to interior, 16°37'S, 72°38'W, 200 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8210* (F 2198771); ca. 16 km S of Camaná on road to interior, 16°35'S, 72°38'W, 400 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8212* (E, F 2198756, GH); ca. 18 km S of Camaná on road to interior, 16°34'S, 72°38'W, 400 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8215* (F 2198758, GH); Lomas of Camaná, ca. 18 km S of Camaná on road to interior, 16°34'S, 72°38'W, 400 m.a.s.l., 22 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8217* (CONC, E, F 2198760, GH, SGO); a 3 km del Peaje de Camaná, Quebrada El Toro, 16°35'S, 72°38'W, 430 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8949* (F 2276708, HSP 005234, US 3512542); Quebrada El Toro, 16°34'S, 72°37'W, 680 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8961* (F 2276710, GH, HSP 005242, US 3512519); Lomas de Camaná, 600–700 m.a.s.l., 13 November 1949, *R. Ferreyra 6439* (USM 80835); Lomas de Camaná, Km 169–170, 180–200 m.a.s.l., 10 November 1952, *R. Ferreyra 8826* (USM 80838); Lomas de Camaná, 500–600 m.a.s.l., 10 November 1952, *R. Ferreyra 8857* (USM 80837); Lomas de Camaná, 700–750 m.a.s.l., 7 October 1957, *R. Ferreyra 12635* (USM 80839); Quebrada del Toro, 16°35'31"S, 72°37'49"W, 442 m.a.s.l., 18 July 2014, *A. Pauca T. 396* (HSP 003046); Quebrada del Toro, 16°32'58"S, 72°36'22"W, 980 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2879* (HSP 000328); Quebrada del Toro, 16°32'58"S, 72°36'22"W, 980 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2881* (HSP 000330), Quebrada del Toro, 16°32'58"S, 72°36'22"W, 980 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2883* (HSP 000332); Quebrada del Toro, 16°32'58"S, 72°36'22"W, 980 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2886* (HSP 000334, HUSA 4346); Dist. Quilca, Quebrada del Toro, 16°32'58"S, 72°36'22"W, 980 m.a.s.l., 18 September 2003, *V. Quipuscoa S. 2890* (HSP 000335); Dist. Samuel Pastor, Quebrada de El Toro, 16°35'30"S, 72°37'52"W, 432 m.a.s.l., 16 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3483* (HSP 000647); Quebrada de El Toro, 16°35'30"S, 72°37'52"W, 432 m.a.s.l., 16 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3488* (HSP 000648); Dist. Quilca, Lomas de Quilca, ca. Km 871 carretera Panamericana, 16°34'17"S, 72°33'21"W, 981 m.a.s.l., 5 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6527* (HSP 10557); Dist. Samuel Pastor, ca. Km 866 Panamericana Sur, Quebrada el Toro, 16°33'19"S, 72°36'58"W, 752 m.a.s.l., 5 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6542* (HSP 8792); Quebrada del Toro, Km 82 Panamericana Sur, 16°35'02"S, 72°37'43"W, 458 m.a.s.l., 4 May 2018, *V. Quipuscoa S., M. Balvin A., M. Bedoya C. & J. Muñuico M. 7865* (HSP 011924, HUT 60400); Lomas de Atico, 50–100 m.a.s.l., 21 November 1961, *O. Tovar 3471* (USM 80836); Lomas de Camaná, 600 m.a.s.l., 31 July 1940, *C. Vargas C. 2000* (CUZ 21403, GH); Lomas de Camaná, 600–700 m.a.s.l., 30 October 1966, *C. Vargas C. 18151* (CUZ 21404).

F8. ***Nolana confinis*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 78. 1936. Fig. 211–214.

Basionym: *Bargemontia confinis* I.M. Johnst., Contrib. Gray Herb. 85: 176. 1929. TYPE: PERU. Tacna: Candarave, 2900–3000 m, 11–13 March 1925, *A. Weberbauer 7382* (Holotype: GH [00282375]; Isotypes: F [F 552612, FM neg. 56676], G [G00383962, G00383965], HG [GH00282376], K [K000532279], S [S04 2769], US [US 1474542, US00121970]).

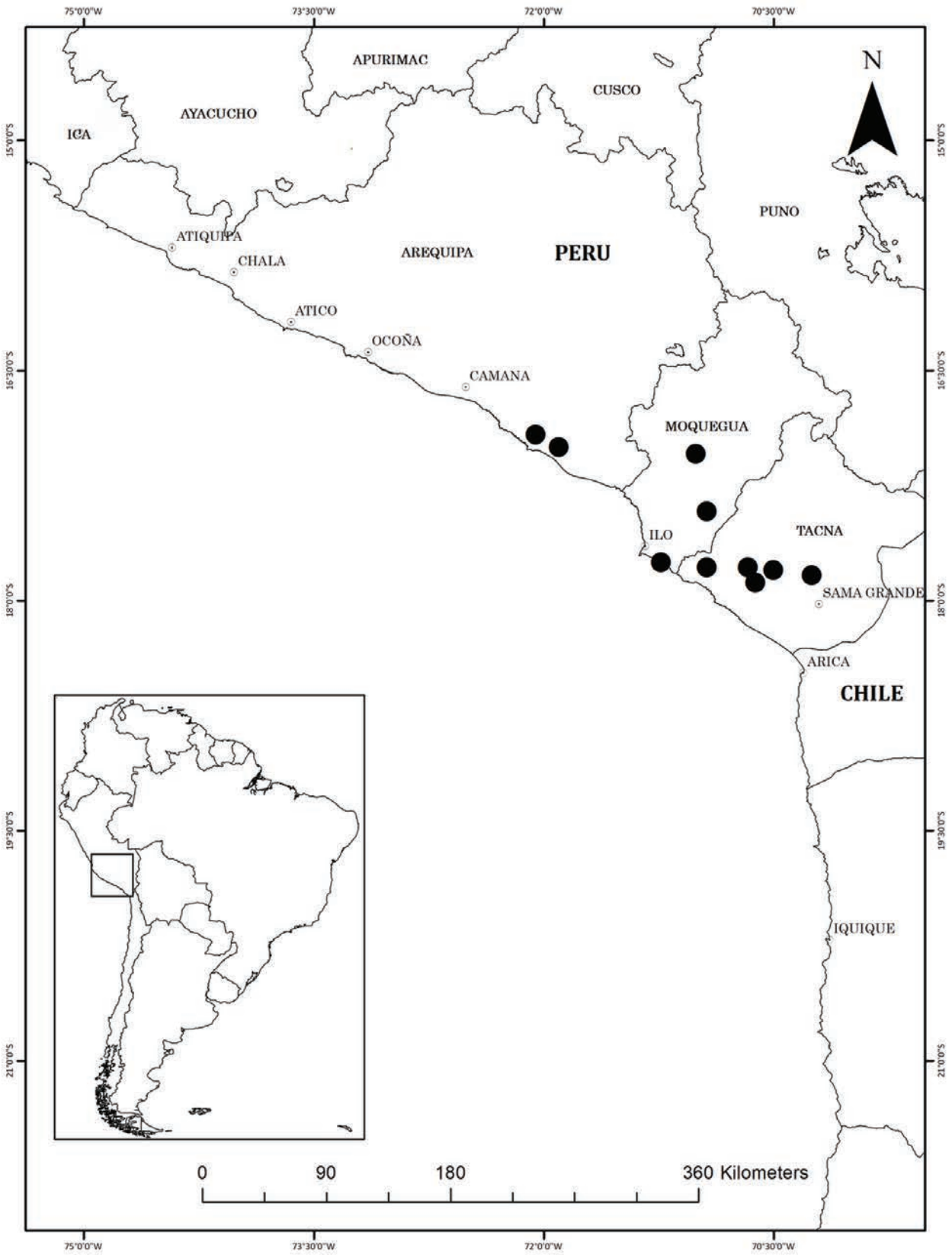


FIGURE 211. Distribution of *Nolana confinis* I.M. Johnst.

Digital image: Holotype of *Bargemontia confinis* from Harvard University Herbaria, Cambridge [GH00 282375]. https://s3.amazonaws.com/huhwebimages/0ADAAE891FB7485/type/full/282375.jpg

Homotypic synonym: *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *confinis* Mesa, Fl. Neotrop. Monogr. 26: 103. 1981.

Rounded, perennial *herbs* or *subshrubs*, 35–50 cm tall; roots to ca. 32 cm long, 5–15 mm in diam.; stems procumbent, flexulose, to 4 mm in diam., conspicuously branched, lanuginous or rarely glabrescent. *Leaves* fasciculate, blades obscurely spathulate, sessile, semisucculent, scarcely pubescent with elongate curly trichomes, 6–14 mm long, 1.6–1.8 mm wide, acute to obtuse, margins revolute, uninerved. *Inflorescences* of solitary flowers, terminal and axillary, and occasionally appearing spicate; pedicels 3–13 mm long, more or less lanuginous. *Flowers* 5-merous; calyces 3.0–3.5(–4.0) mm long, 2.5–3.5 mm in diam., campanulate, glandulose-glabrescent outside, glabrous inside, tube 0.5–1.0 mm long, 1.8–2.0 mm in diam., lobes equal, 2.5–3.0 mm long, 1–2 mm wide, margins pilose, acuminate; corollas infundibularis, blue, dark purple band in the throat, 10–13 mm long, 7.0–9.0(–10.2) mm wide, unequally lobed, ciliolate, ovate-triangulate, obtuse, glabrous, tube lanuginous outside, inconspicuously villous inside; stamens unequal, three larger 6.5–10.0 mm long, united to tube for 1/3 to 1/4 its length; anthers blue; style 6.2–9.0 mm long. *Mericarps* 4–5, rarely 6, globose to reniform, 1-seriate, unequal, larger, 2.5–3.5 mm long, 1.8–2.0 mm wide, , 1.6–2.0 mm long, 1.2–1.5 mm wide, black, rugose, shiny; seeds 2–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *confinis*, bordering on, adjoining, but the reference to this species is obscure.

Distribution and Ecology: Peru, Departments of Moquegua and Tacna; (500–)900–3000 m.a.s.l. (Fig. 211). It is recorded from sandy/rocky soils, at some distance from the coast. The type locality is at 3000 m.a.s.l. and well outside of the influence of coastal fog.

Nolana confinis is a woody shrub with a variable habit, more erect in upper elevation habitats (Fig. 212A–D), such as those at the type locality well above 2000 m.a.s.l. The flowers are lavender to blue with a dark purple band in the throat, that is common to Peruvian taxa (Fig. 213A). The stems are covered by sparce arachnoid pubescence, as are the leaves that are from 6–14 mm long, but never over 2 mm wide (Fig. 213B). As in many *Nolana* species, the fruits and pedicels nod downward at maturity (Fig. 213C). At elevations below 500 m.a.s.l. and much nearer coastal fog, it takes on a low spreading habit (Fig. 214A–C).

The origins of the populations at lower elevations, closer to the coast, appear to have been derived from upslope populations. The type is described from the uppermost populations at 3000 m.a.s.l. and over 100 km distant from the coastal populations at under 500 m.a.s.l. Before recognizing the population above Ilo as distinct, it is best to await additional data. *Nolana confinis*, as suggested by available marker data, is related to *N. johnstonii* (Dillon et al., 2007c). Further sampling and analysis are needed to clarify the relationships of this species.

Additional specimens examined: PERU. **Moquegua**: Prov. Ilo, Lomas of Ilo, 260–460 m.a.s.l., 18 October 1983, *M. O. Dillon & D. Dillon 3656* (E, F 1950179, GH), flowers white, *3657* (F 1950178); N of Ilo, ca. 1 mile inland, [100 ft], 23 September 1937, *D. B. Stafford 912* (BM000941274, K); Ilo, Lomas de Mostacilla, 400–800 m.a.s.l., 28 October 1966, *C. Vargas C. 17982* (CUZ 21407). **Tacna**: Prov. Candarave, Dist. Curibaya, ca. 7 km Suroeste de la laguna Aricota, carretera hacia Candarave, 17°23'20"S, 70°20'23"W, 2328 m.a.s.l, 20 November 2021, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., & J. Muñuico M. 8033* (F 2330853); Prov. Locumba, Lomas de Sama, 300 m.a.s.l., 15 October 1976, *C. Vargas C. 22886* (CUZ 21412). Prov. Tacna, ca. 21 km SE of Moquegua/Tacna border, 850–900 m.a.s.l., 16 February 1983, *M. O. Dillon, P. Matekaitis, & L. Wantanbe 3383* (F 1919546, US 3470031); Lomas of Tacna, 20 October 1983, *M. O. Dillon & D. Dillon 3693* (E, F 1950174, GH, USM); Lomas of Tacna, 530–620 m.a.s.l., 20 October 1983, *M. O. Dillon & D. Dillon 3677* (E, F 1950175, GH, K); Lomas of Tacna, ca. 45 km N of Tacna, ca. 620 m.a.s.l., 9 November 1983, *M. O. Dillon & D. Dillon 3899* (CONC, E, F 1950504, GH, K, USM); 29–32 km WNW of Tacna, Pampa de Sama, 550–630 m.a.s.l., 14 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4778* (CONC, E, F 2014376, GH, HUT 22758, K, US, USM); ca. 99 km SE of Moquegua, road E to Shintari, 17°47'S, 70°40'W, 810 m.a.s.l., 27 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8236* (F 2199335, F 2199337); Lomas de Sama, ca. 50 km N de Tacna, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11654* (GH, USM); Lomas de Sama Grande, 500–600 m.a.s.l., 4 October 1957, *R. Ferreyra 12499* (K, USM); 25 km N de Tacna, 500–600 m.a.s.l., 6 October 1957, *R. Ferreyra 12530* (USM); 60 km N de Tacna, 700 m.a.s.l., 7 October 1957, *R. Ferreyra 12644* (USM); Lomas de Sama, 50 km al N. Tacna, 500–600 m.a.s.l., 1 December 1955, *R. Ferreyra 11652a* (USM); cerca de Puquio-Tacna, 800 m.a.s.l., 30 April 1983, *R. Ferreyra et al. 8604* (USM); Lomas de Sama Grande, 500–600 m.a.s.l., 4 October 1957, *R. Ferreyra 12499* (K [2 sheets]); Lomas de Sama Grande, 500–600 m.a.s.l., 4 October 1957, *R. Ferreyra 12506* (USM); 10 km N of Tamasiri, Lomas de Sama, 200 m.a.s.l., 25 November 1957, *P. C. Hutchison 1845* (F 1555877, GH, K, US 2406446, USM); ca. 25 km S of Camiara, 630 m.a.s.l., 26 November 1964, *P. C. Hutchison & J. K. Wright 7150* (F 1641533, K, US 2502849, USM); Tacna, September 1864, *R. Pearce s.n.* (BM000941352, K [2 sheets]); Dist. Inclán, Sama Grande, 17°47'43"S, 70°38'06"W, 574 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3414* (HSP 002667); 10 km S of Camiara, 70 km N of Tacna, 500 m.a.s.l., 13 April 1973, *A. Richardson 2131* (USM); Lomas de Sama, 450–500 m.a.s.l., 28 October 1966, *C. Vargas C. 18046* (CUZ); 500–600 m.a.s.l., *C. Vargas C. 18063* (CUZ); Lomas de Sama, 700 m.a.s.l.,

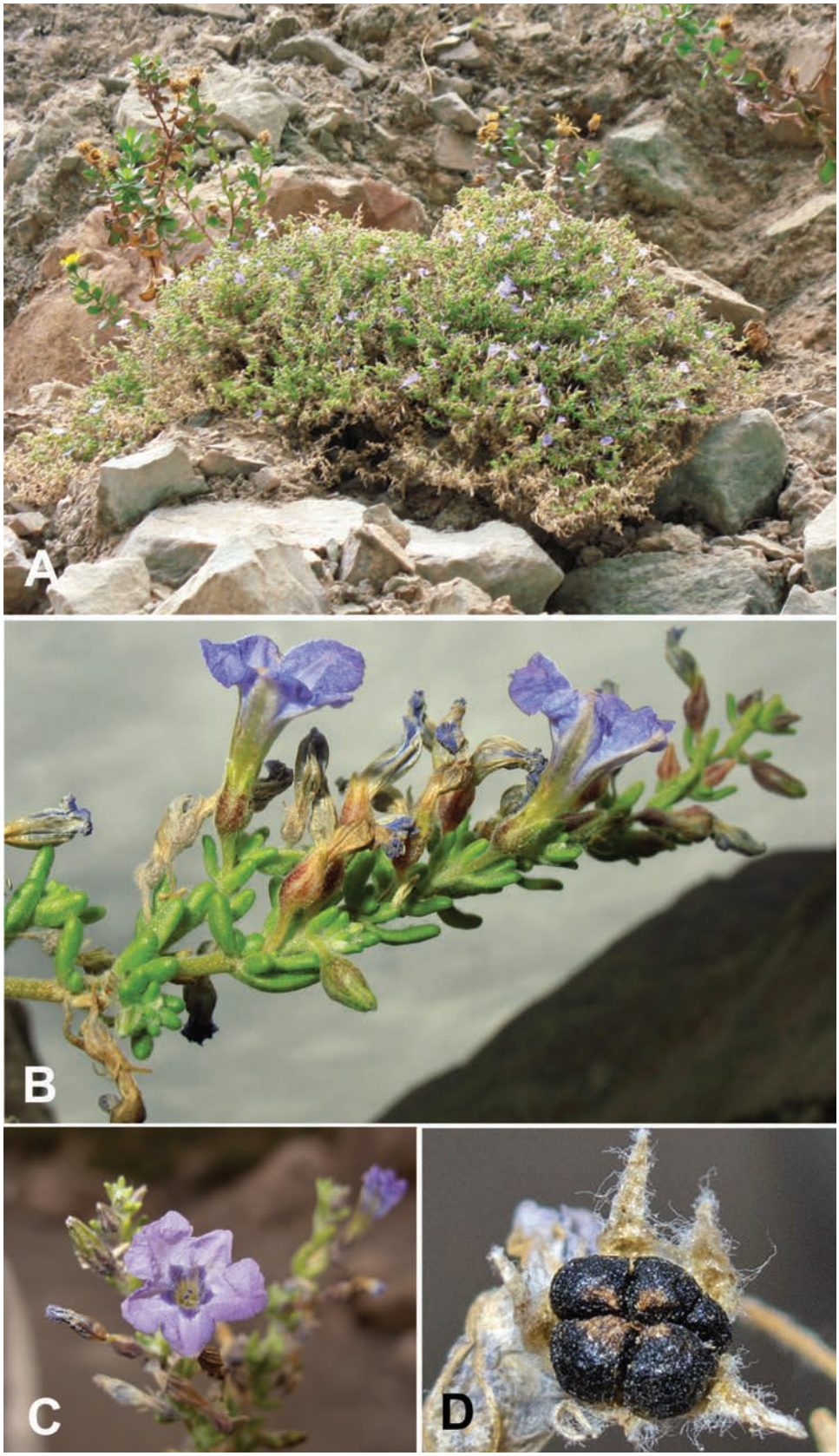


FIGURE 212. *Nolana confinis*. **A**, Low shrubs at 2000 m.a.s.l.; **B**, Flowering and fruiting branch; **C**, Corollas lavender to blue with a dark purple band in the throat common to most Peruvian species; **D**, Ripe, connate mericarps.

FIGURE 213. *Nolana confinis*. **A**, Cylindrical leaves covered with arachnoid pubescence; **B**, Flowers on pedicels; **C,** Nodding peduncles as fruit matures.

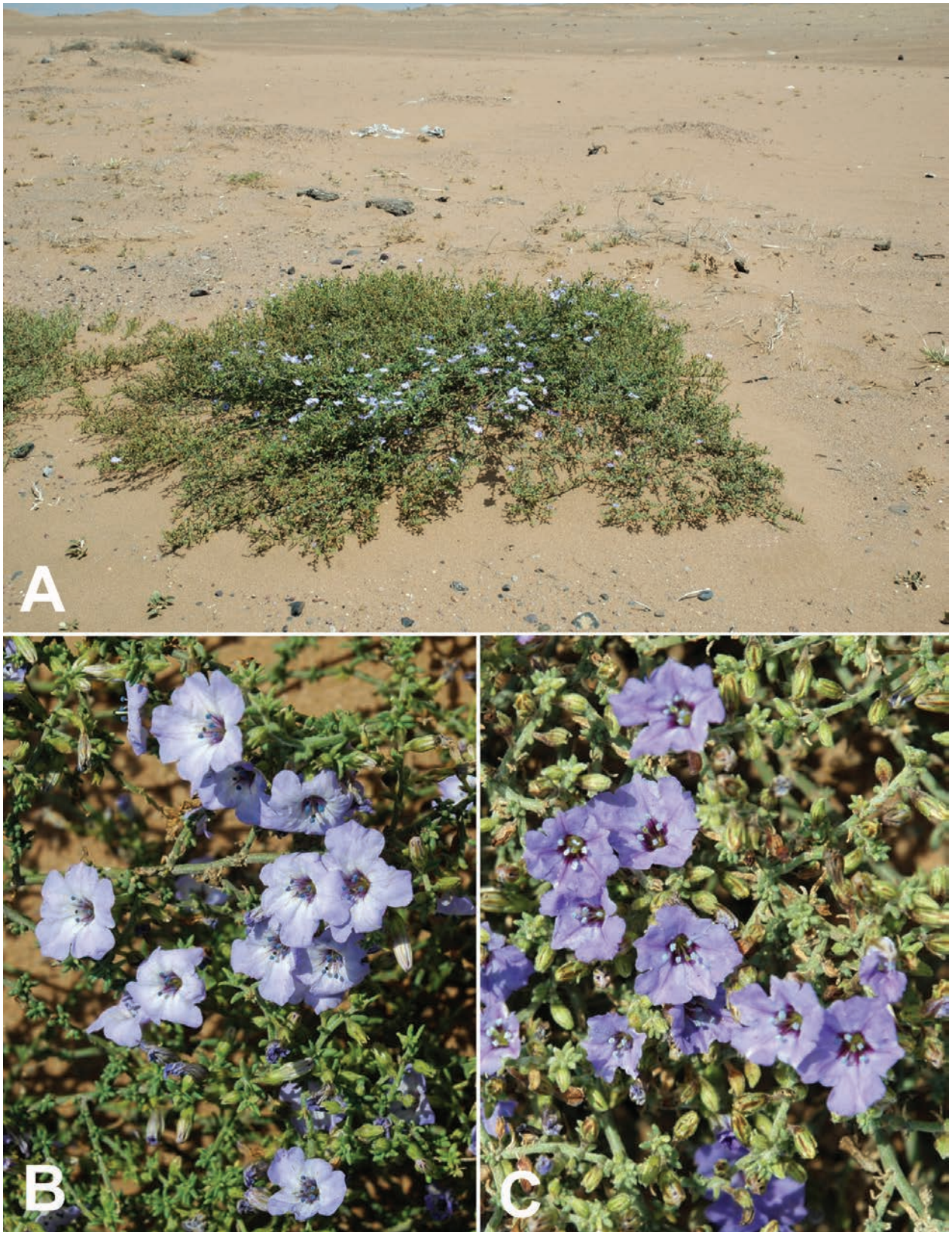


FIGURE 214. *Nolana confinis*. **A**, Low, spreading shrubs at elevations below 500 m.a.s.l.; **B–C**, Corollas blue to lavender.

30 November 1959, *C. Vargas C. 13045* (CUZ); ca. 650 m.a.s.l., August 1925, *E. Werdermann 720* (BM000941353, CONC 55628, E00273876, F 564165, GH, K). Prov. Tarata, 7 km S Candarave on road to Tarata (211 km W of Ilave), 3035 m.a.s.l., 9 October 1997, *M. Weigend & H. Förther 97/800* (MSB, not seen). **No exact Locality**: "Bolivia", *R. Pearce 657, 659* (K).

F9. ***Nolana coronata*** Ruiz & Pav., Fl Peruv. 2: 7, tab. 112b. 1799. TYPE: PERU. Arequipa: Prov. Camaná, entre Pongo y Atiquipa, 30 November 1777, *J. Tafalla s.n.* [*Hb. Pavón 434*] (Lectotype designated by Dillon and Quipuscoa, 2023: MA [815123]; Isolectotypes: B-W 03451-010, F [F 712543, F 843660, F 845176, F 845335, F 341432, F 341434, F 341435, F 341436], G [G 23240, G00383540, G00383541], HAL [HAL0115088], K [K000532272], MA [MA815121, MA815122, MA817983], MPU [MPU012108]). Fig. 215–216.

Digital image: Lectotype of *Nolana coronata* from Royal Botanical Garden, Madrid [MA815123]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.ma815123

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var *humifusa* Mesa, Fl. Neotrop. Monogr. 26: 129. 1981.

Annual or perennial *herbs*, 5–28 cm tall, erect, root simple, with age becoming woody and persistent, 3–17 cm long, 2–4 mm wide; stems ascending, few-branched, 5–20 cm long, 1.0–2.5 mm in diam., glabrous. *Leaves* alternate, blades lanceolate to ovate, 10–40 mm long, 6–30 mm wide, apically acute, basally attenuate, glabrous; petioles 15–30 mm long. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 4–18(–60) mm long, glabrous. *Flowers* 5-merous; calyces 10–15 mm long, 7–9 mm in diam., campanulate, glandular outside, pubescent inside, tube 5–7 mm long, lobes 5, triangular, 5–8 mm long, 2–5 mm wide, prominently pleated at the sinus, evenly rounded off beneath it, acuminate, glandular dorsally, hirsute inside; corolla infundibularis, regular, (20–)30–40 mm long, 7–13 mm wide, violet, glabrous, lobed, lobes 7–9 mm long, unequal, obtuse, tube short, pubescent; stamens subequal, united to tube for 1/3 its length, two larger 8–9 mm long, three smaller 6.8–7.2 mm long; style 4.2–8.0 mm long. *Mericarps* 5, reniform, shiny, black, 3–5 mm long, 2–3 mm wide; seeds ca. 3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *coronatus*, and was mentioned by Ruiz and Pavón in reference to the display of the anthers that are basally connate to the corolla throat.

Distribution and Ecology: Peru, Department of Arequipa; (260–)300–900(–1080) m.a.s.l. (Fig. 215). It is recorded from a very small area around the Lomas of Atiquipa, typically in denser soils with clay, not pure sand.

Nolana coronata is a glabrous herb with showy corollas to 4 cm wide (Fig. 216A) and calyces with extended and undulating margins (Fig. 216B). Its leaves are clearly petiolate with completely glabrous ovate blades. The floral coloration pattern most closely resembles that of *N. spathulata*; however, it is readily distinguished from the latter species by a fundamentally different calyx. Furthermore, the overall shape and size of the gynoecia are very different, although both have only five mericarps (Fig. 216C). *Nolana aticoana* grows in the same geographic area and has been confused with *N. coronata*, but these two species are easily distinguished; the former species has densely villous to glandular pubescent herbage and different mericarps. It also occurs sympatrically with *N. inflata* at the Lomas of Atiquipa; the calyx and mericarp characters serve to separate these two congeners.

There are three sheets of *N. coronata* housed at Madrid, each determined by E. Werdermann and labeled with "no 11/16": MA815121, MA815122, and MA815123. Only one has a chit in the original script as Ruiz and Pavón. A fourth collection is assumed to be another duplicate of the type collection, MA817983. There are four sheets at F that appear to have come from the original Ruiz and Pavón collection at Madrid. In Geneva, there are two sheets from Herbarium Pavón, one is numbered *434* and the other has no number.

Nolana coronata was published in Flora Peruviana et Chilensis (v. 2: 7, tab. CXIIb. 1799) and was typified by a collection attributed to *Tafalla s.n.* (holotype: MA) from near Atiquipa. These collections have ovate to lanceolate leaf blades with obvious petioles and five primary mericarps joined at their faces. Johnston determined a narrow-leaved collection (*Raimondi s.n.* [USM 10856], B) with large, inflated calyces as in *N. coronata*. This caused confusion in the application of the name by Ferreyra (1961). He followed Johnston's concept for *N. coronata* and determined a suite of collections as *Nolana coronata*, all with narrow to linear leaves and large flowers with inflated calyces; e.g., *Ferreyra 11727*, *Ferreyra 11745*, *Hutchinson 1288*, and *K. Rahn 063*. All of these collections are here placed in *N. chancoana,* a species with linear leaves and inflated calyces, quite distinct from authentic material of *N. coronata*.

Additional specimens examined: PERU. **Arequipa**: Prov. Caravelí, Atiquipa, a 2 km E del Cementerio de la Comunidad de Atiquipa, 15°46'16"S, 74°20'54"W, 394 m.a.s.l., 14 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8813* (F 2776731, HSP 005129, US 3512463); Atiquipa, 2 km E of Cementerio de la Comunidad de Atiquipa, 15°45'49"S, 74°20'56"W, 496 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8834* (F 2776734, HSP 005145, US 3512497); cima de las lomas, por el camino a Cahuamarca, 1079 m.a.s.l., 8 August 2013, *C. Fernández A., D. Sotomayor M., I. Revilla P., & M. Espinoza R. 42* (HSP 003222); Lomas de Atiquipa, 988 m.a.s.l., 9 August 2013, *C. Fernández A. & A. Pauca T. 49* (HSP 003229); en la cumbre del Yoque, 15°46'02"S, 74°22'55"W, 961 m.a.s.l., 11 May 2013, *A. Pauca T. 352* (HSP 003089); arriba de Atiquipa, 15°45'59"S, 74°22'07"W, 980 m.a.s.l., 19 August 2006, *V. Quipuscoa S., M. Laura Q., & Y. Cano B. 3375* (HSP 000609); arriba de Atiquipa en Ventiaderos-Avalos, 15°45'59"S, 74°22'52"W, 920 m.a.s.l., 14 September 2006, *V. Quipuscoa S., M. Celis, & M. Laura Q. 3391* (HSP 000596); Cerca a la plaza de Atiquipa, 15°47'47"S, 74°21'52"W, 305 m.a.s.l., 28 November 2017, *V. Quipuscoa S., M. O. Dillon,*

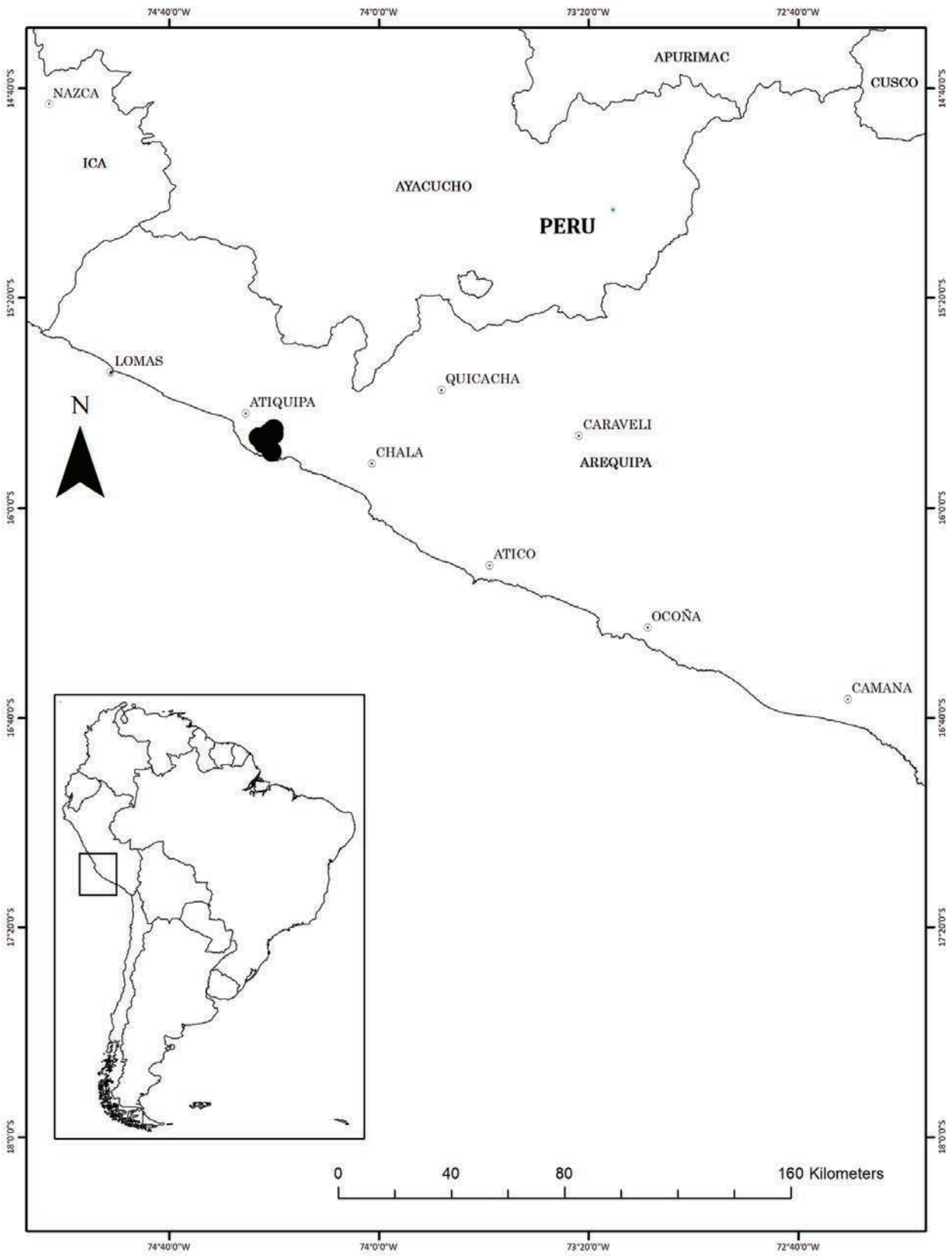


FIGURE 215. Distribution of *Nolana coronata* Ruiz & Pav.

FIGURE 216. *Nolana coronata*. **A**, Glabrous herbs with showy corollas; **B,** Calyx lobes with extended margins; **C**, Gynoecium with five connate mericarps.

M. Balvin A., S. Huamaní Q, M. Bedoya C., & W. Ancalla C. 6638 (HSP 011450); ca. la cima de las lomas de Atiquipa, 15°46'32"S, 74°22'49"W, 929 m.a.s.l., 28 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6662* (HSP 8812); Dist. Atiquipa, alrededores de los neblineros-Lloque, 15°45'57"S, 74°22'54"W, 977 m.a.s.l., 30 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7663* (HSP 011866); entre Chala y Santa Rosa, Km 606 Panamericana, 15°49'15"S, 74°20'22"W, 287 m.a.s.l., 29 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q, M. Bedoya C., & W. Ancalla C. 6702* (HSP 011475).

F10. ***Nolana gayana*** (Gaudich.) Koch, Ind. Sem. Berol. 12. 1855. Fig. 217–220.

Basionym: *Alibrexia gayana* Gaudich., Voy. Bonite, pl. 105. 1851; p. 81. 1866. TYPE: PERU. Lima, based upon material collected at Callao or Lurín, 11–21 July 1836, *C. Gaudichaud s.n.* [Johnston accepted the illustration as the type until the type could be located (see below). Neotype (designated by Dillon and Quipuscoa, 2023): PERU, Lima, "Tablada de Lurín", *A. Mathews 837* (E00793138); Isoneotypes: BM [BM000941268], E [E00793139], K).

Digital Image: Neotype collection of *Nolana gayana* from Royal Botanic Garden, Edinburgh [E00793138]. https://data.rbge.org.uk/herb/E00793138

Holotypic synonym: *Nolana crassulifolia* Poepp. ssp. *revoluta* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 93. 1981.

Perennial *herbs*, sometimes becoming *subshrubs*, 20–150 cm diam.; stems procumbent, suffrutescent, branched, gray-tomentose, trichomes dendritic. *Leaves* alternate to fasciculate, blades spathulate to oblong, rarely becoming linear, 3–20(–42) mm long, 1–13 mm wide, margins revolute, apically acute to obtuse, both adaxial and abaxial surfaces equally dendritic-tomentose; sessile. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 10–48 mm long, recurved in fruit. *Flowers* 5-merous; calyces campanulate, 4–10 mm long, 2.5–6.0 mm wide, tomentose with dendritic trichomes, tube 3–5 mm long, 2–3 mm wide, lobes erect, equal, 3.0–3.5 mm long, 1.0–1.2 mm wide, acute; corollas infundibularis, violet or, more rarely, white, 12–28 mm long, 7–30 mm wide, lobes obtuse; stamens unequal, fused to tube for 1/3 its length, widened at base; anthers lilac; nectary disc patelliform, margin sinuate; style ca. 5 mm long, shorter than the filaments, gynobasic; stigma capitate. *Mericarps* 5, reniform, black, the largest 2.8–3.5 mm long, 1.2–1.8 mm wide, the smallest 2.0–2.2 mm long, 1.0–1.2 mm wide; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Claudio Gay (b. 1800–d. 1873), a French botanist, naturalist, illustrator, and author of some of the first investigations covering the Chilean flora, fauna, geology and geography in the early 1820s. In 1838, he was a founding member of the Museo Nacional de Historia Natural in Santiago.

Distribution and Ecology: Peru, Departments of Ancash, Arequipa, Ica, La Libertad, Lima, and, potentially, Piura; 100–500 m.a.s.l. (Fig. 217). It is recorded from sandy soils in habitats above 100 m.a.s.l., but typically not too distant from the effects of coastal fog.

Illustration: Fig. 218. Illustration of *Nolana gayana* as *Alibrexia gayana*, Plate 105. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana gayana is a perennial herb, or sometimes develops into a shrub with a woody stem, with blue flowers with guides, and succulent leaves (Fig. 219A–B). The leaves are revolute and the flowering peduncles are erect (Fig. 220A). The corollas are light to dark blue with blue anthers and pollen (Fig. 220B), and the calyx lobes are cut to the middle (Fig. 220C). The gynoecium is subtended by a prominent orange nectary (Fig. 220D), and there are five principal, reniform mericarps (Fig. 220E). It is distinguished from its congeners in the north as the only *Nolana* possessing herbage with dendritic trichomes. Johnston (1936: 33) stated that the fruit consisted of five sharply angular mericarps and several more minor mericarps that are wedged in between the bases of the major ones. In several localities in northern Peru, *N. gayana* occurs sympatrically with *N. humifusa*, a species that is easily distinguished by its spurred calyx lobes and the lack of dendritic pubescence.

After studying this taxon throughout its range, the geographic distribution of *Nolana gayana* is expanded to areas south of Lima to include populations in the Department of Ica and northern parts of the Department of Arequipa. Collections with a more southern distribution were initially considered to be *Nolana pallida* (e.g., *Dillon et al. 3237*, *Dillon et al 3242*, *Dillon et al. 8879*, *Fernández & Fernández 55*, *Quipuscoa et al. 3378*, *Quipuscoa et al. 3525*, and *Quipuscoa et al. 3580*). These collections have calyces that are deeply cut to half or more than half the length of the calyx tube. They are here listed as conspecific with *N. gayana*; however, at the risk of undue emphasis on this character, further sampling and analysis are warranted.

Recently, photographs of a plant resembling *Nolana gayana*, taken of a plant collected near Cerro Illescas, Department of Piura in the Sechura desert, were sent to the author (Victor Pariapaza Liviapoma, pers. comm.). Weberbauer (1945) mentioned an unidentified *Nolana* from the Cerro Illescas region, and I visited that area but did not encounter any *Nolana* species. I had assumed that Weberbauer had observed an *Exodeconus* species, but now his observation should not be doubted. This would mark a range extension of over 300 km for *Nolana gayana* and mark the northernmost terminus for the genus in Peru.

Ferreyra (1961) called attention to his numbers *12420* and *13364* from Pasamayo as having only 4 mericarps. He also observed sterile members and suggested that they represented hybrids with *N. humifusa* (Ferreyra, 1961; p. 15). I have not examined these two collections; however, no indications of hybridization have been detected in the material examined in this study.

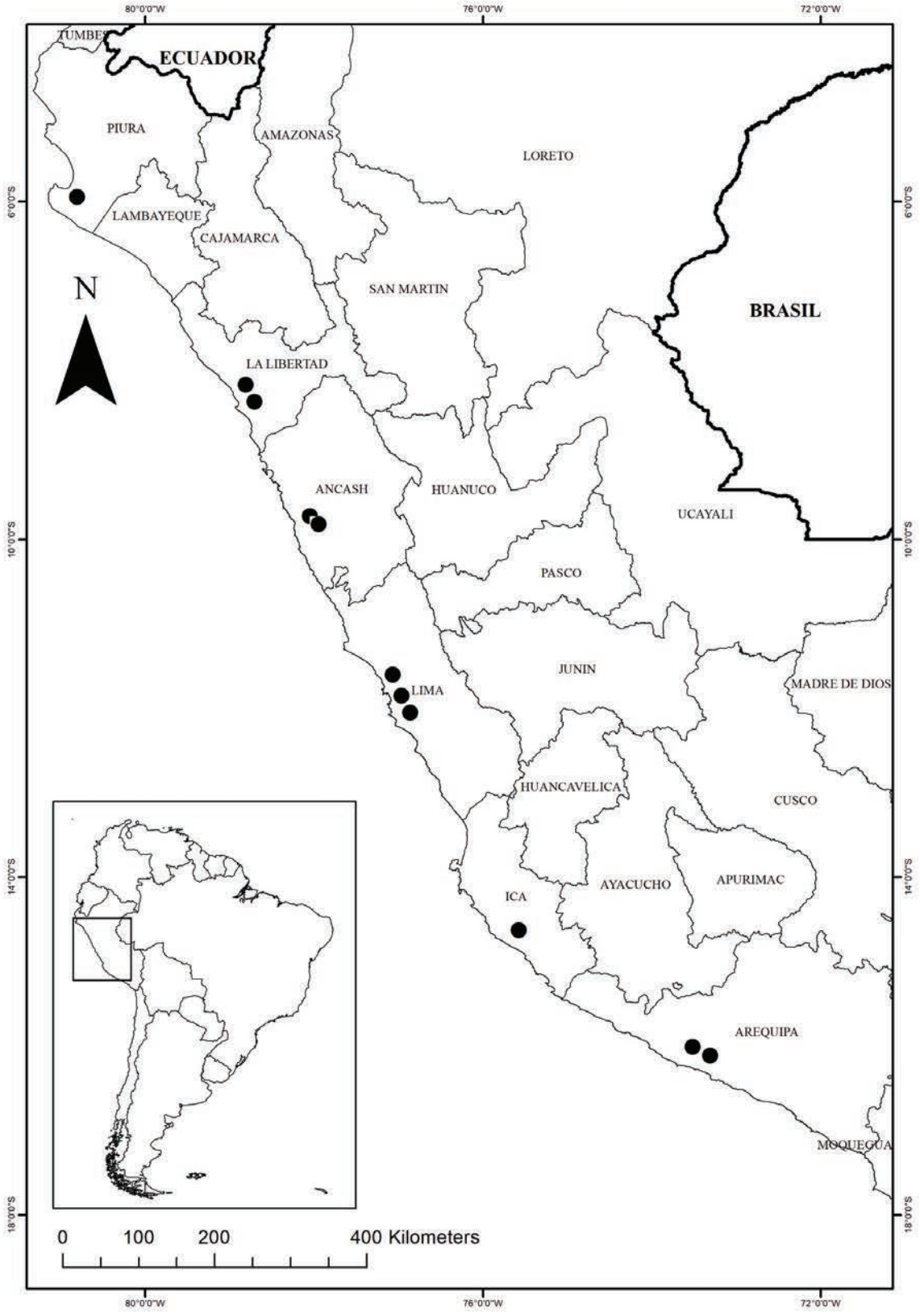


FIGURE 217. Distribution of *Nolana gayana* (Gaudich.) Koch.

FIGURE 218. Illustration of *Nolana gayana* as *Alibrexia gayana*, Plate 105. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 219. *Nolana gayana*. **A**, Shrub with woody stems, blue flowers with guides; **B**, Succulent leaves with revolute margins. Photographs by Victor Quipuscoa Silvestre.

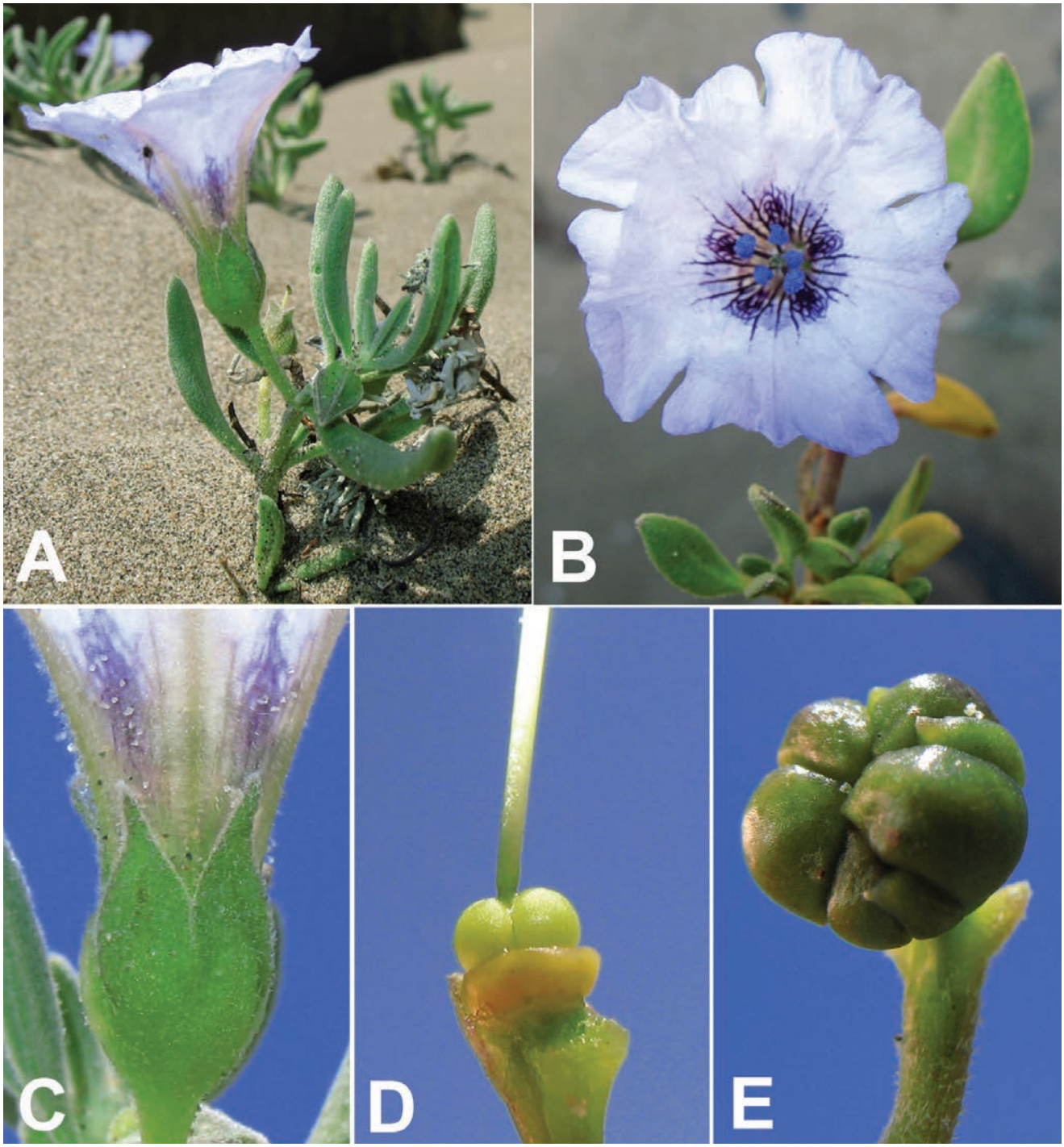


FIGURE 220. *Nolana gayana*. **A**, Lateral view of flower; **B**, Light blue corollas with blue anthers and pollen; **C**, Calyx lobes are cut to the middle; **D**, Gynoecium subtended by orange nectary; **E**, Five principal, reniform mericarps. Photographs by Victor Quipuscoa Silvestre.

Johnston (1936) made his description of *Nolana gayana* largely from Gaudichaud's published plate (Fig. 218), remarking that it was a very distinct species. He speculated that the Gaudichaud illustration had been drawn from material collected by Claudio Gay; however, no collections of *Nolana gayana* by Claudio Gay have been encountered in this study. The neotype chosen here was selected from material collected by Mathews, examined by Johnston (1936: 33), and originated from the geographic region near Lima. Several duplicates exist, and images are available via the internet. It is a pleasure to acknowledge Andrew Mathews, a British botanist who collected plants in Chile and Peru in 1833, married a Peruvian woman, and died at Chachapoyas, Peru. His surname is occasionally cited as 'Matthews', and his specimens are hand-labeled or marked simply with "A. M.".

Additional specimens examined: PERU. **Ancash**: Prov. Casma, Lomas de Mongón, Km 350, 27 November 2001, *S. Leiva G., P. Lezama A., M. O. Dillon, & E. Rodríguez R. 2603* (HUT 38847); Lomas de Mongon near San Rafael, between Casma and Huarmey, 450 m.a.s.l., 17 September 1938, *H. E. Stork, O. B. Horton, & C. Vargas C. 9187* (GH, K). **Arequipa**: Prov Caravelí, ca. 33 km WNW of Chaviña, ca. 300 m.a.s.l., 7 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3242* (F 2043420); Lomas de Jahuay, ca. 33 km WNW of Chaviña, ca. 300 m.a.s.l., 7 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3237* (CONC, E, F 2043422, GH, SGO, US); Lomas of Jahuay, ca. 89 km S of Nazca, ca. 15 km N of Chaviña, 15°34'S, 74°50'W, 30 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3773* (E, F 1950161, GH, SGO, US); al sur de Chala, 15°52'S, 74°11'W, 230 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8879* (F 2276739, HSP 5181, US 3512529); Quebrada a 10 m de carretera Panamericana, antes de llegar a Puerto Inca, 231 m.a.s.l., 16 November 2013, *C. Fernández A. & M. Fernández Z. 55* (HSP 003235); entre Silaca and Ocopa, 15°49'06"S, 74°23'32"W, 203 m.a.s.l., 20 August 2006, *V. Quipuscoa S., M. Laura Q., & Y. Cano B. 3378* (HSP 000612, HUSA 560); Lomas de Cápac, 15°51'48"S, 74°11'30"W, 197 m.a.s.l., 20 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3580* (HSP 002517, HUSA). **Ica**: Prov. Ica, Dist. Santiago, Lomas de Amara, 14°43'47"S, 75°41'48"W, 780 m.a.s.l., 18 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3525* (HUSA 7498). **La Libertad**: Prov. Trujillo, Cerro Chiputur, 420 m.a.s.l., 4 June 1950, *N. Angulo E. s.n.* (F 1746418, HUT 1239); Lomas of Cerro Chiputur, ca. 12 km S of Trujillo on PanAmerican Norte, 200–500 m.a.s.l., 14 October 1986, *M. O. Dillon, A. Sagástegui A., J. Santisteban, & S. Keel 4676* (CONC 109911, F 1981600, HUT 23103); Cerro Chiputur, 150–200 m.a.s.l., July 1948, *A. López M. 145* (US 2058228), Cerro Chiputur, Salaverry, 350 m.a.s.l., 24 February 1983, *A. Sagástegui A., A. López M., & S. López M. 9140* (F 1998998, GH, HUT 17485), *9141* (HUT 17503, US 3264903). Cerro Chiputur, 300 m.a.s.l., 11 November 1983, *A. Sagástegui A. & J. Mostacero L. 11031* (F 1933658, HUT 18131, US 3470034). **Lima**: Prov. Lima. Barranco, in dry sandy places at the lower edge of the lomas formation, 50–200 m.a.s.l., October 1902, *A. Weberbauer 1606* (B). Cañete. ca. 25 km S of Lima, Lomas of Atocongo, 100–200 m.a.s.l., 22 June 1947, *R. Ferreyra 2057* (US 1998570); Lomas de Atocongo, 100–200 m.a.s.l., 28 September 1947, *R. Ferreyra 2457* (F 1488890, US 1998573); Pasamayo, Km 53 carretera Lima–Chancay, 120 m.a.s.l., 24 September 1952, *R. Ferreyra 8756* (GH); Tablada de San Juan, February 1874, *J. B. H. Martinet 287* (P); Tablada de Lurín, *A. Mathews 836* (E00793137, K), *837* (BM000941268. E00793125, E00793139, E00793138, K); Lurín, ca. 200 ft, 23 September 1923, *J. F. Macbride 5937* (F 536941, GH)); Lurín, ca. 200 ft, 23 September 1923, *J. F. Macbride 5941* (F 536945, GH, US 1474565); Huaral, ca. 54 km N of Lima on PanAm Hwy, 24 December 1978, 200 m.a.s.l., *M. O. Dillon & B. L. Turner 1491* (F 1895788). Prov. Chancay, Lomas de Pasamayo, ca. 65 km N of Lima on Panamericana Norte, 450 m.a.s.l., 5 November 1986, *M. O. Dillon, J. Santisteban, M. Chanco, & C. Diaz 4739* (F 1981529, HUT 22742); Lomas de Pasamayo, ca. 450 m.a.s.l., 5 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4740* (F 1981528, HUT 22743); Lomas de Lachay, between Chancay and Huacho, 300–350 m.a.s.l., 14 July 1948, *R. Ferreyra 3846* (US 1998588); Lomas de Chancay, cerca a Chancay, 200–300 m.a.s.l., 17 March 1953, *R. Ferreyra 8989* (GH [2 sheets], K [2 sheets]); Lomas de Ancon, 23 October 1980, *M. Ono et al.s.n.* (MAK 197078), Pascamayo, 23 October 1980, *M. Ono et al. s.n.* (MAK 197079); Atocongo, 250–500 m.a.s.l., 28 June 1925, *F. W. Pennell 14789* (F 558729); Atocongo, 500 m.a.s.l., 9 October 1949, *J. Soukup 3942* (F 1416059, US 2027393); Lomas de Lachay, 4 March 1998, *H. van der Werff, R. Vasquez & B. Gray 14456* (BM000522391). Prov. Huaral, Carretera Panamericana Norte, ca. Km 50, 50 m.a.s.l., 21 July 1992, *A. Cano, M. I. La Torre, K. Young, & B. León 5085* (F 2151241). Lomas de Cerro Negro, ca. 10 km ESE of Ancon, 2 October 1966, *S. S. Tillett 6610-8* (GH); Prov. Lima, 20 km N of Lima along Panamericana Hwy, 100 m.a.s.l., 5 February–2 April 1997, *M. Weigend, N. Dostert, & Drieβle 97/469* (F 2179256). **No exact locality**: South America, 1831, *H. Cuming 1068* (E00130954, K [2 sheets]); Near Lima, *J. J. McLean s.n.* (K); Lima suburbs, 1943, *J. Soukup 2158* (US 1876950).

F11. ***Nolana humifusa*** (Gouan) I.M. Johnst., Contrib. Gray Herb. 112: 50. 1936. Fig. 221–227.

Basionym: *Atropa humifusa* Gouan, Hort. Reg. Monsp. 106, tab. 1762. TYPE: PERU. Described from garden material raised from Peruvian seeds, (Lectotype: MPU028298).

Digital image: Lectotype of *Atropa humifusa* from Université Montpellier—Herbier de Institut de Botanique [MPU028198]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.mpu028198

Heterotypic synonyms: *Nolana prostrata* L. fil., 1762. Decas Pl. Rar. Upsal. 1: 3, t. 2. TYPE: Described from garden material attributed to Adriaan von Royen; *Nolana polymorpha* Gaudich., Bot. Voy. Bonite pl. 101. 1851. TYPE: PERU. Lima: Prov. Callao, Isla San Lorenzo, 11–21 July 1836, *C. Gaudichaud s.n.* (Lectotype designated by Mesa-M., 1981: P [00605851]; Isolectotypes: F [F 679046, F 1000362, F 680842], FI-Webb, GH [GH00282329], NY [NY00312359], US [US 1706494, US00121961]); *Nolana parvifolia* Phil., Anal. Univ. Chile 91: 35. 1895. TYPE: PERU. (No exact locality), 1895, *P. Ortega s.n.* (Holotype: SGO [55135, SGO000004384]).

Annual or short-lived perennial *herbs*, or, more rarely, woody, semisucculent; stems erect to decumbent, glabrous, 8–15 cm long. *Leaves* alternate to opposite, occasionally fasciculate, blades 10–40(–55) mm long, 6–27 mm wide, elliptic or broadly lanceolate, apically obtuse, rarely acute, basally abruptly attenuate, margins revolute, glabrous; petioles 10(–20) mm long. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 5–45 mm long. *Flowers* 5-merous; calyces 5–10(–18) mm long, campanulate,

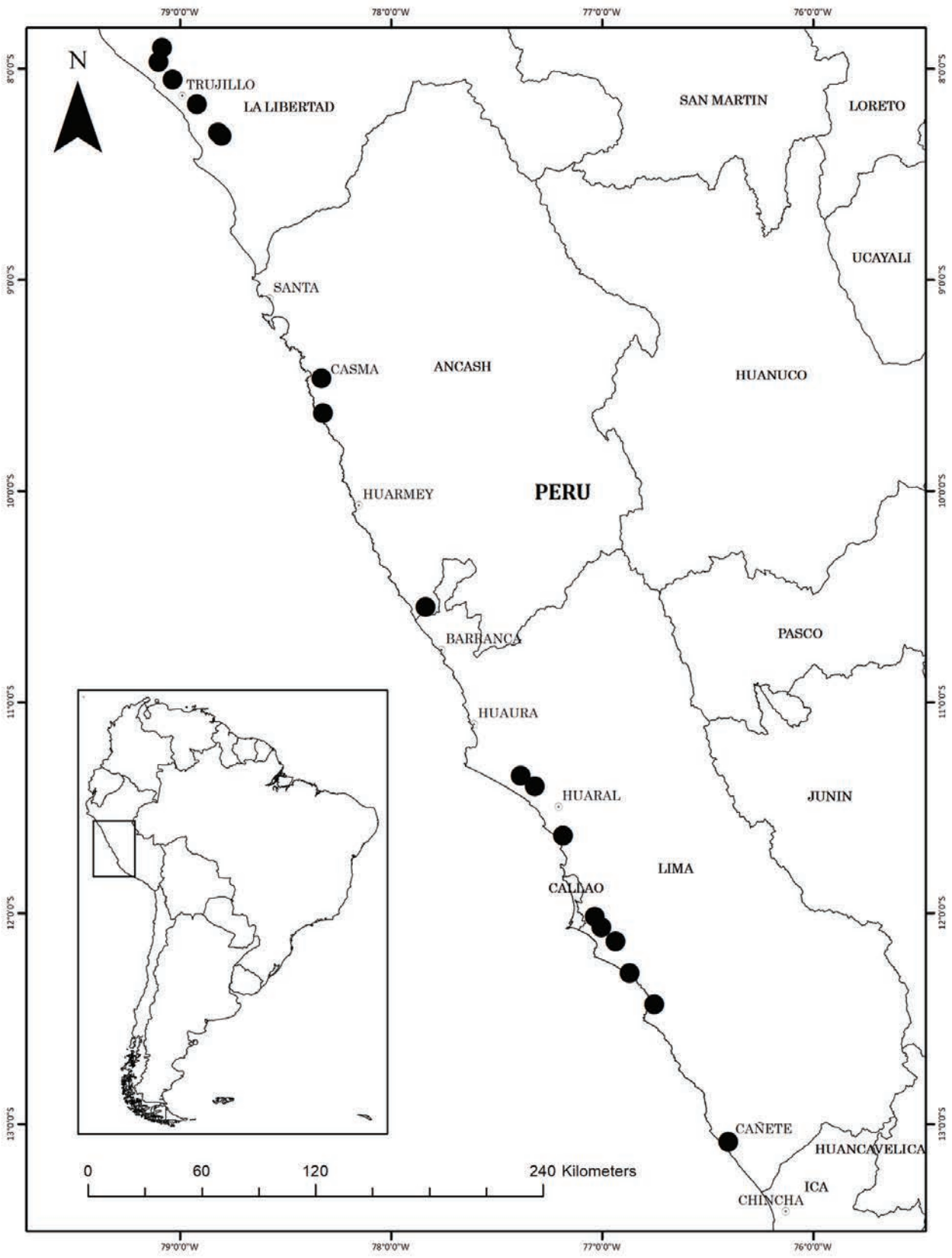


FIGURE 221. Distribution of *Nolana humifusa* (Gouan) I.M. Johnst.

glabrescent, tube short, conspicuously bilabiate, 2.5–3.0 mm long, 6–8 mm wide, lobes 6.5–9.0 mm long, 7–10 mm wide, acute; corolla infundibularis, blue, infrequently white, 15–28 mm long, 15–26(–40) mm wide, lobes rounded; stamens 8–12 mm long, filaments united to tube almost to the middle; stamens unequal; filaments widened at the base, pubescent or not; anthers lilac; nectary disc crateriform, 3.0–3.5 mm in diam.; style 7–8 mm long, gynobasic; stigma capitate-globose. *Mericarps* 5, rarely with 1 or 2 smaller, 1-seriate, 2.2–4.0 mm long, 2.0–3.5 mm wide, reniform, black, shiny; seeds 3–5(–7) per mericarp. Chromosome number: 2*n*=24.

Etymology: The species epithet is from the Latin, *humus*, earth or soil, and *humifusus*, spread out over the ground, procumbent, likely referring to the spreading habit of this species.

Distribution and Ecology: Peru, Departments of Ancash, La Libertad, and Lima; 100–600 m.a.s.l. (Fig. 221). It is recorded from rocky or sandy hills from within the fog zone. USA. Cultivated as a garden ornamental.

Illustration: Fig. 222. Illustration of *Nolana humifusa* as *Nolana polymorpha*, Plate 101. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication see Table 3, adapted from Johnston (1944).

Nolana humifusa is an annual, but plants can perennate when sufficient moisture is available. When conditions are optimal, such as during an El Niño phenomenon, there can be mass blooming, and populations can attain large numbers with nearly 100% ground cover (Fig. 224A). The corollas are blue to purple with a dark band within the throat (Fig. 224B). One distinctive character is the bilabiate calyx lobes that are prolonged into projections and referred to as a plicate sinus or "spurs" (Fig. 224C–D). When sufficient moisture occurs for multiple years, a woody perennating base can develop (Fig. 225A). The corollas can be pale lavender, but whatever color, they develop purple guides in the throat, and have blue anther thecae and pollen (Fig. 225B–C). As in other species of *Nolana*, individuals with all white flowers have white anthers and pollen (Fig. 226A–C).

Nolana humifusa has populations that extend for nearly 600 km from northern to central Peru and is the most common species in northern Peru. Within a large, expansive collection from the Lomas of Pachacamac (Fig. 227A–B), the variation in floral guides and color patterns is considerable (Fig. 227C). Marker data has indicated that *N. humifusa* is related to *N. coronata* in southern Peru, sharing the character of calyx lobe projections.

Nolana adansonii, collected by Feuillée in 1710, was the first *Nolana* known to European botanists; however, *Nolana humifusa* was the first member of the genus to be introduced to European gardens due to its ease of cultivation. It has been used in several breeding studies and has shown high degrees of fertility with *N. paradoxa* of southern Chile (Saunders, 1934). The various breeding studies are discussed under Hybridization.

Johnston (1936: 56) admitted to only knowing *N. polymorpha* from Gaudichaud's plate; however, when Gaudichaud's collections were located, they appeared to represent a perennating plant corresponding to *N. humifusa*. Isla San Lorenzo is eight kilometers long and two kilometers wide and is the largest island off the Peruvian coast. Recently, I was sent photographs of some collections made on Isla San Lorenzo (Paul Gonzáles Arce, pers. comm.). Until a closer examination of this material is possible, it will remain in synonymy.

Additional specimens examined: PERU. **Ancash**: Prov. Casma, Lomas de Mongón, 430 m.a.s.l., 27 November 2001, *S. Leiva, P. Lezama A., M. O. Dillon, & E. Rodríguez R. 2601* (HUT 38849); near San Rafael, between Casma and Huarmey, Mongón Lomas, 400 m.a.s.l., 17 September 1938, *H. E. Stork, O. B. Horton, & C. Vargas C. 9158* (GH, K). Prov. Huarmey, Lomas de Lupin, 31–32 km N of Paramonga, Km 239–241, ca. 330 m.a.s.l., 1 November 1986, *M. O. Dillon & J. Santisteban 4714* (CONC 109908, F 1981561); Panamericana Norte Km 589, 330 m.a.s.l., 10 October 2000, *M. Weigend, H. Förther, & N. Dostert 2000/645* (F 2229810, HUT 38387). Prov. Santa, Cerro Chimbote, 620 m.a.s.l., 1 July 1951, *N. Angulo E. s.n.* (HUT 1386); Lomas de Lupín, entre Paramonga y Huarmey, 200–300 m.a.s.l., 22 April 1953, *R. Ferreyra 9148* (GH, K); Cerro Chimbote, Cerro La Paz, 620 m.a.s.l., 26 September 1986, *J. Mostacero L. & F. Mejía 1471* (HUT 22260); Cerro Chimbote (Cerro La Paz), 620 m.a.s.l., 26 September 1986, *J. Mostacero L. & F. Mejia C. 1473* (HUT 22288); lomas along Pan-American highway, 33 – 38 km N of Pativilca, 23 October 1965, *R. M. Tryon & A. F. Tryon 6574* (GH). No exact locality data, 2000 m.a.s.l., 5 July 1954, *W. Rauh & G. Hirsch P1957* (F 1578067). **La Libertad**: Prov. Trujillo, Cerro Campana, June 1941, *N. Angulo E. 31* (HUT 0014); Cerro Cabras, 100 m.a.s.l., 6 August 1949, *N. Angulo E. s.n.* (F 1711944, HUT 1202); Cerro Chiputur, 510 m.a.s.l., 23 August 1953, *N. Angulo E. s.n.* (HUT 1991); Quebrada de León, 420 m.a.s.l., 24 September 1940, *N. Angulo E. & A. López M. s.n.* (HUT 1291); E slope of Cerro Campana, 150–600 m.a.s.l., 4 January 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 2714* (E, F 1912896); Cerro Campana, ca. 15 km N of Trujillo, 400–680 m.a.s.l., 23 January 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3058* (F 2043425); Lomas de Cerro Chiputur, ca. 12 km S of Trujillo, 200–500 m.a.s.l., 14 October 1986, *M. O. Dillon, A. Sagástegui A., J. Santisteban, & S. Keel 4694* (F 1981582, HUT 23114); Cerro Campana, 300–700 m.a.s.l., 10 October 1986, *M. O. Dillon, J. Santisteban, & B. León 4654* (F 1978721, HUT 23084); SE side Cerro Campana, 250 m.a.s.l., 24 September 1957, *P. C. Hutchison 1354* (F 1555883, US 2406374); Cerro Cabezón, Km 580, 330 m.a.s.l., 10 February 1998, *S. Leiva G., M. O. Dillon, A. Sagástegui A., & V. Quipuscoa S. 2158* (F 2190621, HUT 31956); Cerro Chiputur, 300 m.a.s.l., September 1949, *A. López M. 880* (HUT 4639). Cerro Campana, 350 m.a.s.l., 10 September 1952, *A. López M. s.n.* (HUT 4817); Cerro Campana, 500 m.a.s.l., 9 June 1985, *J. Mostacero L., S. Leiva G., F. Mejía C., F. Peláez P., & J. Guevara B. 703* (F 1994333, HUT 22147); Cerro Campana, 500 m.a.s.l., 17 July 1985, *J. Mostacero L., S. Leiva G., F. Mejía C., & F. Peláez P. 0811* (HUT 22515); Cerro Campana, 450 m.a.s.l., 19 August 1985, *J. Mostacero L., S. Leiva G., F. Mejía C., & F. Peláez P. 1064* (HUT 22700); Cerro

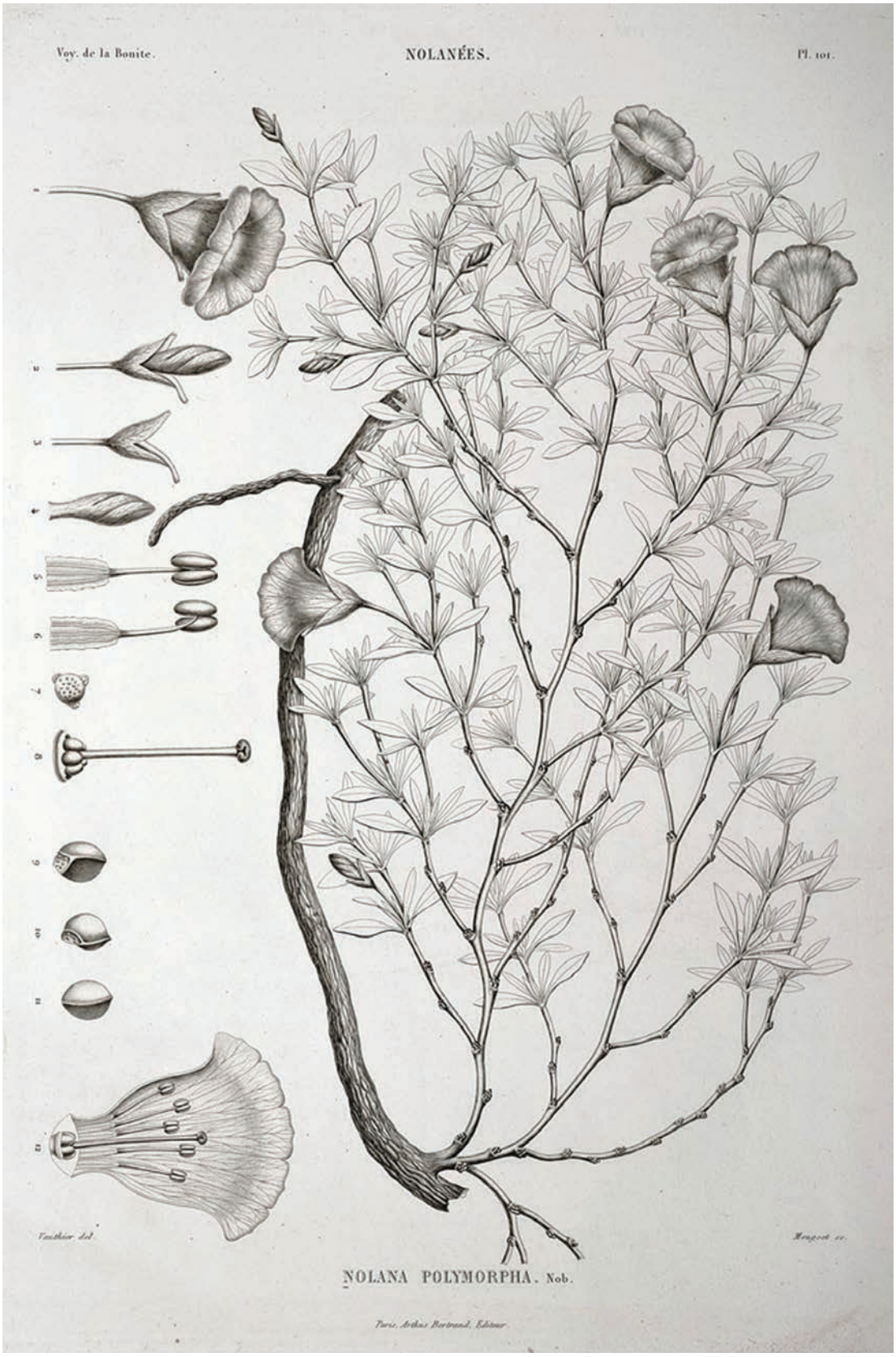


FIGURE 222. Illustration of *Nolana humifusa* as *Nolana polymorpha*, Plate 101. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

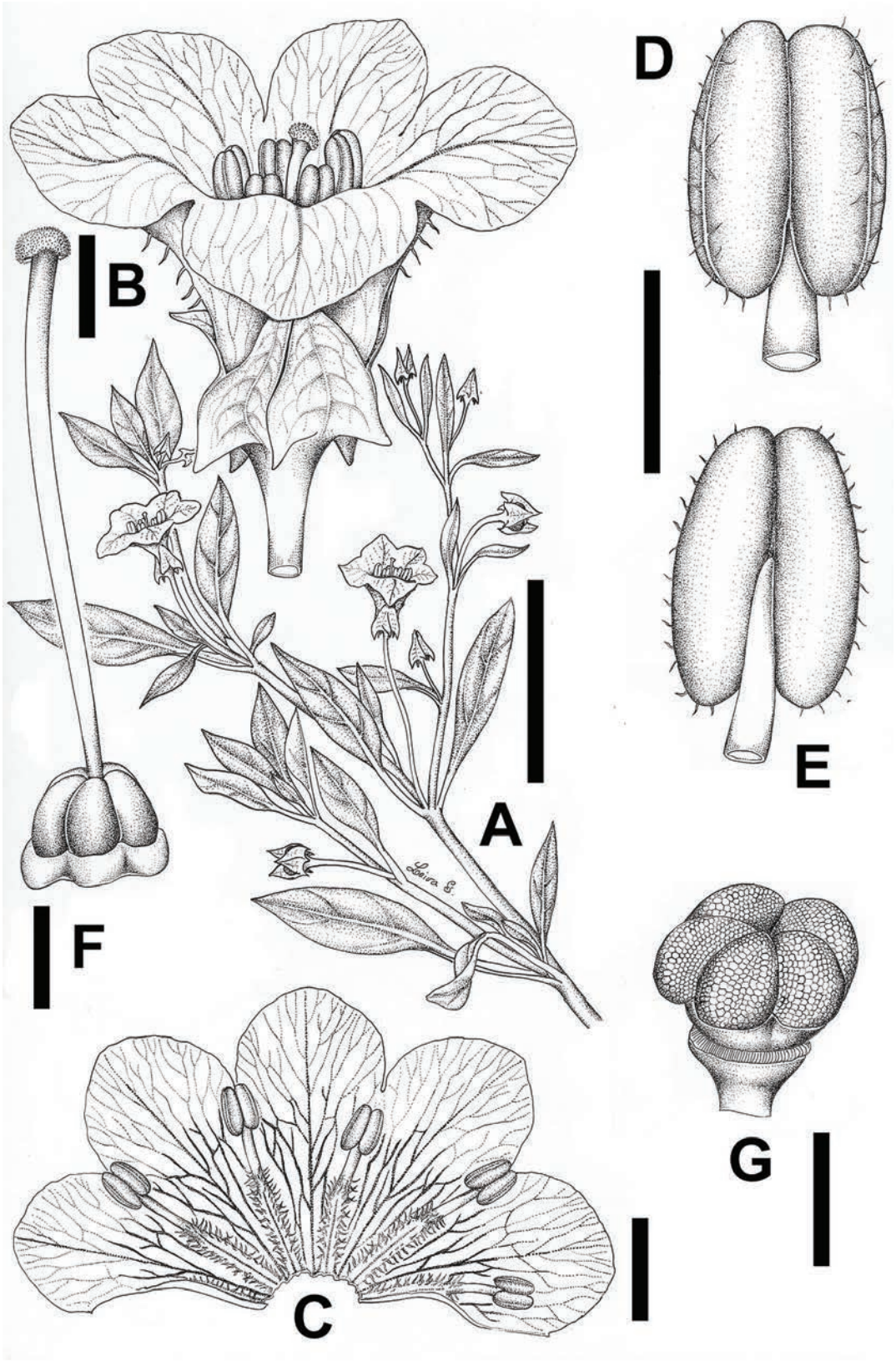


FIGURE 223. Illustration of *Nolana humifusa*. **A,** Flowering branch; **B**, Flower with spurred calyx lobes; **C**, Dissected corolla; **D**, Ventral view of anther thecae; **E**, Dorsal view of anther thecae; **F**, Gynoecium, style, and stigma; **G**, Gynoecium with mature mericarps. Drawn by Segundo Leiva Gonzáles.

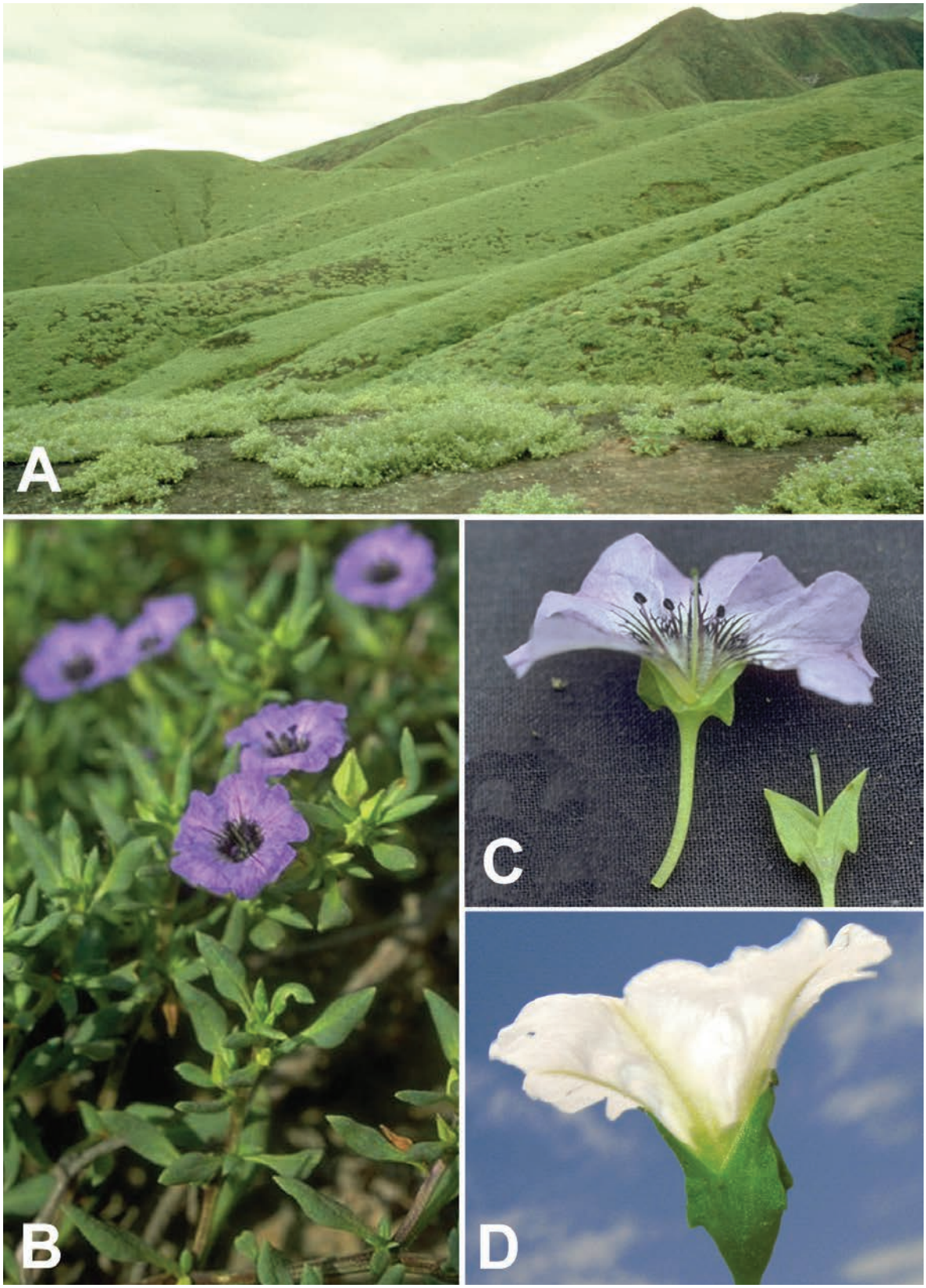


FIGURE 224. *Nolana humifusa*. **A,** Lower slopes of Cerro Cabezon, Peru, during El Niño year 1998, nearly 100% ground cover; **B**, Corollas are blue to purple with a dark band within the throat; **C**, Dissected flower shows bilabiate calyx with lobes prolonged into spur-like projections; **D**, Lateral view of flower.

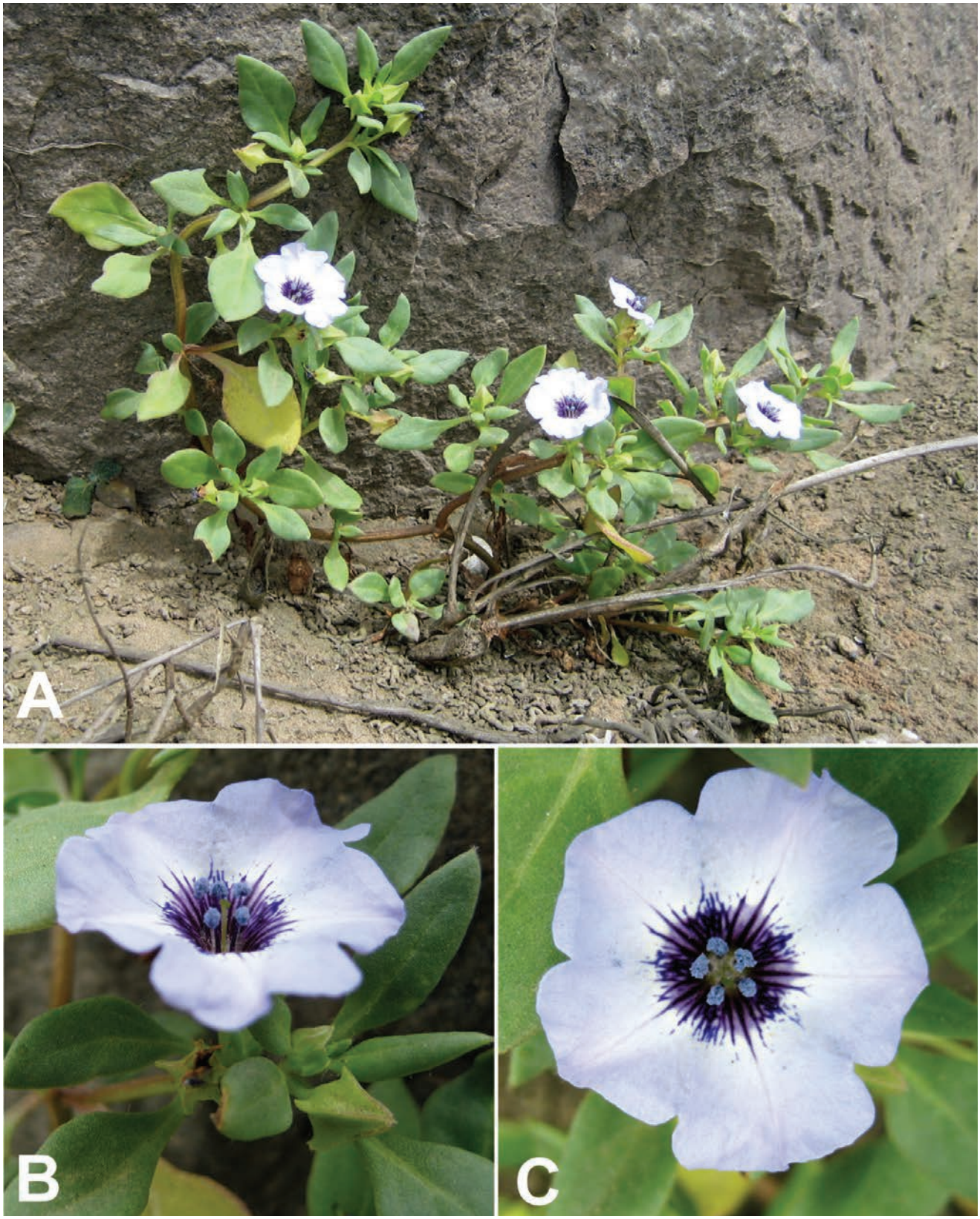


FIGURE 225. *Nolana humifusa*. **A**, Woody perennating base with last season's stems; **B–C**, Lavender corollas with purple guides in the throat, blue anther thecae and pollen.

FIGURE 226. *Nolana humifusa*. **A–C**, A small percentage of individuals have white flowers with white anthers and pollen.

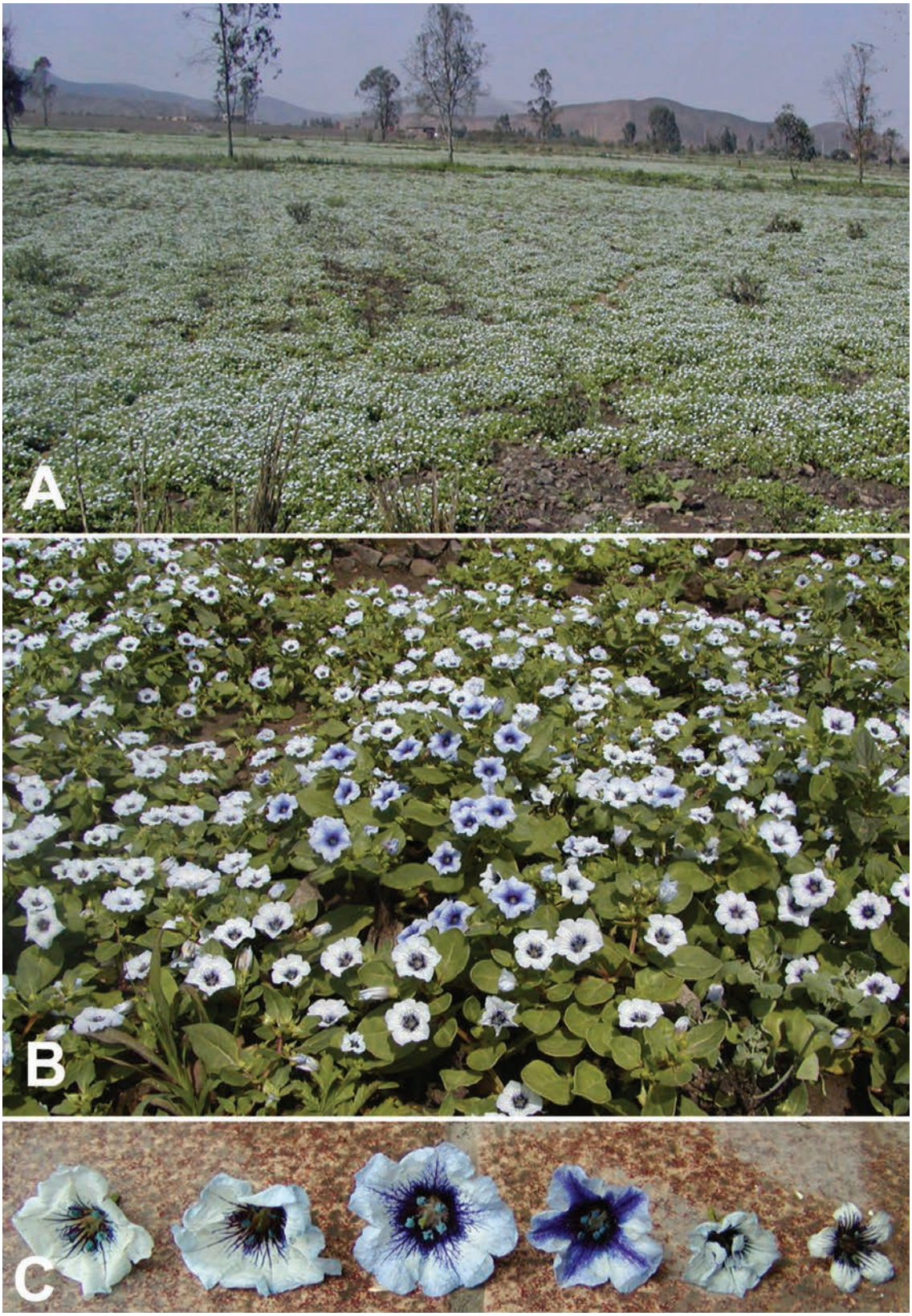


FIGURE 227. *Nolana humifusa*. **A–B**, Dense population from disturbed area at the Lomas of Pachacamac, Peru; **C,** Variation in corolla shape, floral guides, and color patterns. Photographs by Rosanna Freyre.

Campana, 500 m.a.s.l., 9 June 1985, *J. Mostacero L., F. Mejía C., J. Miller, & R. Vásquez 3300* (HUT 28020); Quebrada de San Idelfonso, 100–300 m.a.s.l., 13 April 1998, *E. Rodríguez R. & W. Aguilar T. 2072* (HUT 31979); Cerro Campana, 450–850 m.a.s.l., 14 August 1999, *E. Rodríguez R., & E. Alvítez I. 2257* (HUT 33792); Cerro Campana, 400 m.a.s.l., 25 October 1983, *A. Sagástegui A. 10944* (F 1934184, HUT 17931); Cerro Cabezón, 400 m.a.s.l., 23 September 1976, *A. Sagástegui A. & J. Cabanillas S. 8754* (HUT 14132); Cerro Campana, 400 m.a.s.l., 23 January 1983, *A. Sagástegui A., S. López M., & J. Mostacero L. 10427* (HUT 17425); Cerro Cabezón, 400 m.a.s.l., 20 February 1983, *A. Sagástegui A. & J. Mostacero L. 10436* (F 2037462, HUT 17408); Cerro Cabezón, 450 m.a.s.l., 4 November 1983, *A. Sagástegui A. & S. López M. 10998* (F 1933612, HUT 18129); Cerro Campana, 400 m.a.s.l., 30 October 1985, *A. Sagástegui A., J. Mostacero L., E. Alvítez, S. López, R. Ramírez, S. Leiva, F. Mejía, & F. Peláez 12940* (F 1994372, HUT 22276). Cerro Negro, 300 m.a.s.l., 16 December 1983, *A. Sagástegui A., J. Mostacero L., & M. Diestra Q. 11010* (F 1933648, HUT 17935, US 3470035). Prov. Virú, Km 524, Lomas N of Virú, 330 m.a.s.l., 4 February 1998, *S. Leiva G., M. O. Dillon, A. Sagástegui A., & V. Quipuscoa S. 2144* (F 2190619); Km 524, Lomas N of Virú, 330 m.a.s.l., 4 February 1998, *S. Leiva G., M. O. Dillon, A. Sagástegui A., & V. Quipuscoa S. 2147* (F 2190620); Lomas de Virú, 450 m.a.s.l., 15 September 1986, *J. Mostacero L., S. Leiva G., & J. Guevara B. 1433* (F 1983673, HUT 22652); Lomas de Virú, 400 m.a.s.l., 20 January 1984, *A. Sagástegui A. & J. Mostacero L. 11369* (GH, HUT 11369). **Lima**: Atocongo, 300–350 m.a.s.l., 28 September 1947, *R. Ferreyra 2452* (GH); Prov. Barranca, vicinity of San Juan, 100–120 m.a.s.l., 13 November 1948, *R. Ferreyra 4097* (US 1998596); Lomas of Lurín, 200–250 m.a.s.l., 18 August 1953, *R. Ferreyra 9532* (GH); Barranco, 300 m.a.s.l., 8 September 1910, *A. Weberbauer 5701* (B; F 548539, F 629241, GH, US 1444891); Barranca, 10°25'37"S, 77°55'20"W, 300 m.a.s.l., 10 October 2002, *M. Weigend, M. Ackermann, & J. Alban B. 7362* (B 100094993); 5 km N of Barranca, 40 m.a.s.l., 5 September 1938, *C. R. Worth & J. L. Morrison 9113* (GH, K). Prov. Callao, ca. 8 ft, 18 September 1923, *J. F. Macbride 5883* (F 536887, GH, US 1474535). Prov. Chancay, Lomas de Dona Maria, S of Huacho, 340 m.a.s.l., 19 September 1938, *H. E. Stork, O. B. Horton, & C. Vargas C. 9236* (GH, K); Chancay, Lomas de Pascamayo, 300 m.a.s.l., 4 October 1938, *H. E. Stork & C. Vargas C. 9352* (F 1491924, GH, K); Prov. Huaura, Lomas of Lachay, ca. 105 km N of Lima on Pan-American Highway, 300–500 m.a.s.l., 15 October 1983, *M. O. Dillon, D. Dillon, M. Chanco, & E. Carrillo 3621* (F 1941753). Prov. Huaral, Lachay Reserve, along Pan-American Hwy, 20.1 km N of junction with road to Salinas, 17 September 2001, *M. McMahon, L. Hufford, & J. Opisso 582* (F 2243093); Lomas de Lachay, 30 October 1965, *T. Maekawa et al. s.n.* (MAK 141145), Lomas de Lachay, 100–500 m.a.s.l., 26 September 1997, *M. Weigend & H. Förther 97/537* (F 2211310, HUT 34037). Prov. Huarichirí, Lomas de Pucará, Lurín, 600 m.a.s.l., 20 July 1995, *S. Llatas Q. 3876* (HUT 29310). Prov. Lima, 12°26'08"S, 76°45'10"W, 90 m.a.s.l., 16 February 1994, *E. F. Anderson, J. McAuliffe, K. & F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7844* (F 2143987); San Agustín, 27 September 1940, *E. Asplund 13794* (US 2224745); Atocongo, 25 km S of Lima, 200–250 m.a.s.l., 7 August 1948, *R. Ferreyra 3909* (GH, US 1998591); Lomas de Amancaes, near Lima, 500–600 m.a.s.l., 7 October 1948, *R. Ferreyra 4050* (US 1998594); Lomas de Caracoles entre Lima y Cañete, 200–250 m.a.s.l., 3 September 1950, *R. Ferreyra 8027* (GH); Cerro Agustino cerca a Lima, 370–380 m.a.s.l., 9 August 1952, *R. Ferreyra 8381* (GH); Lomas de Lachay cerca a Chancay, 350–350 m.a.s.l., 24 September 1952, *R. Ferreyra 8725A* (GH); Quebrada de Armendares, Miraflores, 9 km S of Lima, 12°08'S, 77°03'W, 5–20 m.a.s.l., *F. R. Fosberg, R. Ferreyra, & E. Cerrate 28237* (US 2964589); Chorrillos near Lima, ca. 500 ft, 15 September 1923, *J. F. Macbride 5858* (F 536862, GH, K); Chorrillos near Lima, ca. 500 ft, 15 September 1923, *J. F. Macbride 5859* (F 536863); Lurín near Lima, 50 m.a.s.l., 24 October 1965, *T. Maekawa et al. s.n.* (MAK 141144); Dist. Lurigancho, Campoy, 305 m.a.s.l., 12 October 1936, *Y. Mexia 4027* (GH); Capilla de Caringa, ca. 20 km inland of Punta Negura, S. of Lurín, 6 October 1984, *M. Ono & T. Masuzawa s.n.* (MAK 229691); Lomas de Atocongo, 1 October 1980, *M. Ono, T. Masuzawa, & N. Ohga s.n.* (MAK 197081); Lomas de Ancon, 30 September 1980, *M. Ono et al. s.n.* (MAK 197080), Ancon, 23 October 1980, *M. Ono et al. s.n.* (MAK 197082); Amancaes, 200–400 m.a.s.l., 30 June 1925, *F. W. Pennell 14808* (F 558736, GH); vicinity of Lima, 4 July 1914, *Mr. & Mrs. J. N. Rose 18578* (US 761257); Cerro Jerónimo, 700 m.a.s.l., 1946, *J. J. Soukup 3139* (F 1390494). Prov. Yauyos, Lomas de Quilaná, 12°57'13"S, 76°26'29"W, *M. Weigend, M. Ackermann, & M. I. Latorre 7359* (B 1000094995). Prov. Huaral, Lomas de Iguanil vel San Juan vel Loma de Los Grenstros, 2 October 1976, *L. Bernardi 16409* (F 2006551); Pan-Americana Hwy, Km 78 N of Lima, Lomas de San Juan San Cayetano de Chanayllo, ca. 100 m.a.s.l., 17 August 1964, *P. C. Hutchison 6303* (F 1641790). No exact locality: *J. J. Soukup 1284* (F 990359); *Wilkes Explor. Exped. s.n* (US 57458). Cultivated. PERU. **Lima,** Miraflores, ca. 100 m.a.s.l., 2 December 1981, *T. Plowman 11054* (F 1896843, K). USA. **Illinois.** Chicago, 3311 N. Seeley Ave., *T. Plowman 14482* (F 2091591, GH01563471, HUT 24619, US 3212600).

F12. ***Nolana intonsa*** I.M. Johnst., Contrib. Gray Herb. 112: 34. 1936. TYPE: CHILE. Tarapacá: Iquique, 20°13'S, October 1904, *P. Martens s.n.* (Holotype: GH [00282340]). Fig. 228–229.

Digital image: Holotype of *Nolana intonsa* from Harvard University Herbaria, Cambridge [GH00 282340]. https://s3.amazonaws.com/huhwebimages/31768F4B8E44499/type/full/282340.jpg

Homotypic synonym: *Nolana crassulifolia* Poepp. ssp. *revoluta* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 94. 1981.

Spreading perennial *herbs* or *shrubs*; stems decumbent, forming dense mats 0.5–1.0 m in diam., conspicuously shaggy-villous, inconspicuously capitate-glandular. *Leaves*

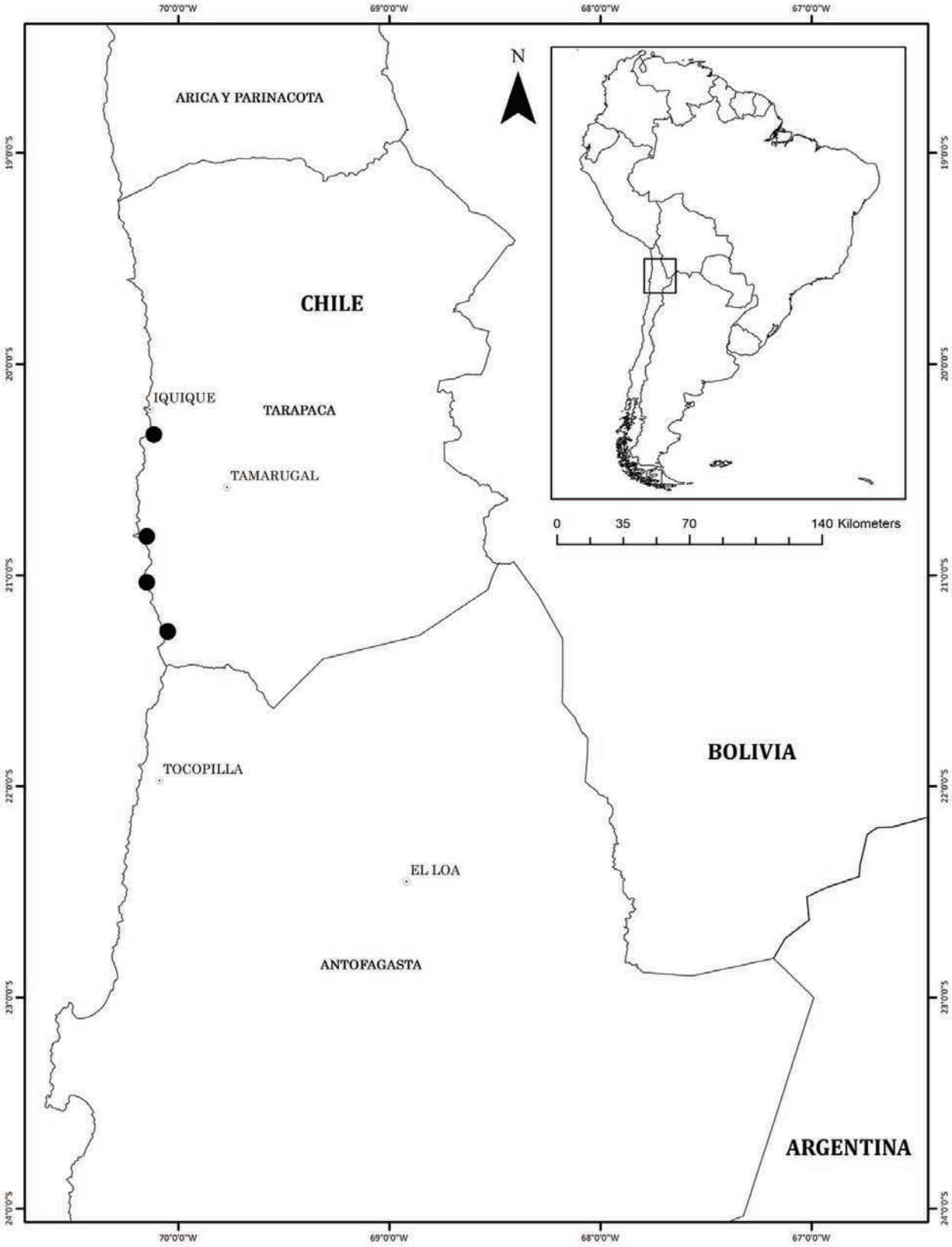


FIGURE 228. Distribution of *Nolana intonsa* I.M. Johnst.

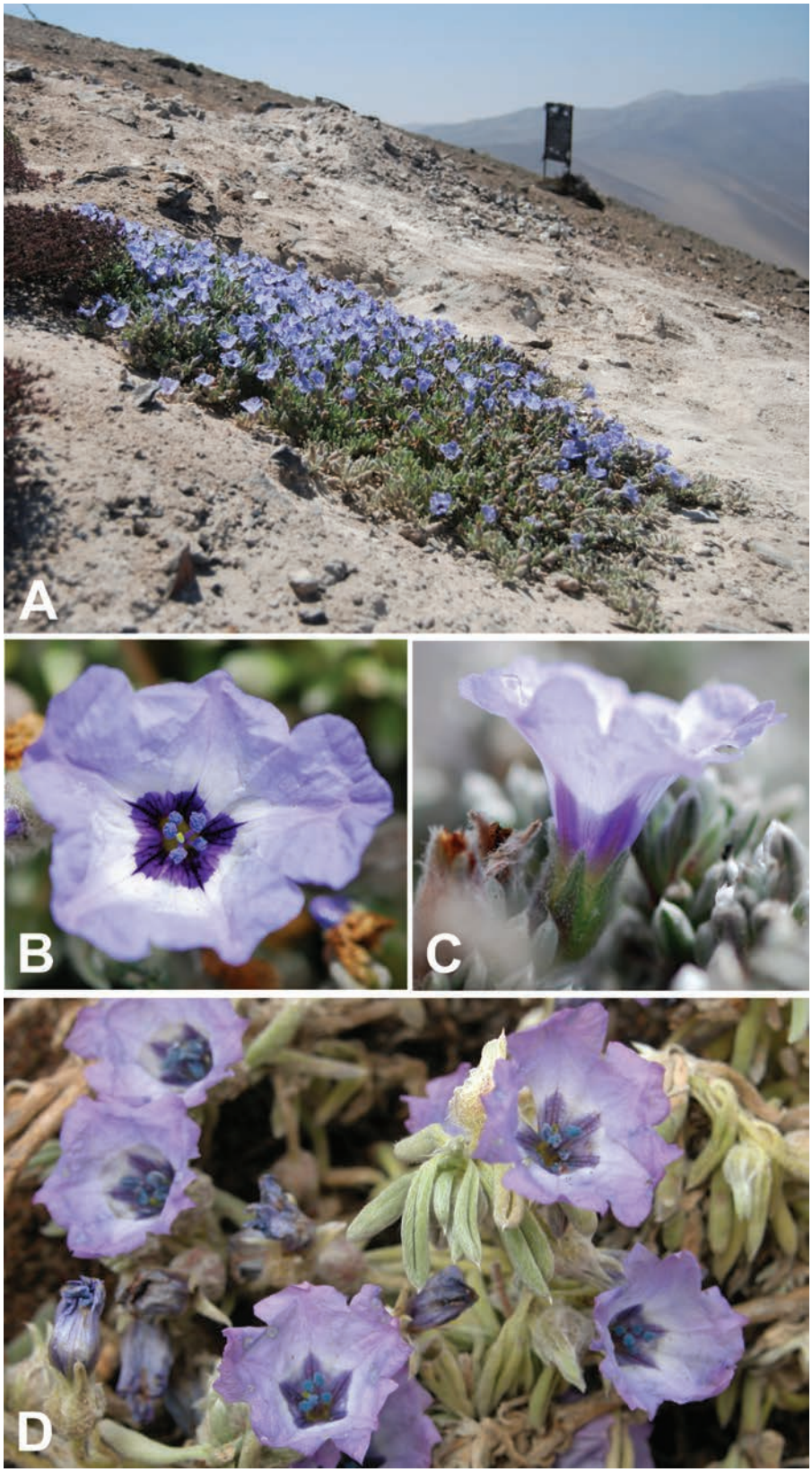


FIGURE 229. *Nolana intonsa*. **A**, Spreading shrubs, small fog trap in background; **B**, Corollas with a dark purple band and guides in the throat, blue anther thecae and pollen; **C**, Lateral view of flower with calyx lobes cut to the middle; **D**, Densely pubescent leaves. Photographs by Josefina Hepp.

alternate, blades narrowly spathulate-linear, 20–30 mm long, 10–20 mm wide, shaggy-villous with non-glandular trichomes, succulent, margins plain, apically obtuse, basally attenuate. *Inflorescences* of solitary flowers, terminal and axillary, pedicels 1.0–4.5 cm long. *Flowers* 5-merous; calyces cupulate, ca. 1 cm long, tube ca. 4 mm wide, ca. 3 mm long, lobes cuneate erect, ca. 2 mm wide, apically long-acuminate; corolla infundibularis, violet, ca. 2 cm long, ca. 2 cm wide, tube ca. 5 mm long, ca. 1 mm wide, 5 deep purple guides, pubescent; filaments unequal, densely pubescent, 4–6 mm long; anthers blue; nectary orange. *Mericarps* 4–5 large, ca. 3.5 mm long, ca. 2.5 mm wide, 8–10 smaller at base; seeds 1–8 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *intonsus*, unshaven, bristly, shaggy, and refers to the obvious pubescence on the vegetative features of the plant.

Distribution and Ecology: Chile, Region of Tarapacá; 300–850 m.a.s.l. (Fig. 228). It is recorded from a few isolated *lomas* formations in sandy soils. It is typically confined to higher elevations; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana intonsa is typically a spreading shrub with sericeous pubescent leaves (Fig. 229A). The corollas possess a dark purple band in the throat and dark purple guides (Fig. 229B), quite unlike any other strictly Chilean species. The sericeous pubescence and corolla pigmentation suggest relationships with species recorded from southern Peru, something Johnston realized (see below). In molecular studies, *N. intonsa*, as well as *N. tarapacana*, are recovered with Peruvian species, specifically *N. aticoana* and *N. cerrateana* (Dillon et al., 2009).

Johnston (1936: 34) commented that *N. intonsa* resembled the Peruvian species, *N. gayana*, in gross habit, but differed in having long attenuate calyx lobes and pubescence consisting of slender elongate simple hairs rather than short dendritic trichomes. Furthermore, it was separated from *N. gayana* by over 1200 kilometers. In his publication on the Flora of the Nitrate Coast, Johnston (1929) listed this species incorrectly as representing *N. gayana*. While Johnston's primary hypothesis that this species was related to Peruvian taxa was correct, the molecular and morphological data do not support a close relationship between *N. intonsa* and *N. gayana*.

Pollinators have been observed visiting *Nolana intonsa* (Fig. 9B), and one of the more conspicuous is the common hawkmoth, *Hyles annei* (Sphingidae). It is likely that any insect visitors are effective pollinators and opportunists.

Additional specimens examined: CHILE. **Tarapacá**: Iquique, Alto Patache, 800 m.a.s.l., 23 November 1997, *E. Belmonte 97-713* (CONC 143507, SGO 149102); Alto Patache, S. de Iquique, 775 m.a.s.l., 12 November 2015, *H. Larrín s.n.* (SGO 169091, SGO 169098); Alto Punta Patache, 20°49'S, 70°09'W, 300 m.a.s.l., 28 October 1997, *R. Pinto s.n.* (SGO 142969); 20°49'S, 70°09'W, 8 November 1997, *R. Pinto s.n.* (SGO 142968); Alto Punta Lobos, 21°02'S, 70°09'W, 500 m.a.s.l., 1 November 1997, *R. Pinto s.n.* (SGO 142977); Alto Punta Lobos, 17 January 1998, *R. Pinto s.n.* (SGO 142978); Alto Chipana, 21°16'S, 70°03'W, 9 November 1997, *W. Sielfeld 15* (SGO 143051); Alto Punta Patache, 20°49'S, 70°09'W, 1 November 1997, *W. Sielfeld 46* (SGO 143052); Cerro Tarapacá, 20°20'S, 70°07'W, 850 m.a.s.l., 5 December 1995, *W. Sielfeld s.n.* (SGO 144338); Punta Lobos, 21°03'S, 70°13'W, 1 January 1999, *W. Sielfeld & R. Pinto s.n.* (SGO 144332).

F13. ***Nolana johnstonii*** Vargas, Rev. Univ. Cuz. 107: 155. 1954. TYPE: PERU. Moquegua: Lomas de Mostacilla, Ilo, 50–300 m, 11–13 November 1949, *C. Vargas C. 8570* (Holotype: CUZ [014168]; Isotypes: GH [GH00282339], USM [USM 242133, USM000563]). Fig. 230–232.

Digital image: Isotype of *Nolana johnstonii* from Herbario San Marcos, Lima [USM000563]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.usm000563

Homotypic synonym: *Nolana laxa* (Miers) I.M. Johnst., Contr. Gray Herb. 112: 59. 1936, fide Mesa-M. (1981).

Perennial suffrutescent *herbs* or weak *subshrubs*; taproot enlarged; stems 30–40 cm long, decumbent, 3–10 mm in diam., densely villous, trichomes stiff and straight or apically bent. *Leaves* alternate, blades obovate, oblanceolate or spathulate, occasionally elliptic, 15–25 (–30) mm long, 10–20 mm wide, apically obtuse to rounded, basally attenuate, strigulose, margins ciliolate with stiff, crooked trichomes. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 7–12 mm long, densely villous with stiff, straight trichomes as on stems. *Flowers* 5-merous; calyx lobes equal, villous with stiff, straight trichomes; corollas infundibularis, violet to white. *Mericarps* 8–12, globose to oblong, black, 2–3 mm long, 1.5–2.2 mm in diam.; seeds 1–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Ivan Murray Johnston (b. 1898–d. 1960), a botanist and systematic monographer from the Arnold Arboretum and Gray Herbarium. Johnston's floristic exploration in northern Chile in 1925 are benchmark studies, recounting biodiversity from a remote geographic area during a strong El Niño event. Johnston authored no fewer than 22 new *Nolana* species recognized here and provided many transfers. His treatment of the flora of northern Chilean (Johnston, 1929) has been translated into Spanish, and the taxonomy has been updated (Muñoz-S. and Moreira-M., 2022).

Distribution and Ecology: Peru, Departments of Arequipa, Moquegua, and Tacna; (100–)350–650(–800) m.a.s.l. (Fig. 230). It is recorded from sandy/rocky soils at some distance from the coast.

Nolana johnstonii is a distinctive annual with ovate to oblanceolate leaves near the base (Fig. 231A–C, Fig. 232A), which is unlike the shape observed in other species. The cauline leaves are considerably smaller but essentially the same obovate to ovate shape. The pubescence of stiff, strigose trichomes on the leaves and peduncles is distinctive. The flower color of the type is white, which is the form most frequently encountered (Fig. 232A, D), but rarer are the pale blue forms with a dark band in the throat and pale purple anthers (Fig. 232C). The mericarps are multiseriate with four or five larger mericarps (Fig. 232B).

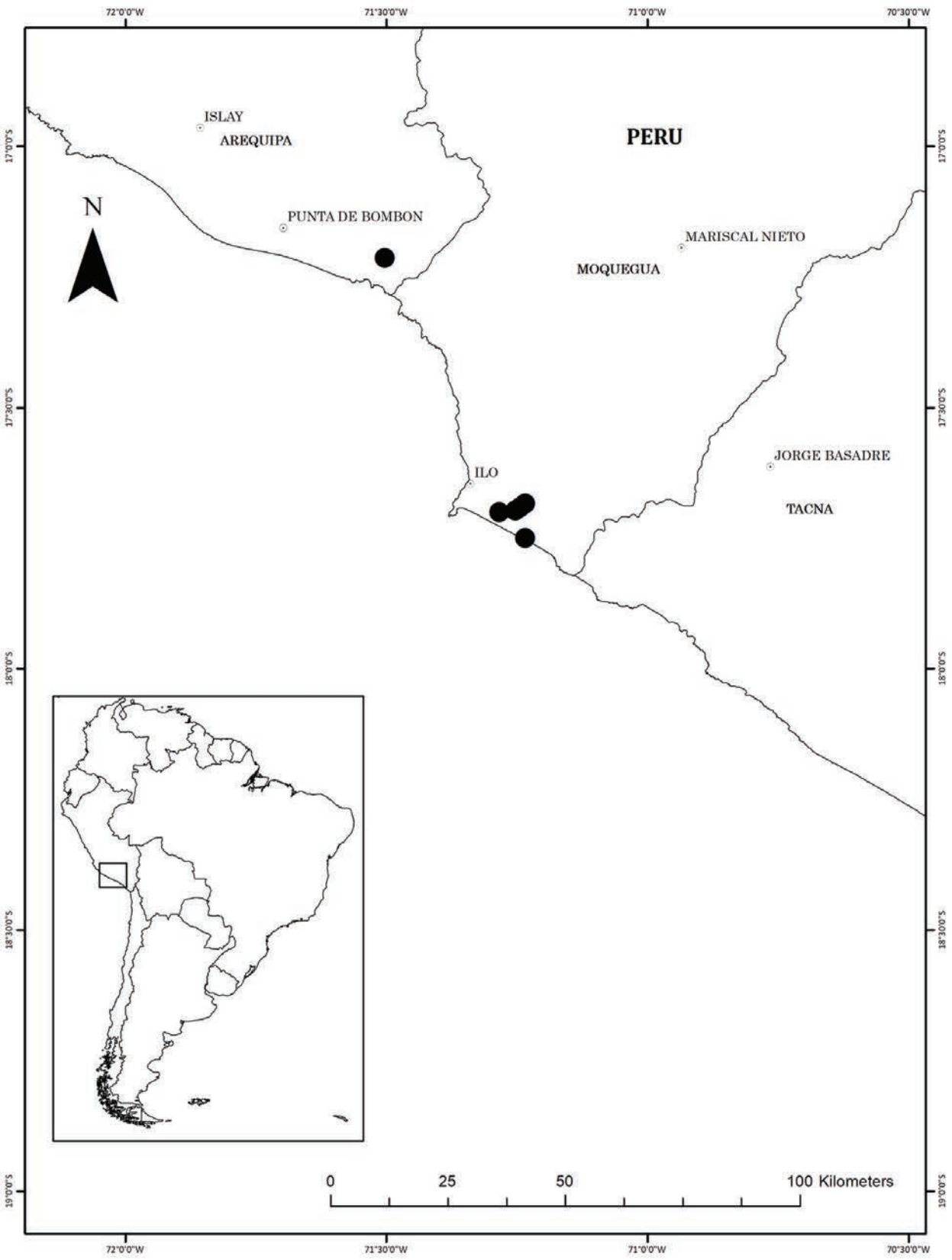


FIGURE 230. Distribution of *Nolana johnstonii* Ferreyra.

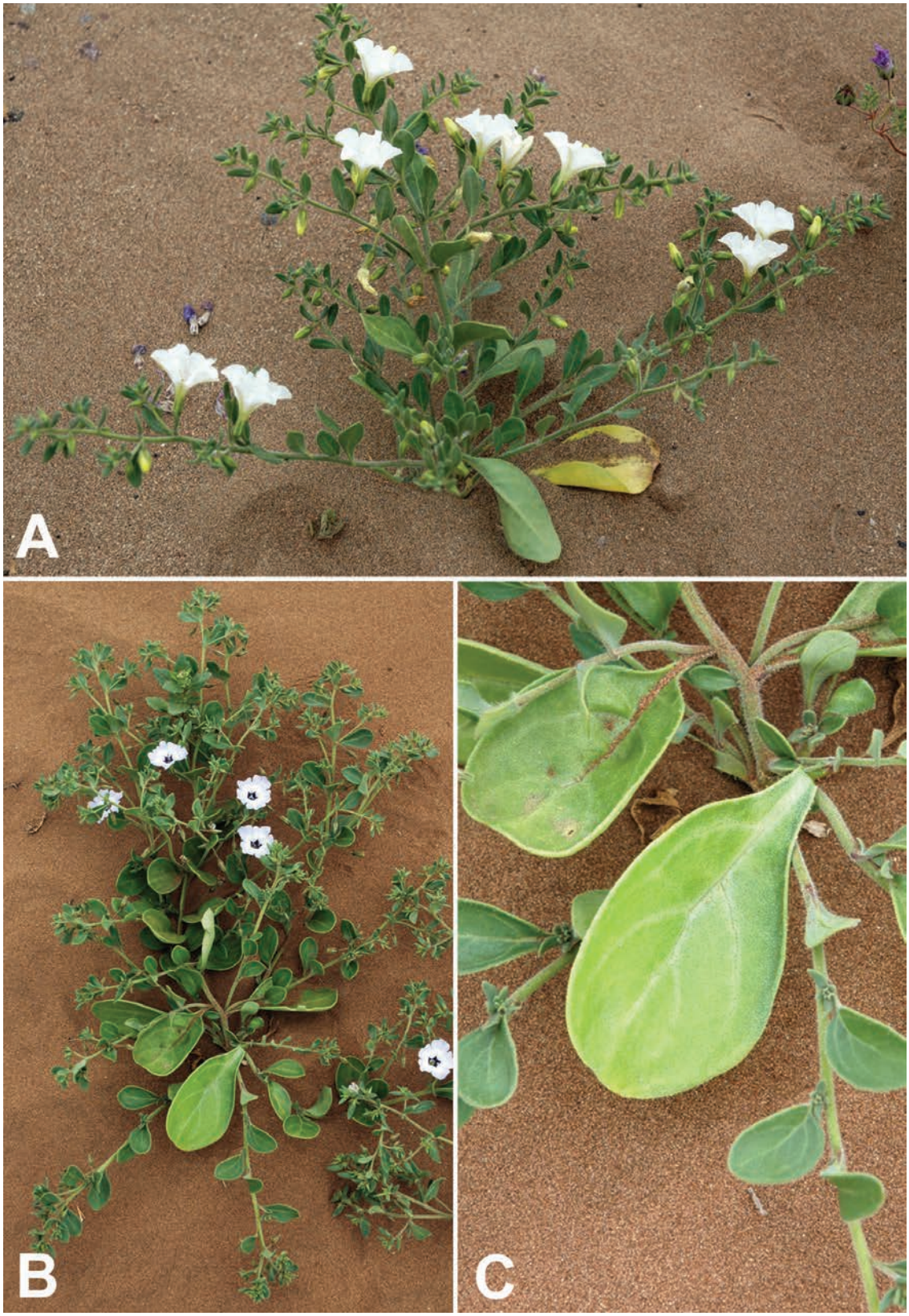


FIGURE 231. *Nolana johnstonii*. **A–B**, Flowering annuals with ovate to oblanceolate leaves near the base; **C**, Obovate to ovate leaves.

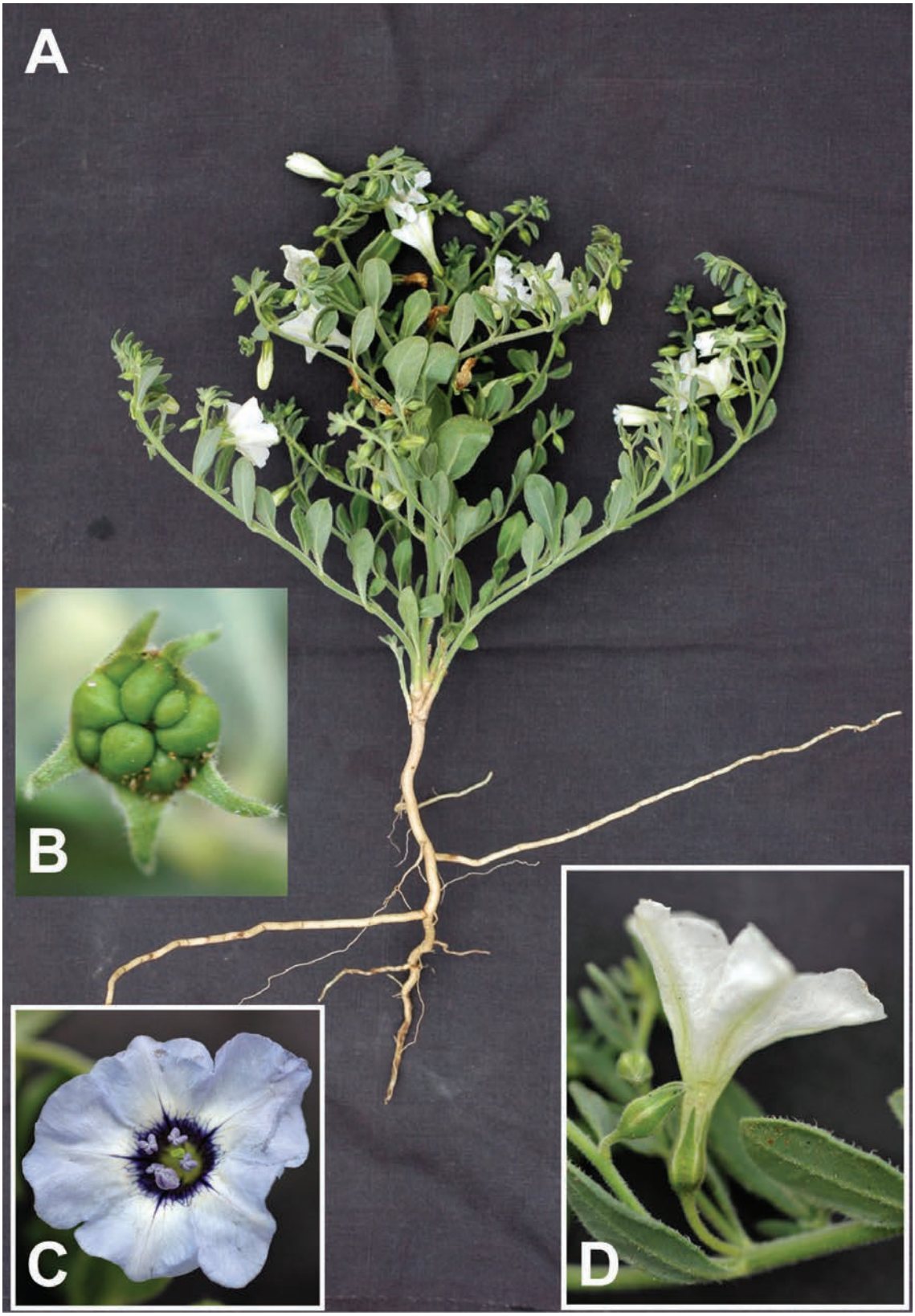


FIGURE 232. *Nolana johnstonii*. **A**, Flowering individual removed from sand; **B**, Multiseriate mericarps; **C**, Frontal view of blue corolla with a dark band in the throat and blue anther thecae and pollen; **D**, Lateral view of the typical white flowers.

Additional specimens examined: PERU. **Arequipa**: Prov. Islay, Dist. Punta de Bombón, cima de lomas de Jesús, 17°12'49"S, 71°30'08"W, 760 m.a.s.l., 29 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6264* (HSP 8770); Islay, 600–900 m.a.s.l., 1 August1940, *C. Vargas C. 2029* (GH). **Moquegua**: Prov. Ilo, Ca. 20 km E of Ilo, 620 m.a.s.l., 12 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3318* (CONC, E, F 1950165, F 2043418, GH, SGO); Ilo: ca. 16 km SE of Ilo, 530 m.a.s.l., 17°41'S, 71°14'W, 25 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8221* (E, F 2199319, GH); Moquegua, Ilo: ca. 15 km SE of Ilo, 17°41'S, 71°17'W, 349 m.a.s.l., 25 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8225* (E, F 2199323, GH, SGO, US); arriba de Ilo, 17°42'S, 71°15'W, 600 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9011* (E, F 2276620, GH, HSP 005282, SGO, US 3512554); Lomas de Ilo (Mostazal), 6 October 1957, *R. Ferreyra 12583* (USM); Lomas de Ilo, 250–350 m.a.s.l., 30 November 1955, *R. Ferreyra 11600* (USM); Lomas de Ilo, 600–650 m.a.s.l., 6 October 1957, *R. Ferreyra 12572* (USM 81185); Lomas de Ilo, 400–500 m.a.s.l., 24 October 1970, *R. Ferreyra 17720* (USM 81193); arriba de Ilo, 17°41'16"S, 71°14'21"W, 21 October 2003, 580 m.a.s.l., *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2919* (HSP 000549); arriba de Ilo, 17°41'16"S, 71°14'21"W, 580 m.a.s.l., 21 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2921* (HSP000550); Lomas de Ilo, 17°41'16"S, 71°14'21"W, 597 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3428* (HSP 002676), Lomas de Ilo, 17°41'26"S, 71°14'35"W, 597 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3431* (HSP 002679), Lomas de Ilo, 17°41'26"S, 71°14'35"W, 597 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3432* (HSP 002680), Lomas de Ilo, 17°41'50"S, 71°15'09"W, 566 m.a.s.l., 15 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3437* (HSP 002684); Lomas de Mostacilla, cerca a Ilo, 400–800 m.a.s.l., 28 October 1966, *C. Vargas C. 17984* (CUZ, USM); Lomas de Ilo, 28 October 1966, *C. Vargas C. 18002* (CUZ, USM), *18005* (CUZ); 400–800 m.a.s.l., *C. Vargas C. 17984* (CUZ); Lomas de Mostazal, ca. 10 km S of Ilo, 100–200 m.a.s.l., 12 October 1997, *M. Weigend & H. Förther 97/837* (F 2211298, HUT 34108). **Tacna**: Prov. Tacna, Lomas de Morro Sama, 7 October 1957, *R. Ferreyra 12648* (USM 81187); Lomas de Sama Grande (ca. 40 km NW Tacna), 700–900 m.a.s.l., 10 October 1997, *M. Weigand & H. Förther 97/806* (F 2211299, HUT 34121).

F14. ***Nolana lezamae*** M.O. Dillon, S. Leiva, & Quip., Arnaldoa 14(2): 184. 2007. TYPE: PERU. Ancash: Prov. Corongo, Dist. Corongo. Tres Cruces, entre La Pampa–Yuramarca, 8°41'S, 77°55'W, 2144 m, 30 June 1998, *S. Leiva G., V. Quipuscoa, P. Lezama A., & E. López 2212* (Holotype: HAO, destroyed; Lectotype designated by Dillon and Quipuscoa, 2023: HUT [032058], Isolectotypes: E, F 2329913, G, GH, HSP). Fig. 233–236.

Digital image: No image is currently available via the internet; the lectotype image of *Nolana lezamae* (Fig. 234) was provided by Universidad Nacional de Trujillo, Trujillo, Peru [HUT-32058].

Succulent, perennial *herbs*; stems prostrate, flexulose, 50–160 cm long, much-branched, minutely glandular pubescent, reddish. *Leaves* verticillate, blades linear, 23–33 mm long, 2–3 mm wide, glabrous, succulent, apically acute, basally cuneate. *Inflorescences* of solitary flowers; pedicels filiform, glabrous, (5–)9–13 mm long. *Flowers* 5-merous; calyx campanulate, 4.0–4.5 mm wide at anthesis, glabrous, tube 4.0–4.5 mm long, 5–6 mm wide; 5-lobed, bilabiate, lobes deltoid, subequal 6–7 mm long, 3.5–4.5 mm wide; corollas narrowly infundibularis, 18–20 mm wide, deep purple, internally glabrous, externally pubescent, trichomes uniseriate and glandular, tube 14.5–15.0 mm long, 27–28 mm wide, 5-lobed, lobes obtuse, 2.5–3.0 mm long, 9–10 mm wide, central acumen obtuse; stamens 5, included, filaments inserted on lower third of corolla, unequal, three 2–3 mm long, two 3.5–4.5 mm long, pilose at the bases; anther thecae 1.5–2.0 mm long, 1.0–1.5 mm wide, purple, pubescent with multicellular trichomes; ovary glabrous, 1.4–1.5 mm long, 1.8–2.0 mm wide, basal nectary, 5 carpels, style included, 7.0–7.5 mm long, stigma capitate, green, sub-lobate, ca. 1 mm in diam. *Mericarps* 5, 3.5–4.5 mm long, 8.5–9.0 mm in diam., included within the expanding calyx; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Pedro Lezama Asencio (b. 1959–), professor at the Universidad Privada Antenor Orrego in Facultad de Medicina, Laboratorio de Bioquimica. Dr. Lezama was born and raised in Corongo, Ancash, a village not far from the type locality. He has been an enthusiastic member of many collecting expeditions throughout Peru.

Distribution and Ecology: Peru, Department of Ancash; 2000–3000 m.a.s.l. (Fig. 233). It is restricted to, but frequent within, a small area of arid vegetation with connections to the coastal *lomas* formations.

Nolana lezamae has a distinctive inland distribution at elevations above 2000 m.a.s.l. and, as a perennial, derives its moisture from episodic rains. Individuals can reach very large proportions with prostrate stems nearly two meters in length (Fig. 236A). It is distinctive with narrow glabrous leaves, bilabiate calyces (Fig. 236B), and purple corollas with a dark purple band within the throat (Fig. 236C). There are invariably five mericarps that are connate at lateral

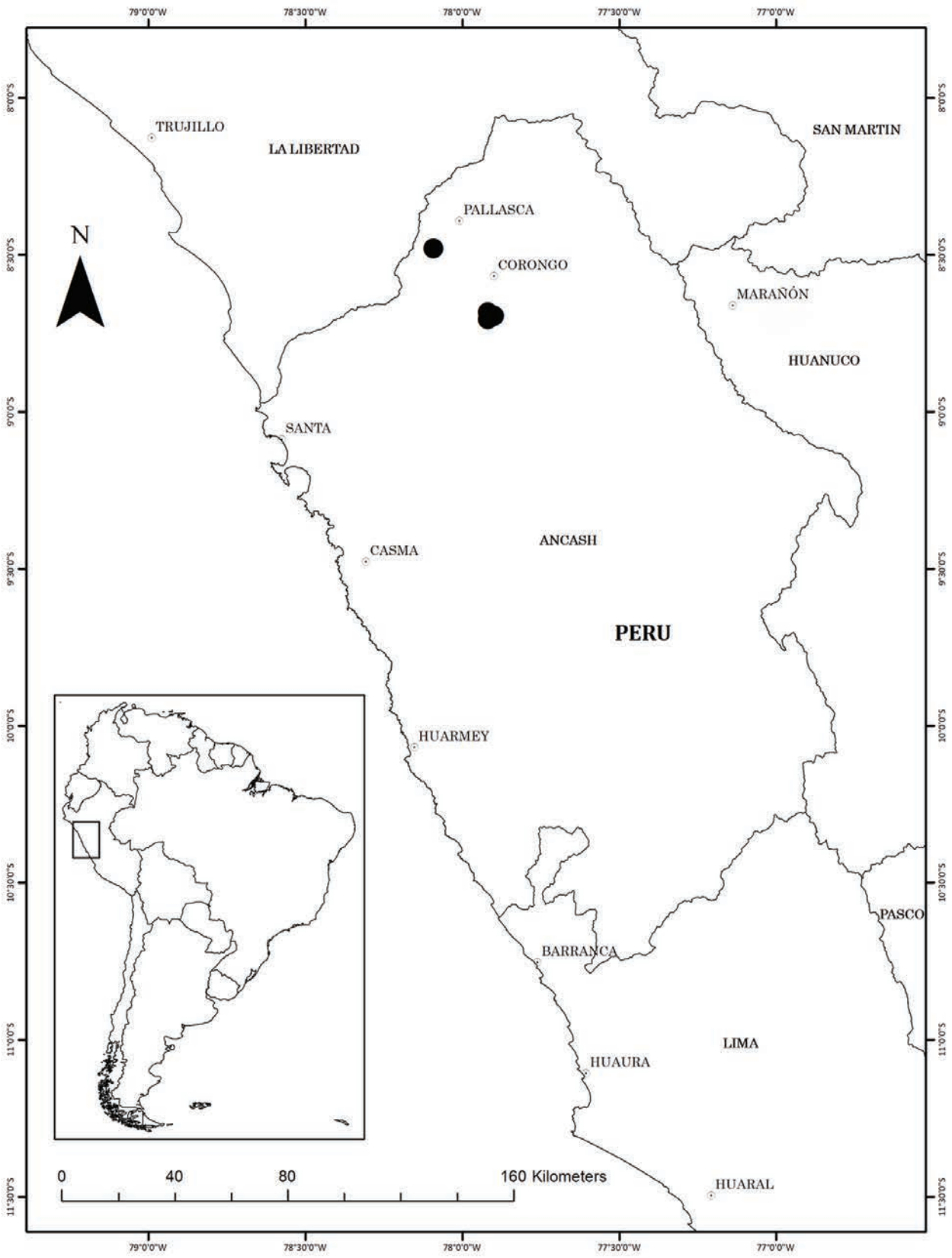


FIGURE 233. Distribution of *Nolana lezamae* M.O. Dillon, S. Leiva, & Quip.

FIGURE 234. Lectotype of *Nolana lezamae* housed at HUT. No digital image is available via the internet.

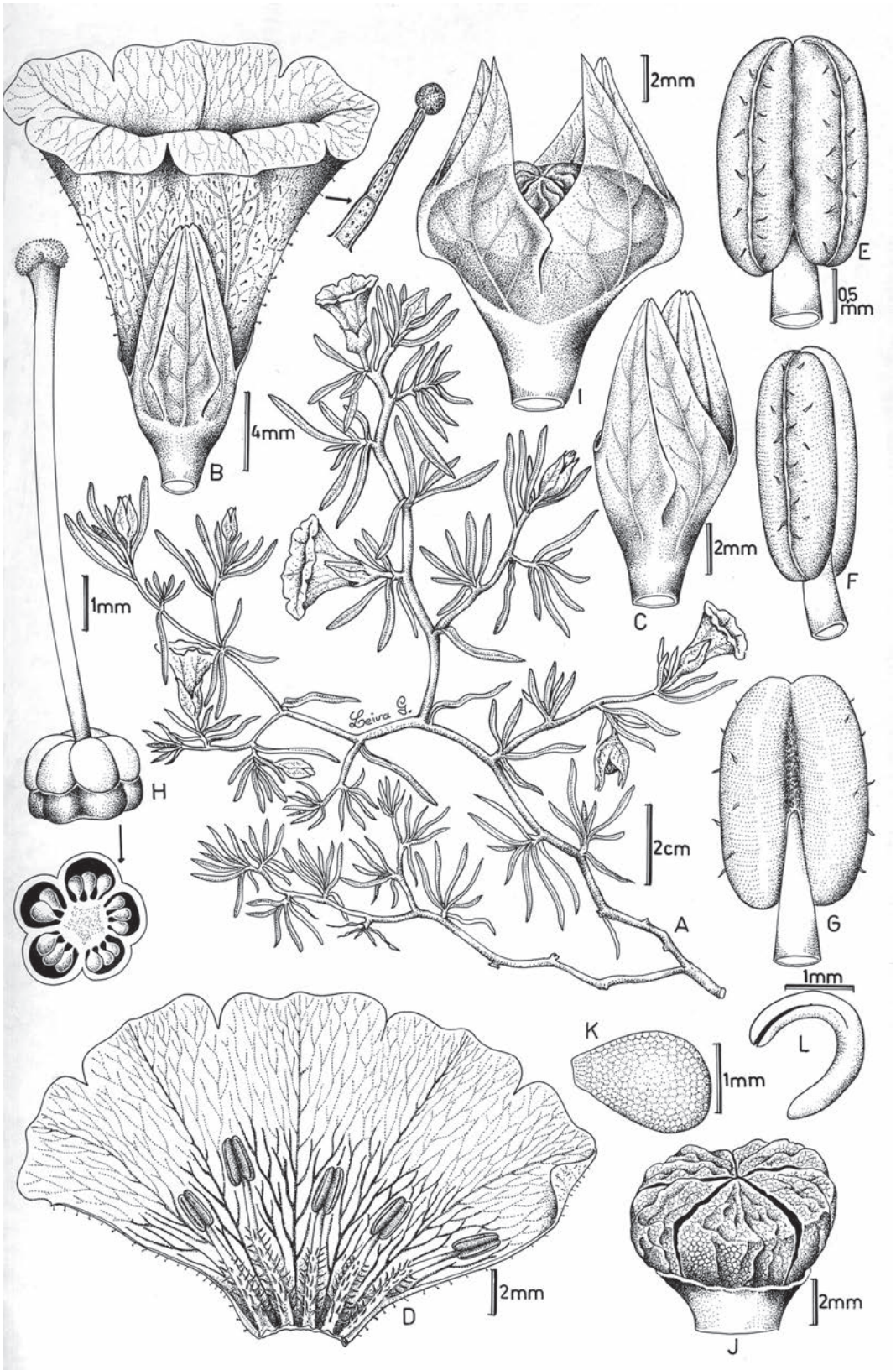


FIGURE 235. Illustration of *Nolana lezamae*. **A**, Habit; **B,** Flower; C, Detail of floral glandular-capitate trichome; **D**, Gynoecium; **E**, Dissected corolla; **F,** Mericarps; **G**, Calyx expanding with mericarps; **H**, Calyx with connate lobes; **I**, Anther thecae dorsal view; **J**, Anther thecae lateral view; **K**, Anther thecae ventral view. Drawn by Segundo Leiva Gonzáles.

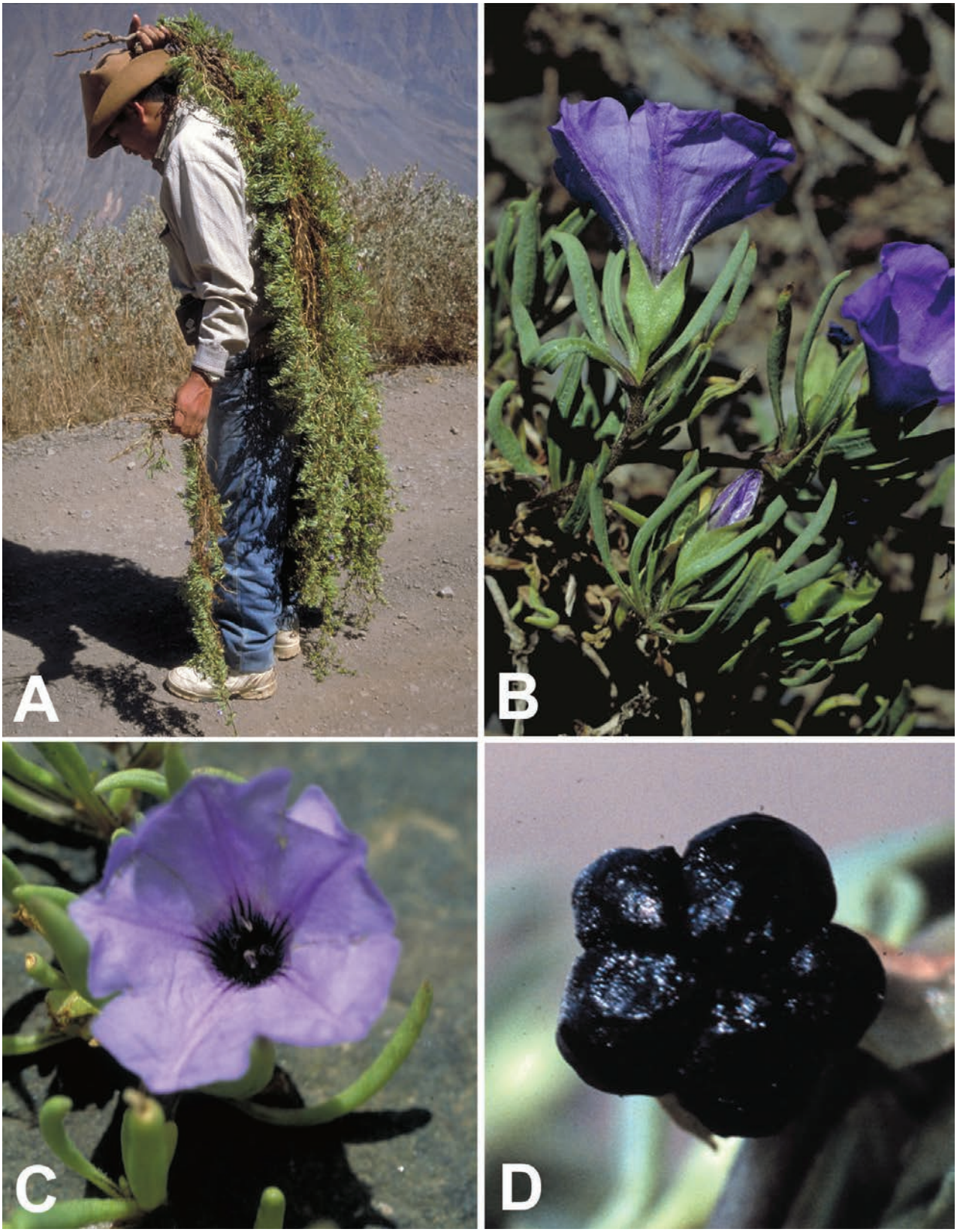


FIGURE 236. *Nolana lezamae*. **A**, Large perennial with prostrate stems to two meters long; **B**, Narrow glabrous leaves and bilabiate calyces; **C**, Purple corollas with a dark purple band within the throat; **D**, Five mericarps connate at lateral surfaces.

surfaces (Fig. 236D). The overall morphology closely resembles that of *N. humifusa*, a species confined to coastal *lomas* environments of northern Peru; however, the latter species is distinguished by its elliptic to ovate leaves and spurred calyces. The presence of trichomes on the anther thecae is an unusual character shared by *N. humifusa* (Fig. 223D–E) and *N. lezamae* (Fig. 235E–G).

Utilizing the GBSSI waxy marker (Dillon et al., 2007c), *N. lezamae* is grouped with *N. aticoana*, *N. humifusa*, and *N. urubambae*, all species that are readily distinguished by their larger laminar leaves and floral morphology.

Additional specimens examined: PERU. **Ancash**: Prov. Corongo, Dist. Corongo. Tres cruces, desvío La Pampa–Sihuas, 1700 m.a.s.l., 6 August 1993, *S. Leiva, P. Lezama A., & E. Larco 842* (F 2329914); Tres Cruces, entre La Pampa–Yuramarca, 2280 m.a.s.l., 4 December 1998, *S. Leiva G., P. Lezama A., & M. O. Dillon 2241* (F 2329916, E); Tres Cruces, 2040 m.a.s.l., 5 December 1998, *S. Leiva G., P. Lezama A., & M. O. Dillon 2250* (F 2329915); Km 1–3 on road to Corongo, 8°41'38"S, 77°53'51"W, 2334 m.a.s.l., 18 May 2013, *T. Särkien, H. M. Baden, E. McAlister, & D. Percy 4688* (BM001120889, E 00700707, HUT 55653). Prov. Pallasca, between Tauca & Chuquicara, 8°28'47"S, 78°05'27"W, 2038 m.a.s.l., 12 May 2013, *S. Knapp, T. Särkien, H.M. Baden, P. Gonzáles, & E. Perales 10643* (E00700840, HUT 55471); alrededores de La Pampa, 8°42'S, 77°55'W, 2200 m.a.s.l., 13 May 2003, *A. Sagástegui A, M. Zapata C., E. Rodríguez R., & V. Medina 17443* (HUT 41666); road Sihuas to Corongo, 8°42'S, 77°00'W, 26 April 2004, *M. Weigend & C. Schwarzer 8043* (F 2284706, HUT 42512).

F15. ***Nolana mariarosae*** Ferreyra, Bol. Soc. Peruana Bot. 7(1-1): 3. 1974. TYPE: PERU. Arequipa: Prov. Caravelí: lomas entre Atico y Ocoña, 3 October 1957, 200–300 m, *R. Ferreyra 12490a* (Holotype: USM [242135, USM000565], Isotypes: USM [USM 242135, USM000566; USM 242135, USM000567; USM 242135, USM000568]). Fig. 237–238.

Digital image: Holotype of *Nolana mariarosae* from Herbario San Marcos, Lima [USM 242135]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000565

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 134. 1981.

Annual *herbs*, 15–40 cm tall, stems branched, ascending, 2–5 mm wide, conspicuously puberulent with capitate-glandular trichomes. *Leaves* alternate, blades lanceolate, succulent, sessile, puberulent with capitate-glandular trichomes, 28–42 mm long, 11–14 mm wide, apically acute, distal leaves linear, 18–22 mm long, 2–3 mm wide, densely puberulent. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 8–10 mm long, pubescent. *Flowers* 5-merous; calyces campanulate, 18–30 mm long, 6–10 mm wide, interior and exterior pubescent, tube 8–10 mm long, zygomorphic, all the lobes on one side, lobes 5, unequal, acuminate, pubescent, the longer 5–8 mm long, 1.0–1.5 mm wide; corollas infundibularis, violet, 32–38 mm long, 24–30 mm wide, slightly lobed, undulate; stamens unequal, 2 larger, 18–20 mm long, 3 smaller, 15–16 mm long, styles 15–16 mm long. *Mericarps* 15–19, ca. 3-seriate, rounded, black, 5 larger mericarps, 2–3 mm long, 1.5–1.8 mm wide, the smaller mericarps 10–14, 1–2 mm long, 0.6–1.6 mm wide; seeds 2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Señora Maria Rosa Gildemeister de Ferreyros (b. 1924–), a benefactor of the Museo de Historia Natural "Javier Prado" in Lima; she donated funds toward the completion of a Pabellón de Botánica at the Museo.

Distribution and Ecology: Peru, Department of Arequipa; 200–300 m.a.s.l. (Fig. 237). It is recorded from the *Lomas* formations between Atico and Ocoña.

Nolana mariarosae has not been encountered in this study and no authentic material has been examined. The calyces are unusually large, with all the lobes on one side (Fig. 238A–B), and they have a trimerous branching pattern, perhaps not unlike the trimerous lax scorpioid cymes in *N. tricotiflora*. Ferreyra (1974: 5) related this species to *Nolana latipes*; however, its overall morphology does not suggest any close relatives. *Nolana mariarosae* has not been included in any molecular studies and is assigned to this clade, based upon overall morphological similarity to other members of the clade, until other data are available.

Additional specimens examined**:** PERU. **Arequipa**: Prov. Caravelí, Lomas de Atico, entre Chala y Camaná, 100–200 m.a.s.l., 3 October 1957, *R. Ferreyra 12492* (GH, USM 80823); Lomas de Atico, 50–100 m.a.s.l., 19 December 1959, *R. Ferreyra 13902* (USM 80824); Lomas de Atico, 50–100 m.a.s.l., 19 December 1959, *R. Ferreyra 13915* (USM 80824); Lomas de Atico, 300–400 m.a.s.l., 31 October 1966, *C. Vargas C. 18219* (CUZ, USM 80820), *18220* (CUZ, USM 80821).

F16. ***Nolana minor*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 4. 1955. TYPE: PERU. Arequipa: Prov. Camaná, La Punta, 20–30 m, 9 November 1947, *R. Ferreyra 2535* (Holotype: USM [242136, USM000569]; Isotypes: F, K [K000532273], MOL [MOL 00547, MOL0004731], US [US 1998577, US00121959]). Fig. 239–240.

Digital image: Holotype of *Nolana minor* from Herbario San Marcos, Lima [USM 242136]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000569

Annual *herbs*, 2–5 cm tall; root simple, filiform, stems simple or few-branched, glabrous. *Leaves* alternate, blades linear-spathulate, 8–14 mm long, 1–4 mm wide, glabrous or inconspicuously glandular-pubescent, margins scarious, apically obtuse, bases largely attenuate, lower leaves with amplexicaul bases, uninerved, sessile. *Inflorescences* of solitary flowers; pedicels 3–4 mm long, pubescent with capitate-glandular trichomes or glabrescent. *Flowers* 5-merous; calyces tubular, glabrous, 3.2–3.5 mm long, lobes 2.3–2.5 mm long, 1.8–2.8 mm wide, bilabiate, obtuse; corolla narrowly hypocrateriformis, blue, 9.6–11.8 mm long, 6.5–7.5 mm wide above, 5-lobed, unequal, obtuse, tube narrow, pubescent internally; stamens unequal, united to tube for 2/3 of its length; 2 larger, 8.5–10.5 mm long,

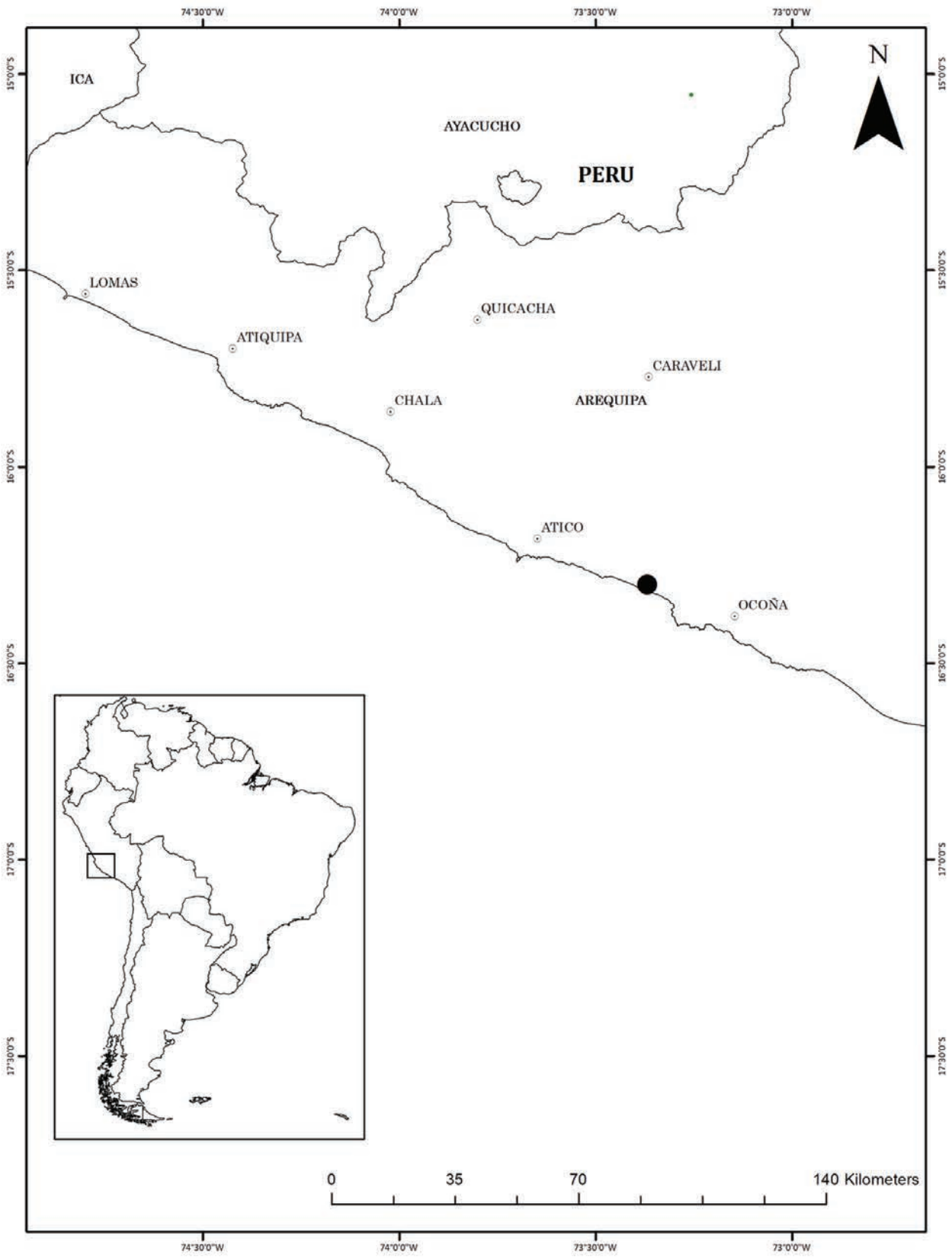


FIGURE 237. Distribution of *Nolana mariarosea* Ferreyra.

FIGURE 238. *Nolana mariarosae*. **A–B**, Flowering branch with large calyces with all lobes on one side.

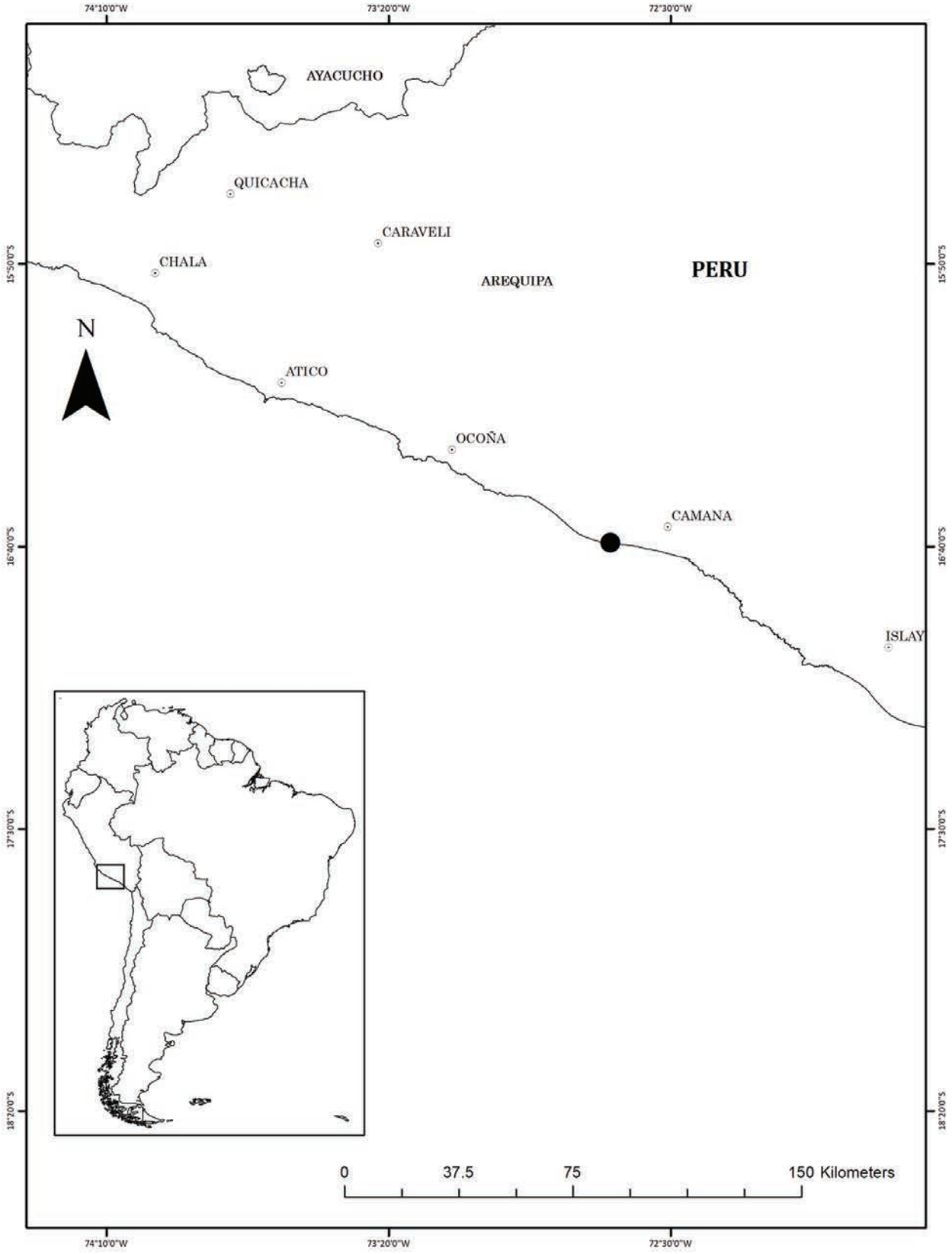


FIGURE 239. Distribution of *Nolana minor* Ferreyra.

3 smaller, 6.5–8.0 mm long; styles 7.5–8.2 mm long. *Mericarps* 2–3, pyriform, brown, 2.6–3.0 mm long, 2.0–2.2 mm wide, obscurely mucronate, contained within the expanding calyx; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *minor*, smaller, inferior, or lesser, and refers to the overall stature of the plant, which is a comparatively minute annual.

Distribution and Ecology: Peru, Department of Arequipa; 20–30 m.a.s.l. (Fig. 239). It is recorded from sandy plains near the ocean, a habitat that would be quite saline and potentially inundated during reoccurring tsunami events that would have covered the area with salt water. The type locality is now complete destroyed by urban development, and it is likely that this species is extinct. It was last collected in 1985 and has not been encountered since.

Nolana minor is a minute, succulent annual only five centimeters tall (Fig. 240), with succulent, terete leaves, and only two mericarps. This species would appear to be related to *N. arequipensis* and *N. thinophila*; however, its relationships have not been tested with molecular techniques. Repeated attempts to locate this rare species have not been successful. The area around La Punta has been the site of extensive housing developments, and, in 2001, the earthquake in southern Peru caused a tsunami that inundated the beachfront of the Camaná area. Given that *N. minor* has not been recollected since 1985, it is feared that this rare species may be extinct.

Additional specimens examined: PERU. **Arequipa.** Prov. Camaná: on sand dune, Camaná beach, ca. 820 km S of Lima, 30 November 1984, *M. Ono s.n.* (MAK 225310); Camaná beach, sand dune, 29 September 1985, *M. Ono, T. Masuzawa, & K. Suzuki s.n.* (MAK 229693).

F17. **Nolana pallida** I.M. Johnst., Contrib. Gray Herb. 112: 69. 1936. TYPE: PERU. Arequipa: Prov. Camaná, Chala, *A. Weberbauer 7183* (Holotype: B, not seen; Isotype: GH [GH00282351]). Fig. 241–247.

Digital image: Isotype of *Nolana pallida* from Harvard University Herbaria, Cambridge [GH00282351]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282351

Heterotypic synonym: *Alibrexia revoluta* Miers, London J. Bot. 4: 508. 1845. *Dolia revoluta* (Ruiz & Pav.) Benth. & Hook.f., Gen. Pl. 2(2): 880. 1876. *Nolana crassulifolia* Poepp. subsp. *revoluta* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 93. 1981.

Plants suffrutescent *perennials*, forming mats to ca. 1 m in diam., branches decumbent, 2–16 cm long, 1–3 mm wide, internodes 2–12 mm long, gray-tomentose with dendritic trichomes. *Leaves* alternate to subfasciculate, blades linear or, at times, lanceolate or oblanceolate, 5–40 mm long, 1.2–9.0 mm wide, margins revolute, apically obtuse, both adaxial and abaxial surfaces canescent with dendritic trichomes; sessile. *Inflorescence* of solitary flowers; pedicels 5–28 mm long, pubescent. *Flowers* 5-merous; calyces 4–11 mm long, 3–7 mm wide, tube campanulate, lobes cut longer than half, 3–4 mm long, 1–2 mm wide at base, more or less equal, acute; corolla infundibularis, lavender-blue, pubescent outside, 12–30 mm long, 8–32 wide, the upper part 5-lobed, lobes obtuse, unequal, tube short; stamens unequal, fused 1/2 length, 10–12 mm long, anthers dark blue; style 10–11 mm long. *Mericarps* 9–14, biseriate, black, globose or reniform, 4–5, 3.2–5.0 mm long, 2.0–3.5 wide, smaller pyriform, 2.2–3.0 mm long, 1.5–1.8 mm wide, more or less opaque; seeds 3–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *pallens*, pale, or *pallidus*, ashen or pale, referring to the dense dendritic pubescence that gives the vegetative parts a gray appearance.

Distribution and Ecology: Peru, Departments of Arequipa and Ica, ranging ca. 400 km; 50–500 m.a.s.l. (Fig. 241). It is recorded from sandy habitats near the ocean.

Illustration: Fig. 246. Illustration of *Nolana revoluta* Ruiz & Pav., Flora Peruviana et Chilensis, plate 113b. (1799).

Fig. 247. Illustration of *Nolana revoluta* Ruiz & Pav., plate 113. Drawings of the Royal Botanical Expedition to the Viceroyalty of Peru (1777–1816).

Nolana pallida is a distinctive element in the southern Peruvian flora. It forms large mats that are buried in the sand and stabilize the shifting, blowing sand (Fig. 242A). The leaves are strongly revolute and densely pubescent with dendritic trichomes, and the calyx lobes are deeply cut to more than half the length of the calyx (Fig. 242B). Typically, in any population, two color forms have a similar morphology (Fig. 242C). The prostrate flowering stems have recurving pedicels that effectively place the mature mericarps into the sand (Fig. 243A). The individuals with lavender or blue corollas have a dark band in the base of the throat, as in many other Peruvian species, and blue pollen (Fig. 243B). The calyces are densely pubescent, and the lobes are cut deeper than the middle of the calyx (Fig. 243C), unlike those in *Nolana gayana*, whose lobes are shorter and cut to no more than the middle of the calyx. The white-flowered individuals are similar in all morphological features except for the white anthers and lack of guides in the throats as in *Dillon & Dillon 3849* (Fig. 244A–B). Occasionally, branches have very densely set leaves that appear decussate (Fig. 245A), but the corollas are like others in the species (Fig. 245B).

Johnston (1936) provided *Nolana pallida* essentially as a replacement name for *Nolana revoluta* Ruiz & Pav., a species known only from an illustration in *Flora Peruviana et Chilensis* (Fig. 246, 247). He admitted confusion about the application of the name for the southern Peruvian taxon, since it was only known from the published plate; no corresponding specimen had been located. Given his doubts, Johnston chose to place it into "Questionable and excluded Species" with the statement that "The only other Peruvian plant at all suggestive of *N. revoluta* is the one I am describing as *N. pallida*, which incidentally does come from the province of Camaná, but that plant differs in shape of the corolla, the very different calyx, its strong perennial root, very woody stem, not evidently veined leaves, etc." After searching the herbarium in Madrid and other herbaria

FIGURE 240. *Nolana minor*. Photograph of a portion of the holotype sheet, minute succulent annuals to five centimeters tall.

with Ruiz & Pavón holdings, no collections corresponding to *Nolana revoluta* were encountered. For that reason, I continue to follow Johnston's treatment until a voucher for *Nolana revoluta* can be located.

Ferreyra postulated a narrow relationship with *N. gayana* to the north; *N. pallida* and *N. gayana* both possess dendritic trichomes and a similar calyx shape; however, they do not appear to be sister species based on molecular marker studies (Dillon et al., 2009).

A series of collections were initially identified as *Nolana tovariana* and cited as such in Dillon et al. (2009). This error was due to an initial examination of the isotype collection of *N. tovariana* at GH, which had been distributed by Ferreyra. The isotype collection was not a duplicate of the type, but was discovered to be a different species, *N. pallida*. For this reason, the following collections are correctly placed under *Nolana pallida*: *Quipuscoa et al. 3517, 3520*, and *3533*. A discussion is presented under *N. tovariana*.

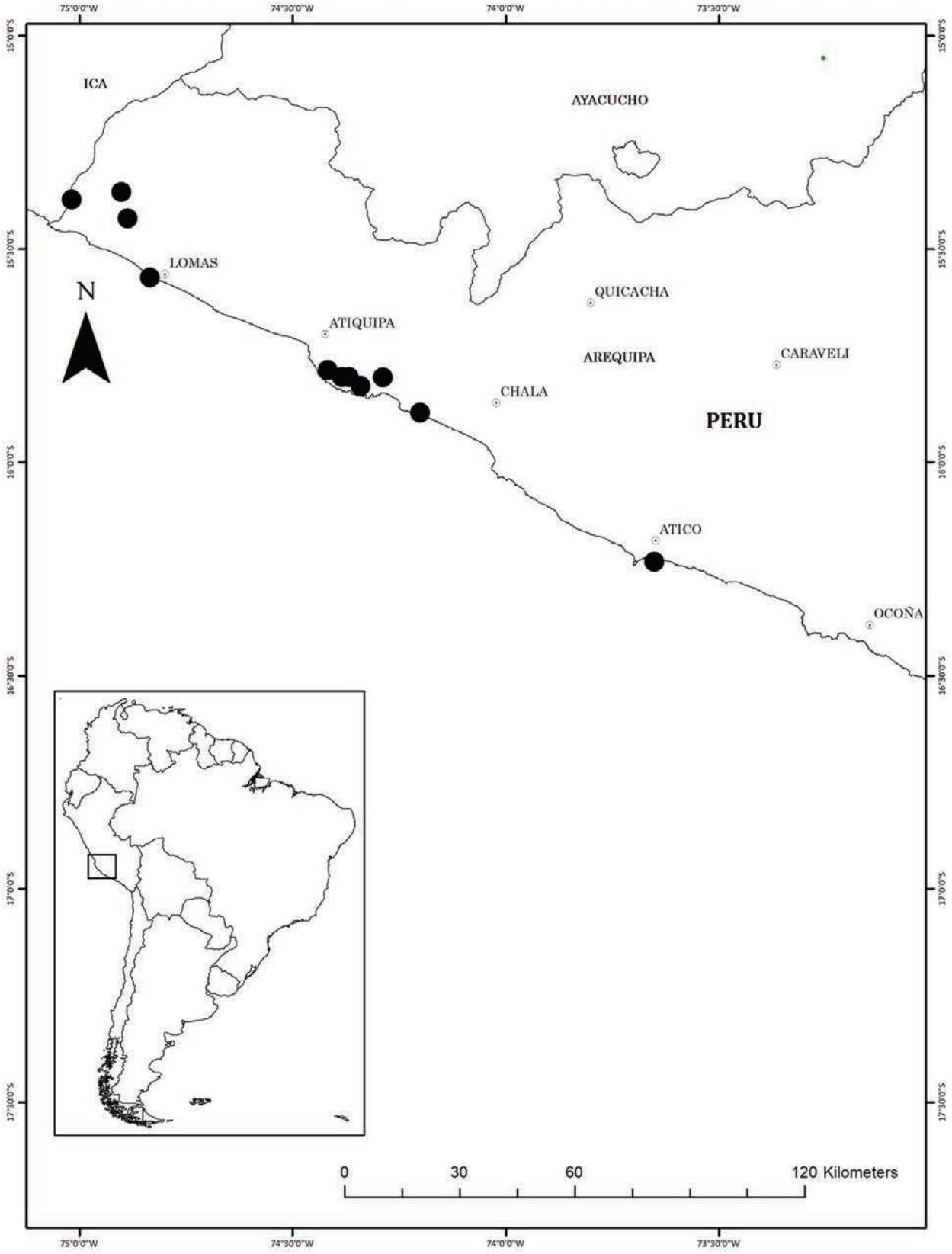


FIGURE 241. Distribution of *Nolana pallida* I.M. Johnst.

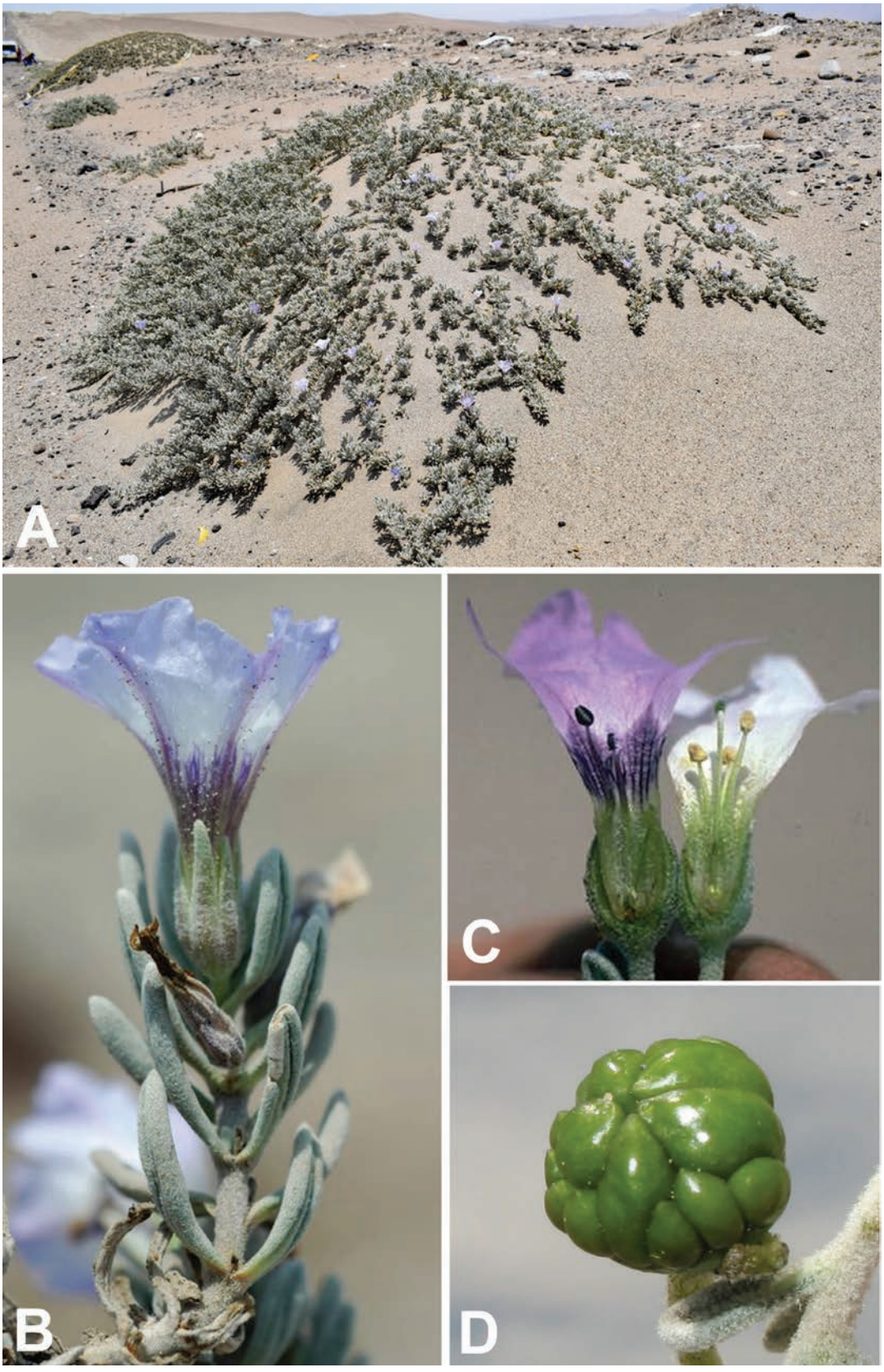


FIGURE 242. *Nolana pallida*. **A**, Large mats buried in sand, stabilizing the shifting dunes; **B**, Flowering branch with strongly revolute leaves, densely pubescent with dendritic trichomes; calyx lobes cut to the base; **C**, Two flowers, one blue and one white, opened to expose anthers; **D**, Gynoecium with connate mericarps.

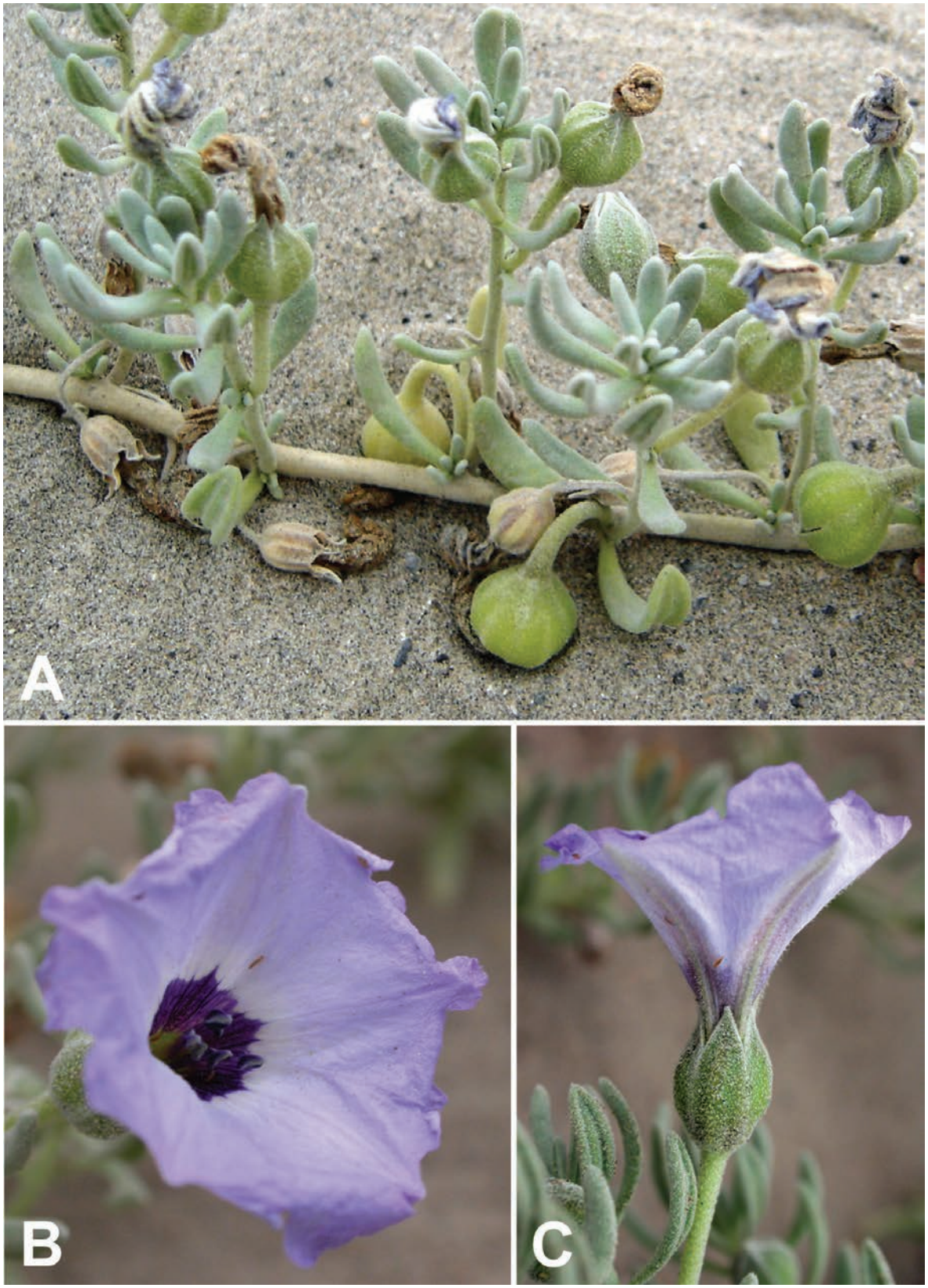


FIGURE 243. *Nolana pallida*. **A**, Prostrate flowering stems with recurving pedicels; **B**, Lavender to blue corollas with a dark band in the base of the throat; **C,** Densely pubescent calyces with lobes cut to the middle.

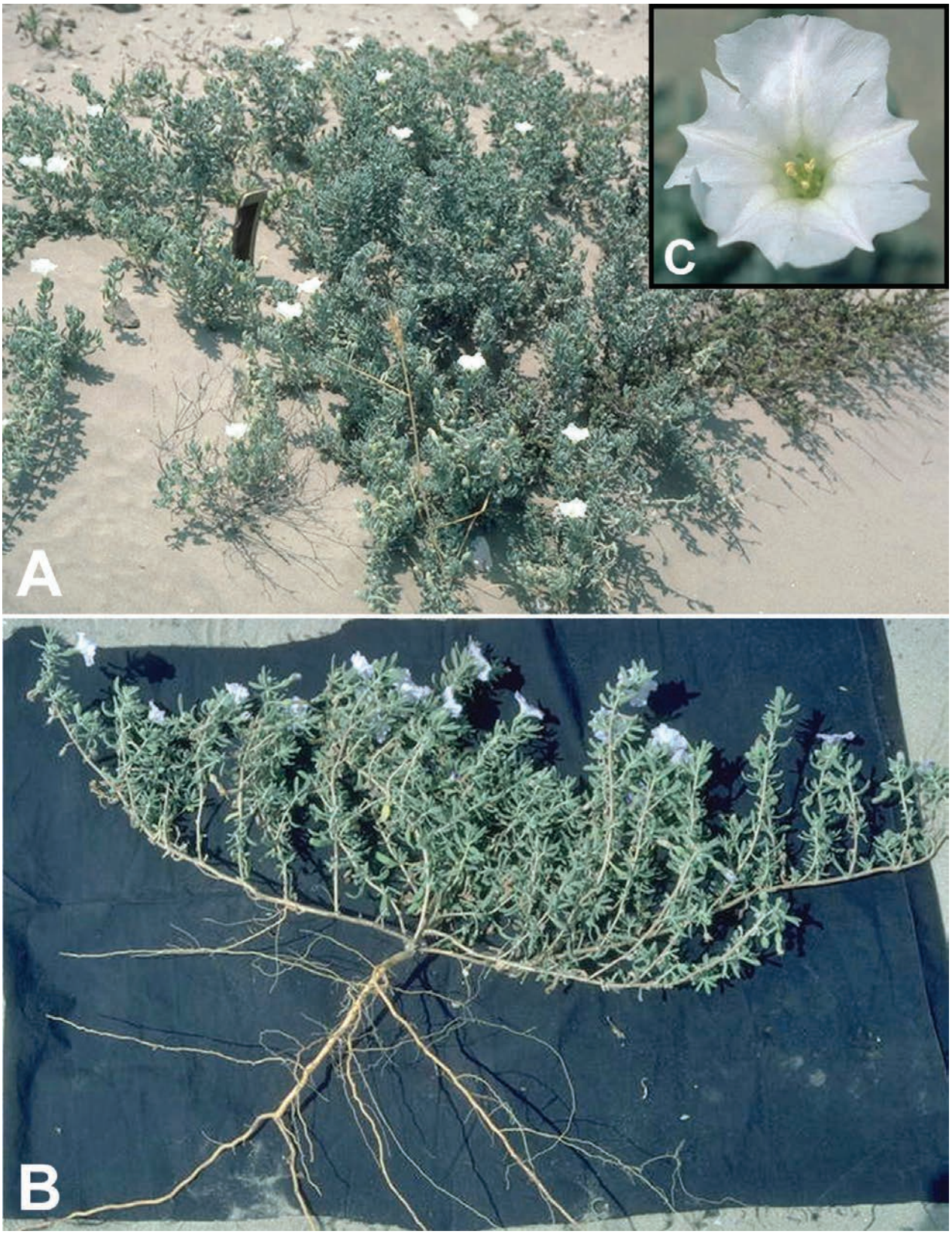


FIGURE 244. *Nolana pallida*. **A–C**, White flowered morphs are similar in most ways to the colored morphs, no guides or coloration in the throats.

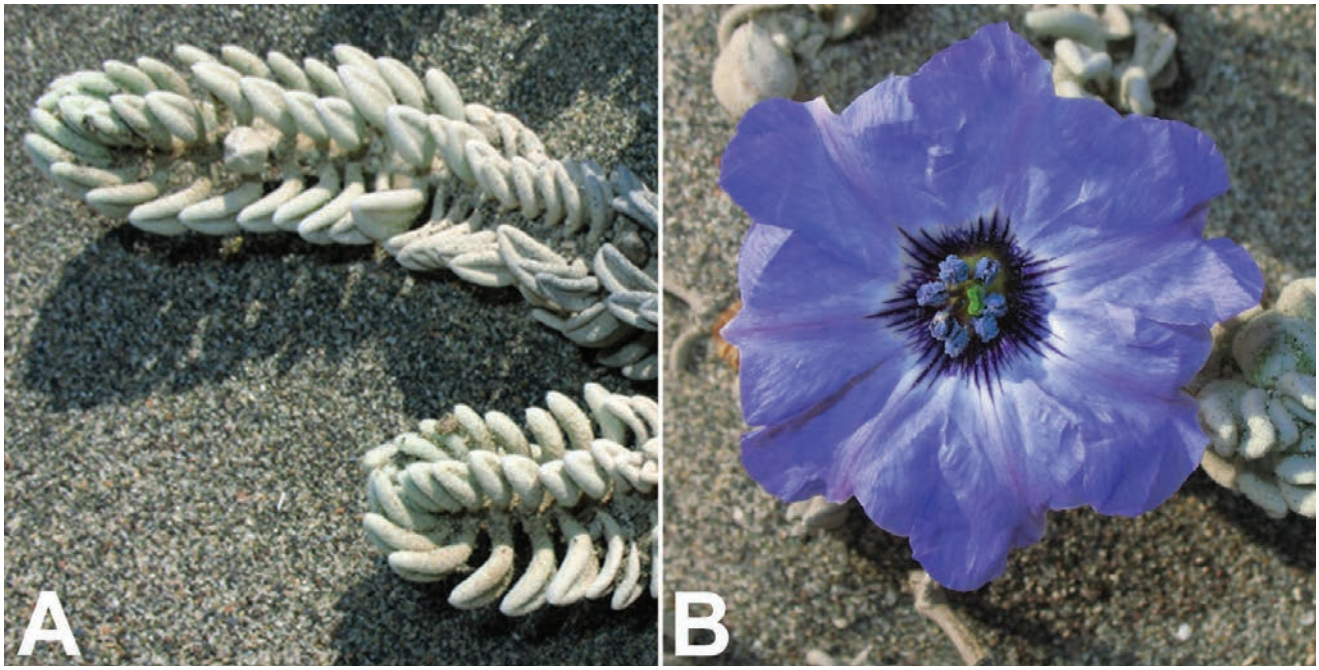


FIGURE 245. *Nolana pallida*. **A**, Branches with densely set leaves appearing decussate; **B**, Corollas are similar with a dark band and guides in the throat. Photographs by Victor Quipuscoa Silvestre.

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, Lomas of Ocoña, ca. 12 km S of Ocoña, Km 788 S of Lima on PanAmerican Hwy, 16°30'S, 73°06'W, 285 m.a.s.l., 4 November1983, *M. O. Dillon & D. Dillon 3853* (CONC, E, F 1950508, GH); Lomas of Ocoña, ca. 285 m.a.s.l., 4 November 1983, *M. O. Dillon & D. Dillon 3860* (F 1941208); entre Ocoña y Camaná, 300–350 m.a.s.l., 13 November 1949, *R. Ferreyra 6452* (USM 81217); entre Camaná y Ocoña, 40 km N, 300–350 m.a.s.l., 13 November 1952, *R. Ferreyra 8876* (GH); 38 km NW of Camaná, 12 km SE of Ocoña, Km 804, 14 January 1963, *H. M., Iltis, C. M. Iltis, D. Ugent, & V. Ugent 1540* (US 2542287); Dist. Ocoña, Lomas de Chira, Km 807 Panamericana Sur, 16°29'06"S, 73°02'00"W, 197 m.a.s.l., 20 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3597* (HSP 002662); Carretera Panamericana ca. al desvio de la caleta del Inca, 16°29'12"S, 73°01'33"W, 271 m.a.s.l., 6 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6550* (HSP 010554). Prov. Caravelí, Lomas de Atiquipa, 220 m.a.s.l., 13 November 1957, *N. Angulo E. s.n.* (HUT 2566); Lomas of Jahuay, ca. 33 km WNW of Chaviña, 15°22'S, 74°54'W, 300 m.a.s.l., 7 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3245* (E, F 1978786); Lomas of Atiquipa, ca. 10.5 km N of turn-off to Atiquipa. KM 584 S of Lima, 150–200 m.a.s.l., 1 November 1983, *M. O. Dillon & D. Dillon 3788* (E, F 1950517, G, GH); ca. 31 km S of Atico & ca. 45 km N of Ocoña along Pan-American Hwy, Km 730 S of Lima, 110–140 m.a.s.l., 4 November 1983, *M. O. Dillon & D. Dillon 3848* (CONC, E, F 1950511, GH, K); Lomas of Atico; ca. 8 km S of Atico along Pan-American Hwy, Km 706–707 S of Lima, 3 November 1983, *M. O. Dillon & D. Dillon 3846* (F 1941214); ca. 31 km S of Atico and ca. 45 km N of Ocoña along Pan-American Hwy, Km 730 S of Lima, 110–140 m.a.s.l., 4 November 1983, *M. O. Dillon & D. Dillon 3849* (CONC, E, F 1950510, GH); ca. 31 km S of Atico, ca. 45 km N of Ocoña along Pan-American Highway, Km 730 S of Lima, 16°14'S, 73°39'W, 110–140 m.a.s.l., 4 November 1983, *M. O. Dillon & D. Dillon 3852* (F 1941212); ca. 42 km N of Ocoña, 16°19'S, 73°24'W, 80 m.a.s.l., 21 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8205* (F 2198776); Atiquipa: N de Atiquipa, Km 593, 15°47'S, 74°25'W, 260 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8802* (F 2276727, HSP 005123, US 3512504); Atico, entre Atico y Camaná, 16°19'S, 73°22'W, 130 m.a.s.l., 15 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8938* (F 2276704, HSP 5223, US 3512538); Pan-American Hwy Km 648 S of Lima, 2 km S of Chala, Lomas de Cápac, hills behind Chala, 200 m.a.s.l., 14 September 1957, *P. C. Hutchison 1289* (F 1559938, K, US 2406357); Dist. Santiago, Lomas de Amara, 14°43'47"S, 75°41'48"W, 780 m.a.s.l., 18 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3517* (HSP 000662, HUSA 7490); Lomas de Amara, 14°43'47"S, 75°41'48"W, 780 m.a.s.l., 18 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3520* (HSP 00664, HUSA 7493); Dist. Lomas, Alto Grande, Km 520 de la Panamericana Sur, 15°26'01"S, 74°52'02"W, 321 m.a.s.l., 19 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M.,*

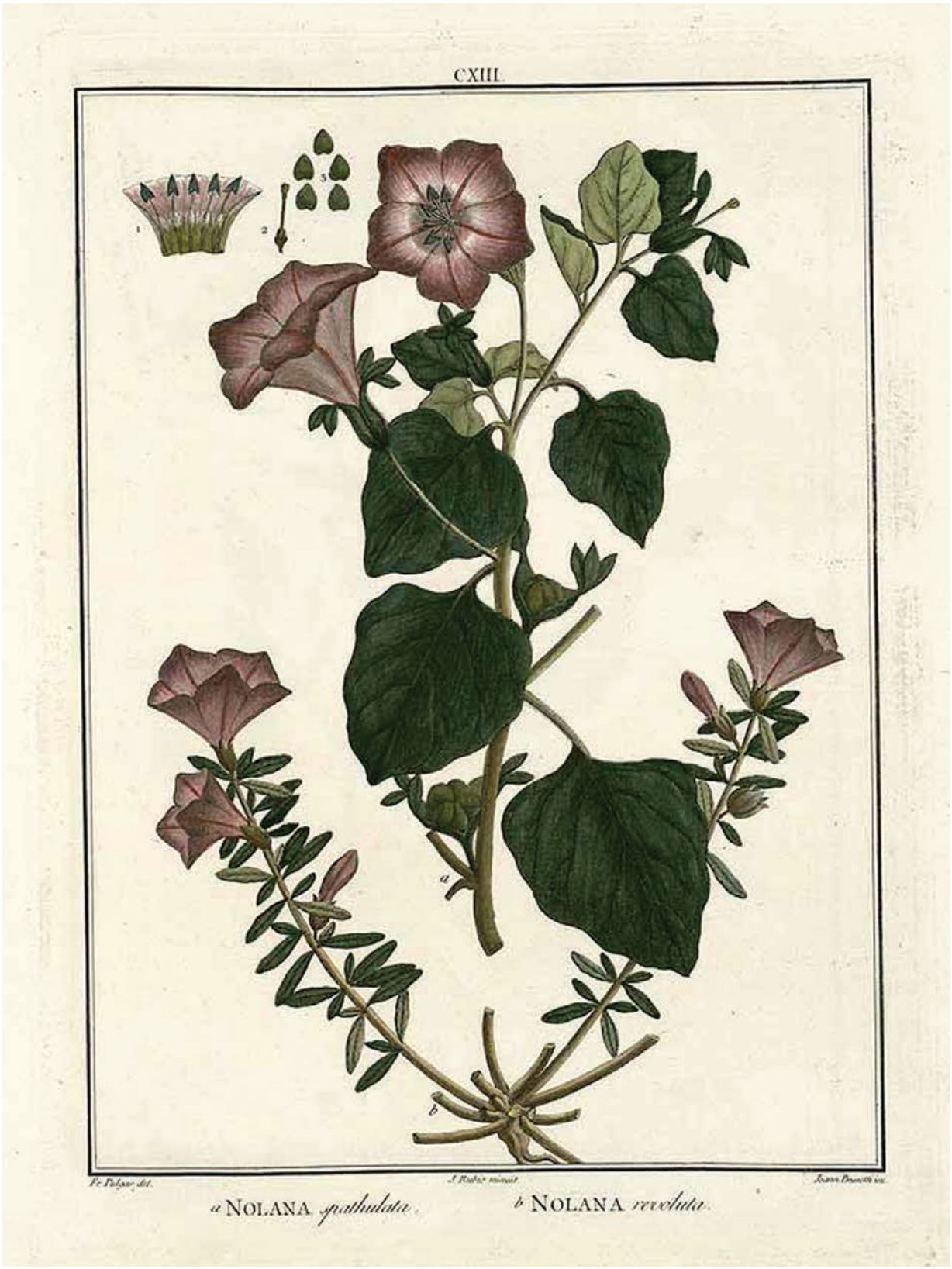


FIGURE 246. Illustration of *Nolana revoluta* Ruiz & Pav., Flora Peruviana et Chilensis, plate 113b (1799).

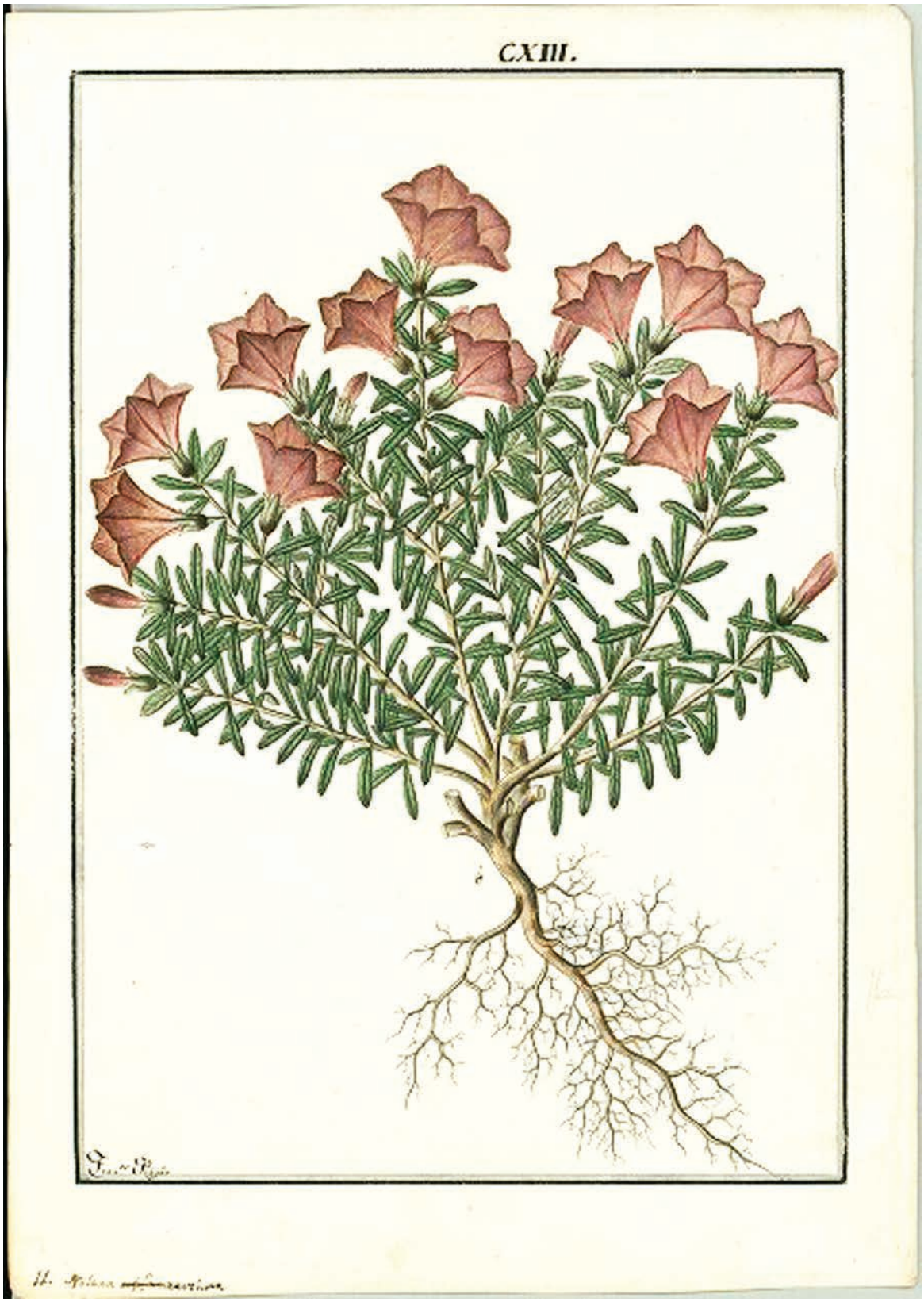


FIGURE 247. Illustration of *Nolana revoluta* Ruiz & Pav., plate 113. Drawings of the Royal Botanical Expedition to the Viceroyalty of Peru (1777–1816).

K. Durand V., D. Ramos A., & N. Castro V. 3533 (HSP 000671, HUSA 7505); Dist. Atico, Pan-Americana Sur Km 716 al sur de Atico, 16°14'31"S, 73°34'23"W, 35 m.a.s.l., 3 December 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & W. Ancalla C. 6847* (HSP 10555); Dist. Lomas, entre Puerto Lomas y Museo Sacaco Desierto, 15°25'42"S, 74°53'06"W, 362 m.a.s.l., 26 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamani Q., & W. Ancalla C. 6590* (HSP 8800, HUT 60427); enter Chala and Santa Rosa, 15°49'15"S, 74°20'22"W, 287 m.a.s.l., 29 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q, M. Bedoya C., & W. Ancalla C. 6698* (HSP 011473); Atiquipa, *A. Raimondi 9086* (GH ex B); Atico, *A. Raimondi 10971* (GH); Km 585 Panamericana Sur, 250 m.a.s.l., 3 October 1997, *M. Weigend & H. Förther 97/719* (F 2211306, HUT 34299); 8 km N of Atiquipa, 100 m.a.s.l., 20 September 1938, *C. R. Worth & J. L. Morrison 15640* (F 1488299, GH, K); 40 km SE of Chala, 16°14'S, 73°39'W, 200 m.a.s.l., 22 September 1938, *C. R. Worth & J. L. Morrison 15706* (F 1488320, GH, K). **Ica**: Prov. Ica. SE of Marcona, along Highway 109, near Km 40, 15°23'15"S, 75°01'54"W, 350 m.a.s.l., 19 February 1994, *E. F. Anderson J. McAuliffe, K. & F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7867* (F 2143428); Lomas de Amara, 14°43'04"S, 75°42'04"W, 824 m.a.s.l., 19 January 2013, *J. P. Cardenas, A. Orellana, & D. Trujillo KPP97* (USM 263989); Prov. Nazca, Marcona: S de Nazca entre Km 518 y Km 590, 15°25'S, 74°53'W, 400 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa S., E. Ortiz V., M. Corrales M., & G. Castillo P. 8784* (F 2276725, HSP 005107, HUSA 6274, US 3512506). Prov. Nazca. San Juan de Marcona, entre Bahia de San Nicolas y San Fernando, 150–200 m.a.s.l., 20 June 2009, *A. Cano, N. Valencia, & C. Valencia 19388a* (F 2295072); Marcona: S de Nazca entre Km 518 y Km 590, 15°26'S, 74°52'W, 80–310 m.a.s.l., 13 November 2005, *M. O. Dillon, J. Wen, V. Quipuscoa, E. Ortiz, M. Corrales M., & G. Castillo P. 8791* (F 2276726, HSP 5114, HUSA 6322, US 3512505).

F18. ***Nolana pilosa*** I.M. Johnst., Contrib. Gray Herb. 112: 79. 1936. TYPE: PERU. Arequipa: Prov. Islay, Mejía, *E. K. F Günther & O. Buchtien 117* (Holotype: HBG, not seen; Isotype: GH [00282333]). Fig. 248–251.

Digital image: Isotype of *Nolana pilosa* from Harvard University Herbaria, Cambridge [GH00282333]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282333

Homotypic synonym: *Nolana crassulifolia* Poepp. ssp. *revoluta* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 93. 1981.

Perennial *herbs*, stems ascending, 4–9 cm long, 1.2–2.0 mm in diam., densely pubescent with capitate-glandular trichomes, 1.0–2.3 mm long; taproot 10–16 cm long, 5–8 mm in diam. *Leaves* alternate, subfasciculate, blades lanceolate, rarely spathulate, 10–18 mm long, 1.2–4.0 mm wide, apically obtuse, base attenuate, almost sessile, densely pilose with moniliform, capitate-glandular trichomes, margins revolute. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 4–7 mm long, pubescent. *Flowers* 5-merous; calyces cupulate, 6–9 mm long, tube short, lobes unequal, 5.0–6.5 mm long, 1.8–2.2 mm wide at base, acuminate, pubescent outside; corollas violet, hypocrateriformis; 16–20 mm long, 8–11 mm wide, rarely pubescent outside, trichomes flexulose; stamens unequal, 5–8 mm long, united to the tube more or less 1/2 the length; style 6–11 mm long. *Mericarps* 3–7, 1-seriate, reniform, 1.8–3.2 mm long, 1.2–2.0 mm wide, black, rugose, shiny; seeds 1–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *pilos*, hair, or the Latin, *pilosus,* hairy with distinct long ascending hairs.

Distribution and Ecology: Peru, Department of Arequipa and Moquegua; 100–800 m.a.s.l. (Fig. 248). It is recorded from sandy soils and inhabits areas receiving coastal fog.

Nolana pilosa is a shrubby, perennial species confined to southern Peru; the plants are often covered with sand (Fig. 249A). It is recognized by its narrow linear-oblanceolate or spathulate leaves that are densely covered with pilose, capitate-glandular trichomes (Fig. 249B). The stalks of the trichomes are lax, multicellular and moniliform; neither are considered lanuginose or villous. Leaves of collections are often coated with sand grains stuck to the apical glandular cells. The corollas are pale violet with a dark purple band at the base of the corolla, which is typical in many Peruvian species (Fig. 249C).

In the coastal area south of Punta Bombón, *Nolana pilosa* occurs sympatrically with *N. thinophila*, and some individuals have characters seemingly intermediate between these two species and may represent hybridization or introgression (Fig. 250). The corollas are pink and the tubes are longer and more narrow than typical *N. pilosa* (Fig. 251A–B) suggesting influence from *Nolana thinophila*. The calyx and mericarps are more like *N. pilosa* (Fig. 251C–D). In molecular analysis, *N. pilosa* is grouped with Peruvian species, specifically with *N. pallida* (Dillon et al., 2009).

Additional specimens examined: PERU. **Arequipa**: Prov. Islay, on the road to Mollendo (Hwy 30), ca. 79.3 km S of Pan-American Hwy, 745 m.a.s.l., 24 February 1994, *E. F. Anderson J. McAuliffe, K. & F. Katterman, C. Diaz, C. Ostolaza, G. Lombardi, & W. Hodgson 7961* (F 2143988); ca. 3 km N of Mollendo, 50 m.a.s.l., 20 November 1983, *M. O. Dillon & D. Dillon 3908* (F 1950503, GH, US, USM); Lomas of Mollendo, ca. 9 km NW of Mollendo, ca. 100 m.a.s.l., 20 November 1983, *M. O. Dillon & D. Dillon 3918* (CONC, E, F 1950502, GH, K, US); Lomas de Mejía, ca. 8 km NNE of Mejía, 160 m.a.s.l., 17 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4819* (CONC, E, F 2330861, GH, HUT 23053, SGO, US); ca. 2 km N of Matarani, 16°59'S, 72°05'W, 150 m.a.s.l., 23 February 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8220* (CONC, E, F 2199343, GH); Mollendo, Sur de Mollendo, 17°01'S, 72°01'W, 150 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva, V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8977* (F 2276714. GH, HSP 5254, US 3512527); Mollendo, Sur de

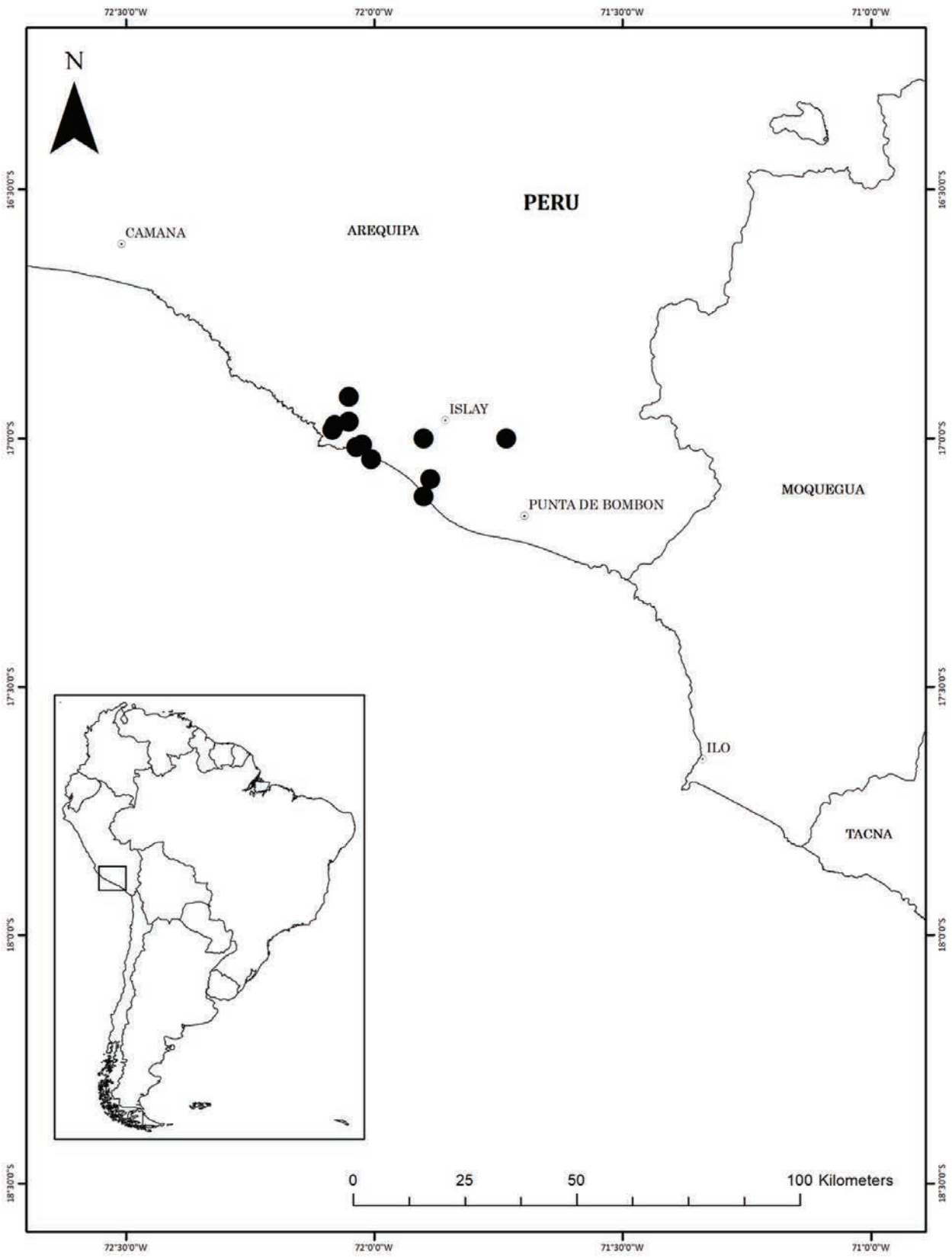


FIGURE 248. Distribution of *Nolana pilosa* I.M. Johnst.

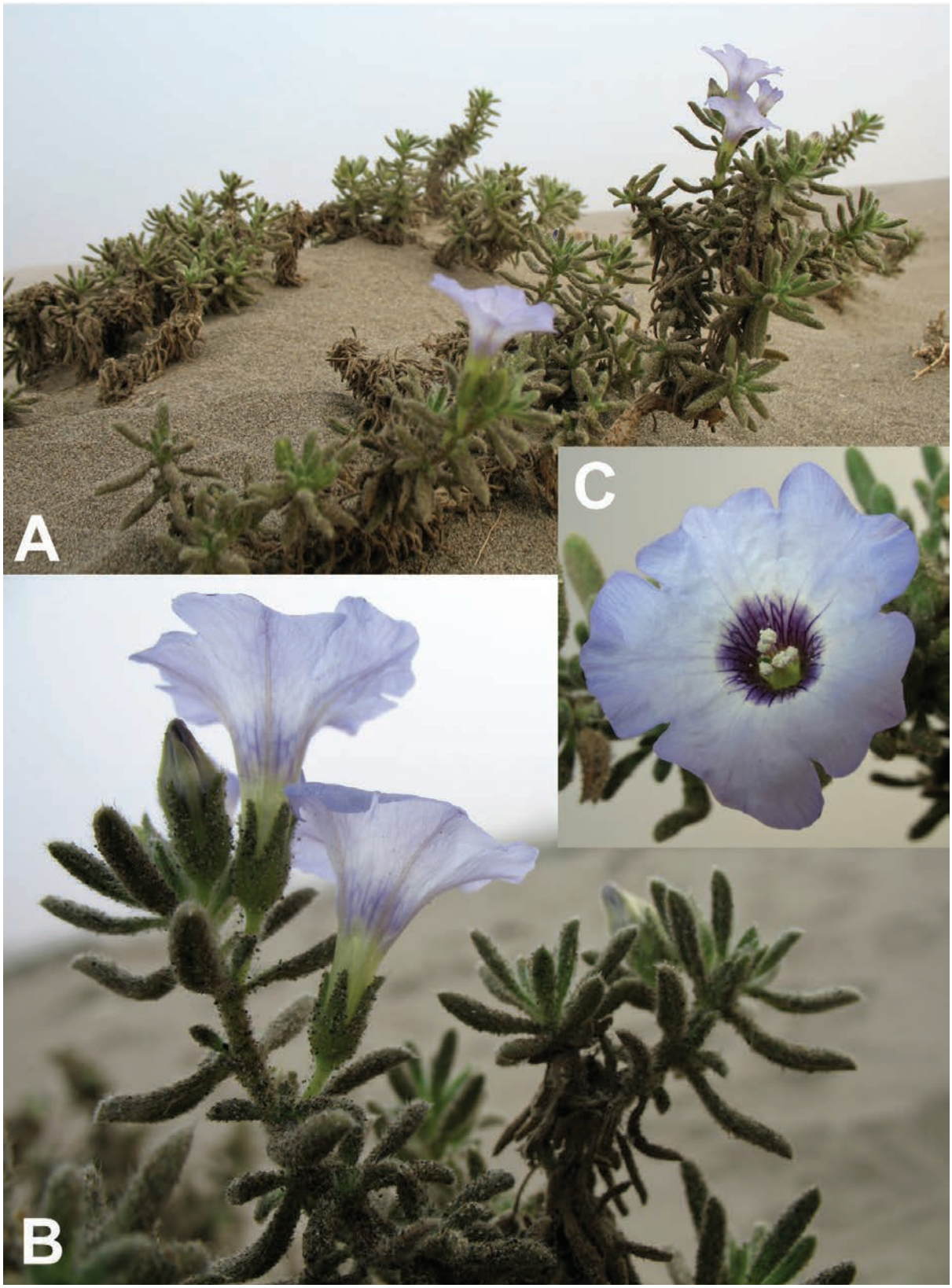


FIGURE 249. *Nolana pilosa*. **A**, Shrubby, perennial plants covered with sand; **B**, Flowering branch with narrow linear-oblanceolate or spathulate leaves, densely pubescent with capitate-glandular trichomes; **C**, Pale violet corollas with a dark purple band at the base of the throat. Photographs by Victor Quipuscoa Silvestre.

FIGURE 250. *Nolana pilosa*. Large individual with putative introgression between *N. pilosa* and *N. thinophila*, south of Mejia, Peru.

Mollendo, 17°01'S, 72°00'W, 100 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8979* (E, F 2276715, GH, HSP 5255, US 3512526); Mollendo, Sur de Mollendo, 17°01'S, 72°00'W, 100 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8983* (F 2276717, GH, US 3512524); Carretera Costanera, ca. 10 km al Sur de Punta Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V, M. Zapata C., M. Corrales M., & G. Castillo P. 8990* (E, F 2276598, GH, HSP 5262, US 3514023); Carretera Costanera, ca. 10 km al Sur de Punta Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8994* (F 2276602, GH, HSP 5264, US 3514027); Carretera Costanera, ca. 10 km al Sur de Punta Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8996* (F 2276604, GH, US 3514029); Punta de Bombón, Carretera Costanera, ca. 10 km al Sur de Punta Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8998* (F 2276606, US 3514031); Punta Bombón, Carretera Costanera, ca. 10 km al Sur de Punta Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8999* (F 2276607, GH, HSP 005267, US 3514032); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9002a* (F 2276611, HSP 5273, US 3514033); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9002b* (F 2276608, GH, HSP 5270, US 3514034); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V.*

FIGURE 251. *Nolana pilosa*. **A**, Individual with influence of *N. thinophila*; **B**, Lateral view of flower; **C**, Closeup of fruiting calyx with capitate-glandular trichomes; **D**, Gynoecium with connate mericarps. Photographs by Victor Quipuscoa Silvestre.

Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9002c (F 2276609, HSP 5271, US 3514035); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9002d* (E, F 2276610, GH, HSP 5272, US 3512545); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°11'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9002e* (F 2276612, US 3512546); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9003* (F 2276613, GH, HSP 5274, US 3512547); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9004* (F 2276614, GH, HSP 5275, US 3512548); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9005* (F 2276615, GH, HSP 5277, US 3512549); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9006* (F 2276616, GHHSP 5277, US 3512550); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G, V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9007* (F 2276618, GH, HSP 5278, US 3512551); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9008* (F 2276618, GH, HSP 5279, US 3512552); Punta de Bombón: Carretera Costanera, approx. 10 km S de Punta de Bombón, 17°14'S, 71°37'W, 30 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 9009* (F 2276619, GH, HSP 5280, US 3512553); Above Mejía, ca. 15 km S of Mollendo, 200 m.a.s.l., 12 November 1949, *R. Ferreyra 6390* (F 1488843); Lomas de Mollendo, 100–200 m.a.s.l., 7 October 1957, *R. Ferreyra 12593* (K); between Mollendo and Matarani, 150–200 m.a.s.l., 29 November 1955, *R. Ferreyra 11560* (K); entre Chucarapi y Pampa Clemesí, valle del Tambo, 700–800 m.a.s.l., 29 November 1955, *R. Ferreyra 11588* (USM 81206); along road from Mollendo to Pan-American Hwy, 15 September 2001, *M. McMahon & L. Hufford 576* (F 2243089); Mejía, 14 m.a.s.l., 4 June 2011, *D. Montesinos T. 3233* (HSP 001334); ca. 1 km de carretera Mollendo–Mejía, 24 April 2019, *M. Quispe T. 193* (HSP 12012); Al Sur de la ciudad de Mollendo, 17°02'31"S, 72°00'19"W, 50 m.a.s.l., 6 November 2002, *V. Quipuscoa S., N. Hidalgo A., D. Sotomayor M., & M. Rodríguez Z. 2805* (F 2293636, HSP, HUSA 4329, HUT 40138, US 3634106); alrededores del INDEHI-UNSA, Catarindo. 17°01'00"S, 71°02'09"W, 20 m.a.s.l., 20 November 2002, *V. Quipuscoa S. N. Hidalgo A., D. Sotomayor M., & M. Rodríguez Z. 2826* (E, F 2293445, GH, HUSA 4599, US); Dist. Mejia, 1 km Sur de Mejia, 17°06'20"S, 71°54'19"W, 10 m.a.s.l., 4 December 2002, *V. Quipuscoa S. & M. O. Dillon 2837* (HSP 000533); al Sur de la Ciudad de Mollendo, 17°02'31"S, 72°00'25"W, 50 m.a.s.l., 5 December 2002, *V. Quipuscoa S. & M. O. Dillon 2839* (F 2293449, HUT 40137, US 3634110); Mollendo, alrededores del INDEHI-UNSA, Catarindo, 17°01'02"S, 72°02'06"W, 0–20 m.a.s.l., 5 December 2002, *V. Quipuscoa S. & M. O. Dillon 2845* (HUSA 4079, HUT 40141); sur de cuidad de Mollendo, 17°2'S, 72°00'W, 0–20 m.a.s.l., 5 December 2002, *V. Quipuscoa S. & M. O. Dillon 2847* (HUSA 1600); Prov. Islay, Dist. Punta Bombón, 17°13'58"S, 71°37'17"W, 146 m.a.s.l., 23 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2931* (HSP 000601), *2932* (HSP 000602). Dist. Mollendo, baja del Cerro San Andrés a 200 m de la carretera hacia Matarani, 16°58'25"S, 72°04'43"W, 340 m.a.s.l., 25 November 2012, *V. Quipuscoa S. & C. Tejada P. 5247* (HSP 004098); Dist. Punta de Bombón, ca. Km 164 carretera Costanera Punta de Bombón–Ilo, 17°13'53"S, 71°36'59"W, 18 m.a.s.l., 28 October 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & M. Bedoya C. 6245* (HSP 12022); Lomas de Mejía, 17°04'58"S, 71°53'10"W, 326 m.a.s.l., 1 November 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., M. Bedoya C., C. Sanz N., & M. Flores M. 6374* (HSP 8775); a la salida de Mollendo, carretera hacia Mejía, 16°58'37"S, 71°59'55"W, 746 m.a.s.l., 2 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., & M. Bedoya C. 6421* (HSP 12025); alrededores del terminal terrestre de Mollendo, 17°00'48"S, 72°01'26"W, 152 m.a.s.l., 4 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., M. Bedoya C., & W. Ancalla C. 6467* (HSP 12027); Mollendo, August–September 1932, sea level to 500 ft, *D. B. Stafford 65* (K); Mollendo, September–October 1933, *D. B. Stafford 282* (K, US 1931285); Mollendo, lower sandy plains, September–October 1933, *D. B. Stafford 288* (BM000941280, K); Mollendo, 600 ft, 25 September1937, *D. B. Stafford 893* (BM00094275, K, US 2056768); Mejia, S of Mollendo, 900 ft, 28 October 1937, *D. B. Stafford 1020* (BM000941278, K); Cachendo, 11 January 1937, *D. B. Stafford 1025* (F 1508574, BM000941277, K); 8 km S of Mollendo, 3 m.a.s.l., 28 September 1938, *C. R. Worth & J. L. Morrison 15734* (K). **Moquegua**: Prov. Ilo, Dist. Ilo, KM 16, 17°40'S, 71°18'W, 268 m.a.s.l., 22 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2924* (HUSA 4356); N of Ilo, sea level, 21 September 1937, *D. B. Stafford 904* (BM000941276, K).

F19. ***Nolana quicachaensis*** Quip. & M.O. Dillon, Arnaldoa 25(2): 247. 2018. TYPE: PERU. Arequipa: Prov. Caravelí; Quicacha, entre Caramba y Quicacha, 15°39'25"S, 73°48'53"W, 1593 m, 30 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q, M. Bedoya C., & W. Ancalla C. 6763* (Holotype, HSP [HSP 007825]; Isotypes, F [F 2322993], HUT [HUT 60417], USM [USM 301276]). Fig. 252–253.

Digital image: Holotype of *Nolana quicachaensis* from Herbario Sur Peruana, Arequipa [HSP 007825]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.hsp022

Shrubs, 0.3–1.0 m tall, stems of dense wood, 3–4 cm in diam., lenticellate, fissured, much-branched, glabrescent. *Leaves* fasciculate, sessile, blades linear to narrowly spathulate, 5–9(–11) mm long, 0.5–1.5(–2.0) mm wide, sigmoid, pubescent with capitate-glandular trichomes, succulent, entire, apically cuspidate, basally attenuate, terete. *Inflorescences* weakly racemose, flowers solitary, axillary, pedicels cylindrical, glandular-pubescent, 5–8(–13) mm long. *Flowers* 5-merous; calyces narrowly campanulate, 3–4 mm wide, glutinous inside and out, 5-lobed, tube ca. 1 mm long, 2.5–3.0 mm in diam., lobes linear-lancelate, unequal, 4–5(–6) mm long, 1.0–1.5 mm wide, apices long attenuate; corollas zygomorphic, tubular-hypocrateriform, 10–12 mm wide at anthesis, 18–20(–23) mm long, tube yellow, lobes white, externally glutinous, internally glabrous; stamens 5, included, filaments inserted in the middle of the corolla, unequal, 12–16 (–18) mm long, bases glabrescent; anther thecae white, 1.5–2.5 mm long, ca. 1 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 1.0–1.5 mm wide, nectary basal, orange, ca. 1 mm wide, carpels 15–18, styles 14–17 mm long, stigma lateral, ca. 0.5 mm long. *Mericarps* 15–18, 2- to 3-seriate, five large, 2.0–2.5 mm long , 1.8–2.0 mm in diam., 10 intermediate, 1.5–1.8 mm long, ca. 1 mm in diam., one to three small, 1.0–1.2 mm long, 0.5–0.8 mm in diam., pyriform, oblong, black, lightly rugose to smooth, contained within the calyx at maturity; seeds 1 per mericarp. Chromosome number: unknown.

Etymology: The specific epithet is derived from the geographic area of Quicacha, near the town of Cháparra in the northern Department of Arequipa.

Distribution and Ecology: Peru, Departments of Arequipa and Ayacucho; 700–1500 m.a.s.l. (Fig. 252). It is growing between granitic rocks in the lower sections of south-facing slopes.

Nolana quicachaensis is a densely branched shrubby species with white flowers (Fig. 253A). The corollas are zygomorphic and invariably white, with white anther thecae (Fig. 253B). The calyx lobes are unequal and bilabiate, and the corollas are tubular (Fig. 253C). The gynoecium has five principal mericarps and a series of minor mericarps (Fig. 253D).

Superficially, *Nolana quicachaensis* most closely resembles *N. lycioides*, with its woody, much-branched habit and linear or spathulate leaves; however, the new species has terete leaves with capitate-glandular trichomes. Furthermore, the solitary axillary flowers form a weak, terminal raceme; the corollas are hypocrateriform with a yellowish tube and white lobes. With its 15–18 mericarps, *N. quicachaensis* is distinct from *N. lycioides*, which has five to nine mericarps. It has not been included in any phylogenetic analysis, and its relationships are here based upon comparative morphology and geographic distribution. It is similar to *N. lycioides* but differs in a range of characters.

Additional specimens examined: PERU. **Ayacucho**: Prov. Lucanas, Dist. Sancos, ca. a San Luis, carretera a Coracora, 15°17'28"S, 74°18'15"W, 703 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7614* (HSP 010556); ca. a San Luis, carretera a Coracora, 15°15'47"S, 74°15'22"W, 843 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7636* (HSP 011853, HUT 60408). Prov. Parinacochas, Dist. Pullo, desvío a Placa, entre San Luis y Carrizal, camino a Coracora, 15°14'22"S, 74°13'57"W, 905 m.a.s.l., 29 April 2018, *V. Quipuscoa S., M. Balvin A., D. Rodríguez P., S. Huamani Q., & M. Bedoya C. 7642* (HSP 011857, HUT 60406).

F20. ***Nolana thinophila*** I.M. Johnst., Contrib. Gray Herb. 112: 56. 1936. TYPE: PERU. Arequipa: Prov. Islay, Mollendo, 0–5 m, 31 May 1925, *F. W. Pennell 14280* (Holotype: GH [00282342]; Isotypes: F [F 558388), K [K000532274], S [S04 2775], US [US 1340773, US00121963], USM [USM 81231, USM000575]). Fig. 254–256.

Digital image: Holotype of *Nolana thinophila* from Harvard University Herbaria, Cambridge [GH00282342]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282342

Homotypic synonym: *Nolana tarapacana* (Phil.) I.M. Johnst. subsp. *thinophila* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 121. 1981.

Perennial *herbs*, procumbent or erect, branched from the base; stems succulent, 5–20 cm long, 1–3(–5)mm in diam., stems terete, internodes 2–5 cm long. *Leaves* alternate, blades linear to spathulate, 9–30 mm long, 3.5–7.0 mm wide, sessile, apically obtuse, basally attenuate, glabrous or sparsely pubescent with capitate-glandular trichomes. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 6–22 mm long, ascending, recurved in fruit. *Flowers* 5-merous; calyces tubular, bifid, 6–8 mm long, 2–3 mm in diam., lobes 1–2 mm long, glabrous; corollas hypocrateriformis, violet to purple, 12–20 mm long, 2–7 mm wide apically, lobes unequal, tube 15–16 mm long; stamens unequal, two 12–13 mm long, united for 1/2 the length of the tube, three 8–9 mm long, united to tube for 2/3 its length; nectary disc crateriform, margin lobed; style 7–8 mm long, gynobasic. *Mericarps* 3(–5), reniform, asymmetrical, black, 3.2–5.2 mm long, 1.8–3.0 mm wide, two larger, globose, three smaller angled, seeds 2–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *thino-*, beach shore or sand, and the Greek, *phileo*, love or regarded with affection.

Distribution and Ecology: Peru, Department of Arequipa; sea level to 100 m.a.s.l. (Fig. 254). It is recorded

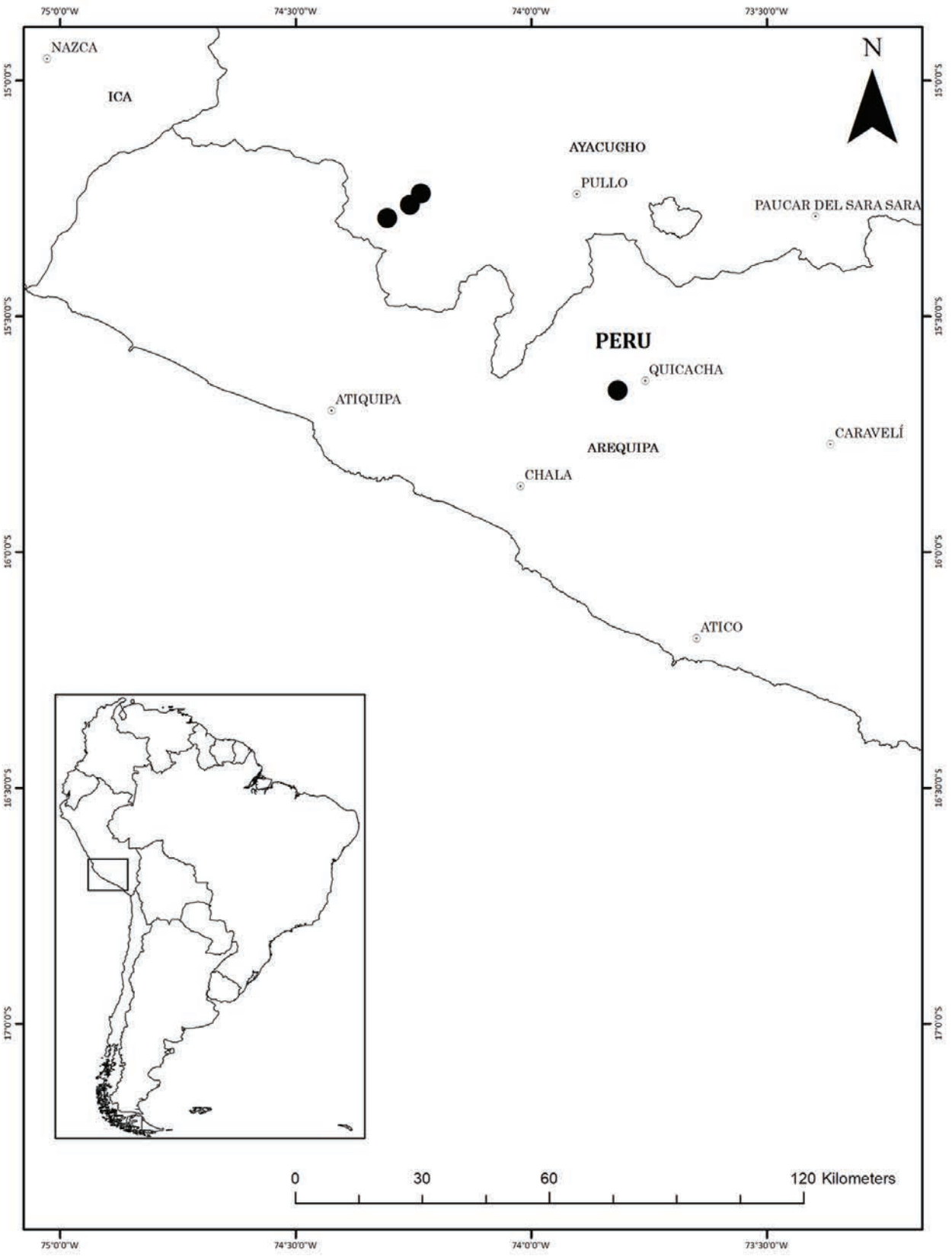


FIGURE 252. Distribution of *Nolana quicachaensis* Quip. & M.O. Dillon.

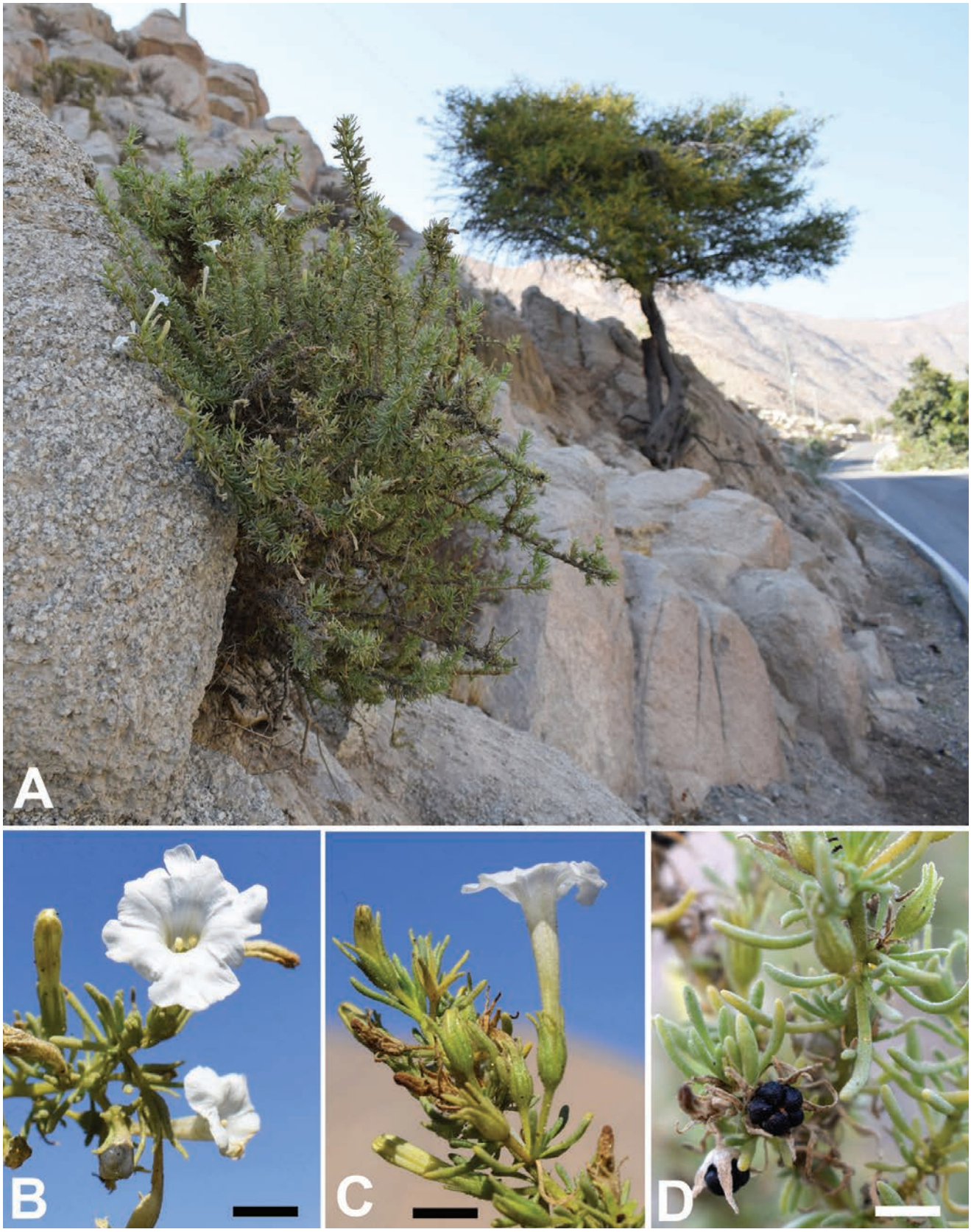


FIGURE 253. *Nolana quicachaensis*. **A**, Flowering shrub; **B**, Frontal view of corollas, scale bar = 8 mm; **C**, Lateral view of apex, scale bar = 8 mm; **D**, Mericarps, scale bar = 5 mm.

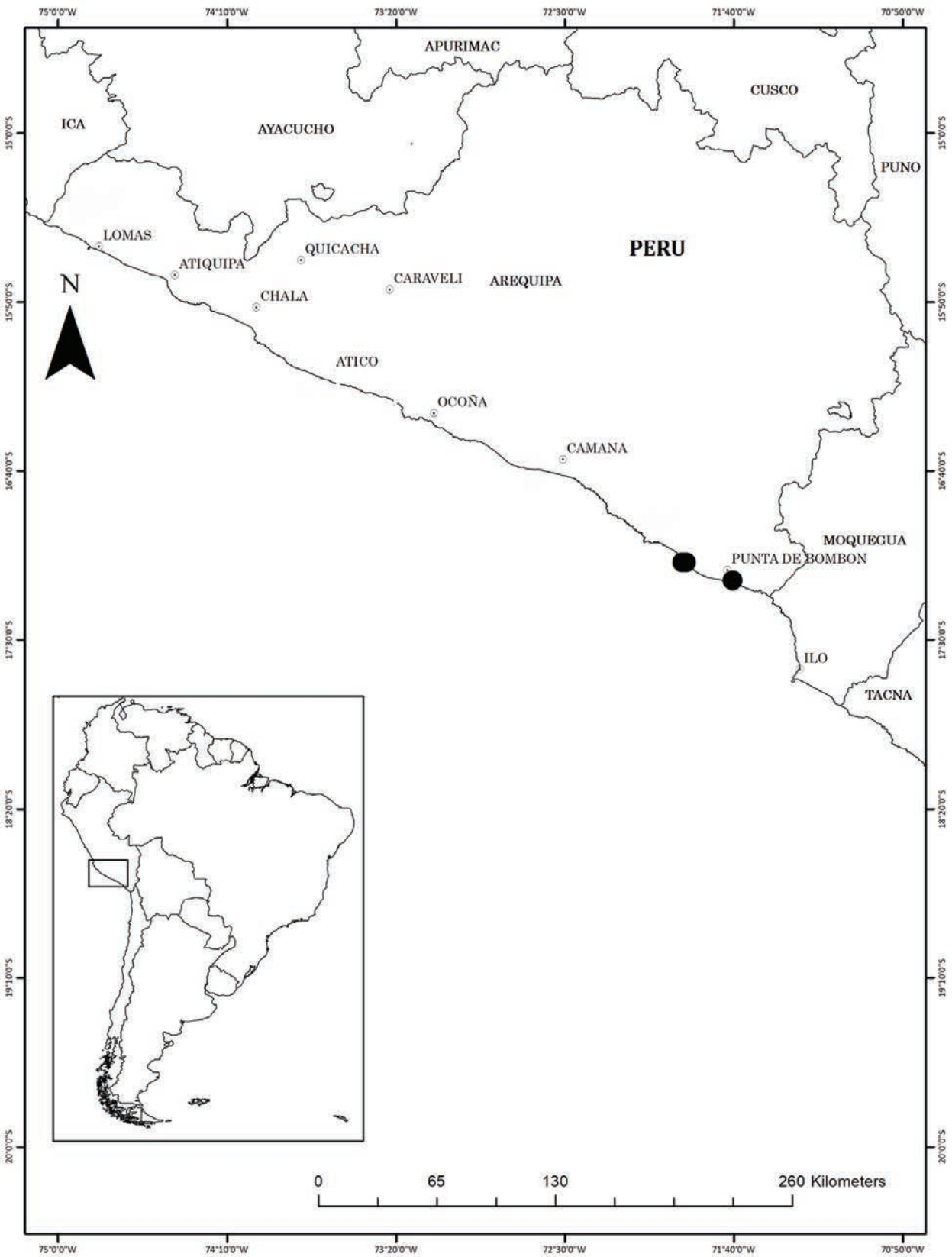


FIGURE 254. Distribution of *Nolana thinophila* I.M. Johnst.

FIGURE 255. *Nolana thinophila*. **A**, Prostrate plants south of Punta Bombón, Peru; **B**, Tubular, succulent leaves, and pink to purple corollas; **C1–3**, Examples of succulent leaves from individuals from very near the ocean.

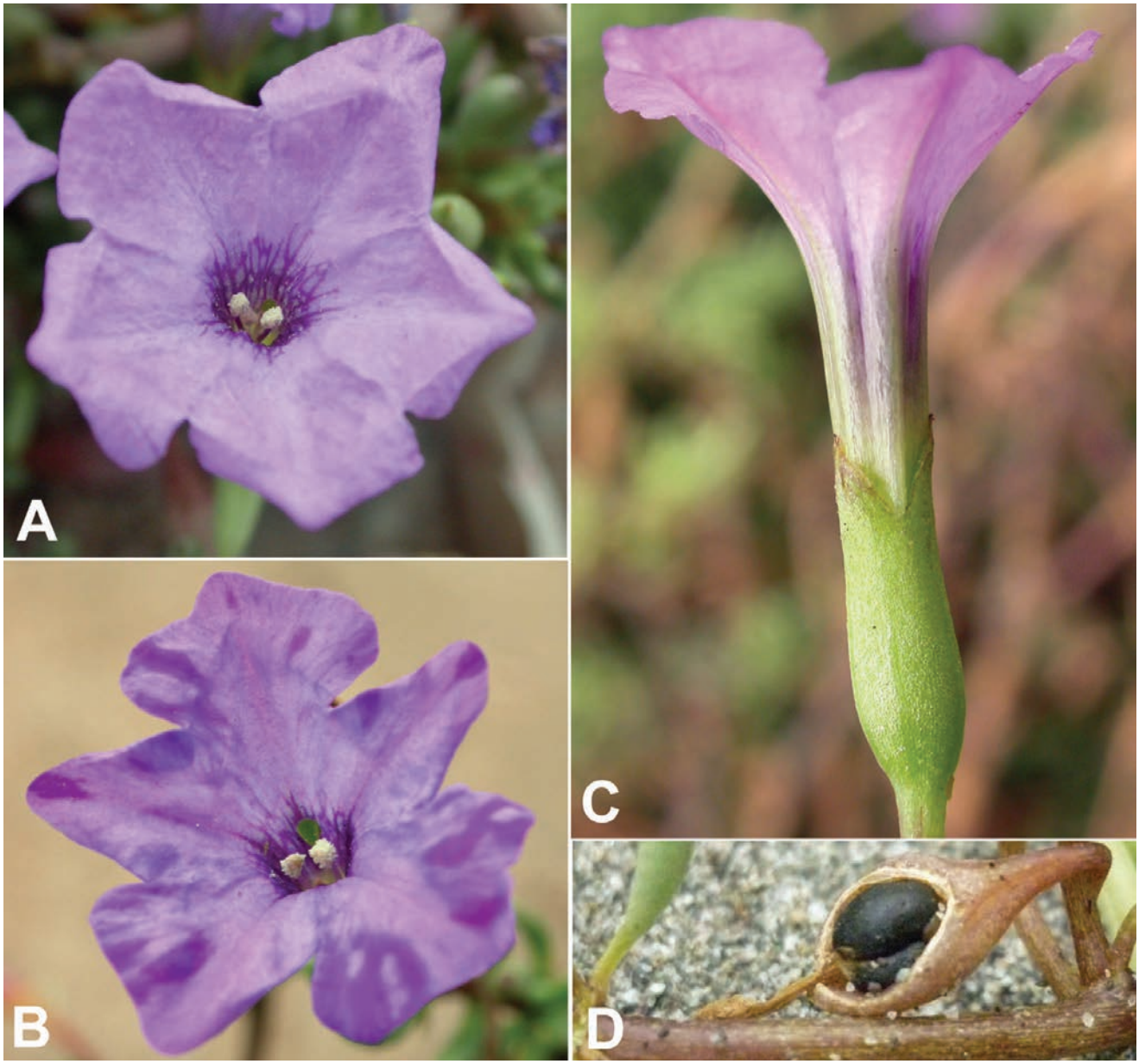


FIGURE 256. *Nolana thinophila*. **A–B**, Corollas variously lobed, pink to lavender with dark guides in the throat; **C**, Calyces tubular, bilabiate; **D**, Gynoecium with three or more mericarps.

from coastal beaches, is largely confined to sandy soils, and can tolerate inundation by salt water during high tides.

Nolana thinophila is largely confined to beachside environments (Fig. 255A) between Mejía and beaches south of Punta Bombón. It is distinctive with its tubular, succulent leaves, and pink to purple corollas (Fig. 255B). When the plants are near the ocean, the leaves can become larger and even more succulent (Fig. 155C, 1–3). The corollas are variously lobed but are invariably pink to lavender with darker guides in the throat (Fig. 256A–B). The calyces are tubular and bilabiate (Fig. 256C), not unlike those in *N. arequipensis* in upland environments. The gynoecium has three or more mericarps (Fig. 256D). Initially, the upland collections were identified as *N. thinophila*, but, when encountered in the living state, they were recognized as distinct and described as *N. arequipensis* (Dillon et al., 2007b). The prostrate, spreading habit and leaf shape (especially when dried) of *N. arequipensis* are like those in *N. thinophila*.

Utilizing the GBSSI waxy marker (Dillon et al., 2007c), *N. thinophila* was shown to be related to, but not the sister species of, *N. arequipensis*. It is recovered in a well-supported clade with several other southern Peruvian taxa, including *N. confinis, N. johnstonii, N. pallida, N. lycioides, N. gayana, N. cerrateana, N. pilosa,* and *N. volcanica*.

Nolana thinophila has been identified as a putative parent of hybrids with *N. pilosa* at a locality near Punta Bombón. Both *Nolana* species occur in close sympatry, and some individuals display intermediate morphology suggesting hybridization between the taxa; the putative hybrids are treated under *Nolana pilosa*.

Additional specimens examined: PERU. **Arequipa**: Prov. Islay, coastal flats between Mollendo and Mejia, [6–10 ft], 8 April 1939, *W. B. Gourlay 124* (K, US 2142199); ca. 3 km N of Mejía, 24 October 1983, *M. O. Dillon & D. Dillon 3703* (F 1950172, USM); S de Mollendo, 17°01'S, 72°00'W, 100 m.a.s.l., 18 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8982* (F 2276716, GH, HSP 5257, US 3512525); alrededores de Mejía, 17°04'S, 71°57'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8988* (F 2276596, GH, HSP 5260, US 3512520); Punta de Bombón, Carretera Costanera, ca. 10 km S de Punta de Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8991* (F 2276599, GH, HSP 005263, US 3514024); Islay, Punta de Bombón, Carretera Costanera, ca. 10 km S de Punta de Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8992* (F 2276600, GH, US 3514025); Punta de Bombón, Carretera Costanera, ca. 10 km S de Punta de Bombón, 17°11'S, 71°43'W, 20 m.a.s.l., 19 November 2005, *M. O. Dillon, J. Wen, S. Leiva G., V. Quipuscoa S., E. Ortiz V., M. Zapata C., M. Corrales M., & G. Castillo P. 8997* (F 2276605, GH, HSP 005266, US 3514030); 10 km S of Mollendo, sea level, 23 April 1939, *W. J. Eyerdam 25171* (K); Santuario Nacional Lagunas de Mejía, 17°07'56"S, 71°53'03"W, 8 m.a.s.l., 22 March 2012, *C. Fernández A. & M. Espinosa R. 005* (HSP 3187); entre Mejía and Mollendo, 5–10 m.a.s.l., 12 November 1949, *R. Ferreyra 6388* (F 1442802, GH, USM 81232); a 1 km Sur de Mejía, 17°07'15"S, 71°53'08"W, 0 m.a.s.l., 6 November 2002, *V. Quipuscoa S., N. Hidalgo A., D. Sotomayor M., & M. Rodríguez Z. 2803* (HUT 40139); 1 km S de Mejía, 17°06'20"S, 71°54'19"W, 10 m.a.s.l., 4 December 2002, *V. Quipuscoa S. & M. O. Dillon 2837* (HSP 000533, HUT 40140, US 3634109); 1 km S de Mollendo, 17°01'02"S, 72°02'01"W, 30 m.a.s.l., 21 October 2003, *V. Quipuscoa S., M. O. Dillon, R. Freyre, & M. Benavides 2918* (HSP 000548); Mollendo, seashore, August–September 1932, *D. B. Stafford K55* (K); Mollendo, seashore, December 1933, *D. B. Stafford 294* (BM000941279, K); Mollendo–Matarani, 100–300 m.a.s.l., August 1949, *C. Vargas. C. 8468* (GH); Las Lagunillas S of Mollendo, 14 October 1997, *M. Weigend & H. Förther 97/862* (F 2211302); 10 km S of Mollendo, sea level, 29 September 1938, *C. R. Worth & J. L. Morrison 15726* (F 1488329, K).

F21. ***Nolana tomentella*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 10. 1955. TYPE: PERU. Arequipa: Lomas de Jahuay, entre Nazca and Chala, 9 September 1952, 300–400 m, *R. Ferreyra 8806* (Holotype: USM [242142, USM000576]; Isotype: K [K000532271, K000532270]). Fig. 257–258.

Digital image: Holotype of *Nolana tomentella* from Herbario San Marcos, Lima [USM 242142]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.usm000576

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var. *plicata* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 133. 1981.

Perennial *herbs*, erect, densely tomentose to ca. 50 cm tall; stems 3–5 mm in diam. *Leaves* alternate, blades spathulate, 15–50 mm long, 4–16 mm wide, densely tomentose with dendritic trichomes, apically obtuse, bases attenuate, margins strongly revolute; sessile. *Inflorescences* of solitary flowers, terminal; pedicels 13–20 mm long; calyces campanulate, 10–14 mm long, 6–7 mm wide, bilabiate, tomentose with dendritic trichomes, tube 5.5–7.0 mm long, lobes triangular, 4.5–7.0 mm long, 3.5–4.0 mm wide, acute; corollas infundibularis, violet, 18–22 mm long, 14–16 mm wide distally, lobes pubescent inside, villous outside; stamens unequal, united to 1/2 their length, 2 larger 11–13 mm long, 3 smaller 10–11 mm long; style 8.5–9.0 mm long. *Mericarps* 10–11, 2-seriate, reniform, the larger 1.5–2.0 mm long, 0.8–1.0 mm wide, the smaller 0.7–1.0 mm long, 0.4–0.5 mm wide; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *tomentum*, woolly with short appressed curled or curved matted hairs, a character that is conspicuous in this species.

Distribution and Ecology: Peru, Department of Arequipa (Fig. 257). It is recorded from interior desert with sparse vegetation.

Nolana tomentella has not been encountered during field studies, and no collections have been personally examined in this study. From photographs by Paul Gonzáles Arce, the plant appears distinct and densely pubescent with dendritic pubescence (Fig. 258A–B). Ferreyra related this species to *N. plicata*; however, currently there is no molecular data supporting its relationships. No authentic material was included in the analysis and results published by Dillon et al. (2009), this taxon was included under the voucher *Dillon et al. 8784*; however, that collection is treated as *N. pallida* in the present treatment.

Additional specimens examined: This species has not been encountered since the type was collected.

F22. ***Nolana tovariana*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 10: 14. 1955. TYPE: PERU. Arequipa: Prov. Camaná, lomas entre Camaná y Ocoña, *R. Ferreyra 8861* (Holotype: USM [242143, USM000578]; Isotype: USM [USM 242143, USM000577, non GH00282359]). Fig. 259.

Digital image: Holotype of *Nolana tovariana* from Herbario San Marcos, Lima [USM 242143]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.usm000577

Homotypic synonym: *Nolana crassulifolia* Poepp. subsp. *revoluta* (Ruiz & Pav.) Mesa, Fl. Neotrop. Monogr. 26: 94. 1981.

Perennial *herbs*, decumbent, 1–2 m in diam., with sparsely pubescent dendritic trichomes. *Leaves* alternate, blades linear, 8–16 mm long, 1–2 mm wide, apex acute, rarely obtuse, green, pubescent with dendritic trichomes; sessile. *Inflorescence* of solitary flowers; pedicels 5–22 mm long, gray-lanuginose. *Flowers* 5-merous; calyces fusiform,

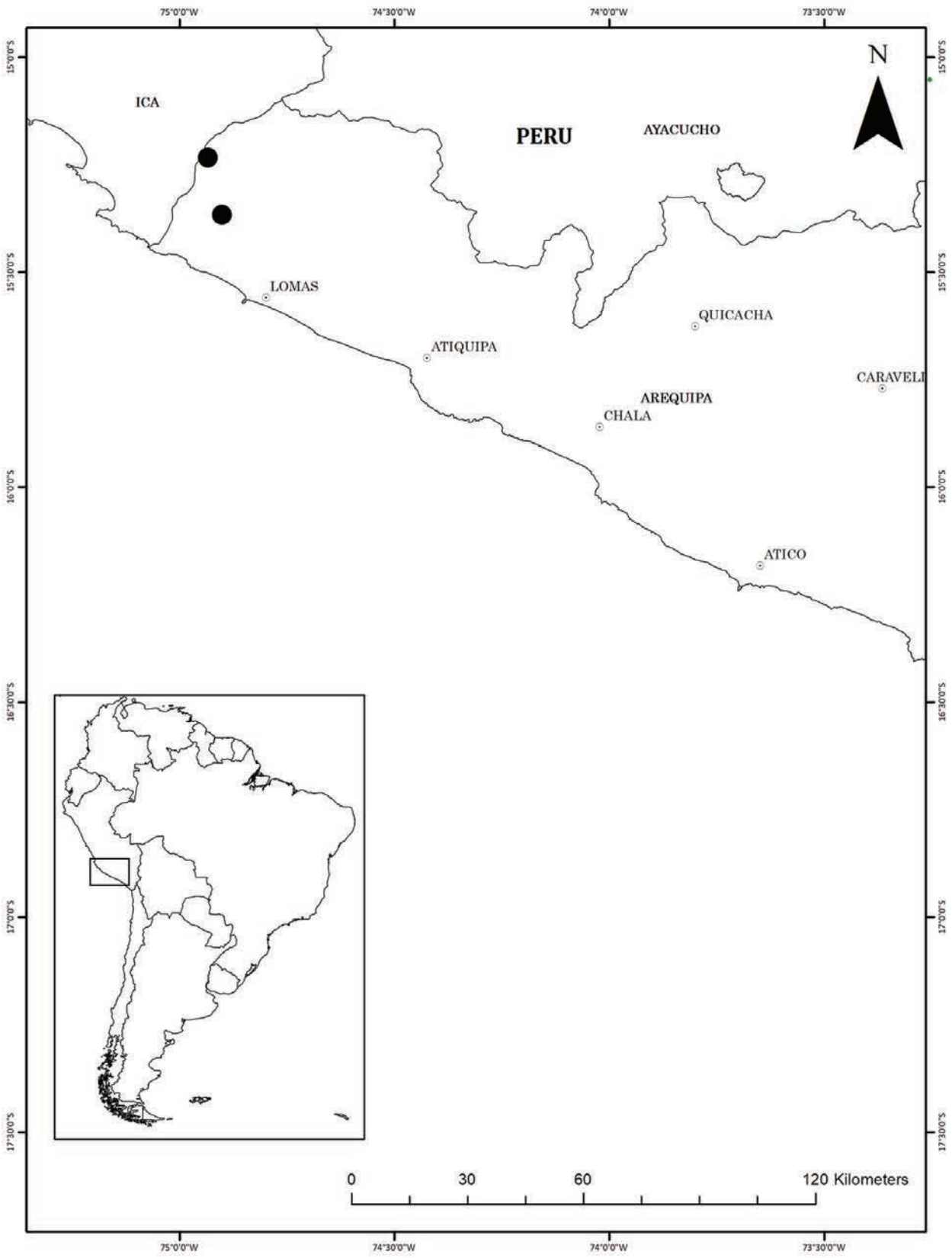


FIGURE 257. Distribution of *Nolana tomentella* Ferreyra.

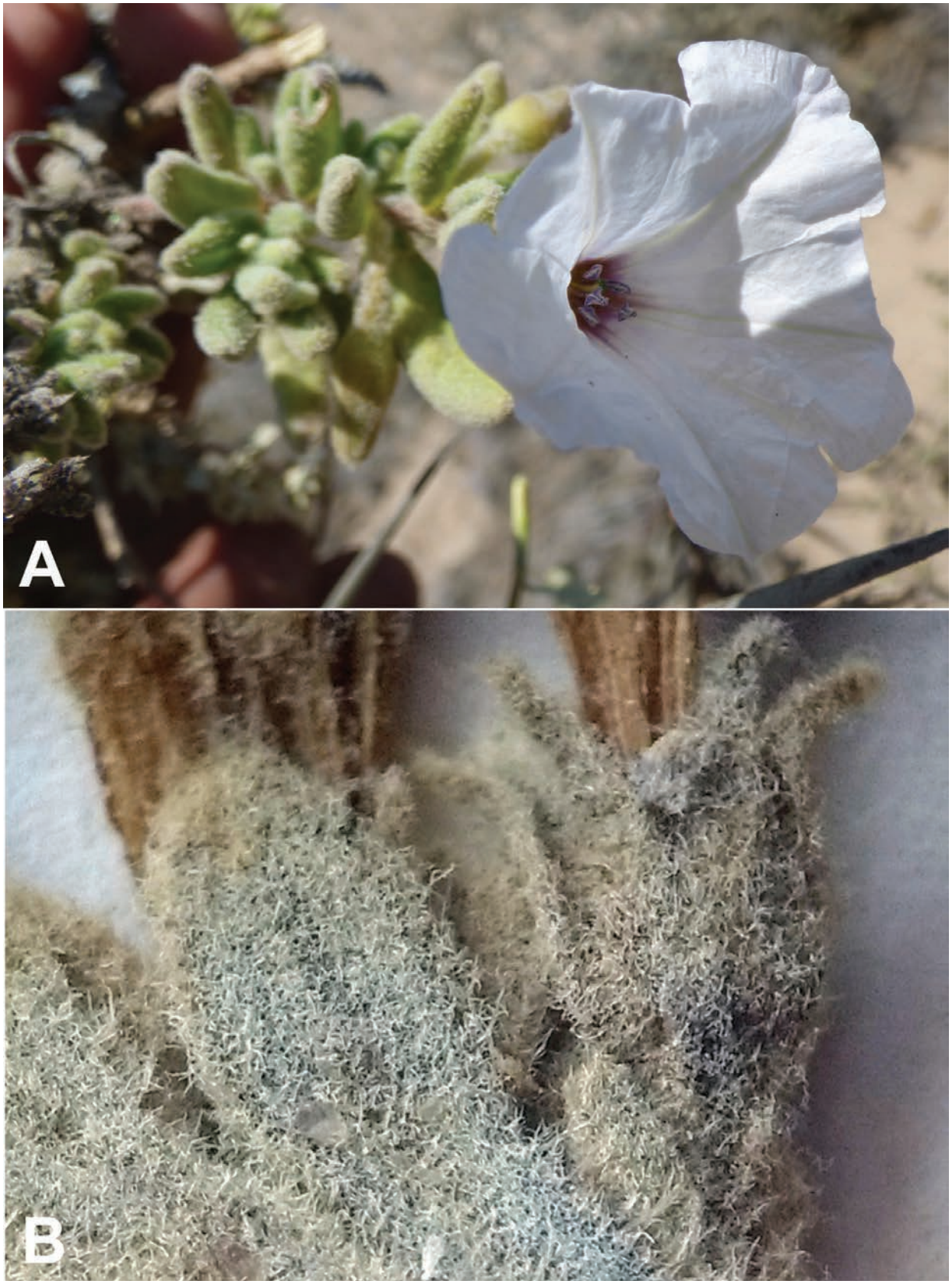


FIGURE 258. *Nolana tomentella*. **A**, Flowering stem photographed by Paul Gonzáles Arce; **B**, Closeup of calyx from type collection.

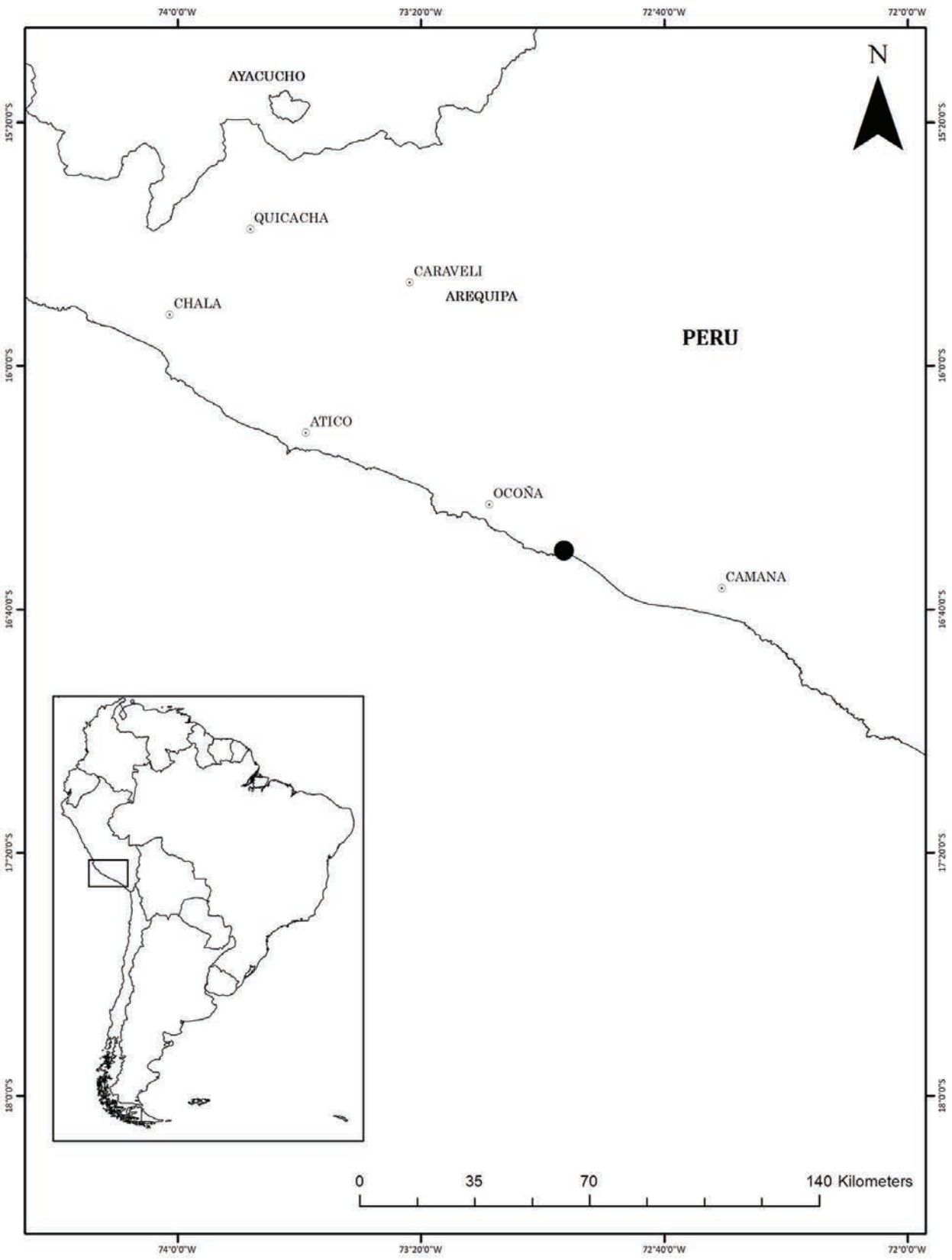


FIGURE 259. Distribution of *Nolana tovariana* Ferreyra.

bilabiate, 9–11 mm long, 2.2–3.2 mm in diam., tube 4.5–6.0 mm long, lobes 4.5–5.0 mm long, 1.2–1.4 mm wide; corollas infundibularis, violet-bluish, 20–22 mm long, 15–17 mm wide, lobes rounded, pubescent, tube villous inside; stamens unequal united to tube for 1/2 its length, two 14–15 mm long, three 12–13 mm long; style 11–13 mm long. *Mericarps* 5, 1-seriate, reniform, black, 0.8–1.0 mm long, 0.4–0.5 mm wide; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Oscar Tovar Serpa (b. 1923–d. 2009), a professor at the Universidad Nacional Mayor de San Marcos and a curator at the Museo de Historia Natural "Javier Prado" in Lima. He was an avid collector and had extensive taxonomic expertise in Peruvian Asteraceae and Poaceae. He contributed to nearly 60 new species to the flora of Peru. I knew him as a kind man, who could best be described as "a gentleman and a scholar".

Distribution and Ecology: Peru, Department of Arequipa; 300–900 m.a.s.l. (Fig. 259). It is recorded from coastal *lomas* formations.

Nolana tovariana has not been encountered during field studies and must be considered rare. I visited the type locality several times, but never encountered authentic material. Because of the confusion surrounding the isotype collection, a series of collections were initially identified as *Nolana tovariana* and cited, as such, in Dillon et al. (2009). The holotype material is housed at the Museo Nacional de Historia Natural "Javier Prado"; however, examination of the isotype collection at GH proved that it is not an isotype, but rather *N. pallida*. For this reason, the following collections which were included in Dillon et al. (2009) are here referred to as *Nolana pallida*, including *Quipuscoa et al. 3517*, *Quipuscoa et al. 3520*, and *Quipuscoa et al. 3533*. On the label of the GH isotype, "*Nolana pallida"* was crossed out and "*Nolana tovariana"* was written above it in ballpoint pen. Furthermore, two other collections of authentic *N. pallida*, *Ferreyra 8876* and *8880*, were collected at the same locality, ca. 40 km north of Ocoña and on the same date, 13 November 1953. In the Herbario San Marcos (USM), two sheets with the type collection number (*Ferreyra 8861*), the holotype (USM000578) and the isotype (USM000577), have the same USM herbarium accession number, USM 242143.

A digital image of the purported isotype of *Nolana tovariana* from the Harvard University Herbaria, Cambridge [GH00282359] has been posted; however, that collection is *Nolana pallida*. A collection of *Nolana tovariana* was discovered at HUH (May 2023) and likely represents the original isotypic material. One explanation is that the labels were inadvertently switched, and the collection, *Ferreyra 8883*, represents an isotype of *Nolana tovariana*, originally meant to be under *Ferreyra 8861*.

Additional specimens examined: PERU. **Arequipa:** Prov. Camaná, ca. Km 40 al N de Camaná, camino a Ocoña, 300–350 m.a.s.l., 13 September 1952, *R. Ferreyra 8865* (USM 81284); entre Camaná y Ocoña, a 40 km al norte, 300–350 m.a.s.l., 13 November 1952, *R. Ferreyra 8880* (GH); entre Camaná and Ocoña, 300–350 m.a.s.l., 13 November 1952, *R. Ferreyra 8883* (GH, USM 81097).

F23. ***Nolana tricotiflora*** Quip. & M.O. Dillon, Arnaldoa 25(2): 248. 2018. TYPE: PERU. Arequipa: Prov. Camaná, Quilca, Lomas de Quilca, Km 62 carretera Costanera, Carrizales, 16°51'19"S, 72°12'21"W, 622 m, 3 November. 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamaní Q., & M. Bedoya C, 6433* (Holotype, HSP [007827]; Isotypes, F [F2322994], HSP [HPS 007828], HUT [HUT 60418], USM [USM 301274]). Fig. 260–261.

Digital image: Isotype of *Nolana tricotiflora* from Herbario Sur Peruano, Arequipa [HSP 007828]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.hsp002

Subshrubs, 30–50 cm tall; single-stemmed, woody, 1–2 cm in diam., brown, lenticellate, cracked, slightly branched at the base, pubescent on mature stems, densely villous with crooked, glandular-capitate trichomes, ca. 2 mm long, young stems greenish purple. *Leaves* whorled, crowded at branch apex, internodes not evident, blades elliptic to linear-lanceolate, 10–14 (–15) mm long, 2.0–3.0(–3.5) mm wide, falcate, distally flexed upwards, both surfaces villous with capitate-glandular trichomes, ca. 1.5 mm long, succulent, entire, apically acute to obtuse, basally attenuate; sessile to subsessile. *Inflorescences* of 3 terminal, lax, scorpioid cymes, 7–12 cm long, each with ca. 12 flowers; pedicels villous, apically capitate-glandular, 2–3(–4) mm long, subtended by reduced, villous, foliar bracts. *Flowers* 5-merous; calyces campanulate, 8–12 mm wide at anthesis, externally villous, glutinous, internally pubescent, 5-lobed, tube 3–4 mm long, 3–5 mm in diam., lobes deltoid, unequal, 7–10(–12) mm long, 3–4 mm wide, apically acute to obtuse; corollas zygomorphic, infundibuliform, 17–22(–25) mm wide at maturity, 17–20(–25) mm long, purple, throat with dark nectar guides, externally and internally glabrous; stamens 5, included, filaments 9–12(–13) mm long, 2 long, 3 short, bases pilose; anther thecae purple, 1.5–2.5 mm long, ca. 1 mm wide, glabrous; ovary glabrous, ca. 1.5 mm long, 1.5–2.0 mm wide, nectary basal, orange, ca. 1 mm wide, carpels (11–)12–18, styles included, flat, 9–12 mm long, ca. 1 mm wide, stigma apical, ca. 0.5 mm long, 1.0–1.5 mm wide. *Mericarps* 12–18, 2-seriate, pyriform, black, 5 large 2.0–2.5 mm long, 1.5–2.0 mm in diam., lightly rugose to smooth, included within the maturing, expanded calyces; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The specific epithet refers to the inflorescence of three terminal, lax, scorpioid cymes.

Distribution and Ecology: Peru, Department of Arequipa; 550–800 m.a.s.l. (Fig. 260). It is recorded from upper ocean-facing slopes bathed in fog in the Carrizales sector; Lomas of Quilca, between Matarani and Quilca.

Nolana tricotiflora was encountered during field studies in 2017 (Fig. 261A), and it contains a combination of characters not found in other congeners. The crooked woody stems are densely leafy, each stem with three branches flowering at the apices (Fig. 261B–C). The inflorescences are lax, scorpioid cymes (Fig. 261D) with long, capitate-glandular pubescence. Only *Nolana mariarosae*, and perhaps *N. pearcei*, have a similar branching pattern.

In most Peruvian *Nolana* species, the flowering stems are unmodified, and the solitary flowers are borne in the

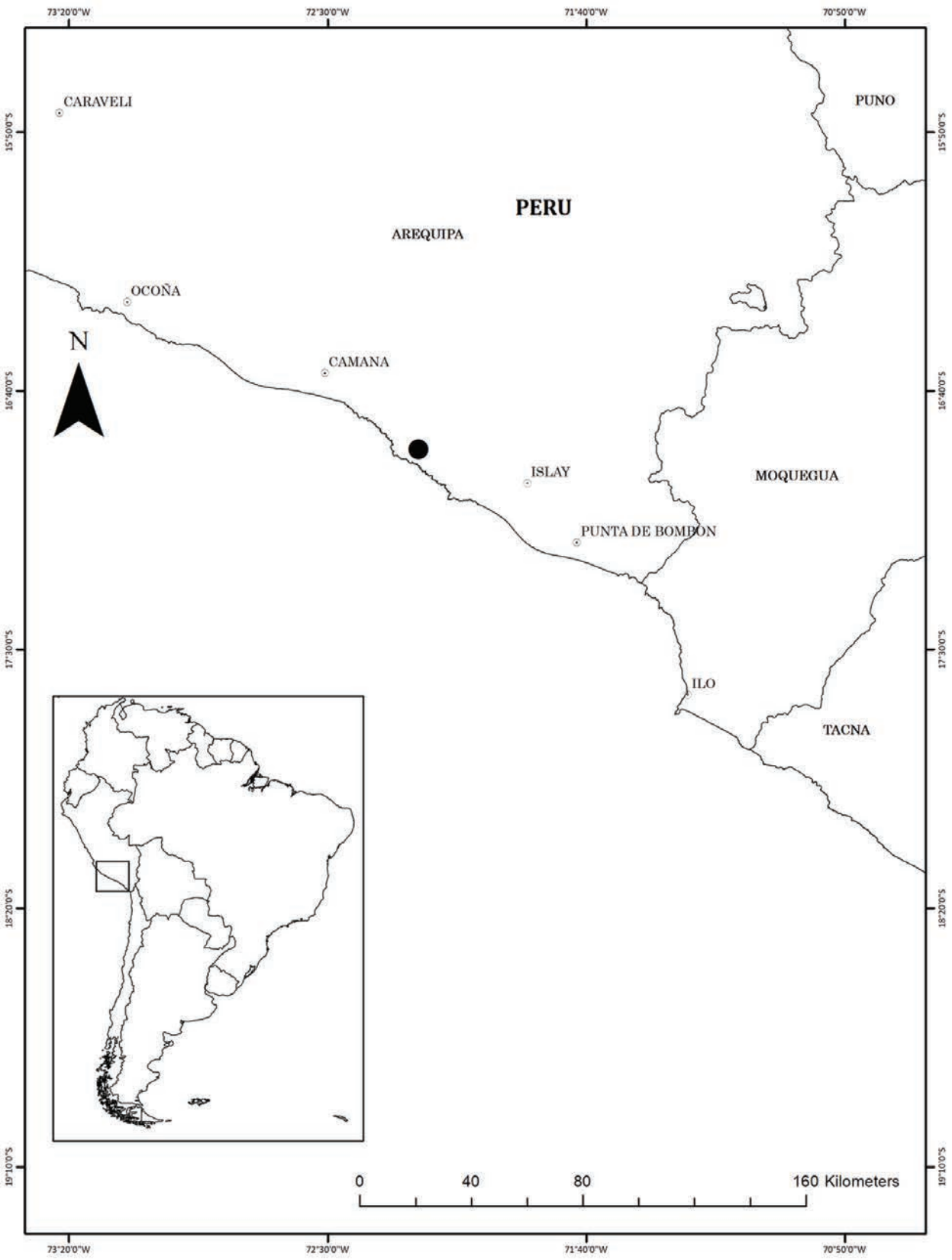


FIGURE 260. Distribution of *Nolana tricotiflora* M.O. Dillon & Quip.

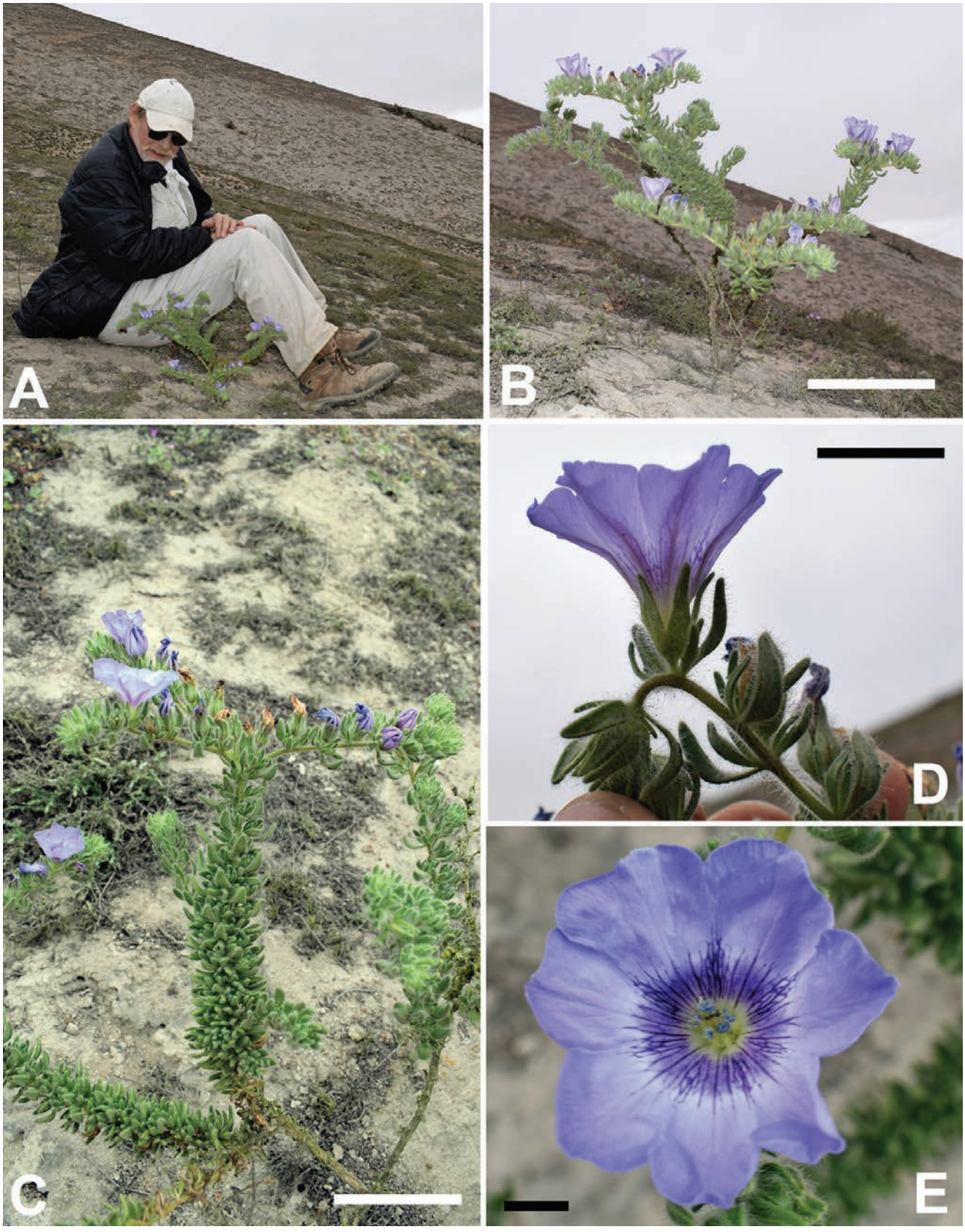


FIGURE 261. *Nolana tricotiflora*. **A**, Photograph of author sitting beside a flowering shrub; **B**, Closeup of shrubby habit, scale bar = 10 cm; **C**, Closeup of leafy stem, scale bar = 5 cm; **D**, Lateral view of flower, scale bar = 10 mm; **E**, Frontal view of corolla, scale bar = 5 mm.

leaf axils. The only exceptions are the southern Peruvian species, which have modifications of flowering stems into recognizable inflorescences with modified bracts subtending individual flowers, but these taxa, *N. inflata* and *N. weissiana*, arise from a basal rosette of modified leaves. In *N. scaposa*, the condition reaches it maximum development, where the inflorescence is a modified branch with subtending floral bracts. None of these species remotely resemble *N. tricotiflora*. *Nolana tricotiflora* has not been included in phylogenetic analysis, and its putative relationships are difficult to establish with comparative morphology and distribution.

Additional material examined: This species has not been encountered since the type was collected.

F24. ***Nolana urubambae*** Vargas, Rev. Univ. Cuz. 107: 154. 1954 [1955]. TYPE: PERU. Cuzco: Prov. Urubamba, Laderas de Yahuarmayo [Yahuarmaqui], 2860 m, 28 February 1949, *C. Vargas C. 7864* (Holotype: CUZ [21440]; Isotypes: GH [GH00282350], USM [USM 81279, USM000579]). Fig. 262–265.

Digital image: Isotype for *Nolana urubambae* from Harvard University Herbaria, Cambridge [GH00282350]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.gh00282350

Homotypic synonym: *Nolana humifusa* (Gouan) I.M. Johnst. ssp. *humifusa* Mesa var *humifusa* Mesa, Fl. Neotrop. Monogr. 26: 129. 1981.

Perennial *herbs* developing a woody caudex, stems 20–40 cm long, prostrate, sparsely pilose, deep purple. *Leaves* alternate, becoming fasciculate, blades oblong to oblanceolate, 5–12 mm long, 2.0–4.5 mm wide, succulent, pubescent with minute curly trichomes but appearing glabrous at 10X magnification; margins thickened, slightly revolute, recurved backwards; petioles 2–4 mm long, dark purple. *Inflorescences* of solitary flowers, terminal and axillary; pedicels ca. 4 mm long, erect in flowering, nodding at maturity. *Flowers* 5-merous; calyx campanulate, lobes lanceolate, (4-)5-merous, 3–4 mm wide, ca. 6 mm long, subtomentose, expanding with maturing ovary to 6 mm wide, broadly ovate; corolla infundibularis, 5-lobed, 15–20 mm long, light blue, central throat dark blue to purple; stamens unequal, 6–8 mm long, pubescent; style exserted, dark blue. *Mericarps* 3–5, 1-seriate, 2.0–3.5 mm long, black, outer surface rugose, faces angled, sometimes with angled or sharp, conic protrusions; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is the latinisation of the geographic locality of the type, Urubamba, Department of Cusco.

Distribution and Ecology: Peru, Department of Cusco; ca. 2860 m.a.s.l. (Fig. 262). It is recorded from only one locality growing in moist calcareous or clay soils.

Nolana urubambae has a small population restricted to calciferous soils on the south bank of the Río Urubamba, opposite the city. These plants are in a habitat over 300 km from the Pacific Ocean and is one of a few inland, high-elevation species in Peru, such as *Nolana chapiensis*, *N. laxa*, and *N. lezamae*. When the locality was visited with Dr. Alfredo Tupayachi in 2000, very few individuals of *Nolana urubambae* were observed (Fig. 263). Those encountered were often growing on exposed rock (Fig. 264A) or in rocky conglomerate soils (Fig. 265A). The surrounding vegetation shared some level of connection with arid, coastal *lomas* formations. A floristic inventory by Tupayachi (2003) indicated that over half of the species of within this floristic pocket have distribution localities that include coastal or near coastal halophytic habitats in southern Peru. The flowering stems of *N. urubambae* are decidedly dark purple in coloration, and the apparently glabrous, succulent leaves are conspicuously recurved, while the pedicels are nodding (Fig. 264B). There are typically five mericarps with rugose dorsal surfaces (Fig. 265B–C).

In molecular analysis utilizing the GBSSI waxy marker (Dillon et al., 2007c), *N. urubambae* is included in a group of Peruvian species, including *N. aticoana*, *N. humifusa*, and *N. lezamae*. In analyses based on sequences of the LEAFY second intron (Dillon et al., 2009), *Nolana urubambae* was included in a weakly supported clade with *N. humifusa*, *N. coronata*, *N. gayana*, and *N. pallida*. Carlos Vargas Calderón (1954) and, later Ferreyra (1961), indicated that this species is related to *N. confinis*; however, no characters warrant such a conclusion. Vargas initially proposed the herbarium name "*Nolana andina*" and annotated herbarium sheets with that name; however, he subsequently changed the species epithet to "*urubambae*".

Additional specimens examined: PERU. **Cusco**: Prov. Urubamba, Cerro Yahuarmaqui, frente de Urubamba, 2890 m.a.s.l., 28 February 1999. *A. Tupayachi 3858* (CUZ, not seen, E, F 2329917, GH, US); ladera de Muyock [Mayuc], arcillo-caizas, 2860 m.a.s.l., 18 January 1963, *C. Vargas C. 014119* (CUZ 21441).

F25. ***Nolana volcanica*** Ferreyra, Publ. Mus. Hist. Nat. Ser. B 12: 42. 1961. TYPE: PERU. Arequipa: Prov. Islay, Mollendo, "sand and volcanic ash", 15 September 1937, 2000 ft [609 m.a.s.l.], *D. B. Stafford 881* (Holotype: K [000532281]; Isotype: BM [BM000021202]). Fig. 266–268.

Digital image: Holotype of *Nolana volcanica* from Royal Botanic Gardens, Kew [K000532281]. http://www.kew.org/herbcatimg/226126.jpg

Homotypic synonym: *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *confinis* Mesa, Fl. Neotrop. Monogr. 26: 103. 1981.

Spreading *shrubs* or perennial herbs, ca. 50 cm tall, 50–100 cm in diam.; stems decumbent, pubescent, flexulose, 1.0–3.5 mm in diam. *Leaves* alternate, blades lanceolate to elliptic, (5–)7–10 mm long, 1.2–2.8 mm wide, laxly to densely lanuginose or, more rarely, glabrescent, margins revolute, 1-nerved, apices obtuse; sessile. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 2–5 mm long. *Flowers* 5-merous; calyces campanulate, 5.0–6.5(–8.0) mm long, 2.5–3.0 mm in diam., tube 1.5–2.0 mm long, lobes linear, acuminate, 3.5–4.5(–6.0) mm long, 1.2–1.5 mm wide, unequal; corollas infundibularis, blue, 9–13 mm long, 8–10 mm wide, pilose outside, lobes obtuse, unequal,

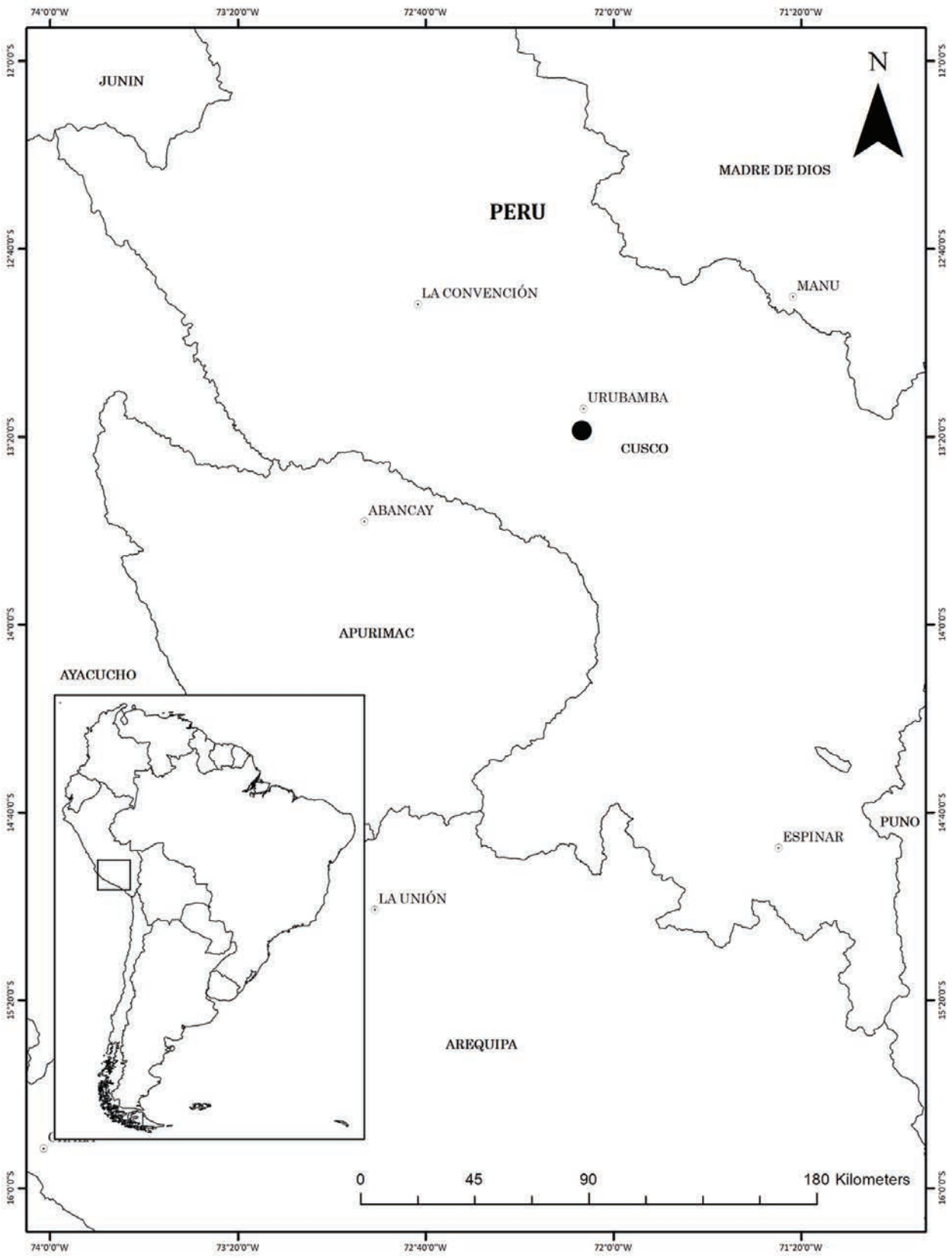


FIGURE 262. Distribution of *Nolana urubambae* Vargas.

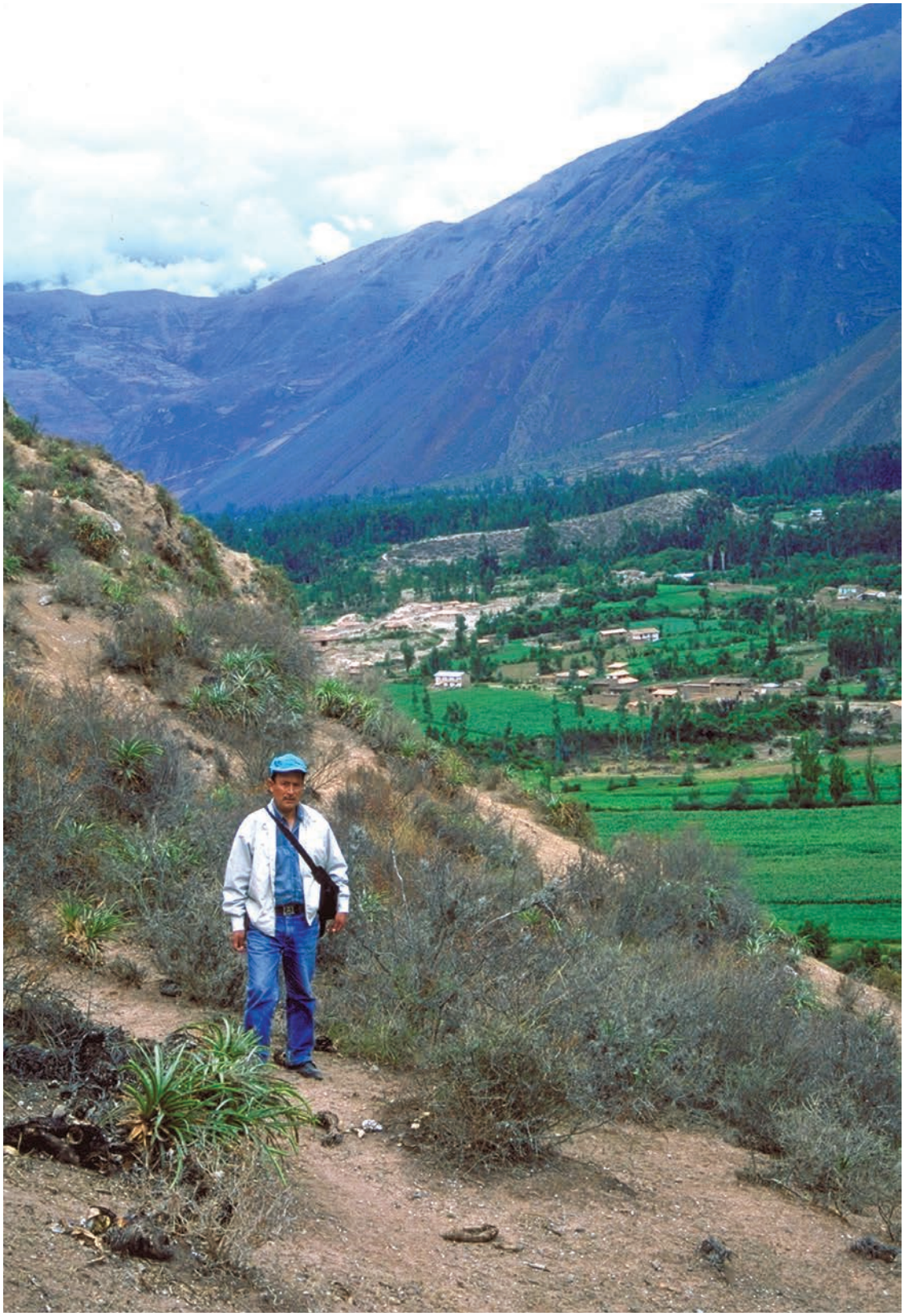


FIGURE 263. *Nolana urubambae*. Dr. Alfred Tupayachi Herrera at the type locality, south of Rio Urubamba. Town of Urubamba, Peru in the background.

FIGURE 264. *Nolana urubambae*. **A**, Plants growing on exposed rock; **B**, Closeup of purple stems with glabrous, succulent leaves and nodding peduncles. Photographs by Alfredo Tupayachi Herrera.

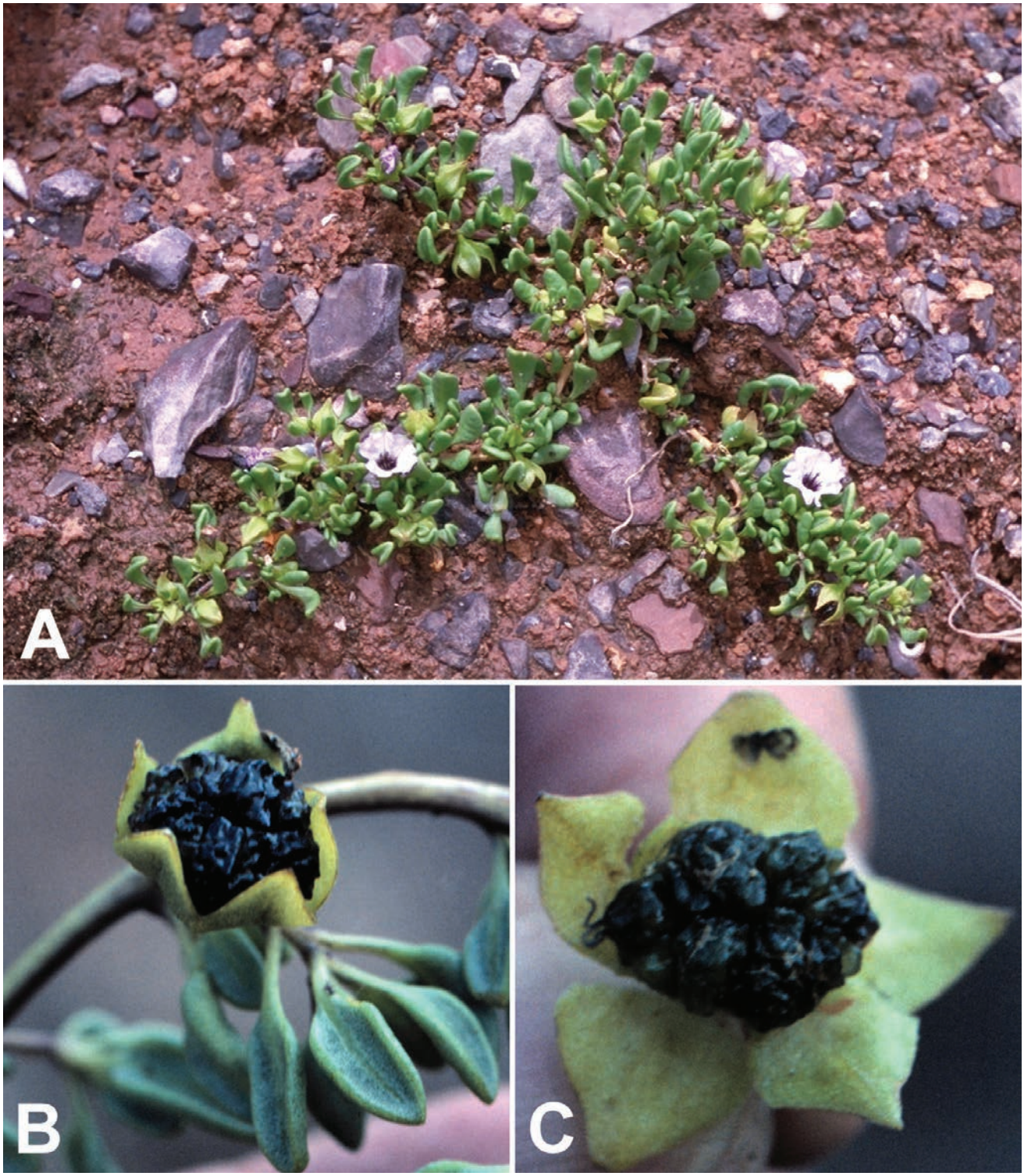


FIGURE 265. *Nolana urubambae*. **A**, Plants growing on conglomerate soils; **B–C**, Mericarps, five, with rugose dorsal surfaces. Photographs by Alfredo Tupayachi Herrera.

tube short; stamens unequal, united to tube for about 1/2 its length, 2 larger 7.5–9.0 mm long, 3 smaller 5.5–7.0 mm long; style 5.0–6.5 mm long. *Mericarps* (4–)5(–6), polyhedrons, black, rugose, 1.5–2.0 mm long; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is derived from comments on the type collection label that indicate that the soil where the species was collected was "volcanic ash"; however, the soils are not volcanic in origin.

Distribution and Ecology: Peru, Department of Arequipa; (100–)500–800(–1000) m.a.s.l. (Fig. 266). It is recorded from *lomas* formations above Mollendo in the Lomas of Yuta; and disjunct populations are recorded from the Lomas de Cachendo and Lomas de Quilca.

Nolana volcanica is a low, much-branched, spreading shrub (Fig. 267A) with a distribution in a few, near-coastal habitats and one inland. The corollas are light blue with a characteristic dark purple band in the throat and blue anther thecae (Fig. 267B, Fig. 268A). The calyces are pubescent with non-glandular, elongate trichomes (Fig. 268B–C), and the lobes have purple striations (Fig. 268C). There are predominately five spherical mericarps (Fig. 268D). Over its altitudinal range from the lower to the upper areas of the Lomas of Yuta, individuals display variation in leaf size and pubescence. At higher elevations, the leaves are more pubescent and are reduced in size. The type collection by Ms. Dora B. Stafford is a densely pubescent specimen that was initially was confused with populations that eventually were designated as *Nolana bombonensis*. One of the collections included in Dillon et al. (2009), *Quipuscoa et al. 2930* (HSP), was assigned to *Nolana volcanica*; however, it was subsequently described as the new species, *N. callae*. Therefore, *N. volcanica* has not been included in any molecular experiments, and its relationships are proposed using comparative morphology.

A disjunct population of *Nolana volcanica* occurs within the Lomas of Cachendo, ca. 25 km east of Mollendo at ca. 1000 m.a.s.l. This population is ca. 30 km from the type locality at the Lomas of Yuta to the west and ca. 20 km from the coast. The population is situated on the leeward side of a series of small mountains that physically separate and isolate the formation. Elevations of the mountains range from ca. 950 to slightly over 1000 meters, and include Cerro Bronce (1059 m.a.s.l.), Cerro Chilenos (984 m.a.s.l.), Cerro Chasca (981 m.a.s.l.), Cerro Gordo (932 m.a.s.l.), and Cerro Chihuanol (967 m.a.s.l.). The area is isolated and has other distinctive species; for example, there is a robust population of *Nolana spathulata*, elements of which have been treated as endemics (see discussion under that taxon). This entire area needs additional collecting and protection from mining development. Another disjunct population is found at Lomas of Quilca at over 800 m.a.s.l., ca. 20 km northwest of the type locality at the Lomas of Yuta.

Additional specimens examined: PERU. **Arequipa**: Prov. Camaná, Lomas de Quilca, Km 62 carretera costañera, Carrizales, 16°50'51"S, 72°12'08"W, 835 m.a.s.l., 3 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & M. Bedoya C. 6456* (HSP 12026). Lomas of Mollendo, ca. 10 km NW of Islay, ca. 670 m.a.s.l., 20 November 1983, *M. O. Dillon & D. Dillon 3955* (F 1950167, GH); Lomas de Mollendo, ca. 100 m.a.s.l., 20 November 1983, *M. O. Dillon & D. Dillon 3921* (F 1941144); Lomas de Mollendo, ca. 9 km E of Matarani on road to Arequipa, ca. 700 m.a.s.l., 17 November 1986, *M. O. Dillon, A. Sagástegui A., & J. Santisteban 4835* (E, F 2014378, HUT 023057, USM); Lomas de Yuta, 16°56'51"S, 72°04'23"W, 818 m.a.s.l., 9 December 2007, *D. Heredia H. & J. Huallpa C. 0029* (HSP 002333); Cerros cerca Islay, 18 August 1863, *J. Isern 2502* (F 1575083); Lomas de Yuta, 16°56'45"S, 72°05'09"W, 904 m.a.s.l., 4 November 2012, *A. Pauca T., E Mamani P., D. Caballero C., & G. Bernedo 311* (HSP 003130); Lomas de Yuta, 16°56'07"S, 72°03'37"W, 718 m.a.s.l., 7 September 2014, *A. Pauca T. & J. K. Chavez V. 482* (HSP 007861); Lomas de Yuta, 16°57'23"S, 72°04'07"W, 521 m.a.s.l., 16 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L. Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3467* (HSP 000636); Dist. Islay, a 800 m de la carretera a Matarani, troche al cerro Yuta, 16°56'18"S; 72°04'20"W, 798 m.a.s.l., 4 November 2012, *V. Quipuscoa S., C. Tejada P., J. Quispe T., & J. Cárdenas R. 5115* (HSP 003854); alrededores del desvío de la troche hacia Cerro Yuta, 16°56'06"S, 72°03'29"W, 693 m.a.s.l., 25 November 2012, *V. Quipuscoa S. & C. Tejada P. 5220* (HSP 004097); Lomas de Mollendo, 16°59'03"S, 71°59'45"W, 576 m.a.s.l., 2 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., & M. Bedoya C. 6403* (HSP 12024); Lomas de Yuta, 16°57'26"S, 72°03'28"W, 532 m.a.s.l., 4 November 2017, *V. Quipuscoa S., M. O. Dillon, M. Balvin A., S. Huamani Q., M. Bedoya C., & W. Ancalla C. 6479* (HSP 12028); bajando a Mollendo, 700 m.a.s.l., 29 October 1966, *C. Vargas C. 18093* (CUZ 21443, USM 81281); bajando a Mollendo, *C. Vargas C. 18100* (CUZ 21442, USM 81280); Quebrada Yura [Yuta] above Matarani, 400–800 m.a.s.l., 14 October 1997, *M. Weigend & H. Förther 97/881* (F 2211312). Prov. Islay, Dist. Cocachacra, Lomas de Cachendo, ca. 900 m.a.s.l., 9 February 1983, *M. O. Dillon, U. Molau, & P. Matekaitis 3287* (F 1950170); Lomas de Cachendo, 17°00'S, 71°44'W, 630 m.a.s.l., 1 March 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8242* (F 2199343); Lomas de Cachendo, 17°00'S, 71°44'W, 630 m.a.s.l., 1 March 1998, *M. O. Dillon, M. Tago, M. Zapata, & L. Martell 8243* (F 2199344, US 3692756); Cachendo, 900 m.a.s.l., 26 October 1976, *C. Ochoa 11258* (US 2910021, US 2982698); Lomas de Cachendo, 16°58'59"S, 71°46'01"W, 939 m.a.s.l., 14 November 2007, *V. Quipuscoa S., M. O. Dillon, E. Ortiz V., L Cáceres M., M. Cueva M., K. Durand V., D. Ramos A., & N. Castro V. 3411* (HSP 002665, HUSA 9109); Lomas de Cachendo, 16°58'53"S, 71°46'21"W, 961 m.a.s.l., 31 October 2017, *V. Quipuscoa S., M. O. Dillon, C. Tejada P., M. Balvin A., S. Huamaní Q., M. Bedoya C., C. Sanz N., & M. Flores M. 6350* (HSP 8771, HUT 60426).

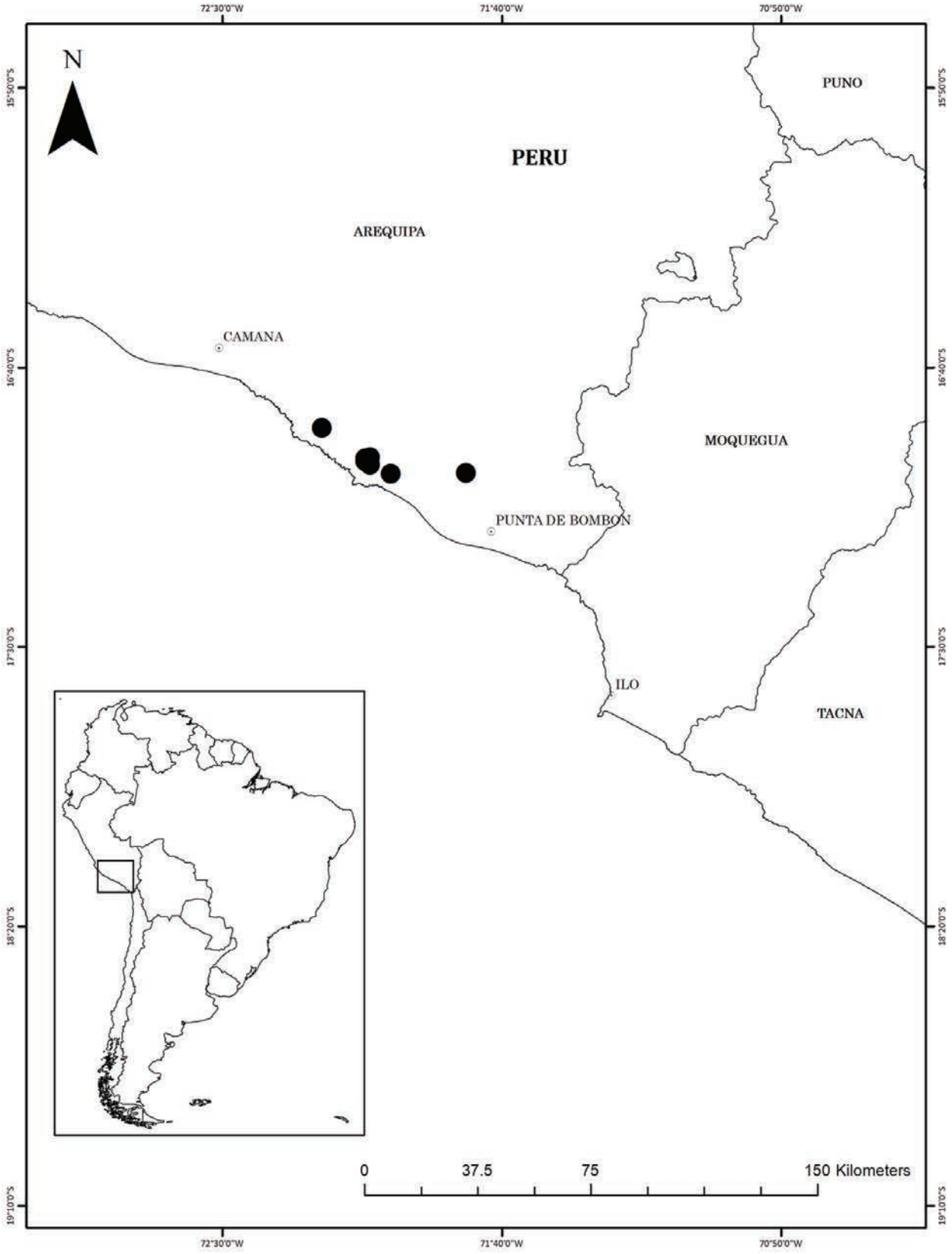


FIGURE 266. Distribution of *Nolana volcanica* Ferreyra.

FIGURE 267. *Nolana volcanica*. **A**, Much-branched, spreading perennials; **B,** Corollas light blue with a dark purple band in the throat and blue anther thecae and pollen. Photographs by Victor Quipuscoa Silvestre.

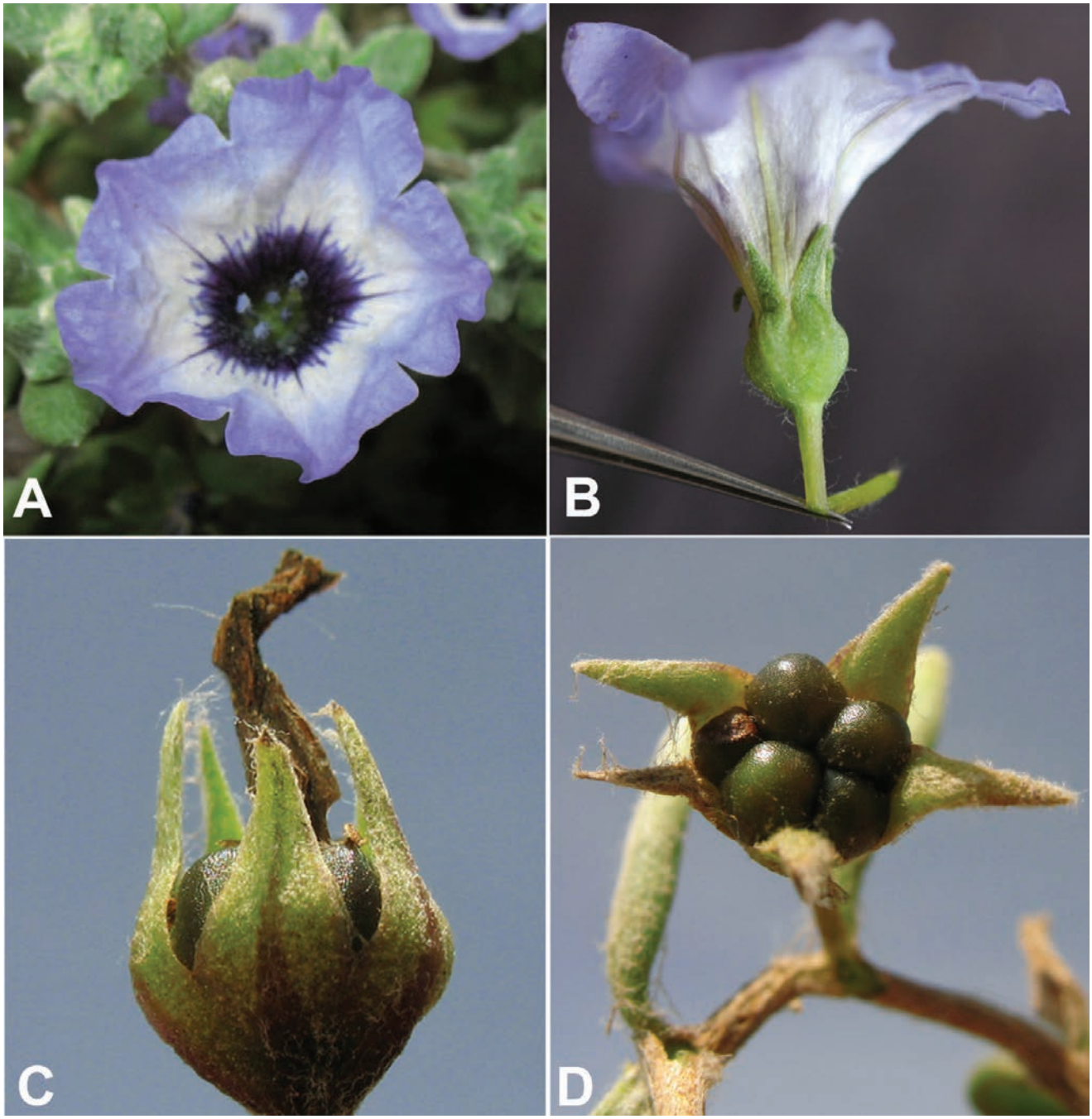


FIGURE 268. *Nolana volcanica*. **A**, Corollas slightly zygomorphic, guides dark purple. **B**, Calyces with arachnoid, non-glandular, elongate trichomes; **C**, Closeup of calyx, lobes with purple striations, cut to middle; **D**, Mericarps spherical. Photographs by Victor Quipuscoa Silvestre.

CLADE G

G1. ***Nolana albescens*** (Phil. ex Wettst.) I.M. Johnst., Contrib. Gray Herb. 112: 66. 1936. Fig. 269–270.

Basionym: *Dolia albescens* Phil. ex Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 4. 1891. *Dolia albescens* Phil., Anal. Univ. Chile. 91: 44. 1895. TYPE: CHILE. Atacama: Monte Amargo [Copiapó–Caldera], September 1885, *F. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55160, SGO000004349]).

Digital image: Holotype of *Dolia albescens* from Museo Nacional de Historia Natural, Santiago [SGO 55160]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004349

Homotypic synonym: *Bargemontia albescens* (Phil. ex Wettst.) I.M. Johnst., Contrib. Gray Herb. 85: 108. 1929; *Nolana crassulifolia* Poeppig subsp. *crassulifolia* Mesa, Fl. Neotrop. Monogr. 26: 88. 1981.

Heterotypic synonym: *Dolia canescens* Phil., Anal. Univ. Chile 91: 46. 1895. TYPE: CHILE. Atacama: Galena, 1889/90, *G. Geisse s.n.* (Holotype: SGO [SGO 55165, SGO000004350]).

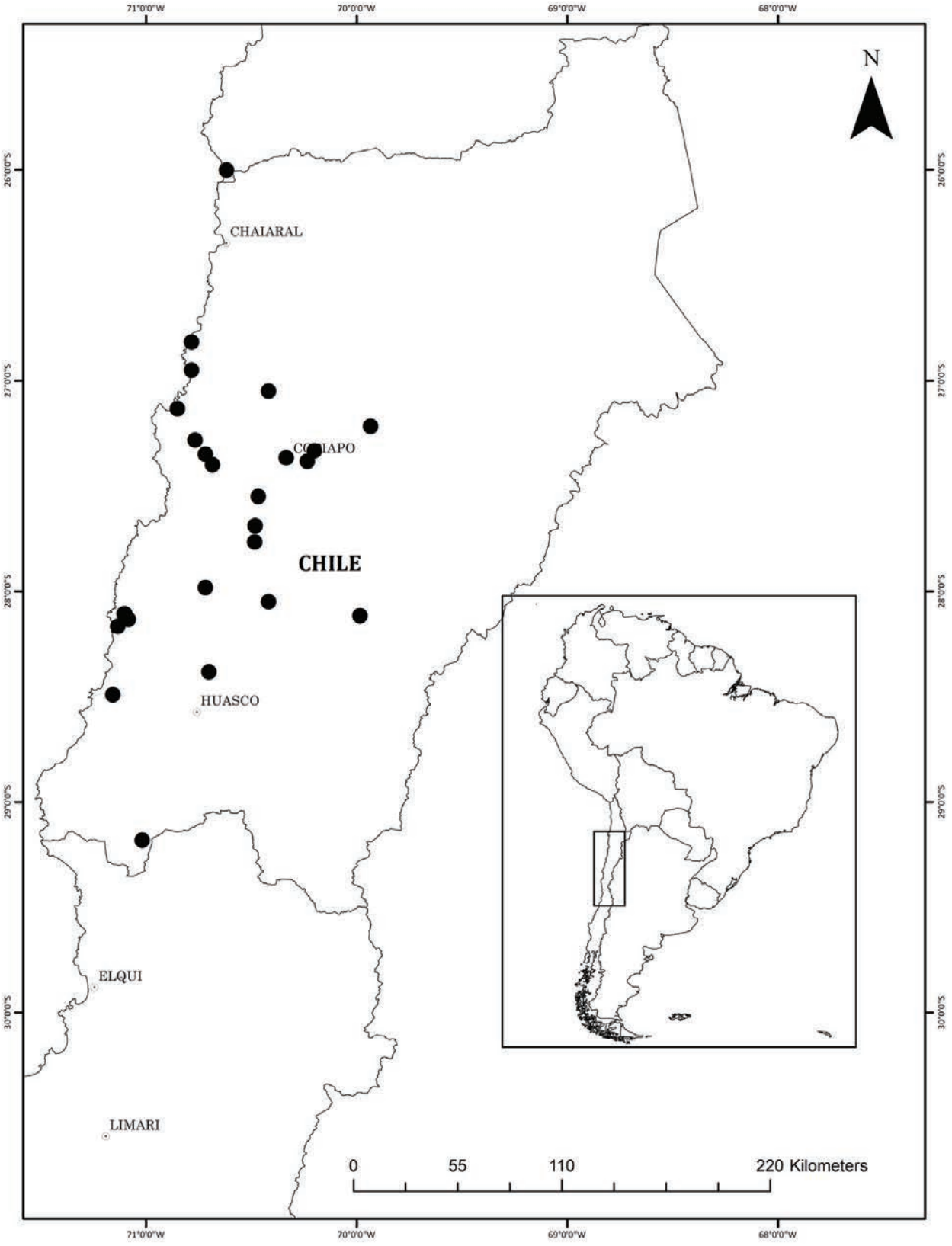


FIGURE 269. Distribution of *Nolana albescens* (Phil. ex Wettst.) I.M. Johnst.

Shrubs to ca. 1 m tall, 1–3 m in diam.; stems erect or ascending. *Leaves* alternate, blades spathulate, clavate, gradually expanded toward the apex, 5–11 mm long, 2–3 mm wide, terete, pubescence compact, dendritic trichomes, gray green, abaxial groove. *Inflorescences* of solitary flowers, terminal and axillary. *Flowers* 5-merous; calyces cupulate, 4.5–5.0 mm tall, ca. 3 mm wide, tube ca. 1.5 mm tall, lobes narrowly deltoid, ca. 3 mm long, ca. 1.5 mm wide, dendritic pubescence, in anthesis the lobes flatten out and appear star-shaped; corollas narrowly tubular, 10–13 mm long, actinomorphic, white, lobes 1.5–2.0 mm long, triangular; anthers blue to violet or purple; filaments villous at base. *Mericarps* 4(–5), 2 large, 2–3 small, oval to elliptic, amber-brown nectary, adhering to calyx; seeds ca. 4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *albus*, white, and *albescens*, signifying becoming white, and refers to the overall whitish or light-gray appearance of this species.

Distribution and Ecology: Chile, Region of Atacama and, potentially, Coquimbo, ranging ca. 300 km; (10–)100–600(–840) m.a.s.l. (Fig. 269). It is recorded from alluvial soils at varying distances from the ocean; Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana albescens is a shrub with erect to decumbent stems (Fig. 270A–B) and vegetative surfaces with dense dendritic pubescence that gives it a whitish or gray-green appearance. The flowers are white and tubular with reddish veins from the tips of the lobes to the base of the corollas (Fig. 271A–B). The gynoecium typically has four mericarps but occasionally has five (Fig. 271C). It is a member of a series of similar looking species with weakly allopatric populations dispersed from north to south, respectively: *N. peruviana*, *N. incana*, *N. albescens*, *N. crassulifolia*, and *N. werdermannii*. The distinctions between *N. albescens* and *N. incana*, a species generally located to the north, are perhaps trivial, but at each end of their distributions they are distinct. The calyces are similar; however, the corollas in *N. albescens* are slightly longer (10–15 mm long) than those in *N. incana* (5–10 mm long).

Johnston (1936: 67) related *N. albescens* to *N. incana* but suggested that the habit of *N. albescens* was bushier, with erect stems up to a meter tall, and evidently distributed to the interior. The ranges of *N. albescens* and *N. incana* overlap at the border between the regions of Antofagasta and Atacama. *Nolana albescens* can also be confused with *N. werdermannii*, a species with longer leaves and shorter corollas. The two do not overlap in distributional range, and *N. werdermannii* is clearly distributed to the south of *N. albescens*.

Johnston [1929: 108] stated that *Nolana albescens* has a firmer and denser indumentum and a more erect habit up to a meter tall. It was often infested with ants, which appear to use gall-like thickenings on the branches as domatia (Fig. 272A). The galls are obvious in fresh material, and, when investigated in 1983, were observed to contain small, white grubs or larvae which have not been identified (Fig. 272B–C).

Additional specimens examined: CHILE. **Atacama**: Copiapó, Nantoco, January 1958, *R. Acevedo s.n.* (SGO 73502); Freirina, Carrizal Bajo, 15 September 1965, *F. Behn s.n.* (CONC 36162); Pampa Caracoles, ca. 17 km N of Caldera, 26°57'S, 70°47'W, 100 m.a.s.l., 24 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5484* (CONC, E, F 2011633, GH, SGO); Km 20 al sur de Copiapó, 27°34'S, 70°27'W, 670 m.a.s.l., *M. O. Dillon & Finger 8613* (F 2331751); ca. 4.8 km E on C-440 from Carrizal Bajo to Ruta 5, 28°06'30"S, 71°06'12"W, 10 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8619* (SGO 158722); road to Aguada Tongoy, ca. 5 km SE of Huasco, 28°29'28"S, 71°09'24"W, 100 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8653* (SGO 158916); W of Ruta 5 towards Carrizal Bajo, 28°06'30"S, 71°06'12"W, 150 m.a.s.l., 29 November 2004, *M. O. Dillon & M. Finger C. 8661* (CONC 179069, SGO 158946); Quebrada de León, 100 m.a.s.l., 30 November 2004, *M. O. Dillon & M. Finger C. 8666* (F 2331752, SGO 158939); 18 km ENE of Chañaral, 731 m.a.s.l., 14 November 2009, *M. O. Dillon & A. Casareggio M. 9104* (CONC, F 2331754, SGO); Quebrada de León, ca. 18 km N of Chañaral, 26°56'00"S, 70°44'30"W, 326 m.a.s.l., 2 October 2010, *M. O. Dillon 9149* (CONC, F 2331759, SGO); 25 km NE of Chañaral along Panamericana towards N (Km 998), *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2683* (B, CONC 138421); 41 km S of Copiapó towards Vallenar, 27°41'22"S, 70°28'51"W, 650 m.a.s.l., 9 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2871* (B, CONC 138496, SGO 146037); Bandurrias, October 1888, *G. Geisse s.n.* (CONC 129679); Copiapó, Quebrada de Chanchoquin, November 1885, *E. E. Gigoux s.n.* (GH00282367); Copiapó, 27 October 1957, *C. Jiles 2083* (CONC 36163); Llano de Chacritas, Km 755, 28°23'S, 70°42'W, 638 m.a.s.l., 11 November 1969, *C. Jiles 5504* (CONC 102457); vicinity of Copiapó, ca. 600 m.a.s.l., 17 November 1925, *I. M. Johnston 5014* (GH, K, US 1473957); camino de Copiapó a Bahía Salada, 27°24'S, 70°41'W, 170 m.a.s.l., 18 October 2005, *F. Luebert & C. Becker 2887* (SGO 159450); Sierra de Los Sapos, 28°03'S, 70°25'W, 840 m.a.s.l., 17 September 2005, *F. Luebert & N. García 2493/887* (SGO 159467); camino de Caldera a Chañaral, Km 30, 24 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1888* (CONC 36136); cercanías de Copiapo, 27°29'40"S, 70°23'22"W, 21 September 2015, *P. Medina 3121* (CONC 186910); cercanías de Copiapó, 27°17'19"S, 70°08'31"W, 794 m.a.s.l., 25 September 2015, *P. Medina 3077* (CONC 186866); Huasco, Quebrada Ñisñiles, Sierra Marañón, 28°30'53"S, 70°46'41"W, 10 November 2011, *G. Mieres s.n.* (CONC 179836); Cerros las Campanitas, 28°27'28"S, 70°48'31"W, 7 December 2012, *G. Mieres s.n.* (CONC 179840); 1st km camino desde Copiapó a Inca de Oro, 27°20'S, 70°12'W, 600 m.a.s.l., 29 September 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2701* (SGO 126129): coastal desert near Totoral, N of Carrizal Bajo, *M. Ono & T. Masuzawa s.n.* (MAK 274963); between Paipote and Puquio, along PanAm Hwy, *M. Ono & K. Suzuki s.n.* (MAK 274059); Llano Seco, ca. 20 km S of Copiapó, *M. Ono & K. Suzuki s.n.* (MAK 274034);

FIGURE 270. *Nolana albescens*. **A**, Spreading, erect to decumbent shrub; **B**, Flowers tubular, white with reddish veins from the tip of the lobes to the base of the corollas.

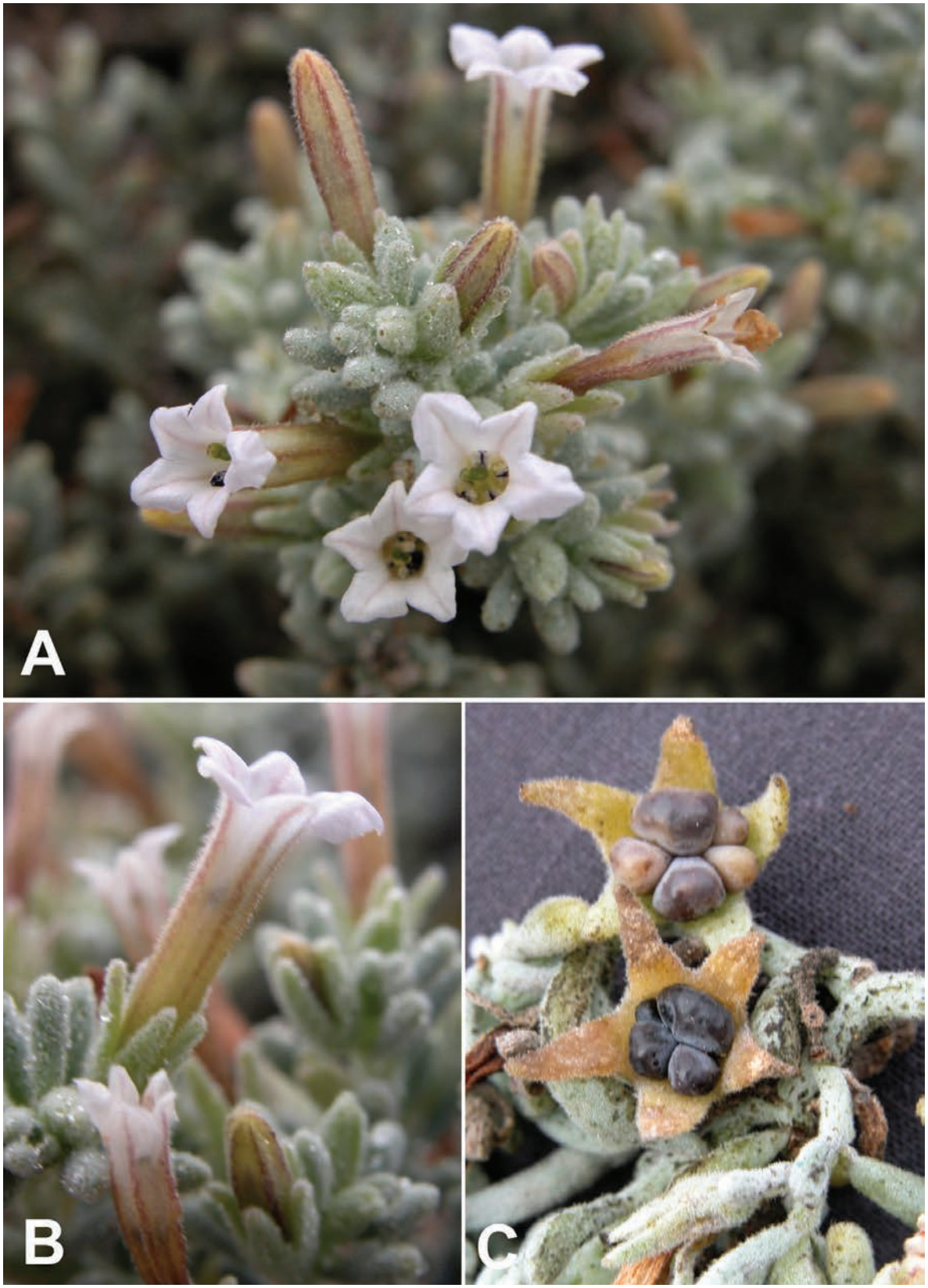


FIGURE 271. *Nolana albescens*. **A,** Vegetative surfaces covered with dense dendritic pubescence; **B**, Corollas three times the length of the calyx; **C**, Gynoecium with four or five mericarps.

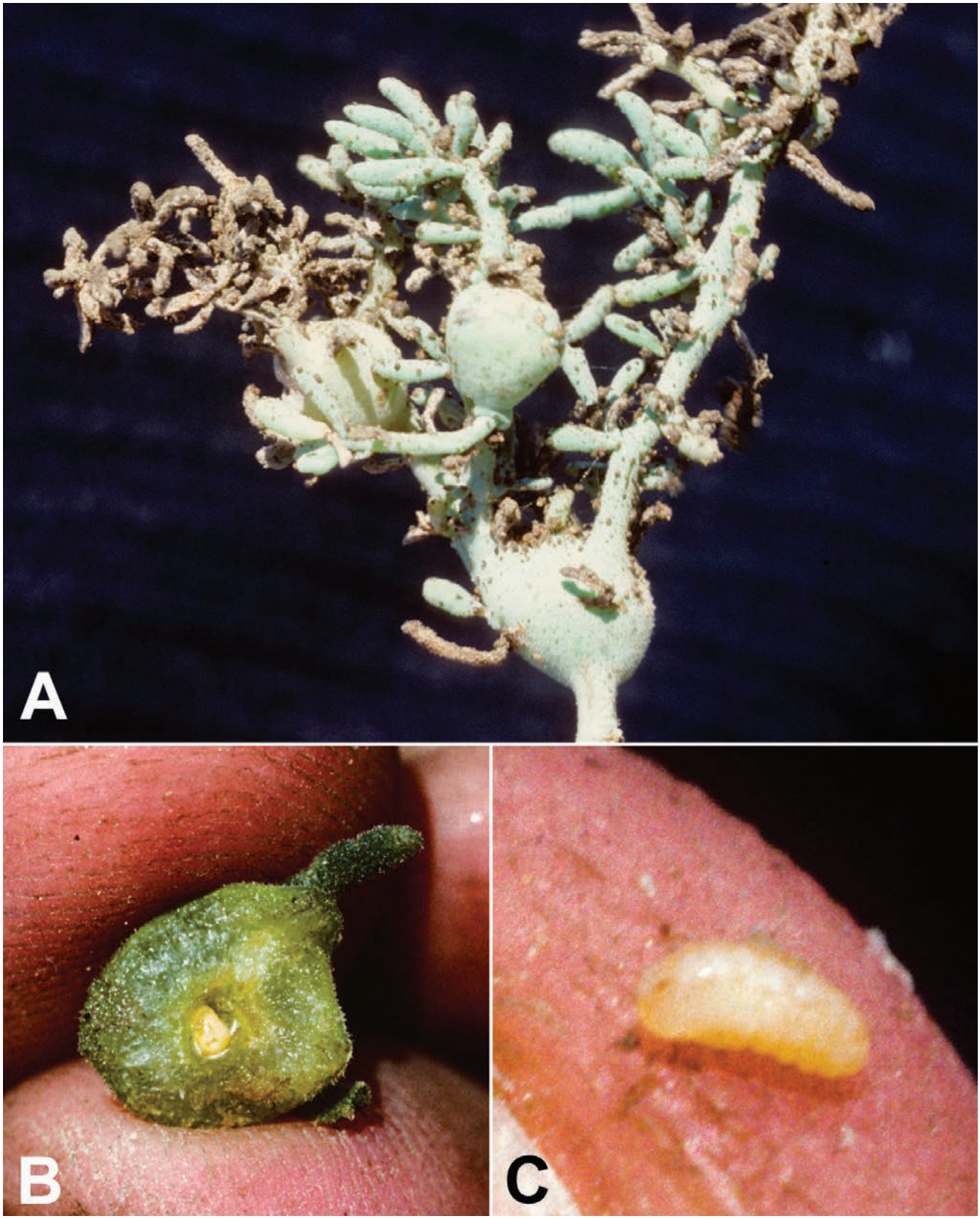


FIGURE 272. *Nolana albescens*. **A**, Branches infested with ants that may use domatia, gall-like thickenings on the branches; **B–C**, Galls contain small, white larvae.

Copiapó, Monte Amargo, 1885, *F. Philippi & A. Borchers s.n.* (BM000941290); Puquios, 800 m.a.s.l., 28 October 1956, *M. Ricardi & C. Marticorena 3676* (CONC 23820); Travesía, 7 November 1956, *M. Ricardi & C. Marticorena 3807* (CONC 23935); Huasco, lomas frente a Las Lozas, 30 m.a.s.l., 14 November 1956, *M. Ricardi & C. Marticorena 3937* (CONC 24054); al norte de Paipote, 550 m.a.s.l., 13 September 1958, *M. Ricardi & C. Marticorena 4602/987* (CONC 25392), *4604/989* (CONC 25394); Copiapó, Quebrada Chuschampis, frente a Punta de Díaz, 27°59'S, 70°34'W, 460 m.a.s.l., 26 November 1980, *R Rodríguez & C. Marticorena 1611* (CONC 92377); Monte Amargo, 18 September 1965, *J. Saá L. s.n.* (CONC 129575), *s.n.* (CONC 129578); 50–60 km S de Copiapó, 24 August 1966, *E. Schlinger s.n.* (CONC 129680); Cerro Negro, 28°10'S, 71°08'W, 18 October 2006, *N. Schulz 17* (SGO 154752); Huasco, al norte de Incahuasi, 29°11'S, 71°01'W, 880 m.a.s.l., 19 March 1988, *F. Squeo 88-201* (CONC 99519); Llano Seco, 7 October 1993, *K. Suzuki s.n.* (MAK 274058); 5 km E de Totoral Bajo, 170 m.a.s.l., *S. Teillier 5535* (CONC 163824); Tierra Amarilla, Quebrada El Buitre, 1 April 1996, *S. Teillier & H. Cofré 96-4240* (SGO 154644); frente a la mina Mantos Verdes, 26°33'54"S, 70°20'23"W, 14 April 2016, *S. Teillier & V. Escobar 8133* (CONC 183662); 7 km S al sur de Inca de Oro, 26°49'20"S, 69°53'13"W, 1770 m.a.s.l., *S. Teillier & R. Lund 7920* (CONC 179567); Caldera, 10 m.a.s.l., September 1924, *E. Werdermann 379* (BM000941293, CONC 109133, E00130922, F 565201, K); Tierra Amarilla, ca. 500 m.a.s.l., September 1924, *E. Werdermann 398* (A, BM000941292, CONC 109127, E00130925, F 565220, K); Huasco, back from town, 10–15 m.a.s.l., 26 October 1938, *C. R. Worth & J. L. Morrison 16219* (GH, K, US 3634882). **Coquimbo**. Tres Cruces, Estación Junta de Chingoles, 29°22'S, 15 September 1935, *C. Muñoz P. B-306* (GH). **No exact locality**: Desert of Atacama, September–October 1890, *T. Morong* (K, US); *T. Morong 1279* (E00130926, F 166486, US 80116).

G2. ***Nolana aplocaryoides*** (Gaudich.) I.M. Johnst., Contrib. Gray Herb. 112: 57. 1936. Fig. 273–277.

Basionym: *Leloutrea aplocaryoides* Gaudich., Voy. Bonite pl. 110. 1842–1846. TYPE: CHILE. Antofagasta: Cobija, *C. Gaudichaud 1* (Holotype: P [00605877]; Isotype: P [P00605880]).

Digital image: Holotype of *Leloutrea aplocaryoides* from the National Museum of Natural History, Paris [P00605877]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.p00605877

Homotypic synonyms: *Bargemontia aplocaryoides* (Gaudich.) I.M. Johnst., Contrib. Gray Herb. 85: 110. 1929; *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa var. *aplocaryoides* (Gaudich.) Mesa, Fl. Neotrop. Monogr. 26: 107. 1981.

Heterotypic synonyms: *Alona pusilla* Phil., Fl. Atac. 45. 1860. TYPE: CHILE. Antofagasta: Caldera and Cachinal de la Costa, *R. A. Philippi s.n.* (Holotype: SGO [55198, SGO000004343]).

Annual *herbs* 10–50 cm tall, or, with sufficient moisture, spreading shrubs; stems sometimes reaching 100–120 cm tall, erect or decumbent, divaricately branched, deep purple, densely hispid with simple trichomes. *Leaves* alternate to fasciculate, clustered towards the apices of branchlets, blades oval to oblanceolate, (3–)5–10(–20) mm long, ca. 5 mm wide, margins revolute, densely pubescent with hispid trichomes. *Inflorescences* of solitary flowers, terminal and axillary. *Flowers* 5-merous; calyces cupulate, 4–5 mm long, lobes 2–3 mm long, lanceolate, unequal; corollas narrowly infundibularis to hypocrateriformis, 13–27 mm long, ca. 20 mm wide, white to light lavender; stamens unequal, filaments not widened at the base, rarely pubescent; nectary disc crateriform, sinuous; style equal to the anthers, gynobasic; stigma capitate or capitate-lobate. *Mericarps* 3(–6), spherical to oblong, ca. 2.5 mm long, ca. 2 mm wide; seeds 1–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is Gaudichaud's suggestion of a resemblance to *Aplocarya* Lindl., a synonym of *Nolana*, and the Greek suffix, *-oides*, indicating resemblance. Lindley named the genus *Aplocarya* by combining the Greek simple, απλός, and nut, κάρυο, containing a single species, *A. divaricata* Lindl.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; 30–100 (–2100) m.a.s.l. (Fig. 273). It is recorded from environments with sandy soils or alluvial gravel fans in near-coast habitats; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Illustration: Fig. 274. Illustration of *Nolana aplocaryoides* as *Leloutrea aplocaryoides*, Plate 110, Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana aplocaryoides is a distinctive annual with a single, purplish-colored stem perhaps 20–30 cm tall that branches toward the apex. Some morphs have been described as a "little trees", and populations of many hundreds of plants can cover large areas (Fig. 275A). The habit of individuals can vary drastically, depending upon the availability of moisture as a plant germinates and reaches flowering maturity. Given sufficient water, as occurs from runoff into *pozos* or small ponds, an individual can grow to a meter tall with dense branches and leaves (Fig. 275B). The stems are purple, the leaves are quite revolute and densely pubescent with hispid trichomes, and the corollas and pollen are invariably white, but are sometimes lavender (Fig. 276A–B). The gynoecium is typically reduced to only three principal mericarps, but occasionally there are as many as five (Fig. 276C–D). The mericarps are initially cream to orange and turn black with maturity (Fig. 276D).

It seems that *Nolana aplocaryoides* (Fig. 277A) has been misinterpreted, especially when collections are dried and flat. For example, the collections of *N. onoana* (Fig. 277B) had been attributed to *N. aplocaryoides*, but when examined in the living condition, they are so very different and impossible to confuse.

Johnston (1929: 110) remarked, "An erect annual herb which is ascending branched above the middle. The stems and foliage are covered with a clammy indumenta of simple spreading hairs. The lavender corolla is completely

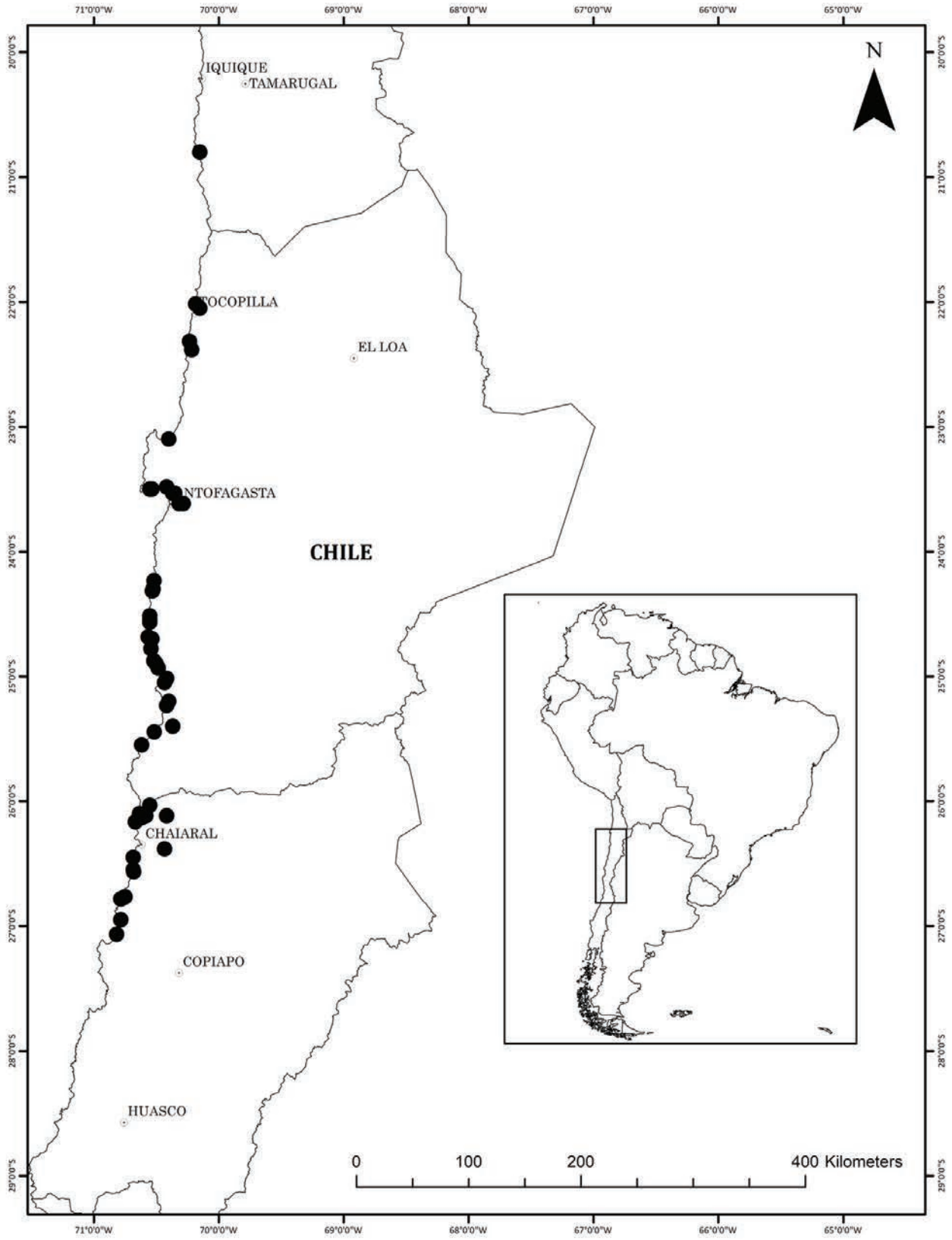


FIGURE 273. Distribution of *Nolana aplocaryoides* (Gaudich.) I.M. Johnst.

FIGURE 274. Illustration of *Nolana aplocaryoides* as *Leloutrea aplocaryoides*, Plate 110. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

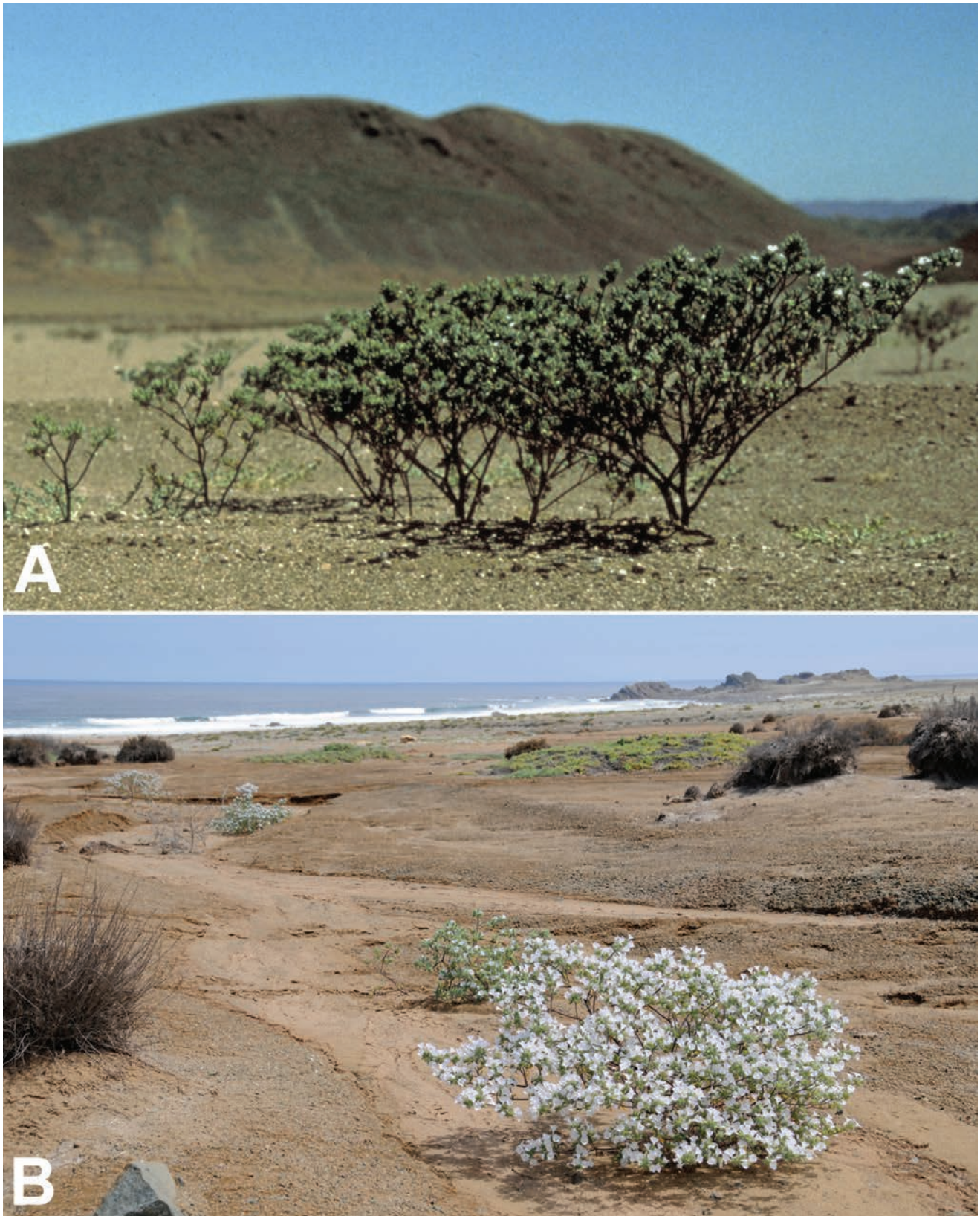


FIGURE 275. *Nolana aplocaryoides*. **A**, Annuals resembling "little trees;" **B**, Flowering robust annual with unlimited available moisture.

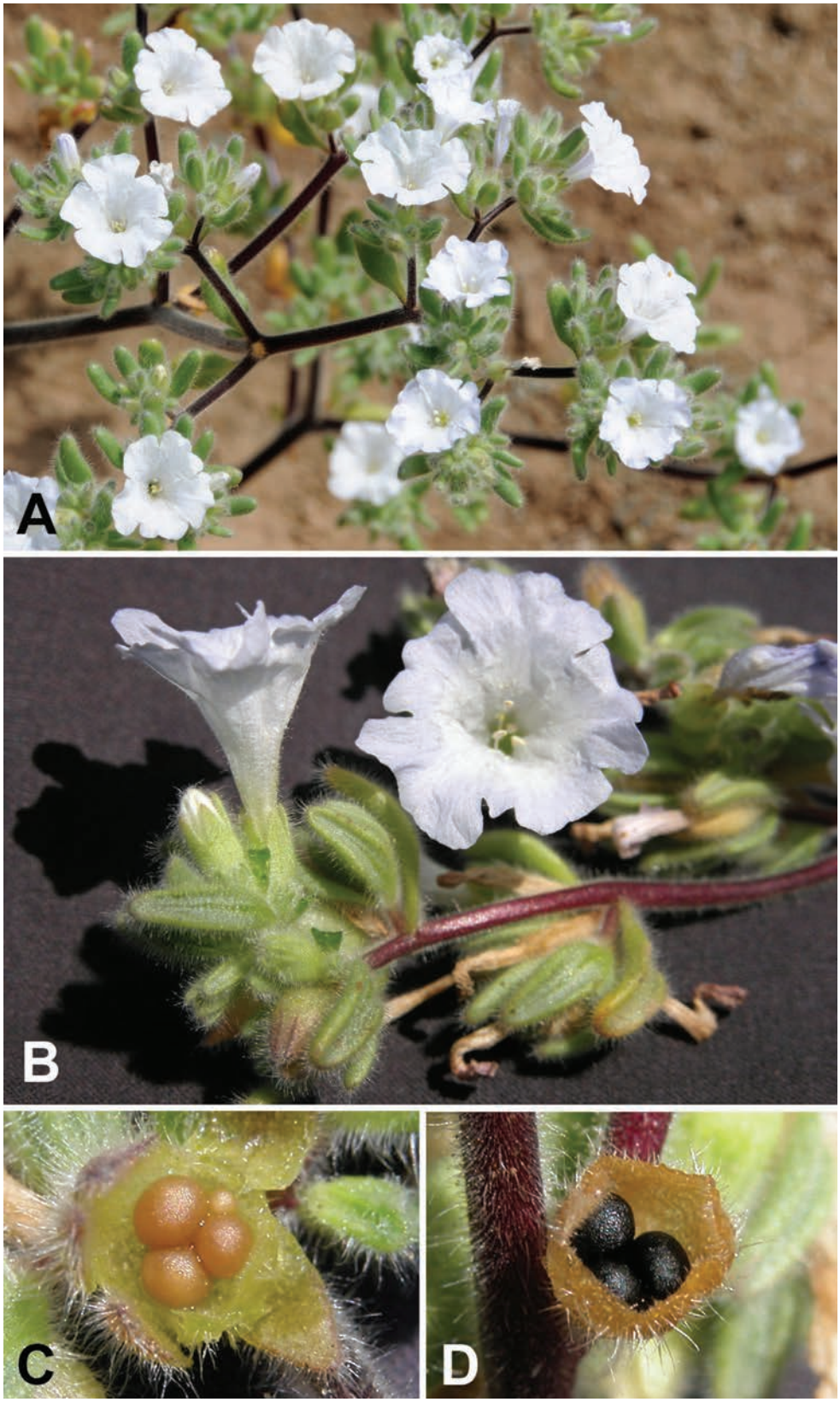


FIGURE 276. *Nolana aplocaryoides*. **A**, Flowering plants with purple stems; **B**, Leaves revolute and densely hispid, corollas and pollen white; **C–D**, Gynoecium reduced, three to five mericarps, initially cream-colored turning black with maturity.

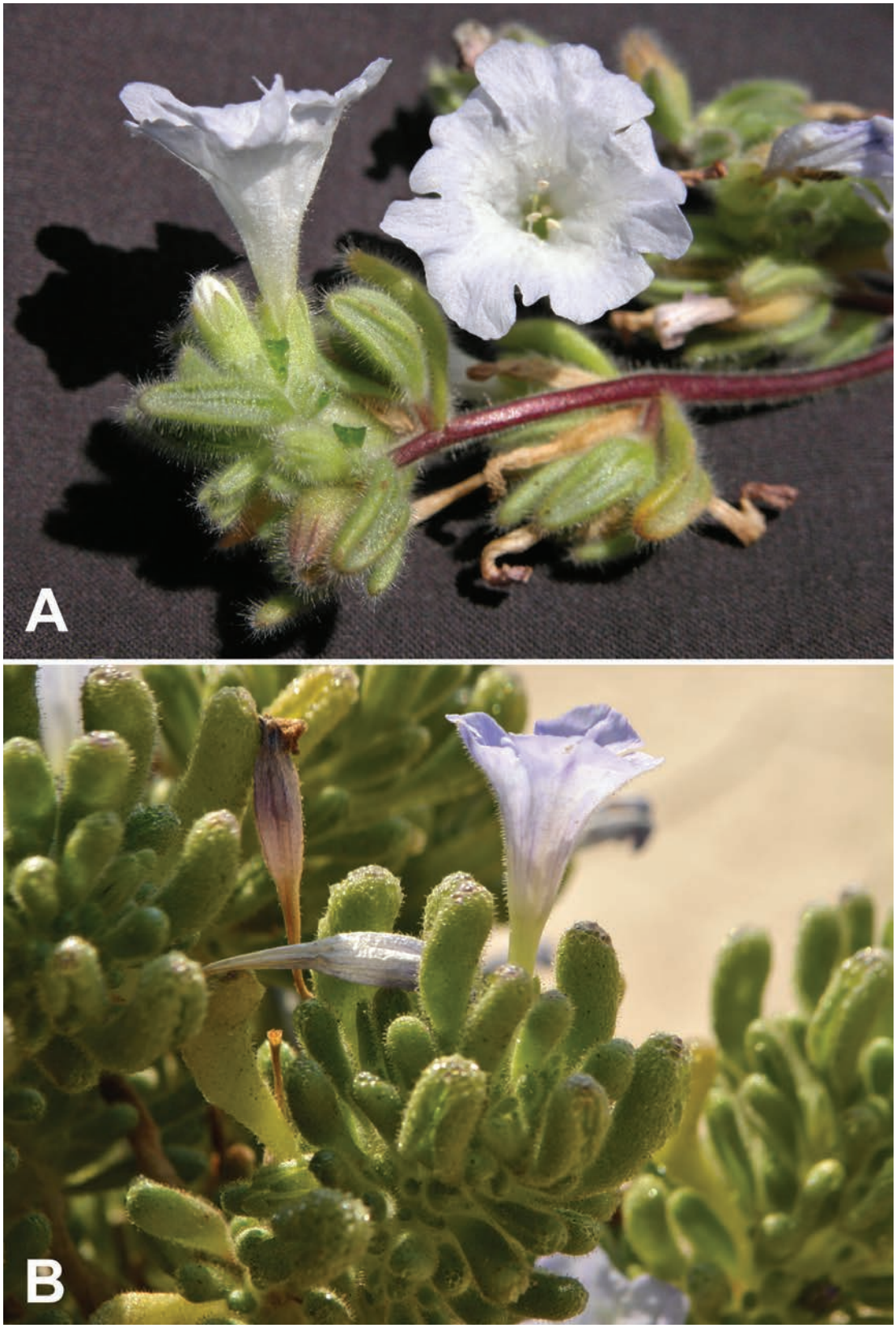


FIGURE 277. *Nolana aplocaryoides*. Comparison of **A**, *N. aplocaryoides* and **B**, *N. onoana* in the living state.

glabrous inside. The plant grows 2–4 dm tall and frequents dry sand and gravel near the coast throughout our area. It has been collected near Barquito (*Johnston 4814*), Taltal (*Werdermann 774*), and Punta Buitre (*Johnston 5243*). Furthermore, Johnston (1929: 157) observed, "Collected on the dry gravelly plain at the base of the hills near Antofagasta (*Johnston 3639*). The specimens upon which the original plate of *L. aplocaryoides* was based were almost certainly collected by C. Gaudichaud at Cobija."

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, lomas de Taltal, 25°26'45"S, 70°30'57"W, 30 m.a.s.l., 25 October 2002, *M. Ackermann 488* (SGO 150968); El Médano, 24°39'S, 70°33'W, 85 m.a.s.l., 1 December 2001, *C. Aedo 7052* (CONC 161707, MA); Cordillera Costa, quebrada paralela a la costa, 8 km al interior, frente a Caleta Coloso, 150–650 m.a.s.l., April 1992, *J. Anabalón s.n.* (SGO 126924); 10 km N from Paposo, 24°55'54"S, 70°30'46"W, 16 m.a.s.l., 21 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 34* (E00230473); 20 km al S de Paposo, 2 February 1947, *W. Biese 2243* (SGO 674412); Aguada Cachina, Cachinal de La Costa, 400 m.a.s.l., 13 December 1949, *W. Biese 3243* (SGO 96847); Quebrada Cachina Planta Esmeralda, Cachinal de La Costa, 200–600 m.a.s.l., 13 December 1949, *W. Biese 3297* (SGO 696901); Quebrada Guanillos, 10 km al N del Cachinal de la Costa, 50–500 m.a.s.l., 14 December 1949, *W. Biese 3345* (SGO 675222); Quebrada Bandurrias, 17 October 1991, *A. Brinck s.n.* (SGO 122821); cercanías Paposo, 25°00'34"S, 70°27'57"W, 20 June 2015, *K. Bull H. 676* (SGO 166633); Vicinity of Miguel Díaz, directly N of Quebrada Iscuña, 24°33'S, 70°33'W, 100–350 m.a.s.l., 15 December 1987, *M. O. Dillon & S. Teillier 5305* (CONC, F 2010883, GH); ca. 7 km SE of Caleta El Cobre on road to Antofagasta, 24°18'S, 70°28'W, 550 m.a.s.l., 16 December 1987, *M. O. Dillon & S. Teillier 5317* (CONC, F 2010939, GH, SGO); near Quebrada Botija, ca. 11 N of Miguel Díaz, ca. 60 km N of Paposo, 24°31'S, 70°33'W, 18 December 1987, *M. O. Dillon 5353* (F 2010905, GH); near Punta Los Tres Picos, ca. 10 km S of Caleta El Cobre, 24°19'S, 70°33'W, 90–100 m.a.s.l., 4 October 1998. *M. O. Dillon & D. Dillon 5628* (CONC, E, F 2013662, GH, K, SGO, US); Near Quebrada Botija, ca. 35 S of Caleta El Cobre, 24°31'S, 70°34'W, 90–100 m.a.s.l., 4 October 1988, *M. O. Dillon & D. Dillon 5633A* (F 2013658); Aguada directly W of Quebrada de Iscuña, ca. 46 km S of Caleta El Cobre, 24°34'S, 70°33'W, 20–30 m.a.s.l., 4 October 1988, *M. O. Dillon & D. Dillon 5637* (CONC, E, F 2013654, GH, SGO, US); Aguada directly W of Quebrada de Iscuña, ca. 46 km S of Caleta El Cobre, 20–30 m.a.s.l., 7 October 1988, *M. O. Dillon & D. Dillon 5660* (F 2014404); Antofagasta: Quebrada Paposo, 5–12 km E of Caleta Paposo, 25°01'S, 70°25'W, 350–950 m.a.s.l., 28 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5563* (F 2012895); N side Punta Dos Reyes, ca. 39 km S of Quebrada El Cobre, 24°32'S, 70°34'W, 5–10 m.a.s.l., 13 November 1988, *M. O. Dillon & D. Dillon 5894* (E, F 2144389, GH, SGO, US); ca. 10 km N of Taltal, 25°20'S, 70°27'W, 50 m.a.s.l., 29 November 1997, *M. O. Dillon 8145* (CONC 149998, E, F 2182960, GH, K, SGO 143704); 36 km N of Paposo ThermoElectric plant, 24°41'05"S, 70°33'52"W, 100 m.a.s.l., 1 November 2004, *M. O. Dillon & M. Finger C. 8639* (CONC 170079, E, F 2329908, SGO 158715); 16 km N of ThermoElectric plant N of Paposo, 24°52'32"S, 70°31'06"W, 110 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8677* (CONC 179103, F 2292799, SGO 158928); 20 km N of Paposo, near ocean in front of Quebrada Panul, 24°46'42"S, 70°32'30"W, 60 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9065* (F 2292850, SGO 158729); Quebrada Médano, ca. 21 km N of Paposo, 24°50'26"S, 70°31'58"W, ca. 102 m.a.s.l., 19 November 2011, *M. O. Dillon 9218* (CONC, F 2331766, SGO); Tocopilla, Chimba, 28 November 1941, *M. R. Espinosa s.n.* (SGO 139539); Rinconada de Paposo, Barrancas, 24°56'S, 70°29'W, 0–250 m.a.s.l., 1 December 1989, *O. Gálvez, A. Cornejo, y M. Villarroel O. 11* (SGO 127373); Rinconada de Paposo, 24°56'S, 70°29'W, 0–250 m.a.s.l., 1 December 1989, *O. Gálvez, A. Cornejo, & M. Villarroel O. 13* (SGO 127375); Rinconada de Paposo, 24°56'S, 70°29'W, 0–250 m.a.s.l., 1 December 1989, *O. Gálvez, A. Cornejo, & M. Villarroel O. 17* (SGO 127379); Tocopilla, 27 October 1930, *F. Jaffuel 1046* (GH); Taltal, September 1931, *F. Jaffuel 2590* (CONC 68823, GH); Caleta Cobre, 8 October 1961, *A. Garaventa 7082* (CONC 68825), *7083* (CONC 92460); Quebrada de La Chimba, 23°32'S, 70°22'W, 100 m.a.s.l., 16 November 1987, *A. Hoffmann y X. Rodríguez 4* (CONC 99182); Tocopilla, Quebrada La Carmelita, 22°03'S, 70°10'W, 700 m.a.s.l., 7 November 1969, *C. Jiles 5325* (CONC 102352); La Chimba, 19 October 1925, *I. M. Johnston 3639* (GH, US 1473982); 10.5 km N of Paposo, La Rinconada, 24°54'S, 70°30'W, 200 m.a.s.l., 15 September 1991, *L. R. Landrum, G. Gutierrez, & S. S. Landrum 7479* (F 2116617, SGO 130277); al sur de Caleta Botija, 24°30'58"S, 70°33'37"W, 85 m.a.s.l., 4 October 2005, *F. Luebert & N. García 2619 / 1013* (F 2290745); Panul, 24°47'S, 70°33'W, 10–200 m.a.s.l., 7 October 2005, *F. Luebert & N. García 2680 / 1074* (F 2290744, SGO 159468); Quebrada Cascabeles, 10 m.a.s.l., 16 September 1941, *C. Muñoz P. & G. T. Johnson 2846* (SGO 118313); 3 km desde Taltal a Paposo, 27 October 1987, *M. Muñoz S. & I. Meza P. 2279* (SGO 137717); Paposo, Quebrada Higuera, 27 January 1957, *S. Nuñez s.n.* (CONC 129676); Quebrada San Ramon, 10–100 m.a.s.l., 25 September 1941, *E. Pisano V. & R. Bravo F. 223* (CONC 144229, SGO 140577); Puerto de Taltal, 60–100 m.a.s.l., 16 September 1941, *E. Pisano V. & R. Bravo F. 251* (SGO 139745); Prov. Tocopilla, Quebrada Chapacase, *M. Quezada & E. Ruiz 10* (CONC 121184); Cerro Copaca, 22°19'S, 70°14'W, 30 m.a.s.l., 28 September 1991, *M. Quezada & E. Ruíz 13* (CONC 121073); Quebrada La Chimba, 23°32'S, 70°21'W, 300 m.a.s.l., 30 September 1991, *M. Quezada & Ruíz 101* (CONC 121144); Quebrada Chinchilla, en la junta con Quebrada La Plata, 24°42'S, 70°32'W, 450 m.a.s.l., 6 October 1991, *M. Quezada & E. Ruiz 310* (CONC 121143, SGO 127874); Taltal, Palo Varado, *M. Ricardi 2515* (CONC 14308); Paposo, Mina Abundancia Posada, 25 September 1953, *M. Ricardi 2647* (CONC 14440); quebrada camino Antofagasta–Calama, Km 10, 12 February 1968, *M. Ricardi*

5508 (CONC 36121); Quebrada Bandurrias, 25°12'S, 70°24'W, 600 m.a.s.l., 5 November 1985, *F. Schlegel 7871* (CONC 99859); ca. 10 km S of Paposo on Rt. 1, ca. 0.5 km S of Santo Domingo, 20°10'S, 70°30'W, 0–2 m.a.s.l., 5 October 1991, *C. M. Taylor, C. von Bohlen, & A. Marticorena 10733* (F 2116659); Punta Morada, 25°22'S, 70°27'W, 20 m.a.s.l., 3 December 2002, *S. Teillier 5972* (CONC 170792); Quebrada de Taltal, 25°26'S, 70°35'W, 130 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2878* (SGO 129358); Paposo, Sector "El Gaucho," 25°26'S, 70°35'W, 50 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. Gracia 2919* (F 2114633, SGO 129359); Paposo, cerca de la playa, 15 November 1959, *J. C. Torres s.n.* (SGO 135488); Quebrada Yumbes, 25–26 August 1992, *J. C. Torres s.n.* (SGO 128749); Taltal, 100 m.a.s.l., October 1925, *E. Werdermann 774* (BM000941306, CONC 22596, CONC 109128, E00130094, F 564219, GH, K 3310757, US 1444769), *974* (B); ca. 10 km SE of Antofagasta, ca. 100 m.a.s.l., 17 November 1935, *J. West 3871* (GH); end of Cifuncho road S of Taltal, 30 m.a.s.l., 15 October 1938, *C. R. Worth & J. L. Morrison 16126* (GH, K). **Atacama**: Prov. Chañaral, hills N of Chañaral, 100 m.a.s.l., 22 February 1939, *A. A. Beetle 26142* (GH, K); Caldera a Chañaral, 4 November 1965, *F. Behn s.n.* (CONC 30861); Parque Nacional Pan de Azúcar, Quebrada de Agua Chica, 5–18 October 1992, *M. E. Cruzat s.n.* (SGO 133709); Near Playa Hippie, ca. 13 km S of Chañaral along Pan American Hwy 5, 26°27'S, 70°41'W, 20 m.a.s.l., 3 December 1987, *M. O. Dillon & S. Teillier 5055* (CONC, E, F 2010278, GH, SGO, US 3470028); Pampa Caracoles, ca. 11 km N of Caldera, 26°57'S, 70°47'W, ca. 60 m.a.s.l., 24 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5472* (CONC, E, F 2012163, GH, SGO, US); 21 km W of Pan-American Hwy 5 on northern route to Parque Nacional Pan de Azúcar, 26°08'S, 70°37'W, 85 m.a.s.l., 30 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5605* (CONC, E, F 2012857, GH); Quebrada to Bahia Tórtolas, S side of Cerro San Pedro, ca. 13 km N of Cifuncho, 25°33'S, 70°37'W, 20–70 m.a.s.l., 12 October 1988, *M. O. Dillon & D. Dillon 5670* (F 2014395); Parque Nacional Pan de Azúcar, Las Lomitas, 6 km E of coast, 26°02'S, 70°33'W, 560 m.a.s.l., 12 November 1997, *M. O. Dillon & C. Trujillo C. 8016* (CONC 149966, E, F 2183316, GH, K, SGO 143721); Parque Nacional Pan de Azúcar, 26°07'S, 70°35'W, 200 m.a.s.l., 1 December 1997, *M. O. Dillon 8149* (F 2182957); ca. 13 km SSW of Chañaral, 26°26'33"S, 70°41'02"W, ca. 15 m, 28 October 2009, *M. O. Dillon & R. Concha 9075* (CONC, F 2293478, SGO); Quebrada El León, 26°58'37"S, 70°46'58"W, ca. 190 m, 30 October 2010. *M. O. Dillon 9171* (CONC, SGO); Pan de Azúcar, 30 October 1980, *J. Grau 2213* (BM000941282); Cerca de Caldera, 7 October 1966, *C. Jiles 4941-A* (CONC 34605), *4941-a* (CONC 103542); Puerto de Chañaral, 26°23'S, 28–29 October 1925, *I. M. Johnston 4814* (GH); Punta Buitre, 24°40'S, 4 December 1925, *I. M. Johnston 5243* (GH); 16 km al S de Chañaral, 19 September 1996, *E. M. L. Kausel 5067* (SGO 137152); camino de Chañaral a El Salado, Km 13 Quebrada El Salado, Pampa Negra, 26°23'S, 70°26'W, 250 m.a.s.l., *C. Marticorena, T. Stuessy, & M. Baeza 9903* (CONC 136240); 12 km del camino acceso costero al Parque Nacional Pan de Azúcar, 26°08'S, 70°38'W, 31 September 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2815* (SGO 126140); Pan de Azúcar, 11 November 1991, *M. Ono s.n.* (MAK 274946); between Caldera and Chañaral, 10 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274035); Quebrada La Quiscuda, entre Pan de Azúcar y Caleta Esmeralda, 50 m.a.s.l., 29 October 1941, *E. Pisano V. & R. Bravo F. 559* (CONC 144227, SGO 156483); 5 km al sur de Obispito, camino Caldera–Chañaral, 10 February 1968, *M. Ricardi 5485* (CONC 36161); carretera Panamericana entre Chañaral y Caldera, Km 65, 23 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1452* (CONC 36158); entre Chañaral y Barquito, 22 February 1969, *M. Ricardi & O. Parra 89* (CONC 33002); Parque Nacional Pan de Azúcar, frente a Cerro Soldado, 26°10'S, 70°40'W, 1150 m.a.s.l., 30 October 1991, *R. Rodríguez 2642-B* (CONC 125792); Cerros frente a Puerto Flamenco, 26°34'S, 70°41'W, 30 m.a.s.l., 29 October 1991, *R. Rodríguez 2678* (CONC 125793); Parque Nacional Pan de Azúcar, 26°07'S, 70°25'W, 15 September 1992, *S. Teillier, P. Rundel, & P. García 2739* (F 2114659, SGO 129357).

G3. ***Nolana crassulifolia*** Poepp., Froriep, Not. Natur- Heilk. 1, 23: 276. 1829. TYPE: CHILE. Valparaíso: "in rupibus marit. ubique prope Concón", *E. F. Poeppig 67* (Lectotype designated by Dillon and Quipuscoa, 2023: W [1889-0301807]; Isolectotypes: BM [BM000021201], HAL [HAL 115090], P [P00605847], W [W0075445]). Fig. 278–282.

Digital image: Lectotype of *Nolana crassulifolia* from Natural History Museum, Vienna [W1889-0301807]. https://herbarium.univie.ac.at/database/detail.php?ID=1103907

Homotypic synonyms: *Bargemontia crassulifolia* (Poepp.) I.M. Johnst., Contr. Gray Herb. 85: 107. 1929. *Dolia crassifolia* Kunth, Revis. Gen. Pl. 3(3): 216. 1898, *Nolana crassifolia* Kunth, Revis. Gen. Pl. 3(3): 216. 1898, in syn.

Heterotypic synonyms: *Alibrexia rupicola* Miers, London J. Bot. 4: 506. 1845. TYPE: CHILE. Valparaíso: Concón, "on rocks upon seashore on which the sea washes", *J. Miers 295* (Lectotype designated by Mesa-M., 1981: BM; Isotypes: K, US [US 1343853, US00121975]). Fig. 279. *Dolia grandiflora* Phil., Ann. Univ. Chile 91: 46. 1895. TYPE: CHILE. Valparaíso: Concón, *F. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: W, not seen; Isolectotypes: SGO [SGO 55152], BM, G, not seen, P). *Alona tomentosa* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Valparaíso: Valparaíso, on rocky cliffs, 1831, *H. Cuming 481* (Holotype: CGE [CGE05019]; Isotypes: BM (BM000021197), BR (BR0000005230389), E (E00130930), FI-Webb, K (K000532252)). Syntype: CHILE. Valparaíso: Valparaíso, *T. Bridges s.n.* (K [K000532253]). *Alibrexia tomentosa* Miers., London J. Bot. 4: 508. 1845. *Alibrexia philippii* A. Braun ex W. Brandt, Bot. Jahrb. Syst. 69(2): 176. 1938, in synonymy. *Nolana grossulifolia* Kunze ex Gay, Fl. Chil. [Gay] 5: 114. 1849, no type designated.

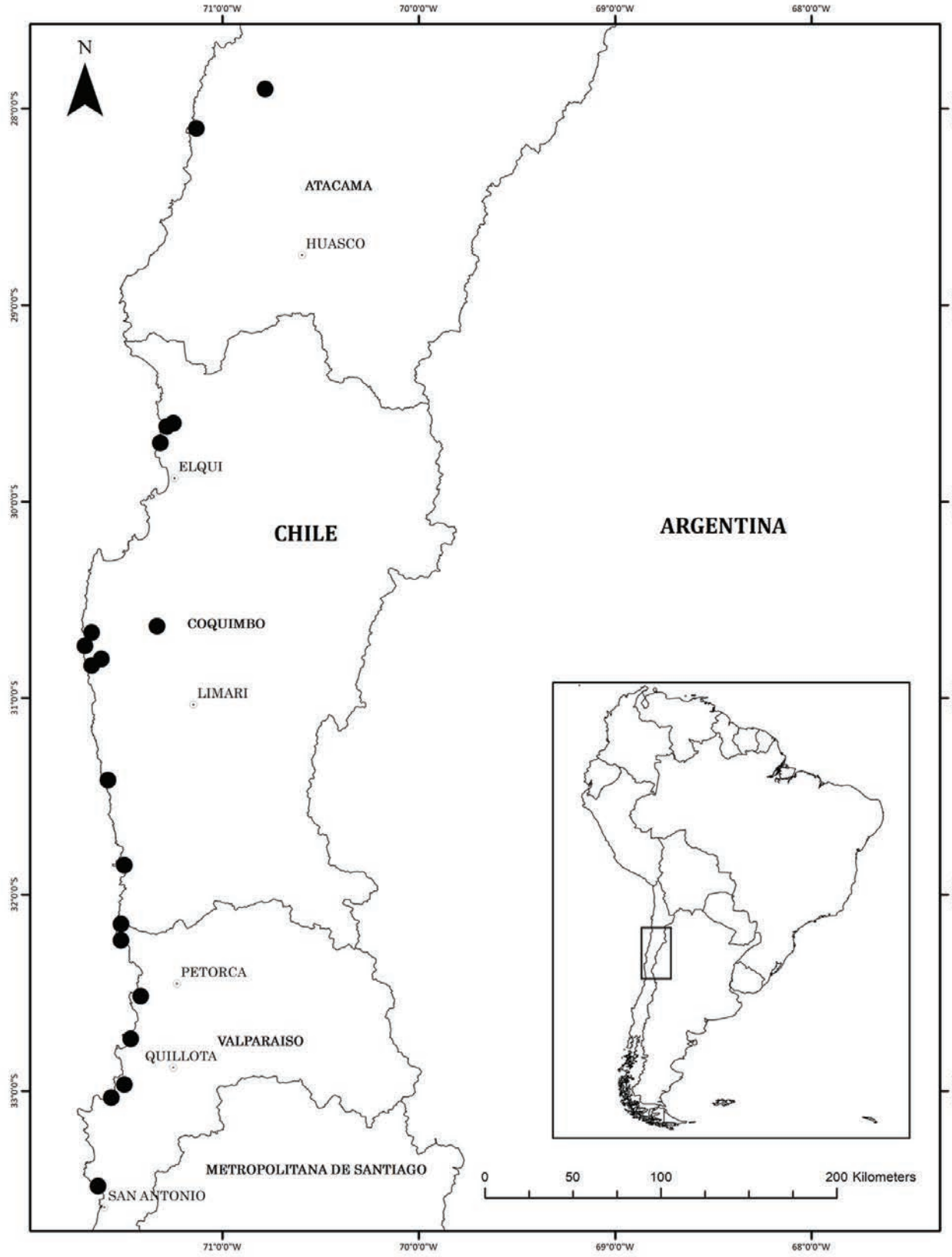


FIGURE 278. Distribution of *Nolana crassulifolia* Poepp.

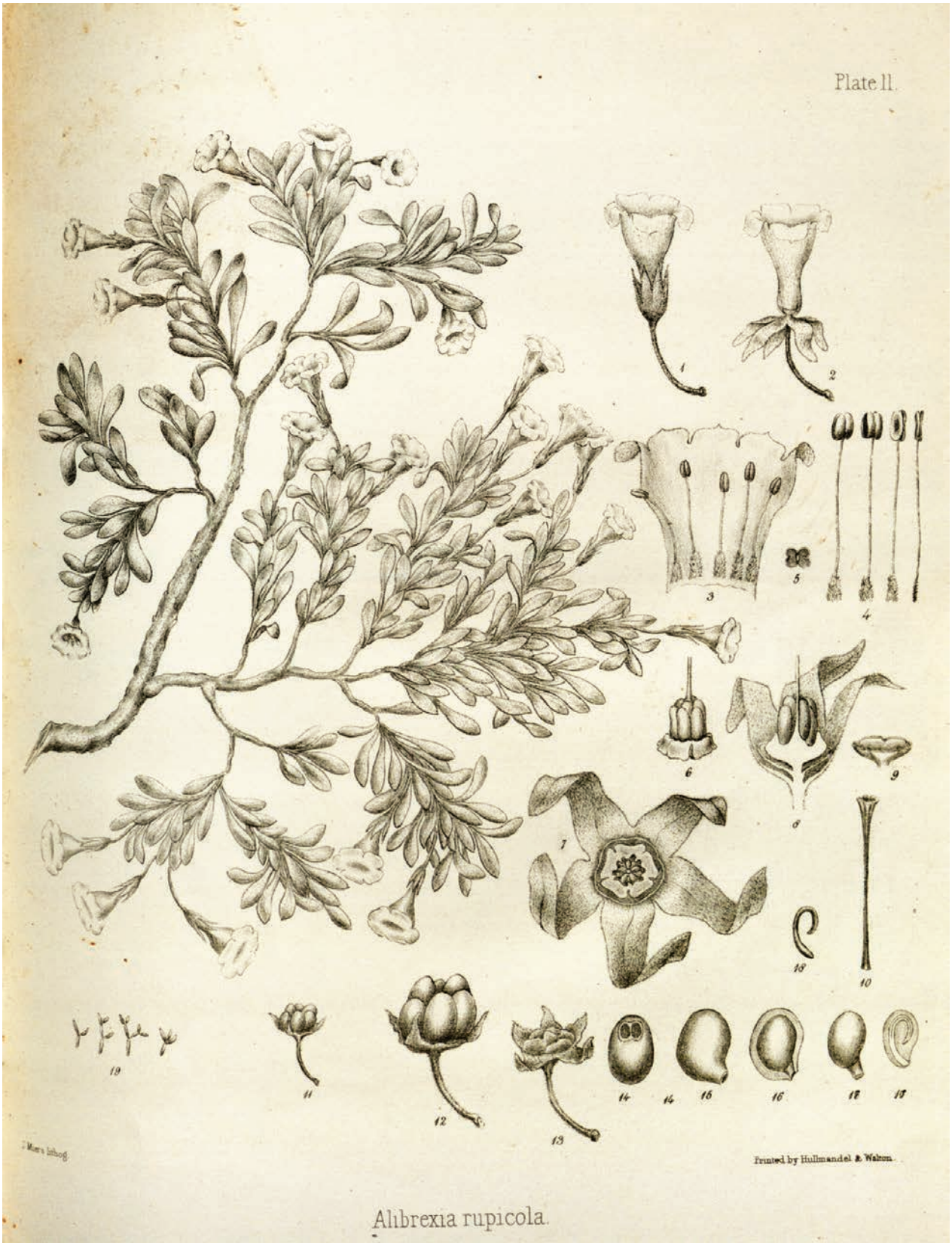


FIGURE 279. Illustration of *Nolana crassulifolia* as *Alibrexia rupicola* Miers (1845).

Sprawling prostrate *shrubs*, often covering coastal rocks, 20–150 cm tall, stems much-branched, to several meters long, not rooting, whitish gray. *Leaves* alternate, blades linear to linear-spathulate, 10–22 mm long, ca. 2 mm wide, succulent, terete to plain, abaxial surface conspicuously grooved, pale green, densely pilose with dendritic trichomes. *Inflorescences* of solitary flowers in apical nodes, pedicels (3–)7–10(–20) mm long, pilose. *Flowers* 5-merous; calyces campanulate, 5–7 mm long, ca. 4 mm wide, lobes ca. 3 mm long, reflexing in fruit; receptacle well-developed; corollas tubular, 7–14 mm long, ca. 2 mm wide, white to pale blue, tube pubescent within; stamens unequal, 6–7 mm long, bases pubescent; nectary disc crateriform, margins sinuate; style ca. 5 mm long. *Mericarps* (3–)5–9, rounded, 2–3 mm in diam.; seeds 1–2 per mericarp. Chromosome number: 2*n*=24.

Etymology: The species epithet is from the Latin, *crassus*, thick, fat, and stout, and *folia*, leaf, and refers to the thickened leaves typical for the species.

Distribution and Ecology: Chile, Regions of Atacama, Coquimbo, and Valparaíso; 0–200 m.a.s.l. (Fig. 278). It is recorded from near-ocean habitats or further inland and is associated with *aguadas*.

Common name: *Sosa brava*.

Illustration: Fig. 279. Illustration of *Nolana crassulifolia* as *Alibrexia rupicola* Miers, London J. Bot. 4: 506. 1845.

Nolana crassulifolia is distributed over 750 km and is one of the more widely recorded species in Chile. The size of individuals and leaf morphology is affected by available moisture, but it is often growing near or in the sea water (Fig. 280A–B). The leaves and calyces are densely pubescent with dendritic trichomes (Fig. 282A, D). Corollas are invariably white with slightly zygomorphic lobes, and all the stamens are level with the green, capitate style (Fig. 282B). There are five to nine corky mericarps, as in *N. prostrata*; the mericarps are quite impervious to the effects of salt water, and this likely leads to its extensive distribution in shoreline habitats.

Nolana crassulifolia is perhaps most closely related to *N. incana* (Ossa et al., 2013), with which it shares a similar corolla shape. These two species appear to have distinct distributions, with *N. crassulifolia* generally occurring more to the south and much closer to the ocean. Other species with dendritic foliar trichomes are sister taxa, including *N. albescens*, *N. peruviana*, and *N. werdermannii* (Tu et al., 2008; Dillon et al., 2009).

Additional specimens examined: CHILE. **Atacama**: Caldera, 10 m.a.s.l., 19 February 1939, *A. A. Beetle 26114* (GH, K); Carrizal Bajo, 28°04'54"S, 71°08'48"W, 0–5 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8617* (SGO 158944); road to Aguada Tongoy, ca. 14 km SW of Huasco, 28°34'09"S, 71°18'31"W, ca. 250 m.a.s.l., 13 November 2004, *M. O. Dillon & M. Finger C. 8658* (SGO 158911); Quebrada El León, 26°57'33"S, 70°44'15"W, ca. 237 m, 30 October 2010; *M. O. Dillon 9172* (CONC, F 2331762, SGO); Carrizal Bajo, 23 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1101* (SGO 108613); Copiapó, Bahía Inglesa, 27°06'17"S, 70°51'12"W, October 2008, *P. G. Ossa 114* (SGO 162562); Bahía Cisne, 27°14'53"S, 70°57'34"W, September 2009, *P. G. Ossa 237* (SGO 162579), *242* (SGO 162580), *244* (SGO 162581); Huasco, Las Hualtatas, 28°07'38"S, 71°09'57"W, September 2009, *P. G. Ossa 256* (SGO 162584), *258* (SGO 162585), *260* (SGO 162586); Elqui, Caleta Hornos, 29°37'00"S, 71°17'11"W, September 2009, *P. G. Ossa 182* (SGO 162571), *184* (SGO 162572); Copiapó, Quebrada el León, a 5 km al interior de ruta 5, 26°57'36"S, 70°44'16"W, September 2009, *P. G. Ossa 321* (SGO 162592); ca. 1–2 km E of Carrizal Bajo, 28°06'09"S, 71°08'12"W, 0 m.a.s.l., 15 April 1994, *C. M. Taylor & A. Pool 11629* (CONC 143564, SGO 147789, US 3354836). Prov. Huasco, 99 km S of Vallenar (measured from Puente Huasco) along the Panamericana, 8 km S of Incahuasi; 14 km N of Trapiche, 29°18'S, 71°02'W, 560 m.a.s.l., 25 October 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 3034a* (B). **Coquimbo**: Fray Jorge, September 1948, 450 m.a.s.l., *B. Collantes T. 21932* (CONC 129607); Punta Arrayán, ca. 20 km N of La Serena, 29°42'S, 71°19'W, 140–150 m.a.s.l., 22–23 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5435* (F 2011542, GH). Prov. Choapa, Mun. Mincha, Caleta Oscuro 3 km W of Puerto Oscuro (Panamericana), 31°25'16"S, 71°35'41"W, 20–100 m.a.s.l., 2 November 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 3089c* (B); Coquimbo, sea level to 300 ft, *C. Elliot s.n.* (K); Coquimbo, January 1903, *G. T. Hastings 586* (US 530457); Caleta El Toro, 30°44'S, 71°42'W, 10 m.a.s.l., *F. Luebert & C. Becker 2914* (SGO 159447); Fray Jorge, 15 September 1947, *J. Ibáñez & G. Kuschel s.n.* (SGO 130625); El Faro, 100 m.a.s.l., 16 September 1936, *G. Montero O. 2827* (GH); Fray Jorge, 30°40'S, 25 September 1935, *C. Muñoz P. B-63* (GH); Choapa, Playa Chigualoco, 31°45'36"S, 71°30'24"W, September 2009, *P. G. Ossa 156* (SGO 162565); Choapa, Chigualoco, 31°45'36"S, 71°30'24"W, September 2009, *P. G. Ossa 159* (SGO 162566); Elqui, Caleta Hornos, 29°37'00"S, 71°17'11"W, 0 m.a.s.l., September 2009, *P. G. Ossa 171* (SGO 162567); Limarí, Caleta Talcaruca, 30°29'40"S, 71°41'26"W, September 2009, *P. G. Ossa 201* (SGO 162576), *203* (SGO 162577), *204* (SGO 162578); La Serena, Choros Bajos, 28 September 1947, *B. Sparre 2801* (SGO 98351); Los Vilos, 5 m.a.s.l., 3 November 2006, *E. J. Tepe, A. Marticorena, & P. B. Pelser 1695* (CONC 167820, GH). **Valparaíso**: Papudo, 9 December 1972, *M. Bassano s.n.* (SGO 137364); costa entre Viña del Mar y Concón, November 1934, *F. Behn s.n.* (CONC 129589); Valparaiso, 1829, *C. L. G. Bertero 1181* (G00137998, GH [2 sheets]); Valparaíso, 1895, *O. Buchtien s.n.* (US 1157076); Cartagena, January 1920, *Bro. Claude-Joseph 979* (US 1057742); San Antonio, October 1921, *Bro. Claude-Joseph 1720* (US 1121274); S of Algarrobo, Playa Canelo, 33°22'04"S, 71°41'25"W, 19 November 2004, *M. O. Dillon & M. Finger C. 8659* (SGO 158945). Prov. Petorca, 21 km N along Panamericana from turnoff to Papudo towards Los Vilos (ca. 49 km S of Los Vilos, ca. 1.0–1.5 km S of Los Molles, rocks on the N side of the bridge Puente El Chivato, 0–20 m.a.s.l., 10 November 1991, *U. Eggli & B. E. Leuenberger 1659* (B, SGO 145673); Mun. Quintero, Quintero, coastal

FIGURE 280. *Nolana crassulifolia*. **A–B**, Growing near or in the sea water.

FIGURE 281. *Nolana crassulifolia*. **A**, Large, sprawling perennial growing near the ocean; **B**, Dense blooming.

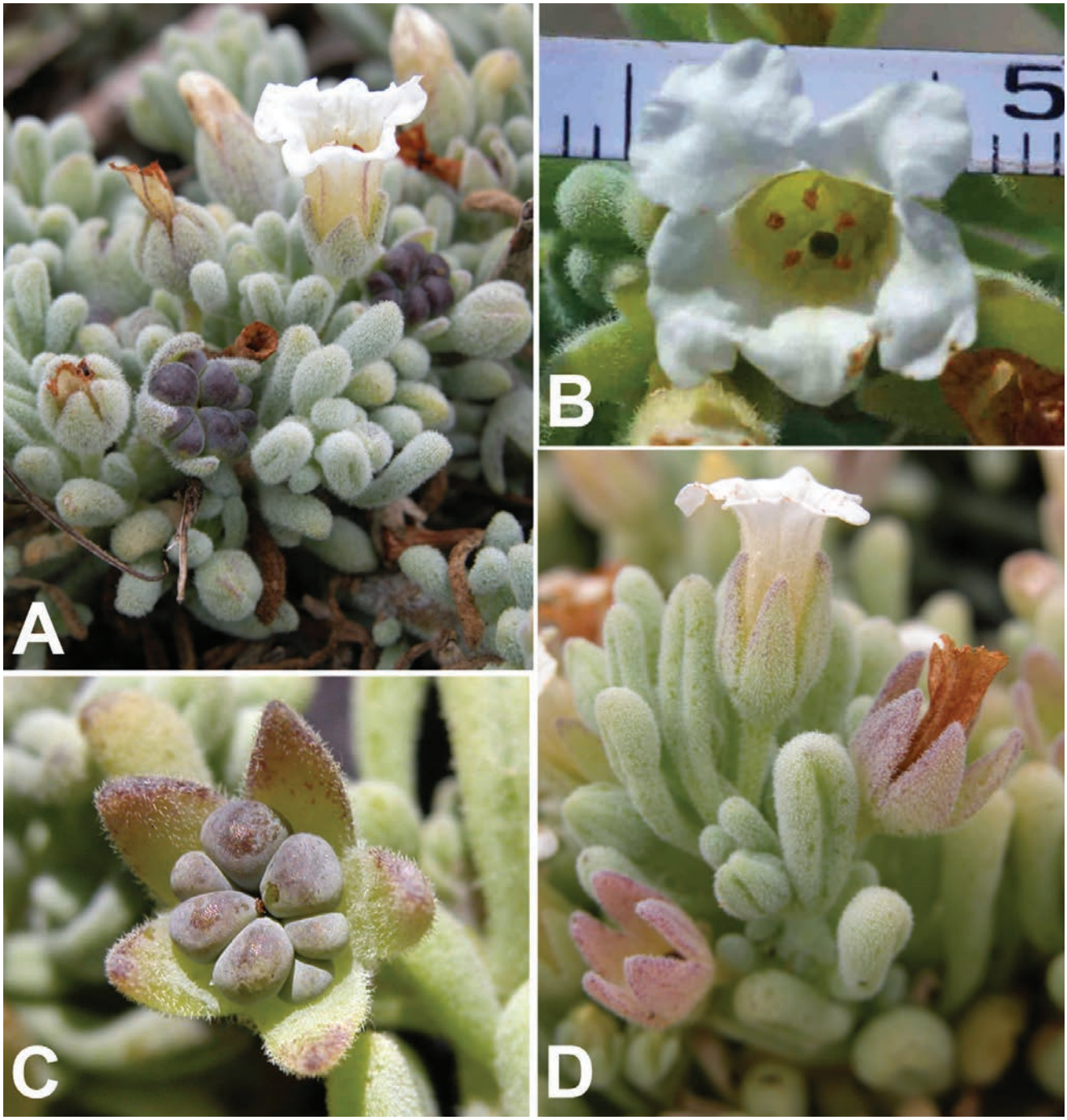


FIGURE 282. *Nolana crassulifolia*. **A**, Leaves and calyces with densely dendritic pubescent; **B**, Closeup of flower, corollas slightly zygomorphic, all stamens at the same level, green capitate style; **C**, Mericarps; **D**, Closeup of leaves and flower. Photograph by Marcelo Rosas.

granitic rocks withering into fine gritty gravel, 32°47'S, 71°33'W, 20–50 m.a.s.l., 5 November 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 3106* (B, CONC 146117, SGO 146155); Valparaiso, 1834, *C. Gaudichaud 120* (G00137907); Quintero, 8 December 1950, *L. H. Gunckel 19047* (CONC 129596); Los Molles, December 1951, *L. H. Gunckel 23426* (CONC 129588); Quintero, 17 October 1951, *L. H. Gunckel 23716* (CONC 129603); Playa de los Enamorados, February 1953, *L. H. Gunckel 23847* (CON 129592); Campiche, November 1959, *L. H. Gunckel 45576* (CONC 129605); Playa de las Conchitas, September 1962, *L. H. Gunckel 39414* (CONC 129606); Concón, 10 m.a.s.l., February 1963, *L. H. Gunckel 40187* (CONC 129600); El Quisco, *L. H. Gunckel 40655* (CONC 129599); Ritoque, January 1961, *L. H. Gunckel 45431* (CONC 129602); Concón, February 1958, 15 m.a.s.l., *L. H. Gunckel 45649* (CONC 129590); El Tabo, *P. L. Gunckel 21392* (CONC 129591); Valparaíso, April–July 1856, *W. H. Harvey s.n.*

(GH, K); Playa de Zapallar, 35 m.a.s.l., 20 February 1953, *U. L. Heins s.n.* (CONC 129593); Algarrobo, 20 m.a.s.l., December 1960, *K. Hochstetter s.n.* (CONC 129597); Playa Mirasol, ca. 36 km N of San Antonio, 33°20'S, 71°40'W, 26 March 1978, *L. R. Landrum 3437* (SGO 126304); Quintero, 21 March 1937, *G. Looser 3664* (GH); Dunas de Concón, 32°56'S, 71°32'W, 11 October 2003, *F. Luebert & L. Kritzner 1882* (SGO 152511); Valparaíso, September 1830, *A. Mathews 310* (GH); El Yeco, 26 December 2004, *I. Meza P. s.n.* (SGO 152449); Tunquén, 5 November 1995, *H. Niemeyer F. & C. Fernández 9594* (SGO 151295); San Antonio, El Quisco, 33°23'14"S, 71°41'32"W, May 2008, *P. G. Ossa 86* (SGO 162559), *87* (SGO 162560); Concón, February 1929, *A. Pirion s.n.* (CONC 129608); camino de Viña de Mar a Concón, 21 February 1930, *A. Pirion 265* (GH); Valparaiso, 1828, *E. F. Poeppig 313* (G00137999); near Valparaíso, December 1928–February 1929, *G. W. Robinson s.n.* (K); Lomas de Fray Jorge, 17 August 1917, *C. J. F. Skottsberg & I. Skottsberg 850* (GH); Valparaíso, 23 September 1917, *C. J. F. Skottsberg & I. Skottsberg 1044* (F 737426, GH); Laguna Verde, 15 km al sur de Valparaíso, 10 m.a.s.l., 24 September 1973, *G. L. Stebbins & P. Weisser 8571* (SGO 139709); Cachagua Norte, 29 March 1972, *B. Torro s.n.* (SGO 135191); Cachagua Norte, 29 March 1972, *B. Toro s.n.* (SGO 135191); near Monte Mar, road from Viña del Mar to Concón, 1–5 m.a.s.l., 27 November 1935, *J. West 3958* (GH); Los Molles, 10 December 1979, *O. Zöllner 10643* (CONC 129601). **No exact locality**: 4 November 1920, *Bro. Claude-Joseph 1201* (US 1059218); Costa, 4 November 1920, *Bro. Claude-Joseph 1201* (US 1059218); *Wilkes Explor. Exped. s.n.* (US 44325).

G4. ***Nolana dianae*** M.O. Dillon, Arnaldoa 14: 192. 2007. TYPE: CHILE. Antofagasta: Prov. Antofagasta, Quebrada above Playa de los Hornos, just N of Punta Hornos, 26 km S of Caleta Michilla, 51 km N of Tropic of Capricorn, 22°55'S, 70°15'W, 300–350 m, 20 October 1988, *M. O. Dillon & D. Dillon 5725* (Holotype: SGO; Isotypes: E, F [F 2045831], G, GH, HSP, US). Fig. 283–285.

Digital image: Isotype of *Nolana dianae* from the Field Museum, Chicago [F 2045831]. https://collections-botany.fieldmuseum.org/catalogue/366169

Succulent, spreading, rounded, facultative annual *herbs*, 30–100 cm in diam.; stems much-branched, 30–40 cm long, prostrate to decumbent, deep purple, pubescent with capitate-glandular trichomes. *Leaves* alternate, blades oblong to oblanceolate, 10–20 mm long, 3–4(–5) mm wide, succulent, strongly concave adaxially, pubescent with capitate-glandular trichomes, dark green, ovate to cordate in section, apically obtuse to rounded, bases cuneate, swollen, margins revolute, sessile. *Inflorescences* of solitary flowers in upper leaf axils, pedicels erect, filiform, 10–15(–20) mm long. *Flowers* 5-merous; calyces campanulate, 7–10 mm long, tube ca. 5 mm long, ca. 4 mm wide; 5-lobed, lobes lanceolate, equal, ca. 4 mm long, ca. 1 mm wide; corollas narrowly infundibuliform, 18–24 mm long, white with deep purple guides, pubescent with capitate-glandular trichomes, 5-lobed, lobes obtuse, 2.5–3.0 mm long, 9–10 mm wide; stamens 5, included, filaments inserted on lower third of corolla, unequal, three, 2–3 mm long, two, 3.5–4.5 mm long, pilose at the bases; anther thecae 1.5–2.0 mm long, 1.0–1.5 mm wide, purple, glabrous; ovary glabrous, basal nectary, 5 carpels, style included, stigma capitate, green. *Mericarps* 4–5, spherical, 2.5–3.0 mm in diam., included within the expanding calyx; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates the second collector of the type, Diane O'Donnell Moran Dillon (b. 1946–), my ex-wife, who accompanied me on several field trips in Chile and Peru. In 1988, as we drove along the coast of Chile north of Tocopilla, I spotted some dark green spots with my binoculars far above the road on the slopes facing the ocean. The plants were upslope; it was a hot day, and I gave my companion the opportunity to stay in the comfort of the truck, but she said, "no", and hiked up to the plants I had seen, about 250 m.a.s.l. straight up. Upon reaching the plants and, after observing the unusual corollas, I exclaimed, "If this is new, I am naming it after you!" I was thrilled that she had chosen to climb the mountain with me and experience a moment of discovery. It took almost 20 years, but I fulfilled my promise.

Distribution and Ecology: Chile, Region of Antofagasta; 300–550 m.a.s.l. (Fig. 283). It is found on rocky gravel of an alluvial fan at the base of the coastal mountains, within 5 km of the ocean and fog influences; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana dianae is a low spreading annual that occurs sympatrically with other species (Fig. 285A). At the type locality above Playa de los Hornos, *N. dianae* is in proximity with *N. balsamiflua* and *N. peruviana*. The leaves are oriented vertically and are densely covered with capitate-glandular trichomes. The star-shaped pattern formed by the guides on the corolla is unique in the genus (Fig. 285B). It resembles, *N. philippiana*, a species with similar leaf form and pubescence, but the corolla shape and floral coloration pattern distinguishes it. Material of these taxa has not been included in molecular studies to date, and further speculation about its relationships will follow those results.

Another collection, *Dillon & Dillon 5728*, was made at the same time at the type locality; field notes indicate the collection was considered to be the same as *Dillon & Dillon 5725,* but the former collection possesses light blue to lavender corollas. Collecting in 1988 was remarkable due to the blooming conditions stimulated by the 1987–1988 El Niño event. Repeated visits to this locality during subsequent years has not yielded new collections of this taxon. Another collection, here considered conspecific, was encountered farther north in a quebrada east of Tocopilla, *Dillon & Dillon 5707*.

Additional specimens examined: CHILE. Antofagasta: Prov. Antofagasta, Quebrada above Playa de los Hornos, just N of Punta Hornos, 26 km S of Caleta Michilla, 51 km N of Tropic of Capricorn, 22°55'S, 70°15'W, 300–350 m.a.s.l., 20 October 1988, *M. O. Dillon & D. Dillon 5728* (CONC, E, F 2045828, G, GH, HSP, SGO, US). Prov. Tocopilla, quebrada ca. 15 km E of Tocopilla, 22°05'S, 70°09'W, 520–550 m.a.s.l., 18 October 1988, *M. O. Dillon & D. Dillon 5707* (F 2014373, G, GH).

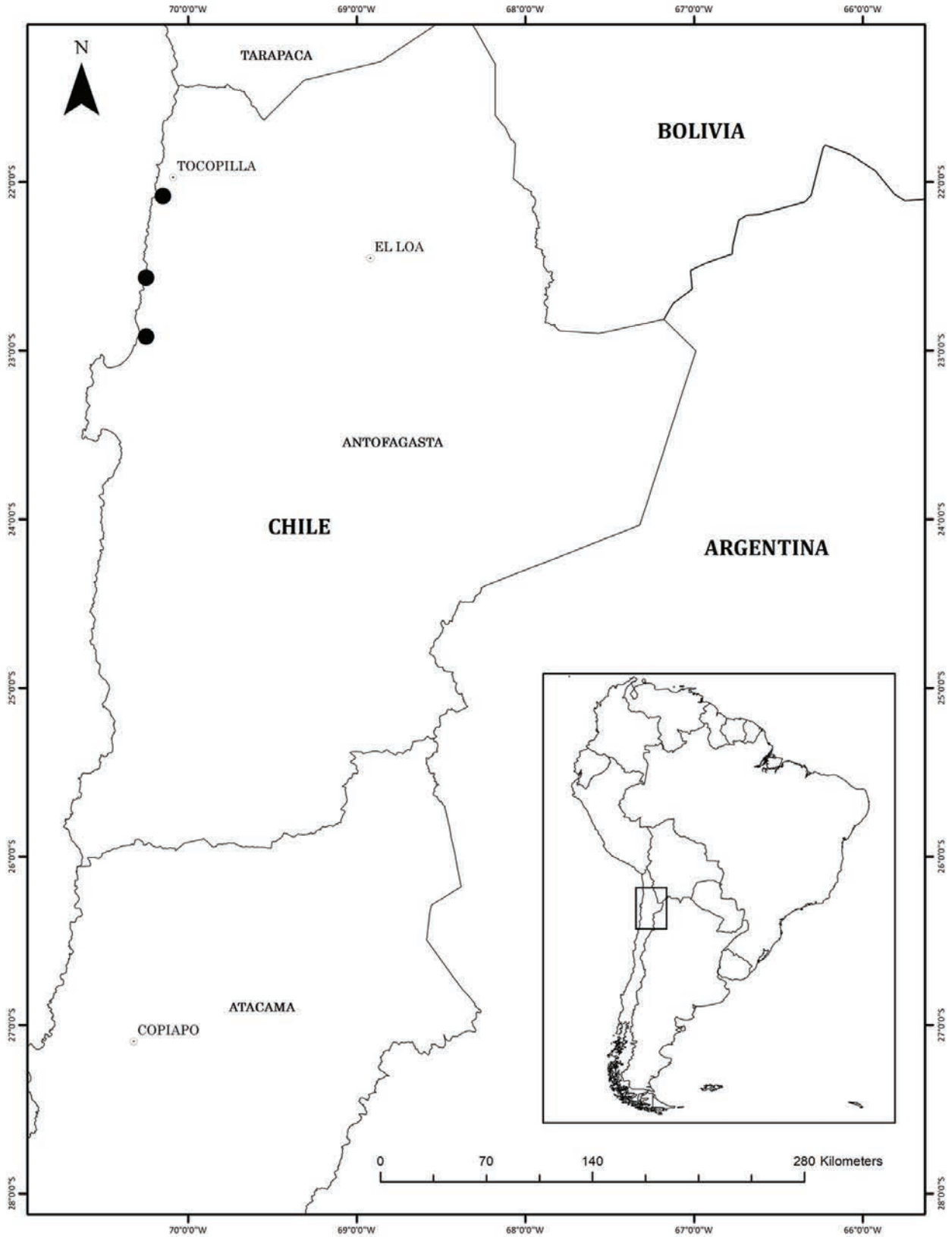


FIGURE 283. Distribution of *Nolana dianae* M.O. Dillon.

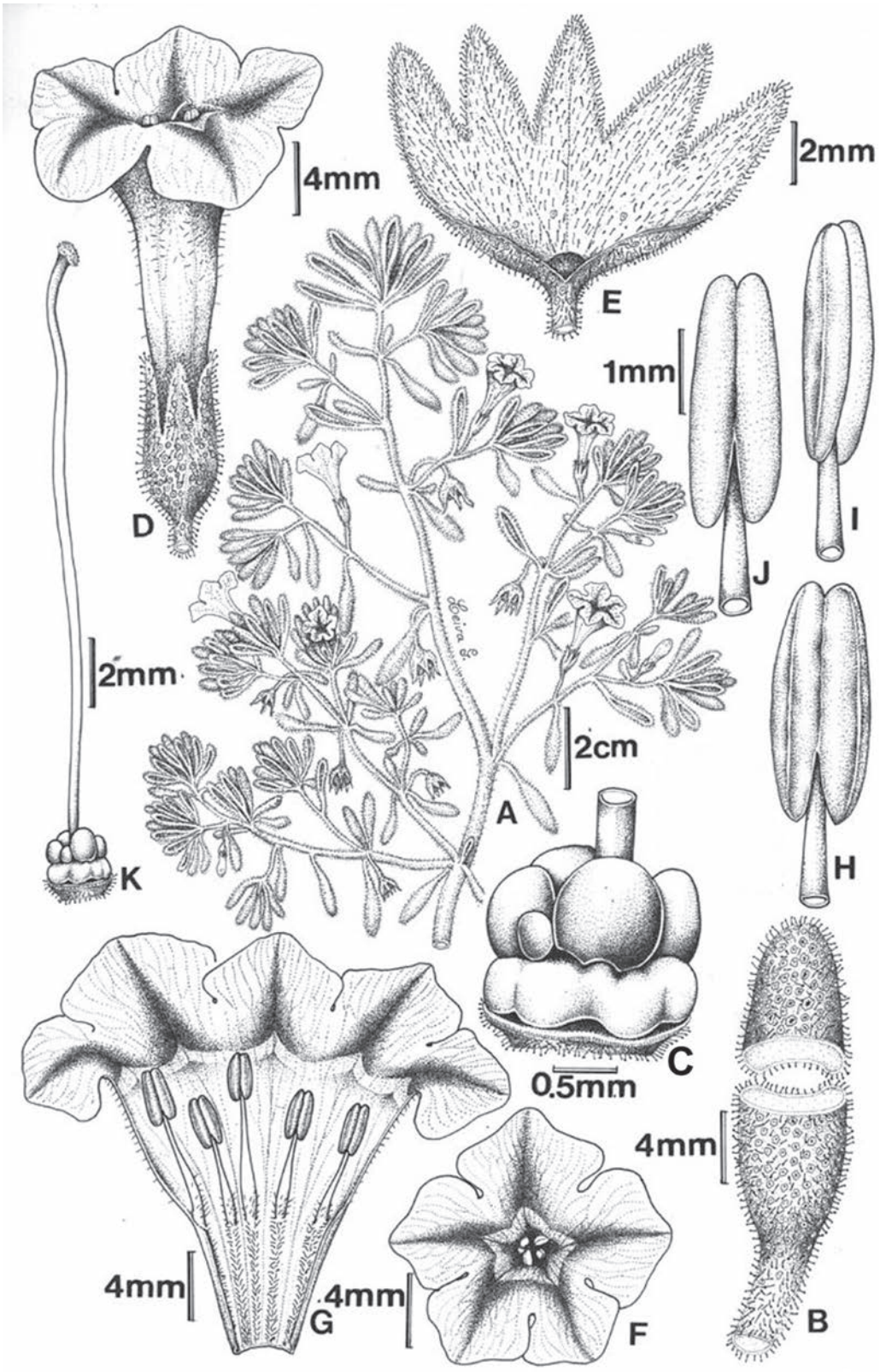


FIGURE 284. Illustration of *Nolana dianae*. **A**, Habit; **B**, Leaf; **C**, Foliar gland; D, Flower; **E**, Dissected calyx; **F**, corolla. **G**, Dissected corolla; **H**, Anther ventral view; **I**, Anther lateral view; **J**, Anther dorsal view; **K**, Gynoecium; **L**, Ovary. Drawn by Segundo Leiva Gonzáles.

FIGURE 285. *Nolana dianae*. **A**, Type locality above Playa de los Hornos, Chile, (1) *Nolana dianae*, (2) *Nolana balsamiflua*, (3) *Nolana peruviana*; **B**, Closeup of leaves and habit; **C**, Closeup of corolla with star-shaped pattern formed by guides.

G5. ***Nolana diffusa*** I.M. Johnst., Contrib. Gray Herb. 112: 77. 1936. TYPE: CHILE. Antofagasta: Prov. Antofagasta, vicinity of Aguada de Miguel Díaz, 1–4 December 1925, *I. M. Johnston 5384* (Holotype: GH [00282372]; Isotypes: K [K000532203], US [US 1473986, US00121958]). Fig. 286–288.

Digital image: Holotype of *Nolana diffusa* from Harvard University Herbaria, Cambridge [GH00 282372]. https://s3.amazonaws.com/huhwebimages/0135582A403D45B/type/full/282372.jpg

Homotypic synonym: *Nolana sedifolia* Poeppig ssp. *sedifolia* Mesa, Fl. Neotrop. Monogr. 26: 99. 1981.

Low, spreading *subshrubs* to ca. 30 cm tall, to ca. 1 m in diam.; stems intricately branched, 3–15 cm long, densely arachnoid-tomentose. *Leaves* alternate to fasciculate, blades 2–4(–6) mm long, 1.5–2.0 mm wide, oblong to oval, terete, densely arachnoid-tomentose, recurved. *Inflorescences* of solitary flowers, axillary and terminal; pedicels 1–3 mm long, arachnoid-tomentose. *Flowers* 5-merous; calyces campanulate, 3–4(–5) mm long, lobes ca. 2 mm long, oblanceolate, obtuse, apices swollen; corollas hypocrateriformis, ca. 6 mm long, 5–6 mm in diam., tube white, lobes light blue to lavender, ovate, subequal; filaments linear, unequal, 3–5 mm long, pilose at the bases; anther thecae purplish; pollen white. *Mericarps* 3–7, ca. 2 mm in diam., black, minutely tuberculate to irregularly rugose; seeds 1(–2) per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *diffusus*, loosely, irregularly, or widely spreading, referring to the overall habit of the plant.

Distribution and Ecology: Chile, Region of Antofagasta; 60–500 m.a.s.l. (Fig. 286). It is recorded from sandy alluvial soils and among rocks on lower slopes; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana diffusa is a small, low shrubby species with a narrow distribution in the vicinity of Paposo (Fig. 287A). Flowers are pale blue to lavender or nearly white in some (Fig. 287B). The leaves are mostly under 4 mm long and are covered with arachnoid-tomentose pubescence (Fig. 288A). Corollas are weakly zygomorphic with no obvious guides; the anther thecae are purplish, and the is pollen white (Fig. 288B). The calyx lobes are expanded and succulent, not unlike those of *Nolana divaricata* (Fig. 288C).

Johnston (1936: 77), in his description of this species, related it to *N. sedifolia*, but distinguished it from the latter species by its more arachnoid-pubescent leaves, its bluish, rather than strictly white, corollas, and by its lower, spreading habit. Furthermore, he suggested that it may also be related to *N. tocopillensis*, from which it differs in its smaller corollas, more crowded leaves, and denser habit. In molecular studies (Dillon et al., 2009), a collection of *N. diffusa* from Quebrada de Miguel Díaz (*Dillon et al. 8076*) was recovered in a clade containing *N. sedifolia* (*Dillon et al. 8721*) from Quebrada Bandurrias. Additionally, one clone of the *N. diffusa* accession was also recovered in a clade containing *N. tocopillensis*, *N. salsoloides*, and *N. ramosissima*, reinforcing observations on overall morphological similarity and geographic distribution (Dillon et al., 2009).

Additional specimens examined: CHILE. **Antofagasta**: Quebrada Cascabeles, *Ch. von Bohlen V. 1297* (SGO 131123); Vicinity of Miguel Diaz, directly N of Quebrada Iscuña, ca. 55 km N of Paposo and ca. 40 km S of El Cobre, 24°33'S, 70°33'W, 100–150 m.a.s.l., 15 December 1987, *M. O. Dillon & S. Teillier 5312* (F 201076, GH, SGO 143712); Hueso Parado, ca. 5 km N of Taltal, 25°24'S, 70°33'W, 60–70 m.a.s.l., 6 October 1988, *M. O. Dillon & D. Dillon 5644* (F 2013648, GH); Quebrada de Miguel Díaz, 24°33'S, 70°33'W, 420–440 m.a.s.l., 22 November 1997, *M. O. Dillon, C. Trujillo C., & M. Villarroel O. 8076* (E, F 2183314, GH, SGO 143712, US); 10 km N of Paposo, 24°55'43"S, 70°30'55"W, 70 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8683* (SGO 158922); 12 km N of ThermoElectric plant north of Paposo, 24°54'32"S, 70°31'20"W, 70 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8676* (CONC 179102, F 2331753, SGO 158929); Blanco Encalada S of Antofagasta, June 1923, *J. E. Harding s.n.* (GH); Taltal, 1 November 1930, *F. Jaffuel 960* (GH); vicinity of Paposo, 9 December 1925, *I. M. Johnston 5570* (GH, K, US 1473987); aluvión frente a Miguel Díaz, 24°33'S, 70°33'W, 275 m.a.s.l., 5 October 2005, *F. Luebert & N. García 2632/1026* (SGO 159475); Paposo, 25°03'S, 70°30'W, 10 October 1983, *M. Elgueta 38* (SGO 145513); Quebrada Miguel Díaz, 250 m.a.s.l., 27 September 2009, *P. Medina & F. Romero s.n.* (SGO 159007); Taltal, 9 September 1936, *G. Montero O. 2883* (GH); Quebrada Taltal, 150 m.a.s.l., 10 September 1936, *G. Montero O. 2902* (GH); Cachinalcito, 100 m.a.s.l., 16 September 1958, *M. Ricardi & C. Marticorena 4631/1016* (CONC 25421); El Médano, 24°51'S, 70°32'W, 8 November 2006, *N. Schulz 16* (SGO 154757); Miguel Díaz, 24°32'S, 70°39'W, 6 November 2006, *N. Schulz 33* (SGO 154753).

G6. ***Nolana divaricata*** (Lindl.) I.M. Johnst., Contrib. Gray Herb. 112: 64. 1936. Fig. 289–294.

Basionym: *Aplocarya divaricata* Lindl., Bot. Reg. 30: tab. 46. 1844. TYPE: CHILE. Coquimbo: Coquimbo, *H. Cuming 862* (Lectotype designated here: E [00130914]; Isolectotypes: E [E00130915], FI-Webb, GH [GH00282371], K [K000532199, K000532200]).

Digital image: Lectotype for *Aplocarya divaricata* from Royal Botanic Garden, Edinburgh [E00130914]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.e00130914

Homotypic synonym: *Dolia divaricata* (Lindl.) Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 4. 1891; *Bargemontia divaricata* (Lindl.) I.M. Johnst., Contrib. Gray Herb. 85: 159. 1929; *Nolana peruviana* (Gaudich.) I.M. Johnst. subsp. *divaricata* (Lindl.) Mesa, Fl. Neotrop. Monogr. 26: 81. 1981.

Heterotypic synonyms: *Dolia clavata* Miers, London Jour. Bot. 4: 503. 1845. TYPE: CHILE. Atacama: Huasco-Coquimbo ["Concepción"], *T. Bridges 1324* (Lectotype designated by Mesa-M., 1981: K (000532202)). *Osteocarpus clavatus* Phil., Anal. Univ. Chile 91: 41. 1895. TYPE: CHILE. Atacama: Copiapó, Caldera, Morro de Caldera, 1886, *G. Geisse s.n.* (Holotype: SGO (55130, SGO000004392)).

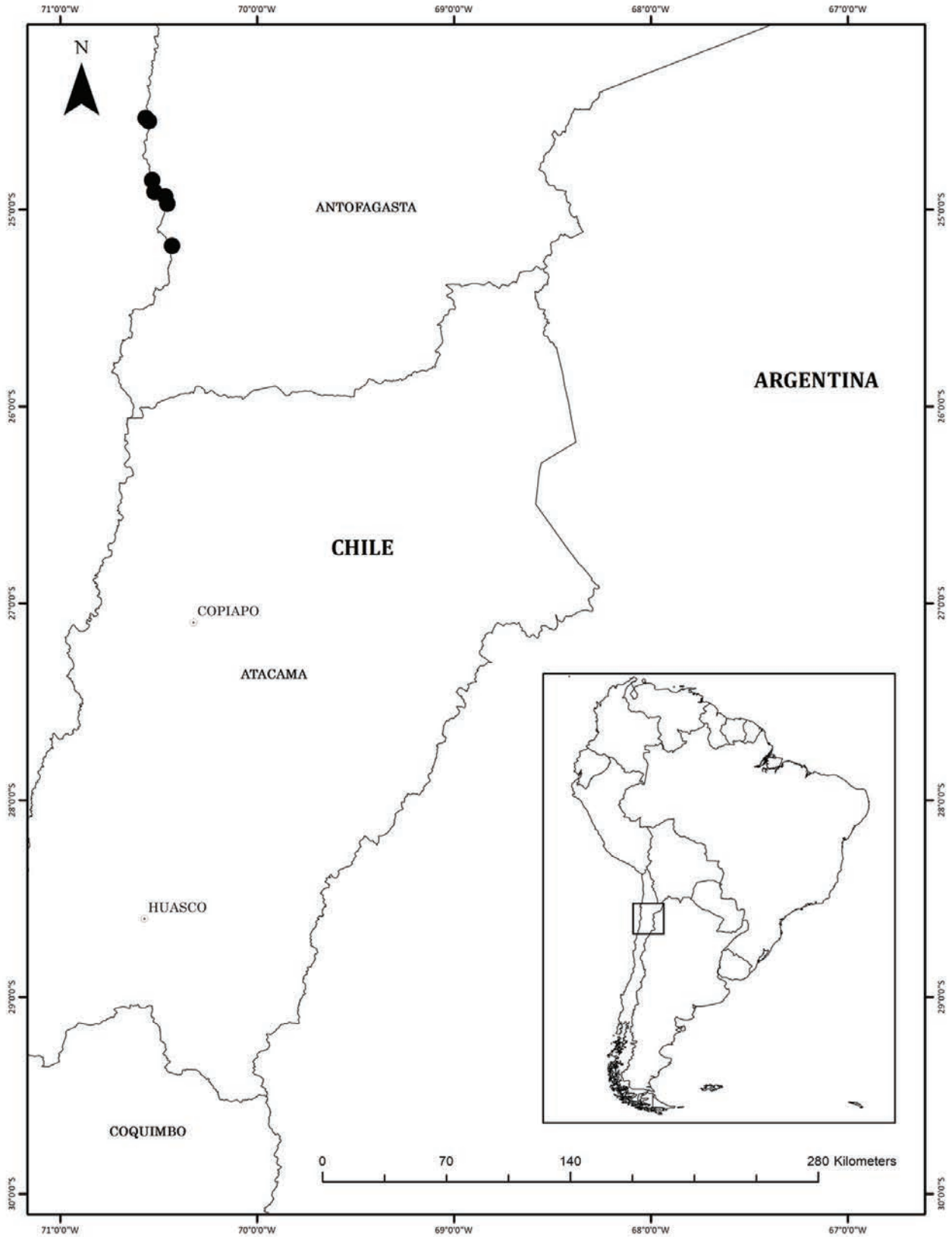


FIGURE 286. Distribution of *Nolana diffusa* I.M. Johnst.

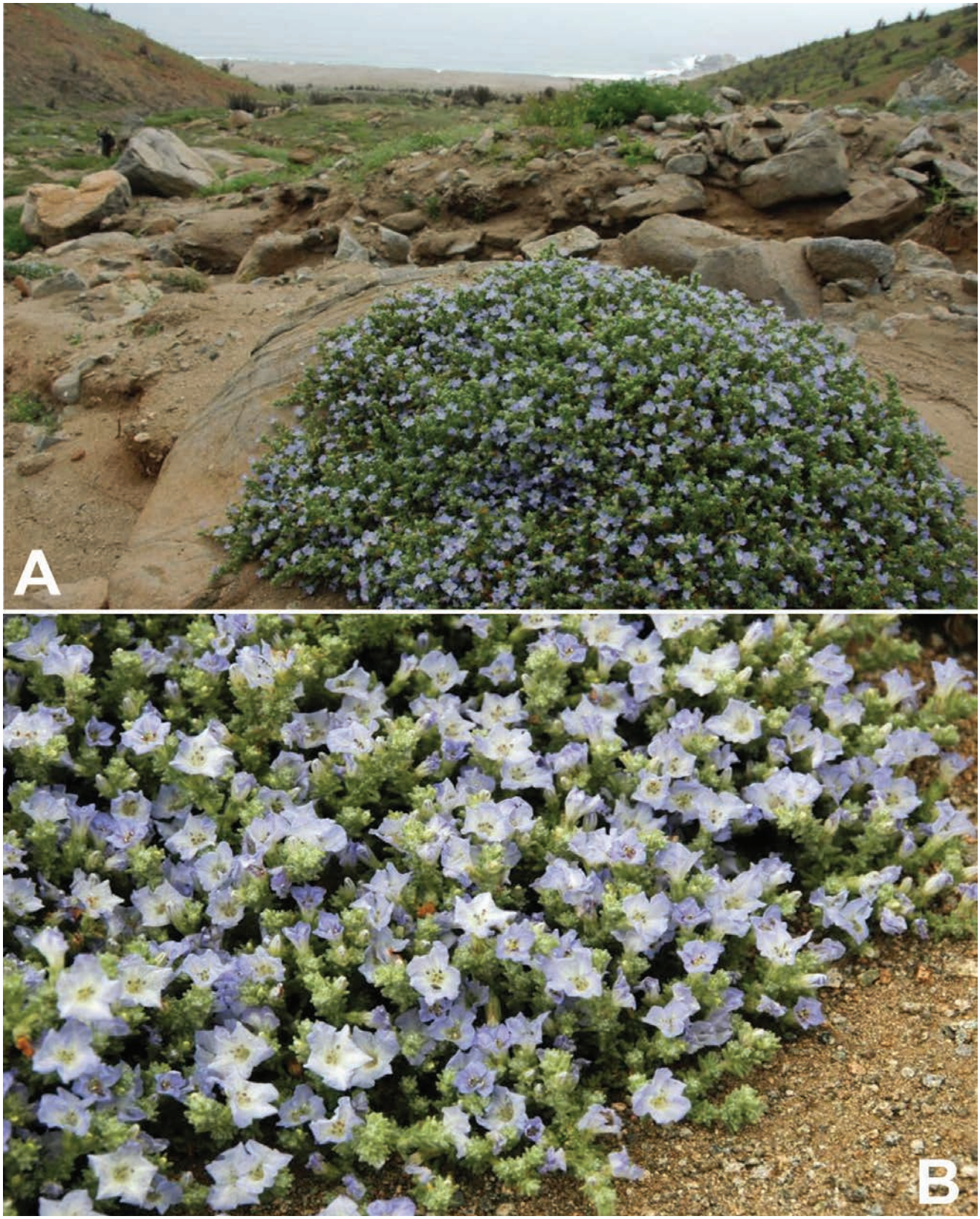


FIGURE 287. *Nolana diffusa*. **A**, Flowering shrubs near the ocean; **B**, Flowers are pale blue to lavender.

FIGURE 288. *Nolana diffusa*. **A**, Flowering branch covered with arachnoid-tomentose pubescence; **B**, Frontal view of weakly zygomorphic corollas with no obvious guides and white anther thecae; **C,** Calyx lobes are expanded and succulent.

Shrubs or perennial herbs, 30–75(–250) cm tall, erect to decumbent; stems densely branched, weakly woody, pale green, essentially glabrous, rarely with short, or long, simple trichomes. *Leaves* alternate to opposite or fasciculate, blades clavate to linear-spathulate, 5–13 mm long, 2–3 mm wide, terete, curving upward, often remaining inflated after drying, glabrous, dark green, margins revolute, abaxial surface weakly canaliculate, apices rounded, bases attenuate; petioles to ca. 1 mm long or absent. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 3–12 mm long. *Flowers* 5-merous; calyces campanulate, actinomorphic, ca. 5 mm long, lobes linear-oblanceolate, acuminate, terete, inflated; corollas infundibularis, ca. 10 mm long, 10–12 mm diam., zygomorphic, solid blue or light blue with white throat; stamens unequal; filaments widened, villous, pubescence of long, slender somewhat curly simple trichomes; inner calyx cup and lobes pilose with short, unbranched trichomes; nectary disc crateriform, margin sinuate; style ca. 15 mm long, gynobasic stigma capitate. *Mericarps* (3–)5, globose to ovoid, shiny, unequal, 2–4 mm in diam.; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *divaricatus*, meaning spreading apart, and refers to the branching habit of the plants.

Distribution and Ecology: Chile, Regions of Antofagasta, Atacama, and Coquimbo; 10–1000 m.a.s.l. (Fig. 289). It is recorded over a 600 km range, from sandy soils in near-coast habitats to upland or inland habitats; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Illustration: Fig. 290. Illustration of *Nolana divaricata* as *Dolia clavata*, Plate 111. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana divaricata consists of highly variable, succulent-leaved shrubs that exhibit a variety of floral forms but have a relatively constant leaf morphology with glabrous surfaces (Fig. 291A). The leaves and calyx lobes are clavate, succulent with swollen and bulbous apices (Fig. 291B, 292A–B). The corollas are often lavender or light blue (Fig. 292C–D), but other colors can be encountered (Fig. 293A–F). There are typically five mericarps that are attached basally (Fig. 292E).

With a distribution over 600 km, populations of *N. divaricata* occupy several different environments (Fig. 289). Sufficient time, range expansion and contraction, and isolation mechanisms have led to variation in leaf morphology, floral color, and corolla shape. The flower color and pigmentation patterns vary from solid blue to blue with an inner white throat, to, rarely, pure white (Fig. 293A–F). Some individuals do not completely conform to the diagnosis of the typical *Nolana divaricata*. While the vegetative morphology is essentially comparable, the corollas are reduced, more tubular, and are completely white (Fig. 294A–B). This group needs more refined analysis to determine if other taxonomic entities need to be recognized.

Nolana divaricata has been confused with *N. salsoloides*, especially when dried as herbarium collections. These two species have a comparable geographic range and many superficial similarities, including the succulent, clavate leaves and swollen, succulent calyx lobes. *Nolana salsoloides* has more spathulate leaves that are uniformly pubescent with capitate-glandular trichomes. Interestingly, molecular studies suggest that *N. divaricata* is most closely related to *N. crassulifolia* (Tu et al., 2009) or *N. incana* (Dillon et al., 2007c).

Johnston (1929) transferred *Dolia clavata* Miers to *Bargemontia* and commented that it was a dense globose bush to ca. 1 m tall; he found it growing on a dry gravelly beach near the waterhole at Aguada Cachina (*Johnston 5694*). It has essentially glabrous, light green spathulate and terete leaves, and blue corollas. He related it to *Nolana peruviana*, a plant which differs by its more northern range, herbage that is covered with a dense canescent indumenta of forked hairs, and a shorter, more cylindrical corolla. The type collection of *Nolana clavata*, *T. Bridges 1324*, came from near the coast between Huasco and Coquimbo and was described by its collector as a 6–9 dm tall bush with pale blue corollas. Johnston (1936) placed *N. clavata* in synonymy with *N. divaricata* and mentioned that the information concerning the type locality was in error. He also placed Philippi's *Osteocarpus clavatus*, a plant collected from the headlands near Caldera, into synonymy with *N, divaricata*.

After examining *Werdermann 834* collections, it was decided that these more closely resemble *N. divaricata* rather than *N. salsoloides*, due to the persistent leaf bases and the lack of trichomes on the stems. The sheets of *Werdermann 834* at US (US 1444776, US 3312702) are more "*divaricata*-like" and are essentially glabrous. The CONC sheets are essentially glabrous, except for a few curly trichomes at the leaf bases; these collections are here treated as *N. divaricata*. Given the overall morphology, *Werdermann 461*, collected at Quebrada León north of Caldera (October 1924), is considered to be *N. divaricata*, not *N. salsoloides*. It should be noted that this sheet appears to have pencil annotations in Johnston's hand indicating "*divaricata*."

A collection by O. Zalensky from Tarapacá is far outside the normal distributional and elevational range for *Nolana divaricata* (i.e., *O. Zalensky XV-857*). Similar observations have been made for other collections by O. Zalensky (cf. *N. rostrata*), and there are unanswered questions concerning the legitimacy of the label data (Sebastián Teillier, pers. comm.).

Additional specimens examined: CHILE. **Antofagasta**: Taltal, Aguada Cachina, Cachinal de la Costa, 400 m.a.s.l., 13 December 1949, *W. Biese 3260* (SGO 96865); Quebrada Taltal, 25°32'S, 70°23'W, ca. 740 m.a.s.l., 23 December 1987, *M. O. Dillon 5382* (CONC, E, F 2010979, GH, SGO, K, US 3470025); Bahía Tórtolas, 25°33'S, 70°38'W, 0 m.a.s.l., 12 October 1988, *M. O. Dillon & D. Dillon 5666* (F 2014397); Quebrada Los Zanjones, 15 km SW of Taltal, 25°31'S, 70°25'W, 610–620 m.a.s.l., 25 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5501* (CONC, E, F

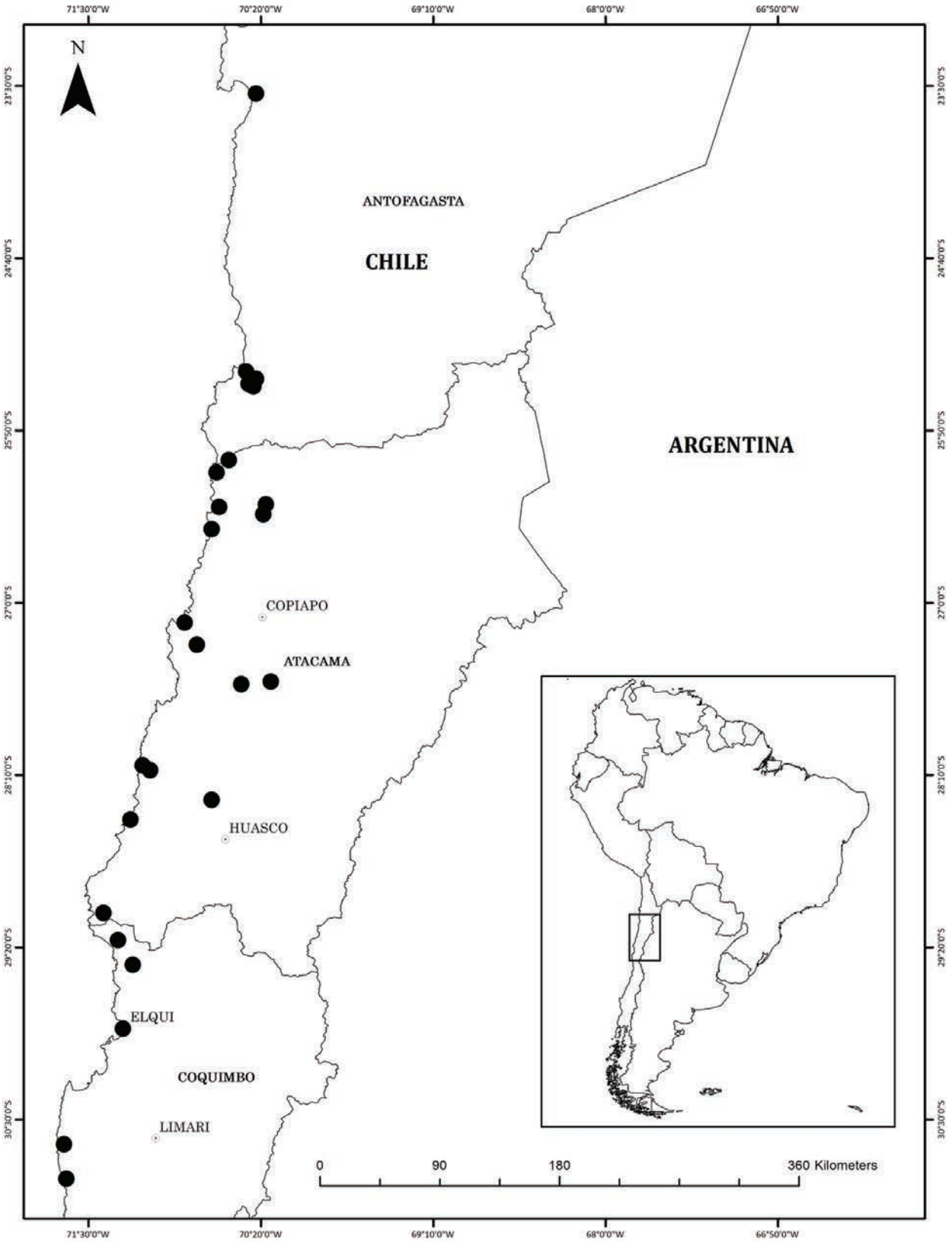


FIGURE 289. Distribution of *Nolana divaricata* (Lindl.) I.M. Johnst.

FIGURE 290. Illustration of *Nolana divaricata* as *Dolia clavata*, Plate 111. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 291. *Nolana divaricata*. **A**, Large shrubs growing in near-ocean dunes; **B**, Leaves and calyx lobes clavate, glabrous, succulent with apices swollen and bulbous.

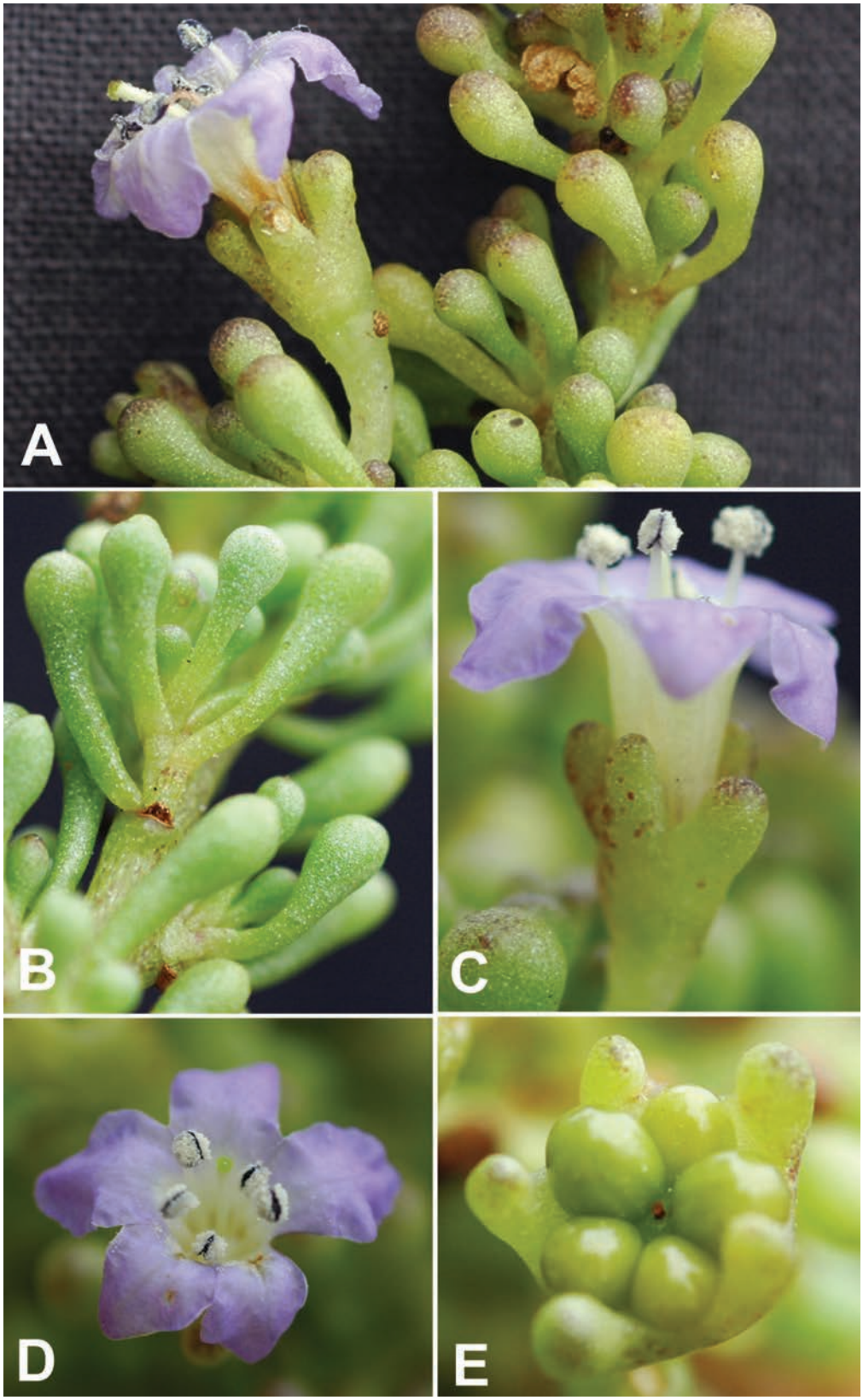


FIGURE 292. *Nolana divaricata*. **A–B**, Glabrous, succulent leaves and calyces; **C,** Lateral view of flower; **D**, Frontal view of corolla, purple anthers with white pollen; **E**, Mericarps.

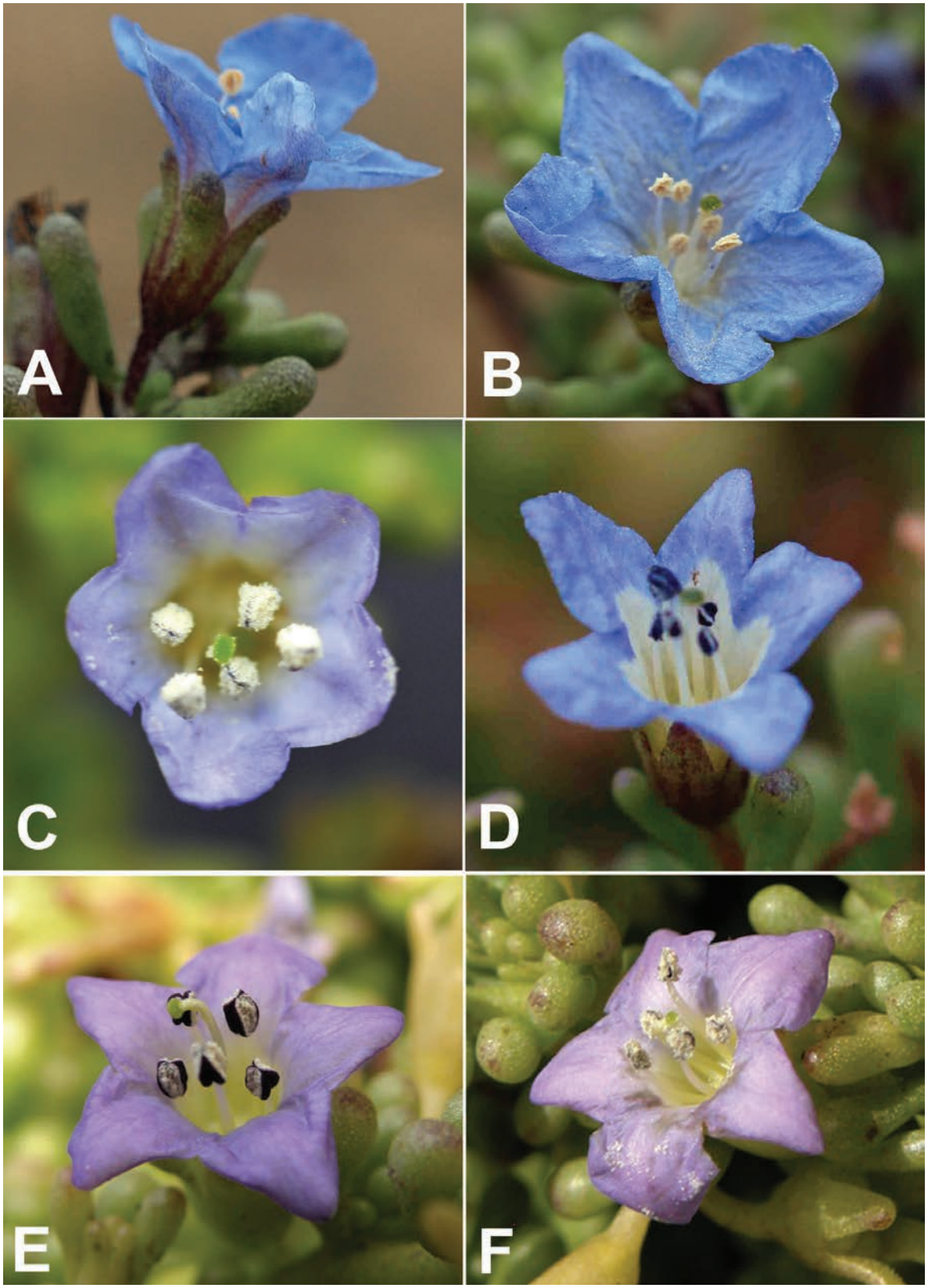


FIGURE 293. *Nolana divaricata*. **A–F**, Diverse corolla shapes and color patterns.

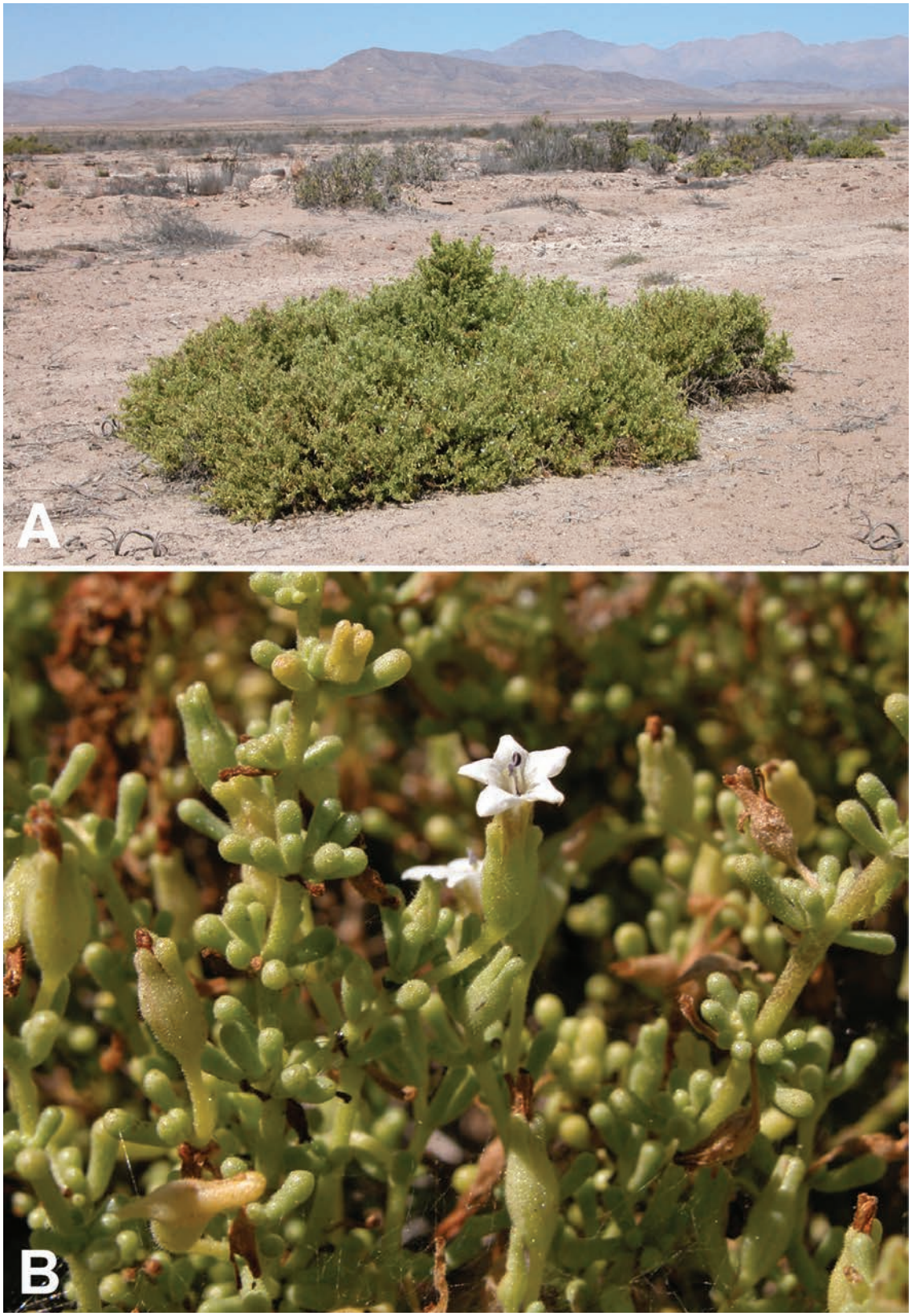


FIGURE 294. *Nolana divaricata*. **A**, Unusual individuals do not completely agree with typical forms; **B**, Corollas reduced, tubular, white.

2011620); 13 km E of Taltal, 0.5 km into Quebrada Estación Brea, 25°30'S, 70°25'W, 600 m.a.s.l., 29 October 1988, *M. O. Dillon & D. Dillon 5803* (E, F 2330868, GH, SGO, US); 11 km E of Breas, 25°27'S, 70°20'W, 820 m.a.s.l., 29 October 1988, *M. O. Dillon & D. Dillon 5810* (F 233084); Quebrada de Taltal, near desvío to Cifuncho, 23°30'35"S, 70°24'47"W, 500 m.a.s.l., 14 October 2004, *M. O. Dillon & M. Finger C. 8566* (F 2292811, SGO 158704); near entrance to Parque Nacional Pan de Azúcar, 25°54'38"S, 70°37'32"W, 280 m.a.s.l., 5 November 2007, *M. O. Dillon & R. Schulz 9055* (F 2292848, SGO 158731); Quebrada de La Chimba, 23°33'S, 70°22'W, 300–550 m.a.s.l., 17 December 1987, *M. O. Dillon & S. Teillier 5339* (F 2010918); Cerro Perales, E of Taltal, 25°26'S, 70°26'W, 890 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8048* (CONC 150025, E, F 2183327, GH, K, SGO 143694, US); Quebrada Agua de Cascabeles, 15 km N of Taltal on Hwy 1, 25°18'S, 70°27'W, 110 m.a.s.l., 28 November 1997, *M. O. Dillon 8137* (F 2182962); Cerro Perales, 25°25'41"S, 70°26'12"W, ca. 860 m.a.s.l., 9 October 2005, *M. O. Dillon, A. Casareggio M., & M. Finger C. 8705* (F 2294690, GH, SGO); 14 km E (above) Taltal towards the Panamericana, 6 km below branching of access roads to the Panamericana towards Antofagasta–Chañaral, Quebrada de Taltal, 25°31'S, 70°25'W, 620 m.a.s.l., 9 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2867* (B, CONC 138493); Sierra Esmeralda, between Posada Hidalgos and Quebrada Cachina via Portezuelo de Mina Carola, 25°50'S, 79°37'W, 14 December 1925, *I. M. Johnston 5675* (GH); region about Aguada Cachina, ca. 25°53'S, 14–15 December 1925, *I. M. Johnston 5694* (F 685189, GH, K, US 1473955); Breas, 25°30'S, 70°24'W, 570 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2736/1130* (F 2290694, SGO 159459); Sierra Esmeralda, camino a Esmeralda, 25°53'32"S, 70°33'33"W, 520 m.a.s.l., 12 October 2005, *F. Luebert & N. García 2777/1171* (F 2290692); Quinchigüe, 26°04'02"S, 70°31'39"W, 330 m.a.s.l., 14 October 2005, *F. Luebert & N. García 2816/1210* (F 2290723); Paposo, Quebrada Guanillos, 690 m.a.s.l., 11 September 1972, *M. Mahu 9261* (SGO 116895); Quebrada Taltal, 100 m.a.s.l., 9 September 1936, *G. Montero O. 2868* (GH), 2906 (GH); entrada nueva a Taltal Km 4, 25°32'40"S, 70°22'48"W, 754 m.a.s.l., 29 September 2005, *M. Muñoz S. 4585* (SGO 153612); near Taltal, between Chañaral and Antofagasta, 22 November 1991, *M. Ono s.n.* (MAK 274965); near Carrizalillo, 20 October 1983, *R. B. Selander 1-83* (SGO 102811); between Caldera and Chañaral, 15 October 1993, *K. Suzuki s.n.* (MAK 274040); 10 km S of Taltal, *M. Ono & K. Suzuki s.n.* (MAK 274067); between Caldera and Chañaral, 10 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274070); 7–15 km N Taltal, 25°24'S, 70°29'W, *K. H. Rechinger & W. Rechinger 63510* (B); Cuesta Barriles, 500 m.a.s.l., 22 October 1964, *M. Ricardi, C. Marticorena, & O. Matthei 1075* (CONC 43020); Quebrada Taltal, Km 15, 25°26'S, 70°35'W, 570 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García 2670* (SGO 129366); Taltal, Quebrada Taltal, camino al aeropuerto, 25°26'S, 70°35'W, 800 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García. 2684* (SGO 129363); Taltal, 400 m.a.s.l., October 1925, *E. Werdermann 834* (A [2 sheets], BM000941340, CONC 22598, CONC 109136, E, F 564279, GH, K, US 1444776, US 3312702). **Atacama**: Chañaral, 5 m.a.s.l., 23 February 1939, *A. A. Beetle 26167* (GH, K); Copiapó, Quebrada Paipote, 13 October 1949, *W. Biese 2659* (SGO 96578); Vallenar, October 1927, *Bro. Claude-Joseph 5020* (US 1422133), *5023* (US 1422136); Quebrada de León, ca. 17 km NNE of Caldera, 26°57'29"S, 70°44'14"W. ca. 287 m.a.s.l. 28 September 2021, *P. Dandois & C. De Schrevel s.n.* (F 2330856); Chañaral: 29 km S of Chañaral, 4 km N of Flamenco, between Chañaral and Caldera, 26°30'S, 70°40'W, ca. 10 m.a.s.l., 28 November 1988, *M. O. Dillon & D. Dillon 6046* (CONC, E, F 2144370, GH, SGO, US); Bahia Inglesa, 27°08'S, 70°51'W, 0 m.a.s.l., 28 November 1988, *M. O. Dillon & D. Dillon 6049* (CONC, E, F 2144366, GH, SGO, US); Mirador, Parque Nacional Pan de Azúcar, 26°07'S, 70°39'W, 320 m.a.s.l., 3 December 1997, *M. O. Dillon 8177* (CONC 149954, E, F 2183340, GH, SGO 143714); Bahía Flamenco, 26.5 km S of Chañaral, 26°34'S, 70°41'W, 50 m.a.s.l., 27 October 2004, *M. O. Dillon & M. Finger C. 8609* (F 222836, SGO 158695); road to Aguada Tongoy, 14 km SW of Huasco, 28°34'S, 71°19'W, 110 m.a.s.l., 13 November 2004, *M. O. Dillon & M. Finger C. 8657* (F 2292782, SGO 158912); Carrizal Bajo, 28°04'54"S, 71°08'48"W, 0–5 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8664* (F 2292810, SGO 158949); 18 km E of Huasco, 28°30'20"S, 71°07'33"W, 200 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8650* (F 2292789, SGO 158919); Parque Nacional Pan de Azúcar, Las Lomitas, 26°02'S, 70°33'W, 560 m.a.s.l., 12 November 1997, *M. O. Dillon & C. Trujillo C. 8017* (CONC 149965, E, F 2183315, GH, K, SGO 143720); Huasco, ca. 100 km S of Copiapó, ca. 49 km N of Vallenar, near Algarrobal, 28°07'06"S, 70°40'18"W, 450 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8616A* (SGO 158950); *8616B* (SGO 158951); ca. 7 km SW of Chañaral, 26°23'02"S, 70°39'49"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9078* (CONC, F 2293475, SGO); ca. 7 km SW of Chañaral, 26°23'02"S, 70°39'49"W, ca. 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9084* (CONC, SGO); ca. 7 km SW of Chañaral, 26°23'02"S, 70°39'49"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9084* (CONC, F 2293472, SGO); Bahia Salada, ca. 14 km S of Caleta Barranquilla at the W end of Ruta C-390, 27°38'23"S, 70°54'37"W, 2 m.a.s.l., 25 October 2010, *M. O. Dillon 9157* (CONC, F 2331760, SGO); Playa Agua de Luna, 28°20'08"S, 71°09'42"W, 0 m.a.s.l., 26 October 2010, *M. O. Dillon 9170* (CONC, F 2331761, SGO); Prov. Huasco, Mun. Huasco, 2 km E of Carrizal Bajo towards Panamericana, 28°06'01"S, 71°08'23"W, 20 m.a.s.l., 8 December 1994, *U. Eggli & B. E. Leuenberger 2595* (B, SGO 145805); Prov. Copiapó, 41 km S of Copiapó towards Vallenar on the Panamericana, 27°41'S, 70°29'W, 650 m.a.s.l., 9 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2875* (B); 22 km N of Huasco Bajo, measured from bridge crossing the Río Huasco, towards Carrizal Bajo, 28 km S of Carrizal Bajo, just N of the mouth of the Quebrada Maisani, 28°18'29"S, 71°09'10"W, 100–200 m.a.s.l., 22 October 1997, *U. Eggli & B. E. Leuenberger 3007* (B); Caldera, November

1886, *G. Geisse s.n.* (SGO 150003); vicinity of Caldera, *E. E. Gigoux s.n.* (GH); Huasco, 30 km N of Vallenar, 550 m.a.s.l., 29 October 1990, *T. C. Lammers, C. M. Baeza, & P Peñailillo B. 7622* (F 2180037); Flamenco, 26˚34'13" S , 70˚40'48" W, 0 m.a.s.l., 15 October 2005, *F. Luebert & C. Becker 2842* (F 2290712); Copiapó, Tierra Amarilla, 27˚26'14"S, 70˚17'00"W, 659 m.a.s.l., 24 September 2015, *P. Medina 3129* (CONC 186918); Cercanías de Copiapó, 27˚30'52"S, 70˚25'27"W, 744 m.a.s.l., 21 September 2015, *P. Medina 3130* (CONC 186919); cercanías de Copiapó, 27˚29'26"S, 70˚22'22"W, 812 m.a.s.l., 22 September 2015, *P. Medina 3131* (CONC 186920); cercanías de Copiapó, 27˚29'41"S, 70˚23'40"W, 761 m.a.s.l., 27 September 2016, *P. Medina 3138* (CONC 186927); Quebradita mano izquierda a 1 hr desde Copiapó a Vallenar, 21 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1014* (SGO 108644); Quebrada 5 km más allá Canto del Agua hacia Carrizal, 170 m.a.s.l., 23 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1075* (SGO 108669); Carrizal Bajo, 23 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1105* (SGO 108615); Poniente de El Salado más o menos 35 km desde Diego de Almagro, 26˚24'S, 70˚19'W, 490 m.a.s.l., 30 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2785* (SGO 126134); Copiapó, Piedra Colgada, 1885, *F. Philippi & A. Borchers s.n.* (BM000941337); Caldera, Quebrada León, October 1924, 30 m.a.s.l., *E. Werdermann 461* (A, F 565283, GH, K, US 1444750); Morro de Copiapó, WSW of Caldera, 10 m.a.s.l., 21 October 1938, *C. R. Worth & J. L. Morrison 16186* (K). **Coquimbo**: La Serena, October 1926, *Bro. Claude-Joseph 4427* (US 1284370); Andacolo, November 1930, *Bro. Claude-Joseph 5452* (US 1470550); Coquimbo, 100–200 ft, November 1929, *C. Elliott 541* (GH, K, US 1587804); 6 km N de Los Villos, 16 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1369* (CONC 43004); Punta Choros, 4 km hacia Carrizalillo, 29˚12'58"S, 71˚27'37"W, 510 m.a.s.l., *A. Moreira M. 699* (SGO 149908); Fray Jorge, 26 September 1935, *C. Muñoz P. B-80* (SGO 57766); Panamericana entre Trapiche e Incahuasi, 17 September 1966, *E. M. L. Kausel 5136* (SGO 79436); Ovalle, Fray Jorge, del Rio Limarí, *B. Sparre 2985* (SGO 98482); Coquimbo, La Serena, 10 m.a.s.l., August 1924, *E. Werdermann 370* (BM000941336, E, F 565192, GH, K).

G7. ***Nolana glauca*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 66. 1936. Fig. 295–297.

Basonym: *Bargemontia glauca* I.M. Johnst., Contrib. Gray Herb. 85: 105. 1929. TYPE: CHILE. Coquimbo: Dept. Chañaral, a pale sprawling shrub on the upper slopes of the hills directly back of Barquito, [26˚22'S], 29 October 1925, *I. M. Johnston 4770* (Holotype: GH [00282374]).

Digital image: Holotype of *Bargemontia glauca* from Harvard University Herbaria, Cambridge [GH00 282374]. https://s3.amazonaws.com/huhwebimages/07357FFC7D8D4E8/type/full/282374.jpg

Homotypic synonym: *Nolana peruviana* (Gaudich.) I.M. Johnst. ssp. *peruviana* var. *glauca* (I.M. Johnst.) Mesa, Fl. Neotrop. Monogr. 26: 80. 1981.

Shrubs, laxly branched, erect to decumbent, glabrous; stems to ca. 1.5 m tall, glabrescent, internodes 5–10 mm long. *Leaves* alternate to fasciculate, blades narrowly tubular to narrowly spathulate, 5–15 mm long, 1.0–2.5 mm wide, succulent, subterete, glabrous, gray, curved upward, apically rounded to obtuse. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 4–5 mm long. *Flowers* 5-merous; calyces obconical, ca. 5 mm long, lobes triangular, apex acute; corollas hypocrateriformis, white to pink, ca. 1 cm long, tube 3.0–3.5 mm long, abruptly expanded 3–4 mm long, 4–5 mm diam., lobes triangular, obtuse, ca. 4 mm wide, ca. 3 mm long, filaments 2.0–2.5 mm long, villous-ciliolate; anthers elliptic, ca. 1.5 mm long; style ca. 1 cm long; receptacles stalked. *Mericarps* 5–8, round, muricate, 2–3 mm in diam., uniseriate, attached basally; seeds ca. 2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *glaukos*, or the Latin, *glaucus*, bluish-green or gray, and refers to the appearance of the leaves.

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 50–750 m.a.s.l. (Fig. 295). It is recorded from a few inland sites, but within the range of coastal fog; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana glauca is a woody shrub with strictly glabrous leaves and small whitish corollas (Fig. 296A–D). The habit can vary from erect, crooked shrubs to spreading, prostrate morphs (Fig. 297A). Its leaf shape most closely resembles other Chilean species that are covered with dendritic trichomes (Fig. 297B). The only other completely glabrous Chilean species is *N. divaricata*, which has blue or lavender corollas, linear-oblanceolate calyx lobes, and succulent leaves with apices tending to be swollen and bulbous. In *N. glauca*, the calyx lobes are invariably triangular with acute apices (Fig. 297C). Mericarps number more than five and are spherical and dark brown (Fig. 297D).

A collection from Coquimbo, (i.e., *C. Marticorena, R. Rodríguez, & E. Weldt 1369*) was determined as *Nolana glauca* by Mesa (22 January 1976), likely based on its glabrous leaves and calyx; however, this collection would greatly extend the known distribution of this species, and it is here recorded as *Nolana divaricata*. This population should be further sampled to confirm this determination.

Additional specimens examined: CHILE. **Atacama**: Chañaral, Parque Nacional Pan de Azúcar, Quebrada Coquimbo; ca. 100 km S of Taltal, 26˚09'S, 70˚39'W, 160–200 m.a.s.l., 5 December 1987, *M. O. Dillon & S. Teillier 5086* (F 1994740); Parque Nacional Pan de Azúcar, Quebrada Coquimbo; ca. 100 km S of Taltal, 26˚09'S, 70˚39'W, 140–190 m.a.s.l., 30 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5592* (E, F 2012869, GH); Bahía Flamenco, ca. 26.5 km S of Chañaral. 26˚34'28"S, 70˚41'00"W, 50 m.a.s.l., 27 October 2004, *M. O. Dillon & M. Finger C. 8608* (F 2292835, SGO 158696); Cuesta Portezuelo Blanco on Ruta 5, 26˚17'39"S, 70˚27'39"W, 740 m.a.s.l., 5 November 2007, *M. O. Dillon & R. Schulz 9059* (F 2292845, SGO 158733); Parque Nacional Pan de Azúcar, Las Lomitas, 2 km E of coast, 26˚01'S, 70˚35'W, 720 m.a.s.l., 12 November 1997,

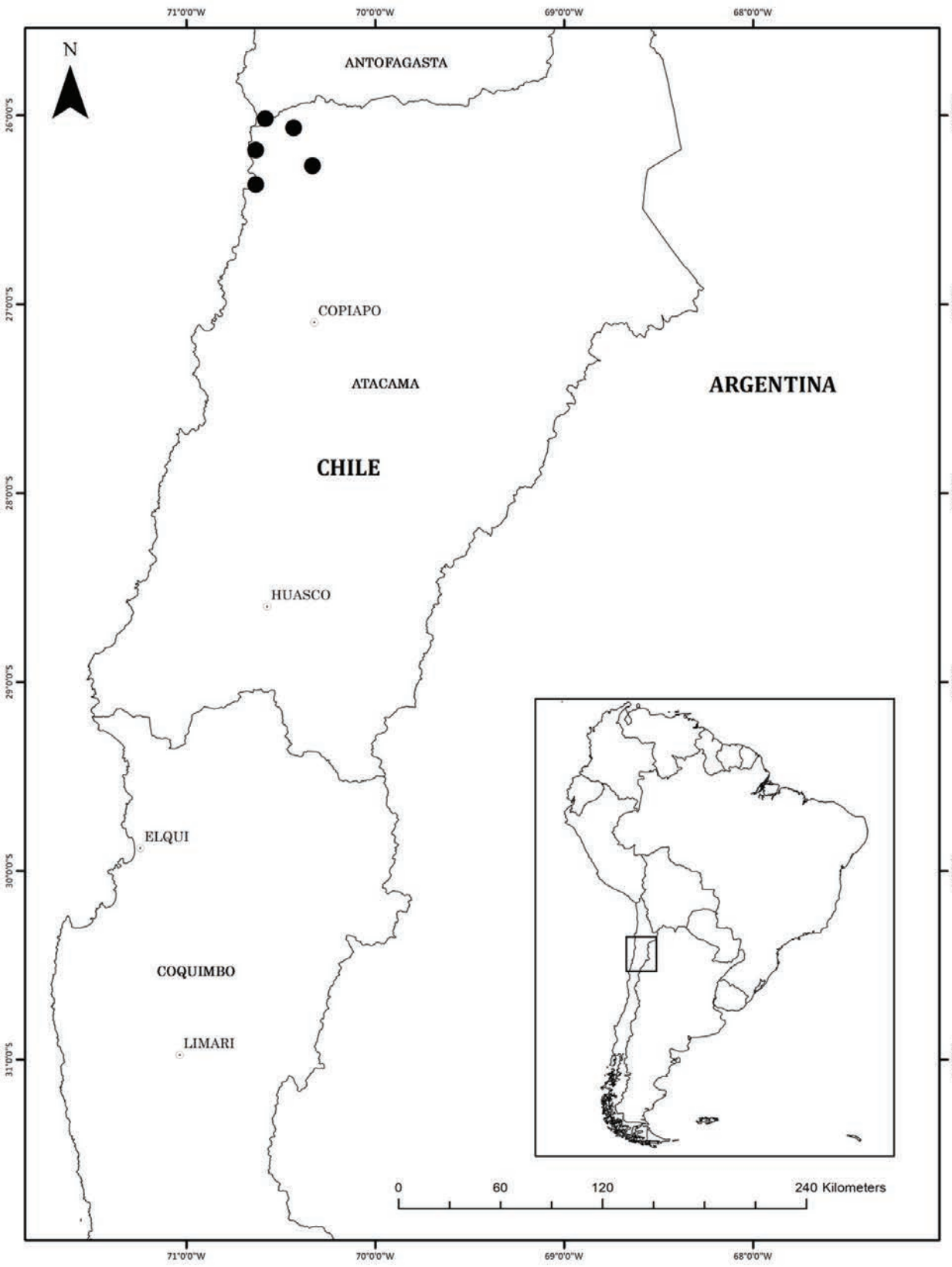


FIGURE 295. Distribution of *Nolana glauca* (I.M. Johnst.) I.M. Johnst.

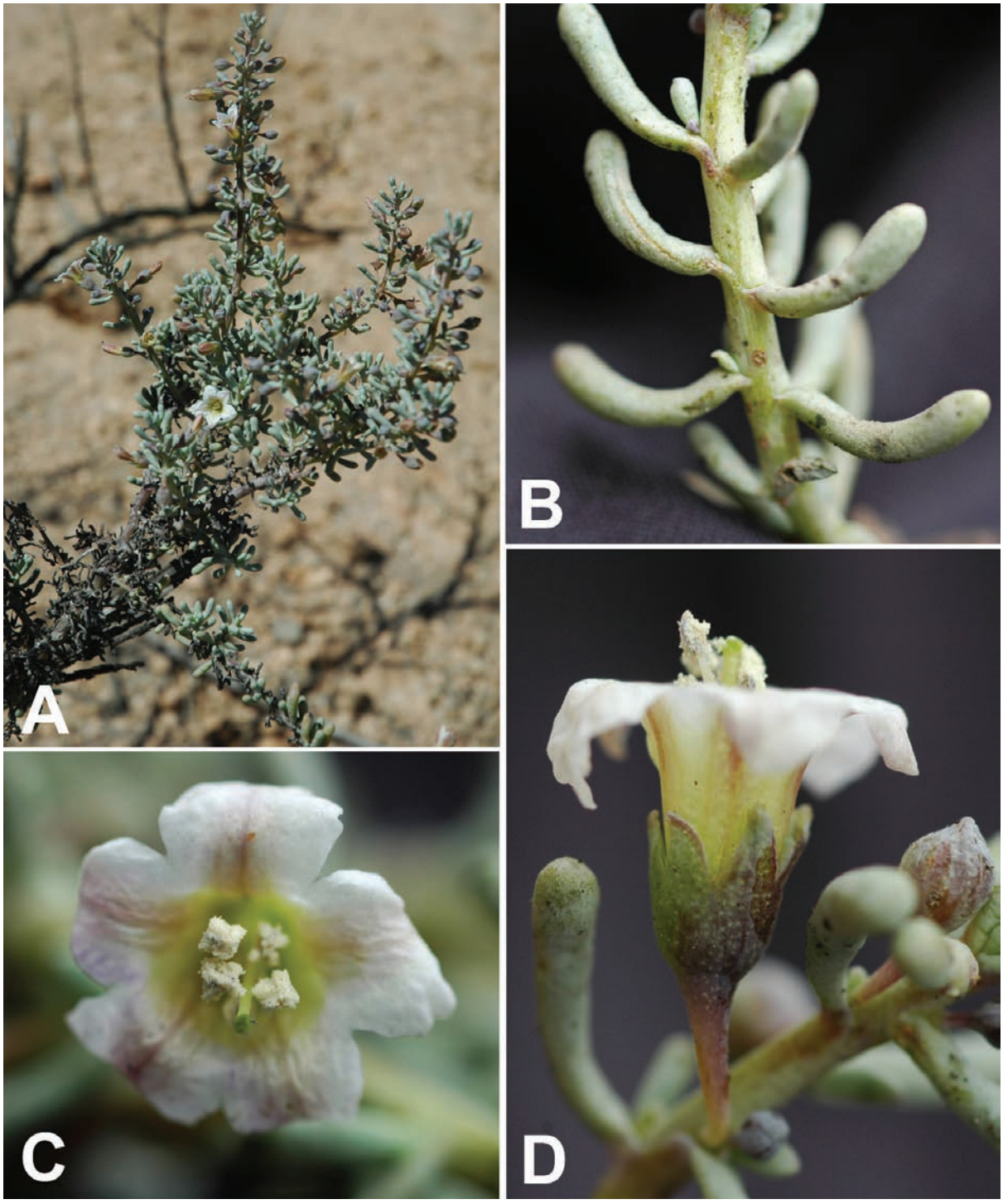


FIGURE 296. *Nolana glauca*. **A**, Shrubs with glabrous leaves and with small white corollas; **B**, Cylindrical, glabrous leaves; **C**, Frontal view of corolla with white anther thecae and pollen; **D**, Lateral closeup view of flower.

M. O. Dillon & C. Trujillo C. 8019 (CONC 149986, E, F 2183338, GH, K, SGO 143718); Parque Nacional Pan de Azúcar, 26°11'S, 70°38'W, 320 m.a.s.l., 1 December 1997, *M. O. Dillon 8157* (F 2182951); ca. 7 km SW of Chañaral, 26°23'02"S, 70°39'49"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9079* (CONC, F 2293437, SGO); ca. 20 km E of Chañaral along Hwy 5, 26°17'35"S, 70°27'40"W, 731 m.a.s.l., 14 November 2009, *M. O. Dillon & A. Casareggio M. 9103* (CONC, F 2293465, SGO); ca. 8 km S of Chañaral, at the mouth of Quebrada Los Infieles, near Playa Caleuche, 26°23'22"S, 70°40'05"W, ca. 5 m.a.s.l., 27 September 2010, *M. O. Dillon 9131* (CONC, SGO); Flamenco, 26°34'13"S, 70°40'48"W, 0 m.a.s.l., 15 October 2005, *F. Luebert & C. Becker 2841* (F 2290720);

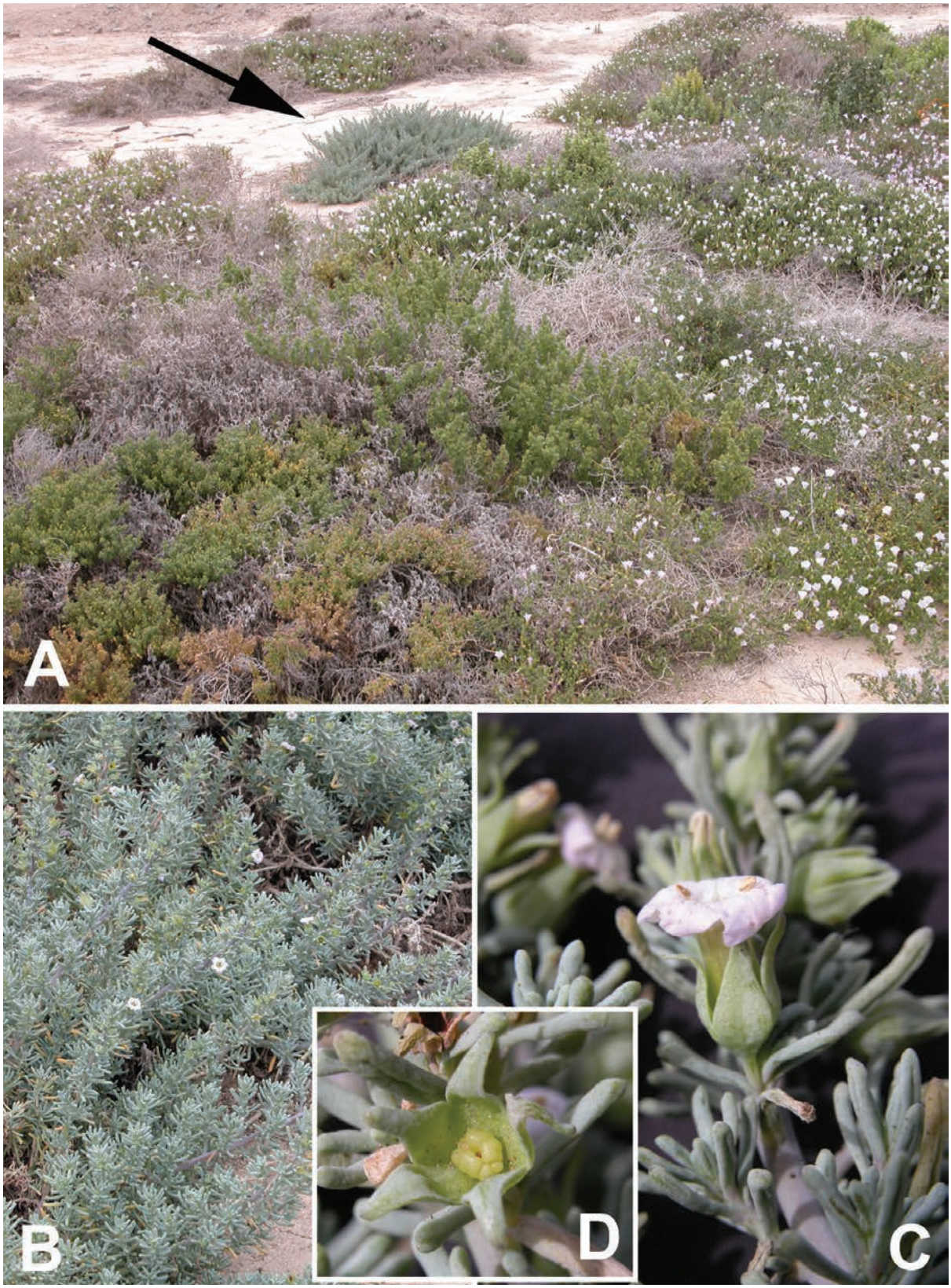


FIGURE 297. *Nolana glauca*. **A**, Shrub (black arrow) growing in runoff pond; **B,** Densely leafy stems; **C**, Calyx lobes triangular with acute apices; **D**, Gynoecium with developing mericarps.

Lalo Seco, ca. 20 km S of Copiapó (ca. 50 km E of ocean), north of Travesía, 30 September 1993, *M. Ono & K. Suzuki s.n.* (MAK 274044), *s.n.* (MAK 274045); 18 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 27406); Chañaral, Barquito, 120 m.a.s.l., 26 October 1941, *E. Pisano V. & R. Bravo F. 512* (CONC 144529, SGO 156437); entre Las Bombas y Chañaral, Km 27, 700 m.a.s.l., 23 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1434* (CONC 36115).

G8. ***Nolana incana*** (Phil.) I.M. Johnst., Contrib. Gray Herb. 112: 68. 1936. Fig. 298–301.

Basionym: *Alibrexia incana* Phil., Flor. Atac. 45. 1860. TYPE: CHILE. Antofagasta: Paposo, January 1854, *R. A. Philippi s.n.* (Holotype: SGO [55126, SGO000004326]; Isotype: W [W0074697], F neg. 33145, GH [GH00282368]).

Digital image: Holotype of *Alibrexia incana* from Museo Nacional de Historia Natural, Santiago [SGO 55126]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004326

Homotypic synonym: *Nolana crassulifolia* Poeppig ssp. *crassulifolia* Mesa, Fl. Neotrop. Monogr. 26: 88. 1981.

Heterotypic synonym: *Dolia eremobia* Phil., Anal. Univ. Chile 91: 45. 1895. TYPE: CHILE. Antofagasta, Breas, 1888, *D. Alamirano Larrañaga s.n.* (Holotype: SGO [SGO 55163, SGO000004351]). *Bargemontia eremobia* (Phil.) I.M. Johnst., Contr. Gray Herb. 85: 107. 1929.

Shrubs, or weakly woody, long-lived perennial herbs; stems reaching over 5 m long, prostrate spreading or occasionally erect, soft and succulent, pale gray green, fragile, somewhat zigzag. *Leaves* alternate, blades clavate, 6–18 mm long, ca. 2 mm wide, terete, abaxial groove, slightly curved upward, canescent, densely pubescent with dendritic trichomes. *Inflorescences* of solitary flowers, axillary and terminal; pedicels ca. 5 mm long. *Flowers* 5-merous; calyces cupulate, 5-dentate, lobes 1–2 mm long, triangular; corollas tubular, (5–)6–10 mm long, 1.0–1.2 mm wide; anther filaments thickened, densely villous. *Mericarps* 3–4(–5), round to oblong, 2–4 mm long, unorganized orange elaiosomes; seeds ca. 2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *incanus*, quite gray, hoary or whitish, and refers to the overall appearance of these plants.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; (5–)100–500(–950) m.a.s.l. (Fig. 298). It is recorded from sandy or clay soils and finds its greatest development in areas of aguadas; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana incana forms extensive prostrate, spreading individuals that can reach several meters in diameter (Fig. 299). The photographs in Fig. 299 were taken in the same *aguada* ten years apart; the picture in Fig. 299A was taken in 1997, and in Fig. 299B, in 2007. Outside of the influence of *aguadas*, in more arid conditions, the size of individuals is smaller (Fig. 300A), and the leaves are densely pubescent with dendritic trichomes (Fig. 300B, Fig. 301A). The flowers are shorter and wider (Fig. 300C, Fig. 301B), than its nearest relative, *Nolana albescens*, and more like *N. crassulifolia*. The mericarps of all of these species are comparable (Fig. 300C, Fig. 301C). All of these are in the group of canescent shrubs with small, white flowers, including *N. peruviana* to the north and *N. albescens* to the south. They are distinguished from *N. peruviana,* that has broadly clavate to globular-obovate leaves, 5–10 mm long; however, the two species do grow in the same general environments at some locations.

Biese 3230 (SGO) is a mixed collection with one branch of *N. incana* and another of *N. divaricata* on the same sheet (SGO 696834); it is filed under *N. incana*.

Additional specimens examined: CHILE. **Antofagasta**: Taltal, Aguada Breas, 780 m.a.s.l., 12 December 1949, *W. Biese 3230 p.p.* (SGO 96834); Aguada Breas, *W. Biese 3231* (SGO 96833); Aguada Cachina, Cachinal de La Costa, 13 December 1949, *W. Biese 3263* (SGO 96868); Quebrada San Ramón, ca. 6 km NE of Taltal, 25°23'S, 70°25'W, 50–80 m.a.s.l., 24 December 1987, *M. O. Dillon 5397* (CONC, E, F 2010964, GH); Aguada directly W of Quebrada Bandurrias, ca. 15 km S of Punta Grande, 20–30 m.a.s.l., 7 October 1988, *M. O. Dillon & D. Dillon 5651* (CONC, E, F 2013642, GH, SGO); ca. 13 km E of Taltal, 0.5 km into Quebrada Estación Breas, 25°30'06"S, 70°25'18"W, 600 m, 29 October 1988, *M. O. Dillon & D. Dillon 5798* (F 2329922, GH); ca. 13 km E of Taltal, 0.5 km into Quebrada Estación Breas, 25°30'06"S, 70°25'18"W, 600 m, 29 October 1988, *M. O. Dillon & D. Dillon 5799* (F 2329921); ca. 13 km E of Taltal, 0.5 km into Quebrada Estación Breas, 25°30'S, 70°25'W, 600 m.a.s.l., 29 October 1988, *M. O. Dillon & D. Dillon 5800* (CONC, E, F 2330869, GH, SGO, US); Cerro Perales, ca. 5 km E of Taltal, 25°25'S, 70°25'W, 550–600 m.a.s.l., 1 November 1988, *M. O. Dillon & D. Dillon 5826* (CONC, E, F 2144383, GH, SGO, US); ca. 60 km S of Taltal, near mouth of Quebrada de La Cachina, 26°00'S, 70°37'W, 50–100 m.a.s.l., *M. O. Dillon & D. Dillon 6040* (F 2144368, GH, US); Quebrada de Taltal, near desvío to Cifuncho, 23°30'35"S, 70°24'42"W, 500 m.a.s.l., 14 October 2004, *M. O. Dillon & M. Finger C. 8563* (F 2292805, SGO 158707); mouth of Quebrada Bandurrias, 25°13'S, 70°26'W, 20 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8046* (CONC 150027, E, F 2183329, GH, K, SGO 143701); Playa Cachinales, ca. 30 km N of Taltal, 25°10'S, 70°27'W, 20 m.a.s.l., 25 November 1997, *M. O. Dillon 8097* (F 2183309); Cerro Perales, 24°46'13"S, 70°32'42"W, ca. 580 m.a.s.l., 9 October 2005, *M. O. Dillon, A. Casareggio M., & M. Finger C. 8704* (E, F 2294691, GH, SGO, US); 14 km E, above Taltal towards the PanAmerican, 6 km below, U. *Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2864* (B, CONC 138507, SGO 146031); ca. 2 km S of Taltal on coastal gravel track to the basural in the Quebrada de Changos, ca. 0.8 km inland from sea, S slopes of Cerro Barazarte, 25°25'23"S, 70°29'56"W, 80–250 m.a.s.l., 16 February 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2685* (B, CONC 138423, SGO 145877); Quebrada de Taltal, 26 July 1960, *G. Hartmann s.n.* (CONC 36263); Parque Nacional Pan de Azúcar, Quebrada La Chicas, 26°03'23"S, 70°32'28"W, 447 m.a.s.l., 9 March 2017, *A. Ibáñez, B. Arnold, & R. Vargas 9170* (CONC 184612); Parque Nacional Pan de Azúcar, Las Lomitas,

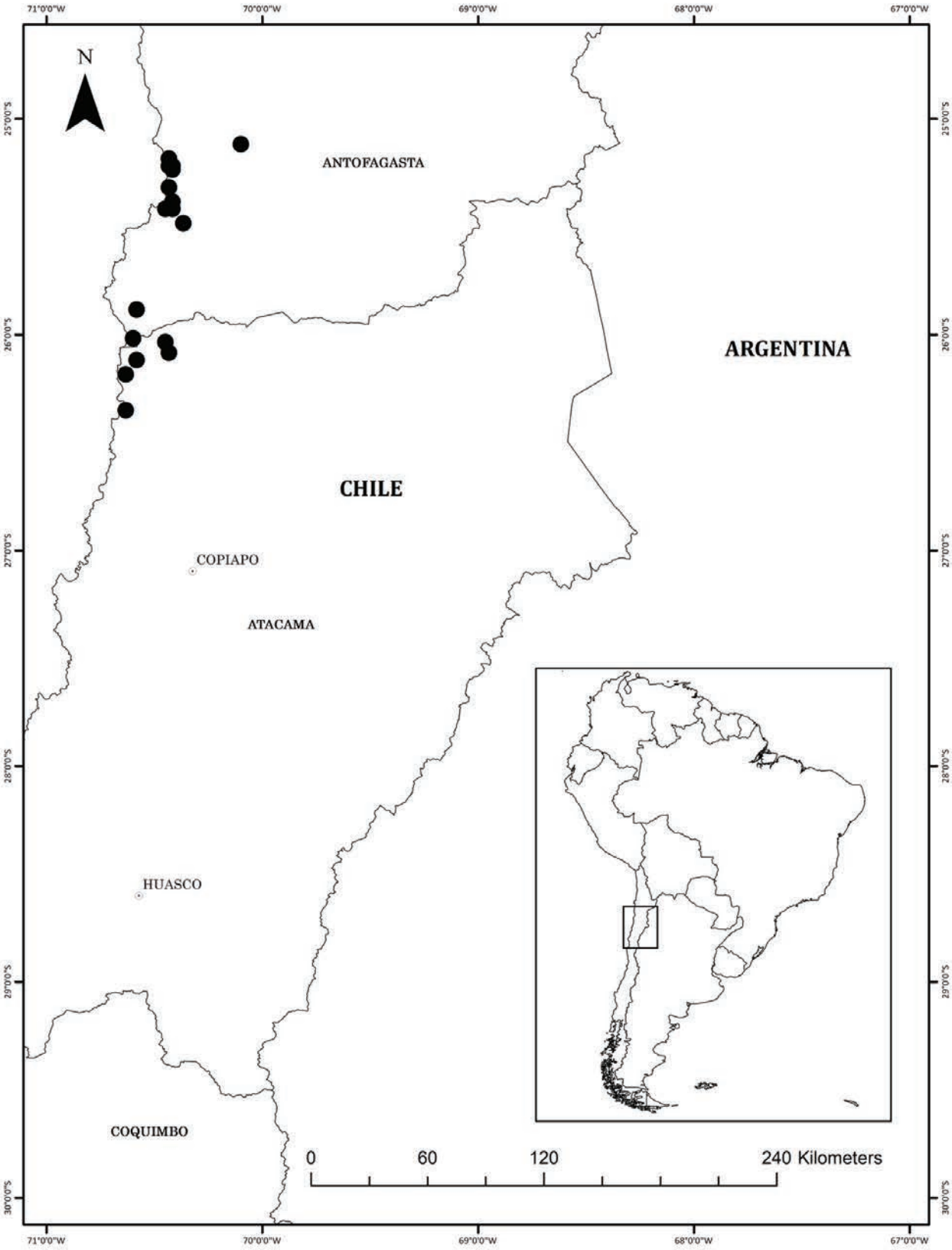


FIGURE 298. Distribution of *Nolana incana* (Phil.) I.M. Johnst.

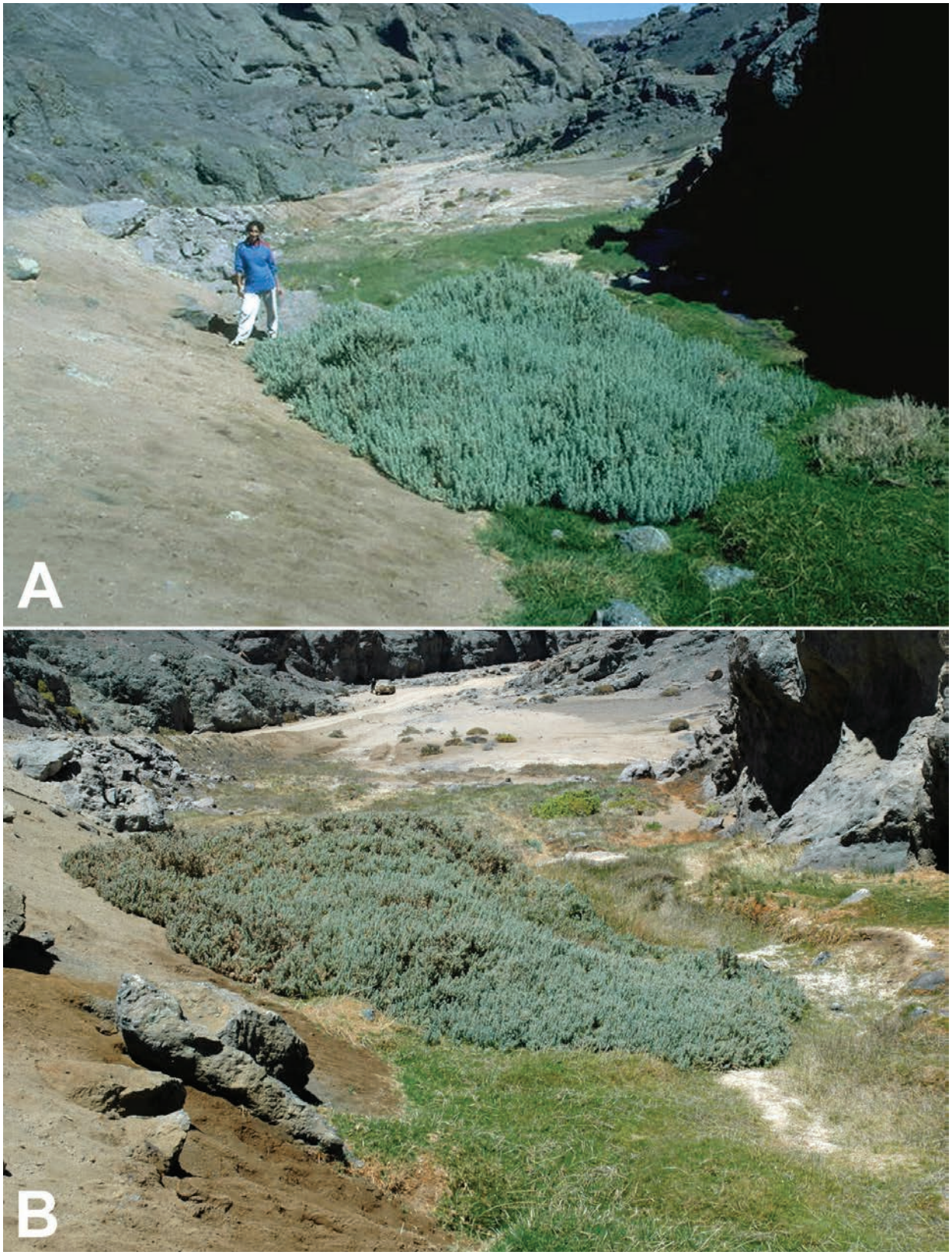


FIGURE 1. FIGURE 299. *Nolana incana*. **A**, Large sprawling plant growing in an *aguada* in 1997; **B**, Same locality in 2007.

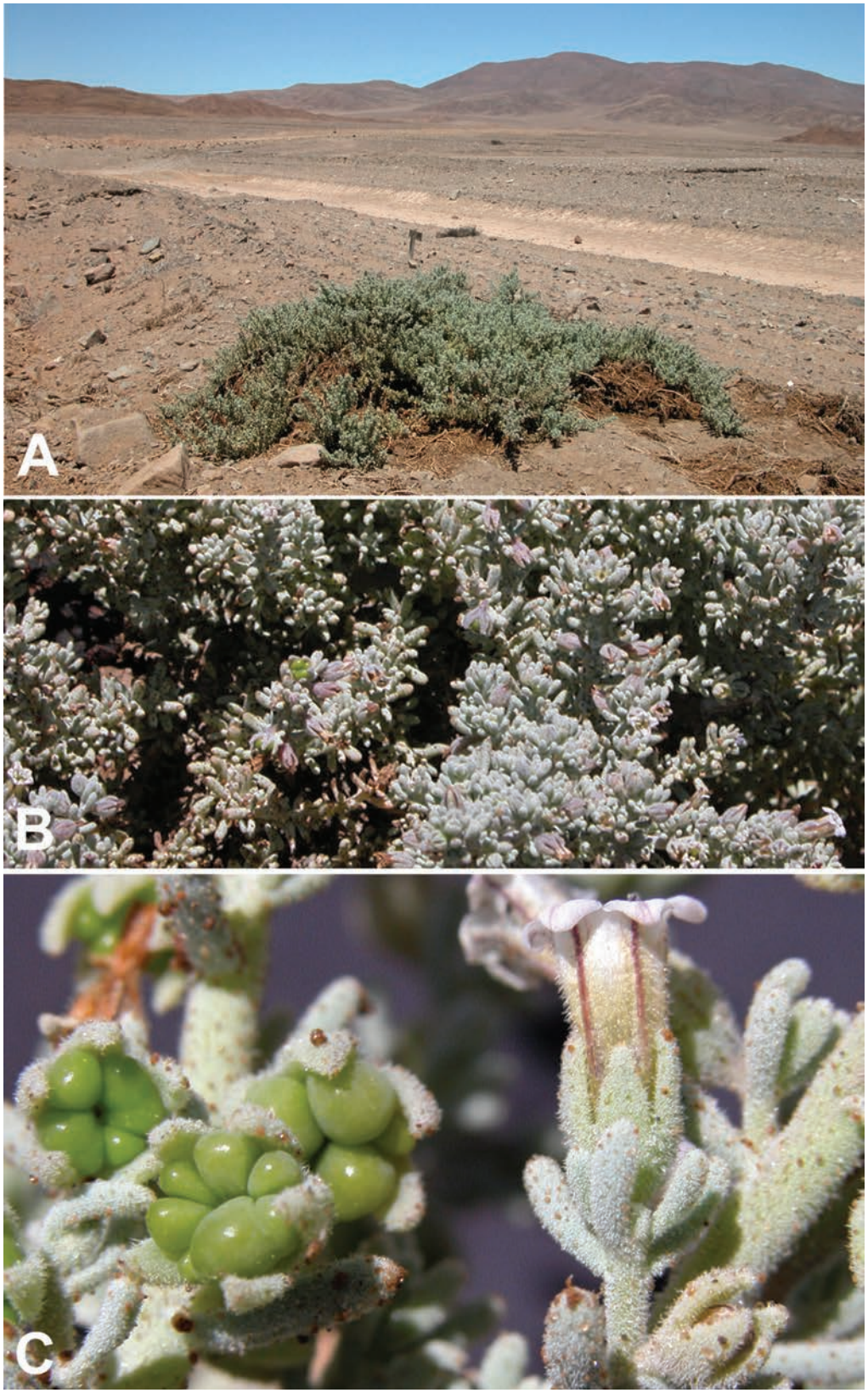


FIGURE 300. *Nolana incana*. **A**, Outside the influence of *aguadas*, individuals are much reduced; **B**, Leaves are densely pubescent with dendritic trichomes; **C**, Flowers are covered with dendritic trichomes, mericarps four to six.

FIGURE 301. *Nolana incana*. **A**, Closeup of flowering branch; **B**, Closeup of corollas with anther thecae equal, green stigma; **C**, Connate mericarps.

26°01'07"S, 70°36'36"W, 780 m.a.s.l., 9 March 2017, *A. Ibáñez, B. Arnold, & R. Vargas 9183* (CONC 184611); Quebrada de San Ramón, 25°21'–24'S, 26 November 1925, *I.M. Johnston 5128* (GH, K, US 1473958); Posada Hidalgos, 13 December 1925, *I. M. Johnston 5662* (GH); Trayecto Agua Verde–Chañaral, 25°30'S, 70°00'W, 1300 m.a.s.l., 26 February 2001, *C. Latorre, C. Villagrán, & A. Maldonado 245* (CONC 150976); Taltal, November 1936, *R. López M. s.n* (CONC 129572), *s.n.* (CONC 129682); playa 10 km al sur de Paposo, 25°04'S, 70°29'W, 5 m.a.s.l., 8 October 2005, *F. Luebert & N. García 2683/1077* (F 2290739, SGO 159473); Breas, 25°30'S, 70°24'W, 570 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2737/1131* (F 2290701, SGO 159456); La Tórtolas, Sierra de San Pedro, 25°34'S, 70°36'W, 170 m.a.s.l., 12 October 2005, *F. Luebert & N. García 2758/1152* (F 2290697SGO 159452): Quebrada Miguel Díaz, 200 m.a.s.l., 29 September 2009, *P. Medina & F. Romero s.n.* (SGO 159008), *s.n.* (SGO 159011); Quebrada La Cachina, 17 September 1953, *M. Ricardi 2486* (CONC 14279); Quebrada Anchuña, 20 September 1953, *M. Ricardi 2536* (CONC 14329); camino Taltal-Paposo, Sector Bandurrias, Quebrada Anchuña, 25°11'S, 70°26'W, 90 m.a.s.l., 14 November 1996, *R. Rodríguez 3113* (CONC 136633, SGO 152816); Quebrada de Taltal, 25°26'S, 70°35'W, 470 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García 2698* (F 2114631, SGO 129361); Paposo, Quebrada Guanillos, 25°03'S, 70°30'W, 950 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2763a* (SGO 129355); Hueso Parado, 400 m.a.s.l., 17 September 1967, *O. Zöllner 1709* (CONC 129681); **Atacama**: 29 km S of Chañaral, 4 km N of Flamenco, 26°30'S, 70°40'W, ca. 10 m.a.s.l., 28 November 1988, *M. O. Dillon & D. Dillon 6048* (E, F 2144390, GH, SGO, US); northern entrance to Parque Nacional Pan de Azúcar, 26°02'S, 70°27'W, 450 m.a.s.l., 26 November 1997, *M. O. Dillon 8103* (F 2182964); Parque Nacional Pan de Azúcar, 26°07'S, 70°35'W, 200 m.a.s.l., 1 December 1997, *M. O. Dillon 8154* (F 2182953); Parque Nacional Pan de Azúcar, 26°11'S, 70°38'W, ca. 320 m.a.s.l., 1 December 1997, *M. O. Dillon 8159* (F 2183342); 30 km E of Chañaral, Quebrada Saladito, ca. 9.5 km E of Salado, 26°20'03"S, 70°19'12"W, 625 m.a.s.l., 4 November 2004, *M. O. Dillon & M. Finger C. 8640* (F 229830, SGO 158714); Cuesta Portezuelo Blanco on Ruta 5, 26°17'39"S, 70°27'39"W, 740 m.a.s.l., 5 November 2007, *M. O. Dillon & R. Schulz 9060* (F 2292849, SGO 158730); Parque Nacional Pan de Azúcar, Las Lomitas, 26°01'S, 70°36'W, 720–780 m.a.s.l., 11 November 1997, *M. O. Dillon & C. Trujillo C. 8010* (CONC 150036, E, F 2183320, GH, K, SGO 143689, US); ca. 7 km SW of Chañaral, 26°23'02"S, 70°39'49"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9077* (CONC, F 2293476, SGO); Las Bombas, 26°05'S, 70°26'W, 750 m.a.s.l., 6 November 1969, *C. Jiles 5308* (CONC 92370); Chañaral, Playa al sur de Chañaral, 13 September 1965, *A. Kohler 103* (CONC 36029); Pan de Azúcar, Las Lomitas, 26°00'20"S, 70°36'19"W, 820 m.a.s.l., 14 October 2005, *F. Luebert & N. García 2818/1212* (F 2290705); al Norte de Sierra Colorado, Km 1020, 27 October 1987, *M. Muñoz S. & I. Meza P. 2262* (SGO 137727).

G9. ***Nolana inconspicua*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 73. 1936. Fig. 302–303.

Basionym: *Bargemontia inconspicua* I.M. Johnst. Contrib. Gray Herb. 85: 158. 1929. TYPE: CHILE. Antofagasta: Antofagasta, *A. Rose & J. N. Rose 19416* (Holotype: US [761944, US00121973]; Isotypes: GH [GH00282341], NY [NY00312357]).

Digital image: Holotype of *Bargemontia inconspicua* from United States National Herbarium, Washington, D.C. [US 761944]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.gh00282341

Erect *shrubs*, 30–75 cm tall, villous with capitate-glandular trichomes; intricately branched, the apical branches 4–8 cm with leaves; internodes 3–10 mm long, lower branches with withered, persistent leaves. *Leaves* alternate to fasciculate, blades 8–10 mm long, 1.0–1.5 mm wide, spathulate to clavatus, pubescent with short, capitate-glandular trichomes, abaxial surface cucullate, apically rounded; sessile. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 1–2 mm long. *Flowers* 5-merous; calyces ca. 12 mm long, tube cylindrical, 3.0–3.5 mm wide, 7–8 mm long, lobes linear to linear-oblanceolate, ca. 5 mm long, subequal, very succulent, pubescent with capitate-glandular trichomes; corollas infundibularis, 12–13 mm long, tube 3–4 mm long, limb 8–9 mm long, ca. 10 mm wide, light blue; anther filaments glabous, 5.0–5.5 mm long; styles ca. 1 cm long. *Mericarps* 5, ovoid, 1.7–2.2 mm long, black, basally affixed; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *inconspicuus*, or not readily visible or not prominent. Johnston did not clearly specify anything in his original description.

Distribution and Ecology: Chile, Region of Antofagasta; 100–1000 m.a.s.l. (Fig. 302). It is recorded from rocky, sandy soils from Cerro Coloso, south of Antofagasta, and ranges south to El Cobre; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana inconspicua is a small to robust erect shrub (Fig. 303A) confined to a small geographic area immediately south of Antofagasta and extends ca. 60 km south to El Cobre. It is characterized by green, succulent, cylindrical or linear leaves with capitate-glandular trichomes, and elongate, succulent, or swollen calyx lobes that are deeply cut to the base of the calyx (Fig. 303B).

Johnston (1929: 158) thought *Nolana inconspicua* was related to *N. clivicola* and suggested that it was perhaps only a "pronounced variety" of that species, since he had not encountered the former species in the field. It differs in having recurved fruiting pedicels, very distended fruiting calyces, is conspicuous villous with glandular-pubescence, and has linear or strap-shaped leaves. While Johnston confessed to being unable to give satisfactory key characters for the separation of *N. inconspicua* and *N. leptophylla*, these two are each very distinct. The calyx lobes are much longer and succulent in *N. inconspicua*, and they are not recurved or revolute as in *N. leptophylla*.

The dried herbarium collection of *Eggli et al. 2692* has

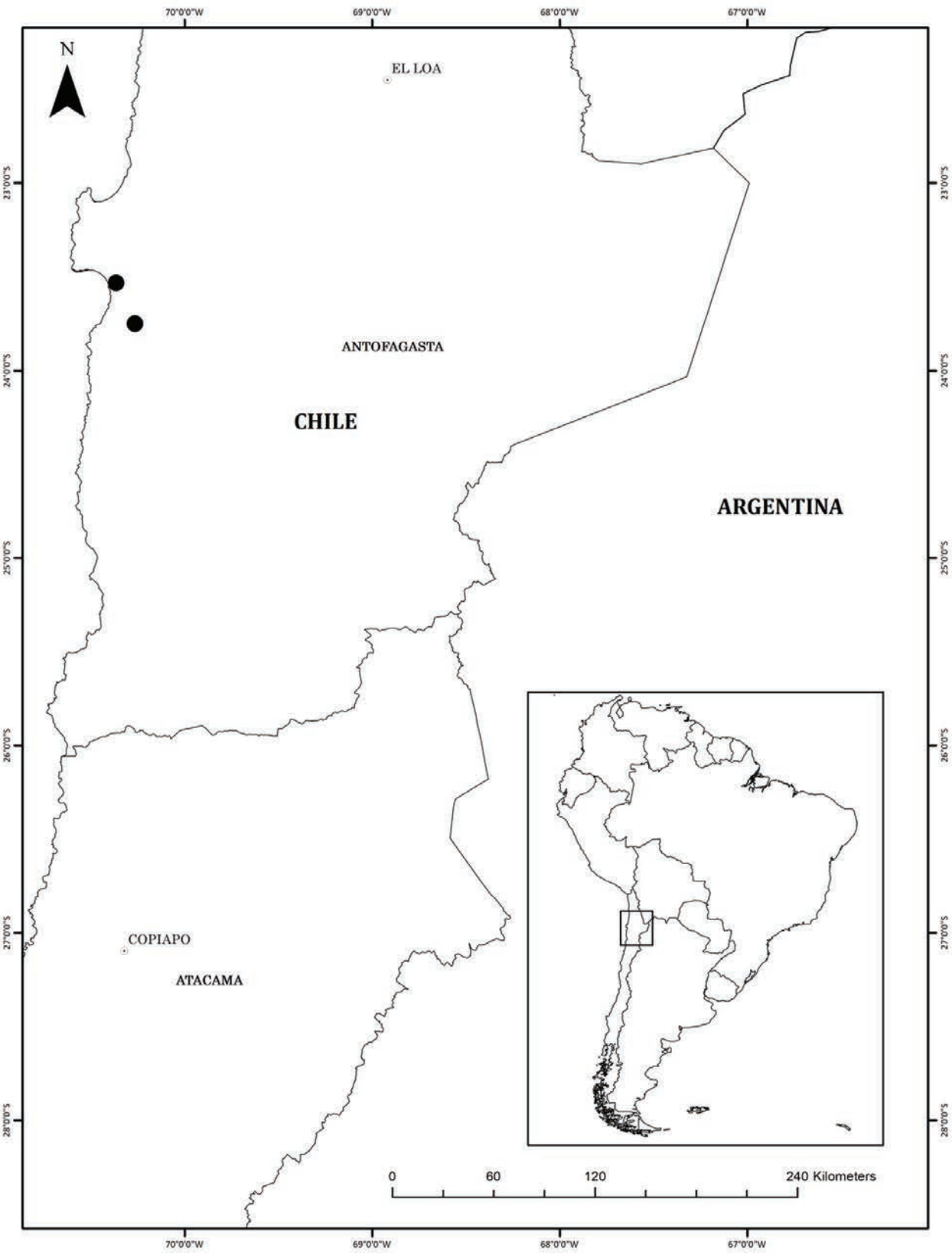


FIGURE 302. Distribution of *Nolana inconspicua* (I.M. Johnst.) I.M. Johnst.

FIGURE 303. *Nolana inconspicua*. **A**, Small to robust erect shrubs; **B**, Leaves succulent, pubescent with capitate-glandular trichomes, calyx lobes elongate, succulent.

the overall appearance of *N. incana*; however, its long calyx lobes are characteristic of *N. inconspicua*, and it is placed here provisionally; the collection of *Eggli & Leuenberger 2846* is placed here with reservations.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Cerro Cerisso, road to airport, SE of Antofagasta, 100 m.a.s.l., 27 February 1939, *A. A. Beetle 26184* (GH, K); Cerro Coloso, 4 December 2021, 23°48'12"S, 70°29'11"W, *M. O. Dillon & M. Villarroel M. 9232* (HSP); S of Antofagasta, Cerro Coloso–Cerro Jarón area, Quebrada del Buey, 3 km W of the coast on mining road towards Pozo Lombriz, 23°46'46"S, 70°27'25"W, 17 February 1997, *U. Eggli & B. E. Leuenberger 2692* (B, CONC 138480); 43 km SW of Panamericana towards El Cobre, 24°19'01"S, 70°27'19"W, 1020 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2846* (CONC 183515, SGO 146073); Antofagasta, 6 November 1931, *F. Jaffuel 2625* (GH); camino entre Ruta 5 y Caleta El Cobre, 24°19'S, 70°27'W, 1020 m.a.s.l., 4 October 2005, *F. Luebert & N. García 2612 / 1006* (E, F 2329909, HPS, SGO 159464); camino de Antofagasta a Taltal, Km 10, 23 October 1964, *M. Ricardi, C. Marticorena, & O. Matthei 1080* (CONC 30062).

G10. ***Nolana lachimbensis*** M.O. Dillon & Luebert, Arnaldoa 14(2): 196. 2007. TYPE: CHILE. Antofagasta: Prov. Antofagasta, La Chimba, quebrada NE of Antofagasta, 23°32'16"S, 70°21'33"W, ca. 500 m, 21 October 2004, *M. O. Dillon & M. Finger C. 8591* (Holotype: SGO [157613], SGO000004372; Isotype; CONC 179070, E, F [2290061], G, GH, HSP, US). Fig. 304–306.

Digital image: Holotype collection of *Nolana lachimbensis* from Museo Nacional de Historia Natural, Santiago [SGO 157613]. https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.sgo000004372

Shrubs to ca. 50 cm tall, much-branched, compact. *Leaves* alternate to fasciculate, blades elliptic to orbicular, 3–4 mm long, 2–4 mm wide, terete, pubescent with capitate-glandular trichomes or, rarely, with dendritic trichomes, margins strongly revolute and forming an abaxial cleft; sessile. *Inflorescences* of solitary flowers in upper leaf axils, pedicels 1–3 mm long, erect, densely pubescent with capitate-glandular trichomes. *Flowers* 5-merous; calyces campanulate, 4–5 mm long, tube ca. 2 mm long, ca. 2 mm wide, 5-lobed, lobes 2–3 mm long, ca. 1 mm wide, equal; corollas hypocrateriformis, ca. 8 mm long, ca. 10 mm wide distally, lavender to white, weakly zygomorphic, lobes ca. 3 mm long, ca. 3 mm wide, obtuse to rounded; stamens 5, included, filaments inserted on lower third of corolla, unequal, three ca. 4 mm long, two ca. 6 mm long, slightly exserted; anther thecae 1.0–1.5 mm long, ca. 1 mm wide, purple, pollen white; ovary glabrous, basal nectary, 5 carpels, style included, stigma capitate, green. *Mericarps* 4–5, immature; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet refers to the type locality, Quebrada La Chimba, which is immediately north of the city of Antofagasta, Chile.

Distribution and Ecology: Chile, Region of Antofagasta; two localities, Quebrada La Chimba and Cerro Moreno, the isolated mountain on the peninsula north of Antofagasta; 500–1000 m.a.s.l. (Fig. 304). It is recorded from only two localities, and both have received some level of disturbance. The individuals from within Quebrada La Chimba were restricted to rock cervices on the sides of the quebrada.

Nolana lachimbensis is a small, globose shrub (Fig. 305A) with leaves ca. 4 mm long and ca. 4 mm wide (Fig. 306B), that have short, capitate-glandular trichomes. The flowers are small (Fig. 305C–D) and approach some morphs observed in *N. divaricata*, but that species has larger leaves and corollas. Within Quebrada La Chimba, several other *Nolana* species are recorded, including *N. linearifolia*, *N. peruviana*, and *N. sedifolia*. Another collection is from the upper reaches of Cerro Moreno (*Luebert & García 2591*), the isolated mountain on the peninsula north of Antofagasta, just 20 km WNW of Quebrada La Chimba (Fig. 306A). This population has exclusively white corollas (Fig. 306B), but it is like the La Chimba population in all other features. The pubescence on *Nolana lachimbensis* is sparsely dendritic, rather than the capitate-glandular trichomes that occur on the foliar and floral surfaces of *N. lachimbensis*. *Nolana peruviana*, *N. sedifolia*, and *N. villosa* are also recorded on Cerro Moreno.

I visited the Quebrada La Chimba first in December 1987 and recorded nearly 40 species. A visit in 1988 yielded fewer species, and, over the ensuing years, the quebrada became increasingly disturbed and largely abandoned because of the encroachment of a large-scale garbage dump near the entrance. The quebrada walls were covered with graffiti and numerous feral dogs were encountered during the last visits in October and December 2004. The continued deterioration of the quebrada is obvious, although it was listed as "Reserva Nacional La Chimba" in 1988 (CONAF, 1993).

In 1999, I photographed a collection by G. Mann (CONC 75594) at the Universidad of Chile, Concepción herbarium. The sheet had originally been annotated as *Nolana leptophylla*. I disagreed with that determination and annotated it as *N. inconspicua*. Since that time, I have not only adopted a more cogent interpretation of what represents *N. inconspicua*, but I also discovered *N. lachimbensis* in October 2004. Now, as I examine the photographed sheet, there appears to be good evidence to place this collection here until further examination.

Collections originally considered to represent *N. inconspicua* from Quebrada La Chimba are treated here as *N. lachimbensis*; i.e., *C. Muñoz P. 3645*, *S. Teillier 457*, *E. Pisano V. & J. Venturelli E. 1677*, and *Ricardi et al. 1412* from Cerro Moreno.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Cerro Moreno, 23°29'14"S, 70°35'20"W, 690–760 m.a.s.l., 2 October 2005, *F. Luebert & N. García 2591/985* (E, F 2329910, SGO 159469); Loma NE Cerro Moreno, 1000 m.a.s.l., *G. Mann s.n.* (CONC 75594); Quebrada de La Chimba, 16 km NO de Antofagasta, 500 m.a.s.l., 16 December 1943, *C. Muñoz P. 3645* (SGO 119113); Quebrada de La Chimba, 300–400 m.a.s.l., 2

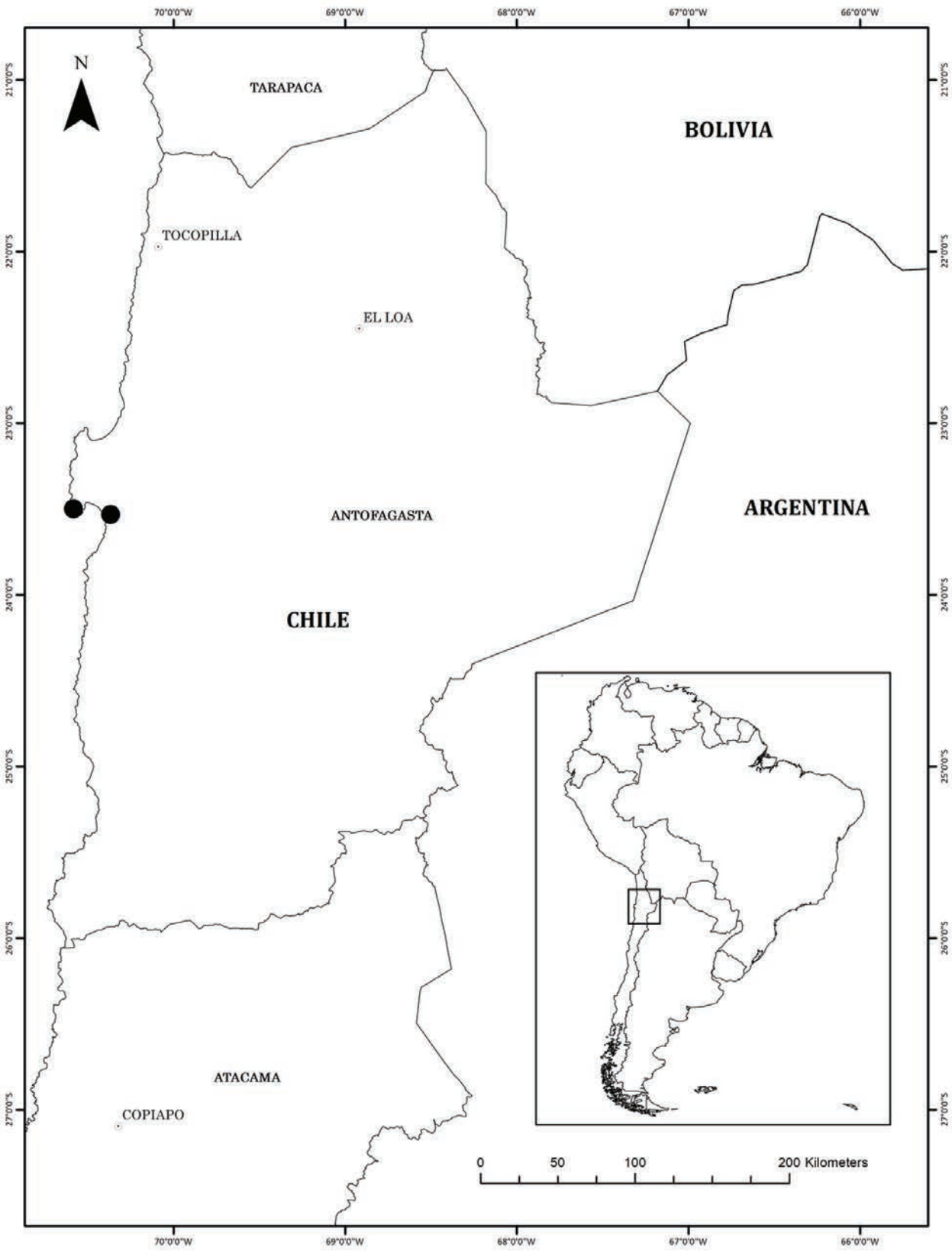


FIGURE 304. Distribution of *Nolana lachimbensis* M.O. Dillon & Luebert.

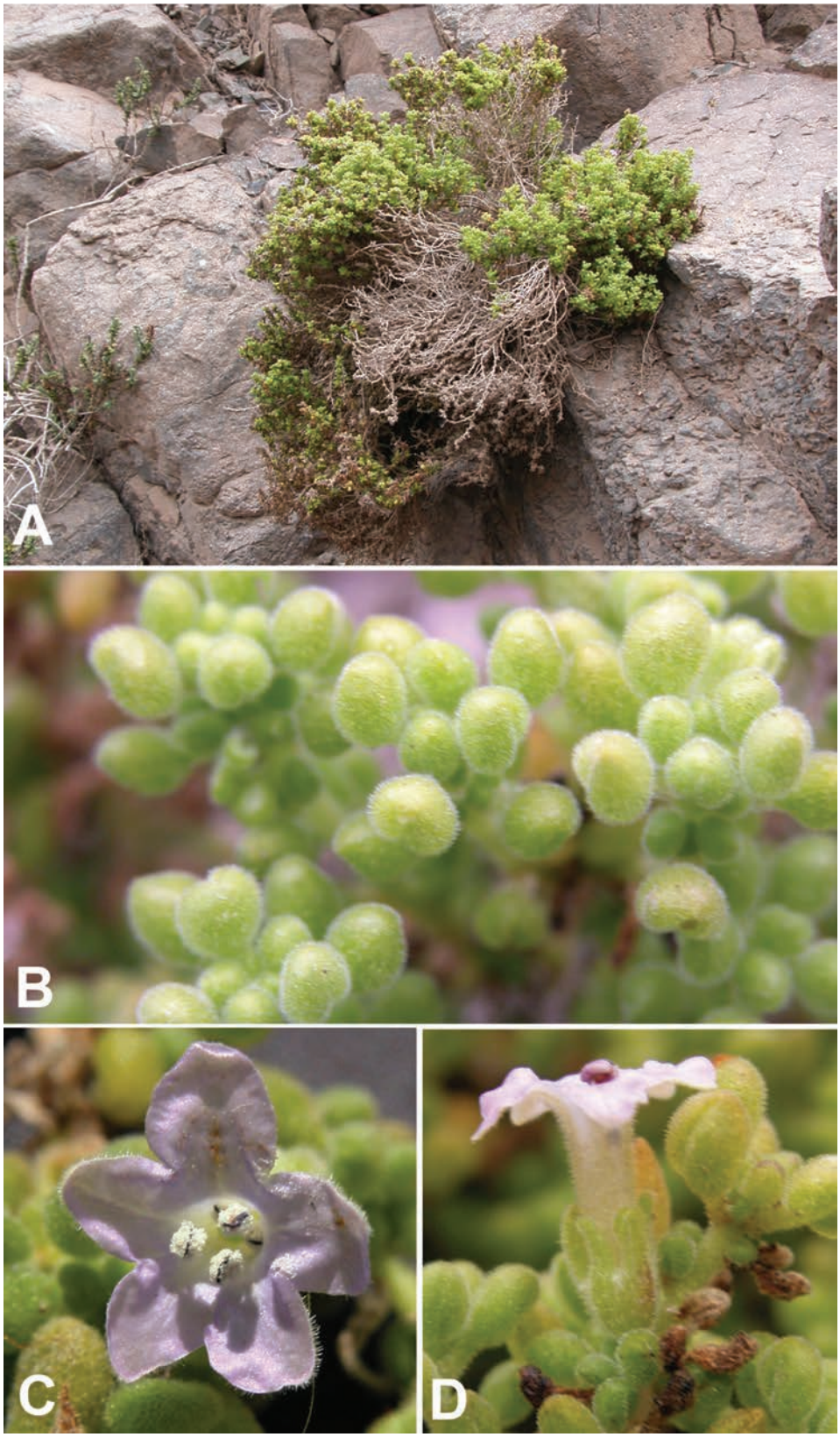


FIGURE 305. *Nolana lachimbensis*. **A**, Habitat, growing in rock cervices and shrubby habit in Quebrada La Chimba, Chile; **B**; Closeup of leaves; **C**, Closeup of corolla showing slightly exserted purple anthers with white pollen; **D**, Closeup lateral view of flower.

FIGURE 306. *Nolana lachimbensis*. **A**, Habitat, growing among rocks on Cerro Moreno, Chile; **B**, Closeup of white corollas.

January 1943, *E. Pisano V. & J. Venurelli E. 1677* (SGO 139175); Quebrada La Chimba, 1 October 1954, *M. Ricardi 3056* (CONC 18289); cumbres del lado sur del Cerro Moreno, 1000 m.a.s.l., 22 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1412* (CONC 36255); Quebrada La Chimba, 23°32'S, 70°25'W, 30 September 1987, *S. Teillier 457* (CONC 138392, SGO 141658).

G11. ***Nolana leptophylla*** (Miers) I.M. Johnst., Contrib. Gray Herb. 112: 73. 1936. Fig. 307–310.

Basionym: *Dolia leptophylla* Miers, London J. Bot. 4: 504. 1845. TYPE: CHILE. Antofagasta: Cobija ["Peru"], Iquiqui et Arica, 1831, *H. Cuming 956* (Lectotype designated here: K [000532197]; Isolectotypes: GH [GH00282330], K [K000532275]).

Digital image: Lectotype of *Dolia leptophylla* from Royal Botanic Gardens, Kew [K000532197]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.k000532197

Homotypic synonym: *Bargemontia leptophylla* (Miers) I.M. Johnst., Contrib. Gray Herb. 85: 159. 1929. *Dolia dubia* (Phil.) W. Brandt, Bot. Jahrb. Syst. 69(2): 188. 1938. *Dolia leptophylla* Miers, London J. Bot. 4: 503. 1845.

Heterotypic synonym: *Velpeaulia alibrexioides* Gaudich., Voy. Bonite pl. 109. 1851–1852. TYPE: CHILE. Antofagasta: Cobija, 1–3 July 1836, *C. Gaudichaud 6* (Lectotype designated by Mesa-M., 1981: P [0065857]; Isolectotypes: F 680792, F 1000374, FI-Webb, GH, P [P00605858, P00605859], US [US 1706284, US00121969]). *Bargemontia alibrexioides* (Gaudich.) I.M.Johnst., Contr. Gray Herb. 85: 159. 1929. *Alona deserticola* Phil., F. Atac. 44. 1860. TYPE: CHILE. Antofagasta: Chaco [3100 m.a.s.l., 25°15'S], February 1854, *R.A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 55077, SGO000004328]; Isolectotypes: SGO [SGO 55079, SGO 55078, SGO000004331, SGO000004330], W [W0074694], F [F neg. 33142]). *Bargemontia deserticola* (Phil.) I.M. Johnst., Contr. Gray Herb. 85: 111. 1929. *Dolia deserticola* (Phil.) W. Brandt, Bot. Jahrb. Syst. 69(2): 190. 1938. *Alona dubia* Phil., Anales Univ. Chile 27: 350. 1865. TYPE: CHILE. Antofagasta: Puquios, *F. Geisse s.n.* (SGO 55079, SGO00004329). *Dolia dubia* (Phil.) W. Brandt, Bot. Jahrb. Syst. 69(2): 188. 1938.

Subshrubs, 30–60 cm; rounded to globose, twigs brittle; stems densely hispidulous with capitate-glandular trichomes. *Leaves* alternate, opposite, or fasciculate, blades linear-oblong, 4–5 mm long, 1–2 mm wide, viscid, green, hispidulous with capitate-glandular trichomes, margins strongly revolute, sessile. *Inflorescences* of solitary flowers, terminal and axillary, rarely appearing weakly cymose; pedicels 8–12 mm long, recurved in fruit, densely hispidulous. *Flowers* 5-merous; calyces ca. 5 mm long, campanulate, hispidulous with capitate-glandular trichomes, 5-dentate, enlarged in fruit, teeth subequal, erect, triangular, ca. 4 mm long, ca. 1.5 mm wide, margins strongly revolute; corollas hypocrateriformis, 10–24 mm long, limb 8–10 mm wide, white to light lavender, villous; stamens unequal; filaments not widened at base, long villous; anther thecae white; nectary disc patelliform; style as long as the shorter filaments, gynobasic; stigma capitate. *Mericarps* 3–4(–5), unequal, oval, 1.5–2.0 mm long; seeds 1–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is derived from the Greek, *leptophyllus*, meaning slender-leaved.

Distribution and Ecology: Chile, Regions of Tarapacá, Antofagasta, and Atacama; (10–) 800–2000(–4200) m.a.s.l. (Fig. 307). It is recorded from rocky soils at elevations of over 1000 m.a.s.l. and often among a few highly xerophytic members of its vegetation community; due to the downslope movement of mericarps from upper elevations, some individuals have been recorded at near sea level (Pinto and Luebert, 2009).

Illustration: Fig. 308. Illustration of *Nolana leptophylla* as *Velpeaulia alibrexioides*, Plate 109. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana leptophylla is a shrubby species (Fig. 309A–B, Fig. 310A) with small, densely hispidulous leaves, calyx lobes with strongly revolute margins (Fig. 310B), and white or pale lavender flowers (Fig. 309B). Seldom does one character serve to distinguish a species, but the distinctly revolute margins of the calyx lobes are one such character. They were drawn in an exaggerated manner in Gaudichaud's illustration (Fig. 308). The maturing gynoecium recurves, or nods, as in other species, and the dense capitate-glandular trichomes are evident on the leaves and calyx (Fig. 310C). The mericarps are shiny and are often reduced to three (Fig. 310D). It has a latitudinal distribution of, perhaps, 500 km, and ranges from sea level to 4000 m.a.s.l. It can be assumed that this species is more typical in the higher elevations and reaches downslope sites via water transport.

Nolana leptophylla is related to other northern Chilean species, and, more specifically, to *N. sphaerophylla*, its sister species in all analyses to date (Tu et al., 2008). Johnston (1936: 74) commented that the type of *N. leptophylla, Cuming 956*, in the Hooker collections at Kew, was labeled by Hooker as from Peru, but, according to a manuscript plant list at the British Museum and one of Cuming's original labels, the specimen belongs to a suite of numbers that Cuming distributed as from 'Cobija, Iquiqui et Arica'. Given the overall distribution of this species, it is most likely that the type came from Cobija.

Johnston also commented that the type of *Velpeaulia alibrexioides*, as exhibited by specimens in Paris, was in all probability *Gaudichaud 6* from Cobija, Chile. This specimen has rigid branching, strongly revolute leaves, and stiff, capitate-glandular trichomes. The type of *N. leptophylla*, having also been collected at Cobija, is a slender plant with much longer, thinner trichomes. Johnston was convinced that the differences between the two collections were their ecological origins. Cuming's plant is very much like the more southerly plants from the interior, along the base of the cordilleras, which Philippi described as *Alona deserticola*.

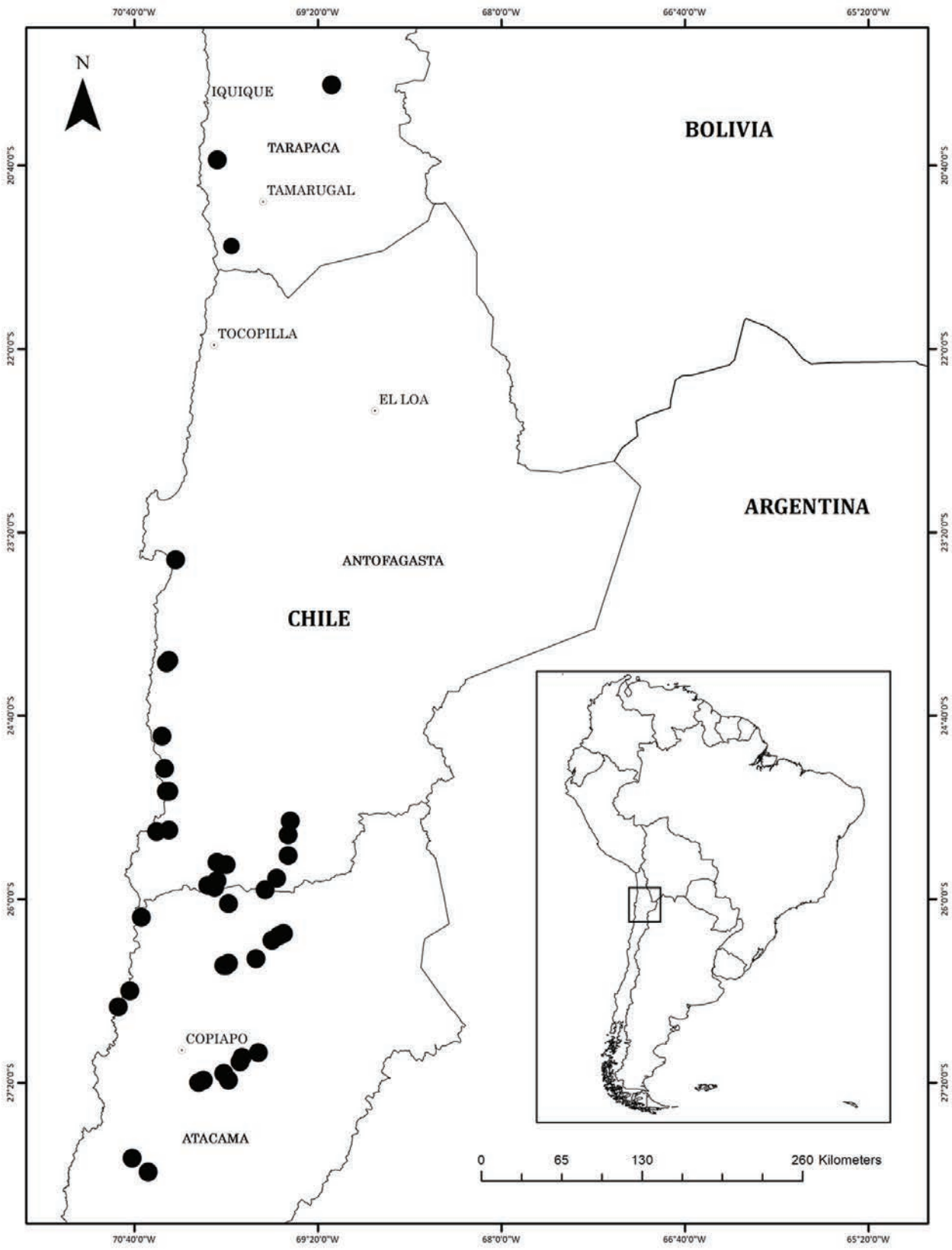


FIGURE 307. Distribution of *Nolana leptophylla* (Miers) I.M. Johnst.

FIGURE 308. Illustration of *Nolana leptophylla* as *Velpeaulia alibrexioides*, Plate 109. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

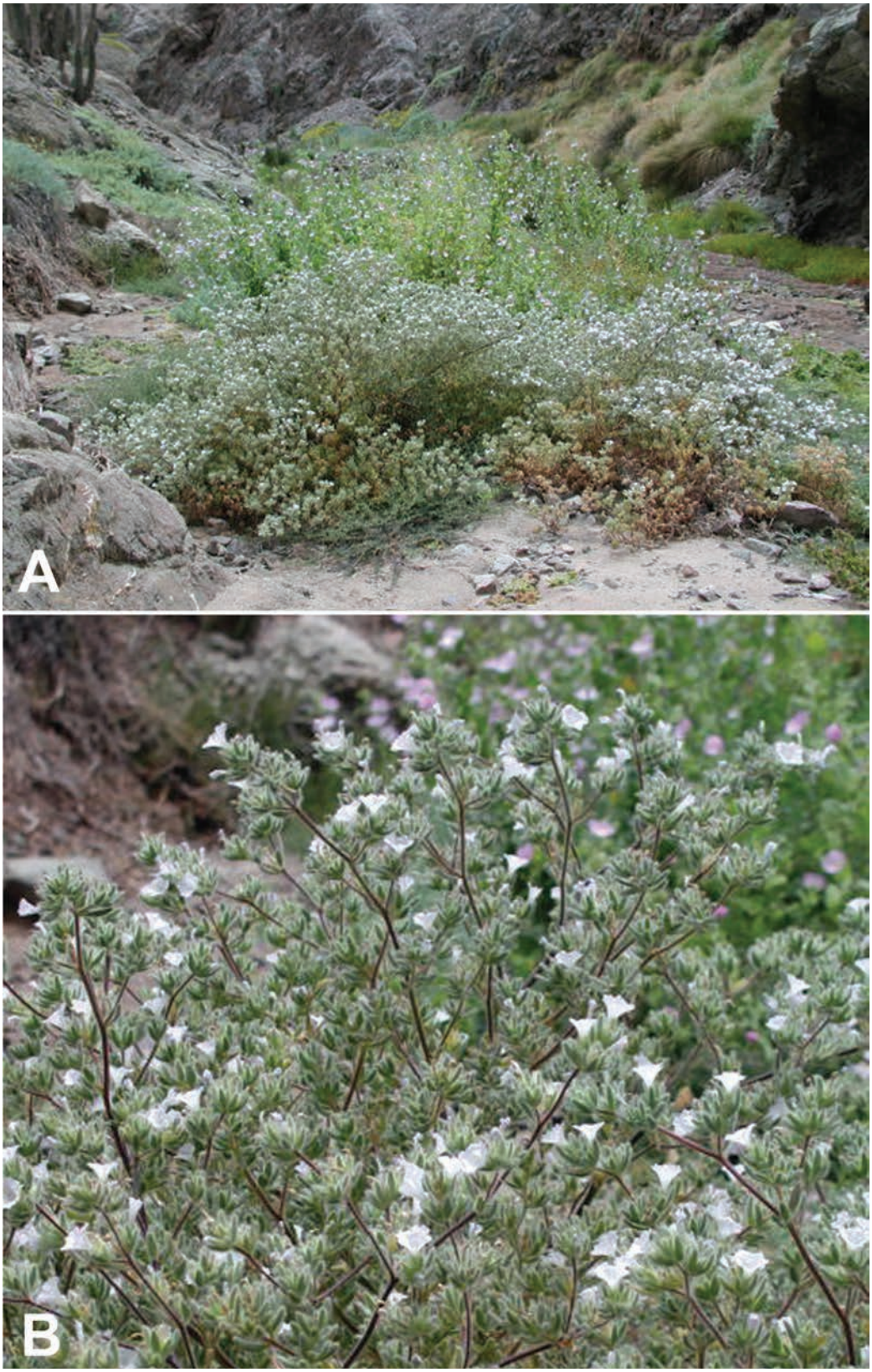


FIGURE 309. *Nolana leptophylla*. **A**, Spreading perennials in mouth of quebrada near sea level; **B**, Flowering branches dark purple, flowers white.

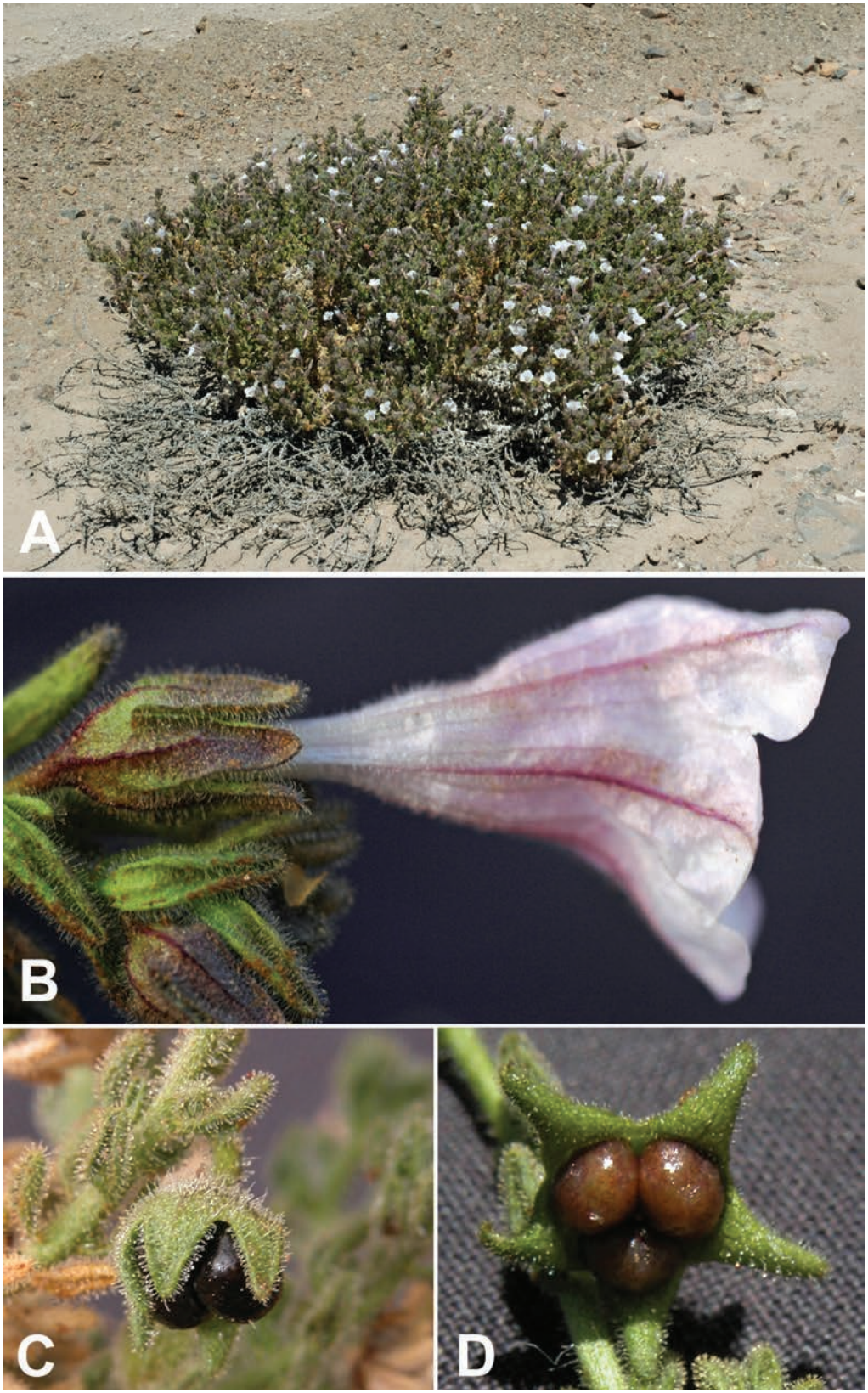


FIGURE 310. *Nolana leptophylla*. **A**, Smaller habits in more arid habitats, note old stems at outer edge; **B**, Small, densely hispidulous leaves, strongly revolute margins of the calyx lobes and white or pale lavender flowers; **C**, maturing gynoecium recurves, dense capitate-glandular trichomes; **D**, Mericarps reduced to three.

Johnston (1936, p, 75) suggested that *Nolana leptophylla* was most closely related to *N. villosa*, and further commented that both were plants inhabiting the arid crests above the fog-bathed fertile slopes of the coastal hills, as well as the desert interior. Except for the collections recorded from near Cobija, which he surmised had come from the arid crests of the coastal hills at 1000 m.a.s.l. or more, *N. leptophylla* was only known from the very arid interior, 75–125 km from the coast and at higher elevations (1500–3000 m.a.s.l.).

There is a suite of specimens that have intermediate morphology between *N. leptophylla* and *N. villosa*. They are all from higher elevation localities east of Copiapó on the road to Tingogasta (Puquios): *F. Behn s.n.* (CONC 28569), *U. Eggli & B. E. Leuenberger 2607*, *T. Lammers et al. 7624*, *M. Ricardi et al. 1111*, *M. Ricardi 3675*, *C. Marticorena et al. 492*, *C. Villagrán & M. Kalin-Arroyo 4501*, and *C. Marticorena et al. 9816*. These specimens are here assigned to *N. leptophylla*. For a discussion of other potential members of this complex, see the discussion under *N. villosa*.

Additional specimens examined: CHILE. **Tarapacá**: Prov. Iquique, Mamiña, 2700 m.a.s.l., *H. Larraín 97-668* (CONC 143387); Alto Chipana, 21°16'S, 70°03'W, 24 October 2001, *R. Pinto 705* (SGO). **Antofagasta**: Taltal, 25°27'50"S, 70°26'42"W, 360 m.a.s.l., 24 October 2002, *M. Ackermann 461* (CONC 157506, SGO 150945); Antofagasta, camino al E de Morro Blanco, 2380 m.a.s.l., *G. Arancio 92-623* (CONC 122261); Quebrada Ciclón, 1380 m.a.s.l., *G. Arancio & F. Squeo 10033* (CONC 140578); Llano de la Pampa de Barreal Seco, 1130 m.a.s.l., *G. Arancio & F. Squeo 10025* (CONC 140327), *G. Arancio & F. Squeo 10028* (CONC 140426); entrada al cerrito Mateo, 1050 m.a.s.l., G. *Arancio & F. Squeo 10029* (CONC 140325); Camino de La Brea a La Pólvora, 1900 m.a.s.l., G. *Arancio & F. Squeo 10041* (CONC 140329), 2200 m.a.s.l., *10047* (CONC 140328); Quebrada Juncal, 2250 m.a.s.l., G. *Arancio & F. Squeo 10069* (CONC 140323); Nuevo Juncal, 2650 m.a.s.l., G. *Arancio & F. Squeo 10158* (CONC 140332); al S de Agua Verde, 1380 m.a.s.l., *G. Arancio & F. Squeo 10381* (CONC 140324); road from Antofagasta to Caleta El Cobre, 24°17'33"S, 70°26'45"W, 1196 m.a.s.l., 20 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 6* (E00230526); Cobija, Quebrada Aguada Cañas, 500–800 m.a.s.l., 16 October 1949, *W. Biese 2782* (SGO 97237); Cobija, Aguada Cañas, 500–800 m.a.s.l., 4 December 1949, *W. Biese 3073* (SGO 96678); Antofagasta, 30 km al Oeste de Caleta Blanco Encalada, 1200 m.a.s.l., 11 December 1949, *W. Biese 3724* (SGO 096720); Quebrada Paposo, ca. 12 km E of Caleta Paposo, 25°01'S, 70°25'W, 910 m.a.s.l., 7 December 1987, *M. O. Dillon & S. Teillier 5136A* (F 2330860); Quebrada Bandurrias, 15 km S of Punta Grande, 25°13'S, 70°25'W, ca. 20 m.a.s.l., 10 December 1987, *M. O. Dillon & S. Teillier 5218* (CONC, F 2011178, GH); ca. 28 km E (by road) of Caleta El Cobre, just below the mirador, 24°16'S, 74°25'W, 1550–1570 m.a.s.l., *M. O. Dillon & D. Dillon 5621* (CONC, E, F 2013669, GH, SGO, US); Upper, eastern end of Quebrada Médano, ca. 22 km N of Paposo, ca. 15 km ENE of coast, 24°49'S, 70°28'W, 1000 m.a.s.l., 23 October 1988, *M. O. Dillon & D. Dillon 5730* (F 2045819); mouth of Quebrada Bandurrias, 25°13'S, 70°26'W, 20 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8045* (CONC 150026, E, F 2183330, GH, K, SGO 143708, US); entrance to La Brea, Km 8 Puente, 25°29'56"S, 70°25'14"W, 10 October 2005, *M. O. Dillon & M. Finger C. 8709* (F 2294686, GH, SGO); above Caleta El Cobre, 24°19'13"S, 70°27'23"W, 980 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9069* (F 2292855, SGO 158726); 40 km SW of the Panamericana towards El Cobre, 20 km NE of El Cobre, 24°17'31"S, 70°26'32"W, 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2844* (B, CONC 138514, SGO 146072); Chañaral, vicinity of Potrerillos, Quebrada de Pasto Cerrado on banks about salt vega just above Encanche, 2100 m.a.s.l., 22 October 1925, *I. M. Johnston 3663* (GH, K, US 1473956); Prov. Estación Agua Verde, *C. Latorre, C. Villagrán, & A. Maldonado 242* (CONC 150767); Trayecto Agua Verde–Chañaral, *C. Latorre, C. Villagrán, & A. Maldonado 243a* (CONC 150768), *248* (CONC 150765); camino entre Ruta 5 y Caleta El Cobre, 24°16'S, 70°26'W, 1530 m.a.s.l., 4 October 2005, *F. Luebert & N. García 2611/1005* (SGO 159465); Quebrada entre Punta Cañas y Punta Médano, 24°52'46"S, 70°30'58"W, 50–100 m.a.s.l., 23 October 2009, *F. Luebert & A. Moreira M. 3002* (SGO 158984); Quebrada Cascabeles, al norte de Taltal, 10 m.a.s.l., 16 September 1941, *C. Muñoz P. & G. T. Johnson 2848* (SGO 118311); Aguas Verdes, 15 April 1993, *H. Niemeyer F. & C. Fernández H2* (SGO 140696); camino entre Varillas y Caleta El Cobre, quebrada frente al Cerro Santa Rita, 1250 m.a.s.l., *M. Quezada & E. Ruiz 135* (CONC 121783); Caleta El Cobre, 24°17'45"S, 70°26'51"W, 1170 m.a.s.l., 10 January 2011, *M. Rosas 7191* [*INIA-1099*] (K); Quebrada Bandurrias, 40 m.a.s.l., 5 November 1985, *F. Schlegel 7877-1* (SGO 105235); Tocopilla, Cerro Mamilla, 22°00'S, 70°10'W, 29 September 1987, *S. Teillier 438* (CONC 138374, SGO 141656); Taltal, Paposo, Quebrada Guanillos, 25°03'S, 70°30'W, 1040 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2746* (F 2114623); Taltal, Quebrada de Taltal, Km 9.96, 25°26'S, 70°35'W, 400 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García 2637* (F 2114626, SGO); Taltal, Quebrada de Taltal, 25°26'S, 70°35'W, 570 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García 2669* (F 2114625); Taltal, Quebrada Guanillos, 25°03'S, 70°30'W, 1040 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2751* (SGO 129380); Taltal, Quebrada de Taltal, 25°26'S, 70°35'W, 410 m.a.s.l., 17 September 1992, *S. Teillier, P. Rundel, & P. García 2839* (F 2114628); Quebrada de Taltal, 2 km E, 25°26'S, 70°35'W, 130 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2867* (SGO 129378); Quebrada Matancilla, 25°26'S, 70°35'W, 185 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2930* (SGO 129376); Taltal, Quebrada Yumbes, 1300 m.a.s.l., 17–18 October 1994, *J. C. Torres M. s.n.* (SGO 133969). **Atacama**: Prov. Chañaral. 16 km al S de Diego de Almagro, *G. Arancio & F. Squeo 10009* (CONC 140543); Quebrada Carrizalillo, *G. Arancio & F. Squeo*

10016 (CONC 140555), *10017* (CONC 140330); Pueblo Hundido, *M. Barros 7091* (CONC 14074); Quebrada de San Andrés, 30 December 1971, *K. Beckett, M. Cheese, & J. Watson 4737* (SGO 110285), *4741* (SGO 110289); Quebrada de San Andrés, *F. Behn s.n.* (CONC 28569); Hacienda Castilla, 27°53'S, 70°41'W, 300–400 m.a.s.l., *F. Behn s.n.* (CONC 30808); Quebrada Garín, 30 km al E de Chulo, 2000 m.a.s.l., 13 October 1949, *W. Biese 2634* (SGO 96553); Quebrada Puquios–Garín, 800 m.a.s.l., 13 October 1949, *W. Biese 2655* (SGO 96574) Quebrada Paipote, 13 October 1949, *W. Biese 2659* (SGO 96579); Quebrada Paipote, 13 October 1949, *W. Biese 2660* (SGO 96579); Totoralillo, falda Este del Valle Copiapó, 700–800 m.a.s.l., 13 October 1949, *W. Biese 2674* (SGO 96593); Quebrada Cerillos, 15 km al E de Estación Checo, 700–900 m.a.s.l., 14 October 1949, *W. Biese 2755* (SGO 97216); 21 km W of Pan-American Highway (5) on Northern route to Parque Nacional Pan de Azúcar; ca. 100 km S of Taltal, 26°08'S, 70°37'W, 85 m.a.s.l., *M. O. Dillon, D. Dillon, & V. Poblete 5607* (F 2012855, SGO); 42 km E of Diego de Almagro, 21 km E of Llanta, 26°24'S, 69°37'W, 1740 m.a.s.l., 4 November 2004, *M. O. Dillon & M. Finger C. 8642* (CONC 179081, E, F 2329901, G, GH, SGO 158711, US); 4 km below Mina Potrerillos, 120 km from coast, 26°24'37"S, 69°30'35"W, 2460 m.a.s.l., 2 December 2004, *M. O. Dillon & M. Finger C. 8644A* (SGO 158921); 4 km below Mina Potrerillos, 120 km from coast, 26°24'37"S, 69°30'35"W, 2460 m.a.s.l., 2 December 2004, *M. O. Dillon & M. Finger C. 8644B* (CONC 179088, F 2292792, F 2292832, SGO 158708); 53 km NE of Copiapó on Camino Internacional, 2.2 km NE of Puquios, 1270 m.a.s.l., 30 October 1990, *T. G. Lammers, C. M. Baeza P., & P. Peñailillo B. 7624* (CONC 113402, F 2075561); Copiapó, 70 km E of Copiapó towards Paso de San Francisco, Quebrada de Paipote, 27°07'S, 69°46'W, 1500 m.a.s.l., 10 December 1994, *U. Eggli & B. E. Leuenberger 2607* (B, CONC 132060, SGO 145813); Puquios, 27°09'36"S, 69°53'11"W, 1290 m.a.s.l., 18 September 2005, *F. Luebert & N. García 2502/896* (F 2290726); Quebrada de Paipote, Puquios, 1250 m.a.s.l., *C. Marticorena, O. Matthei, & M. Quezada 492* (CONC 38723); Camino Internacional de Copiapó a Tingogasta, entre Quebrada Cruz de Caña and Quebrada El Sauce, 1200 m.a.s.l., *C. Marticorena, T. Stuessy, & C. M. Baeza P. 9816* (CONC 136231); camino El Salvador a Chañaral, Km 6, 2200 m.a.s.l., *C. Marticorena, T. Stuessy, & C. M. Baeza P. 9881* (CONC 136251); Quebrada de La Cortadera, Potrerillos, 2100 m.a.s.l., 22 January 1944, *C. Muñoz P. 3934* (SGO 119668); al Norte de Inca de Oro, 28 October 1987, *M. Muñoz S. & I. Meza P. 2319* (SGO 137716); 4 km N del cruce a Negro Francisco por Camino a Inca de Oro, 27°19'S, 70°10'W, 860 m.a.s.l., 29 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2719* (SGO 126131); Quebrada Chañarcito 18 km al Sur de Diego de Almagro, 26°28'S, 69°59'W, 29 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2747* (SGO 126130); Bajando de Potrerillos, en Estación Encanche, 26°24'S, 69°32'W, 2030 m.a.s.l., 30 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2776* (SGO 126132); Quebrada de las Pinturas, 1300 m.a.s.l., 3 July 1987, *H. Niemeyer F. s.n.* (SGO 128296); Chañaral, Inca de Oro, 19 November 1941, 1560 m.a.s.l., *E. Pisano V. & R. Bravo F. 722* (SGO 156552); Canal relave El Salvador, 1622 m.a.s.l., *M. Reyes & L. Letelier 1330* (CONC 168439); Puquios, *M. Ricardi 3675* (CONC 23819); Camino al Salar de Maricunga, cerca de Puquios, *M. Ricardi, C. Marticorena, & O. Matthei 513* (CONC 36256); 10 km al sur de Pueblo Hundido, *M. Ricardi & C. Marticorena 4611/996* (CONC 25401); camino Pueblo Hundido a El Salvador, Cuesta de Llanta, 1250 m.a.s.l., *M. Ricardi, E. Weldt, & M. Quezada 415* (CONC 43010); camino Internacional a Tingogasta, Puquios, *M. Ricardi, C. Marticorena, & O. Matthei 1111* (CONC 30070); camino de Pueblo Hundido a El Salvador, 19 km al interior de Llanta, 2100 m.a.s.l., 13 February 1966, *M. Ricardi, C. Marticorena, & O. Matthei 1565* (CONC 31656, F 2048620); camino a Diego de Almagro, 2775 m.a.s.l., *F. Squeo & Letelier 1236* (CONC 168515); Huasco, Carretera Panamericana, frente a Punta de Díaz, *R. Rodríguez & P. Rivera 56* (CONC 34931); Quebrada de Puquios, 1 February 1997, *S. Teillier 4132* (CONC 143272, SGO 154077); Camino Internacional de Copiapó a Tinogasta, *C. Villagrán & M. Kalin-Arroyo 4501* (CONC 71378); Cord. Maricanga, October 1924, 1800 m.a.s.l., *E. Werdermann 454* (CONC 56030, E00130941, F 565276, US 1444749); Mineral El Salvador, Cerro de la Cruz, 4200 m.a.s.l., *O. Zöllner 890* (CONC 129671). Entre San Andrés y Copiapó, *O. Zöllner 10104* (CONC 129670).

G12. ***Nolana linearifolia*** Phil., Anal. Univ. Chile 91: 28. 1895. TYPE: CHILE. Atacama: "Desierto Atacama" [Sierra Esmeralda], 1884–1885, *F. J. San Román s.n.* (Lectotype designated by Mesa-M., 1981: SGO [055139, SGO000004375]; Isolectotypes: GH [GH00282337], S). Fig. 311–312.

Digital image: Lectotype of *Nolana linearifolia* from Museo Nacional de Historia Natural, Santiago [SGO 055139]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004375

Homotypic synonym: *Bargemontia linearifolia* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 109. 1929.

Heterotypic synonyms: *Nolana decemloba* Herzog, Meded. Rijks-Herb. 29: 20. 1916. TYPE: CHILE. Antofagasta: Antofagasta, *C. T. J. Herzog 2319* (Holotype: L, not seen; Isotypes: S [S04 2770]; W, not seen, F neg. 33147 ex W). *Bargemontia deflexa* I.M. Johnst., Contrib. Gray Herb. 85: 110. 1929. TYPE: CHILE. Atacama: Dept. Chañaral, Carrizalillo, 1921, ca. 50 km NE of Chañaral, *J. E. Harding 2* (Holotype: GH [00282355]); *Nolana deflexa* (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb. 112: 71. 1936.

Decumbent annual or perennial *herbs*, often flowering in the first year, forming mats to ca. 2 m in diam.; stems procumbent or decumbent, densely puberulent with glandular-capitate trichomes, to ca. 50 cm long, becoming lignified with age. *Leaves* alternate to fasciculate, blades linear, 10–30(–40) mm long, 1–2 mm wide, with a slight abaxial depression, erect, densely puberulent with capitate-glandular trichomes, margins revolute or not, with

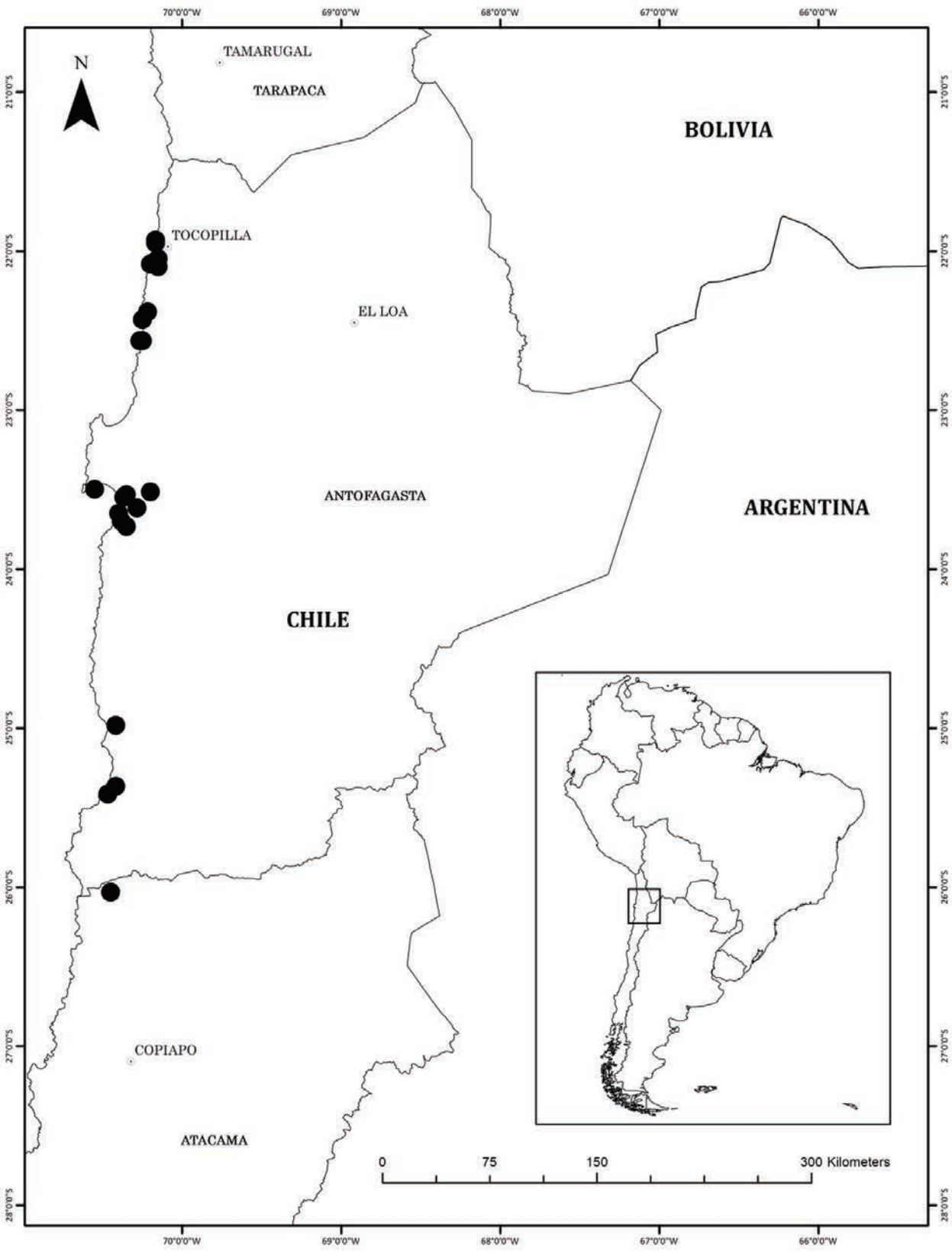


FIGURE 311. Distribution of *Nolana linearifolia* Phil.

callous edges, white salt glands abundant, epetiolate, base slightly restricted and possessing an abaxial, stramineous, thickened or swollen protuberance where it joins the stem. *Inflorescences* of solitary flowers in leaf axils; pedicels (3–)8–15 mm long, densely puberulent with glandular-capitate trichomes, pendent and deflexing in fruit. *Flowers* 5-merous; calyces campanulate, 12–18 mm long, 2–3(–5) mm wide, throat 3–5 mm long, lobes linear-acuminate, unequal, (6–)8–12 mm long, 1.0–2.5 mm wide at base, densely glandular-pubescent externally and internally, succulent, spreading in fruit, apically rounded to obtuse; corollas infundibularis, 12–24(–30) mm long, throat 40–50 mm wide at mouth; plicate, deeply lobed, appearing as 10-lobed, dark lavender to purple or mauvette, a green costa between the calyx lobes, coiling upon drying; anthers unequal, 2 longer and 3 shorter; filaments purple, 4–5 mm long, bases densely villous, anther thecae blue to lavender; nectary disc patelliform, raised 2–3 mm on stalk, alveolate; style as long as the shorter filaments, gynobasic. *Mericarps* (3–)5(–8), spherical, unequal, 2–3(–4) mm in diam., black, attached basally; seeds (1–)4–5 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *linearifolius*, linear-leaved, and refers to the characteristic leaves of this species.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; (30–)100–600(–1040) m.a.s.l. (Fig. 311). It is recorded from dry crests and quebradas in the coastal hills.

Nolana linearifolia is a distinctive spreading annual (Fig. 312A) with terete, linear leaves and showy corollas with deeply cut lobes, making them appear to have ten lobes (Fig. 312B–C). The calyx lobes are unequal (Fig. 312D) and densely puberulent with short, stout capitate-glandular trichomes. This species has been confused with *N. stenophylla*, a species with linear leaves of similar shape and length, but that species has pilose pubescence with elongated, capitate-glandular trichomes and, uniformly, three large mericarps. When collections are dried, the two species look very much alike and are easily confused. In the living condition, these two species are very distinct and could never be confused in the field. The flower colors recorded for *N. linearifolia* range from blue to mauvette, a pale purple that is redder and paler than average lavender; however, the throats are uniform and don't have the distinctive white coloration. In a publication on the flora of Pan de Azúcar (Rundel et al., 1996), *Nolana stenophylla* was listed among the 17 species recorded from that area. After re-examination of the vouchers in that study, it was determined that the collections designated as *N. stenophylla* are collections of *N. linearifolia*.

The type of Philippi's species was collected by San Román in the Sierra Esmeralda (25°56'S, 70°27'W). Apparently, there is a conspecific plant which grows well above the fertile belt on the extremely arid crests at about the upper limit of vegetation on the ridge above Aguada Panulcito (*Johnston 5461*). This plant differs from Philippi's type only in its more abundant glandular pubescence on the stems and leaves and the smaller corollas. The blue corolla is variable in size, ranging from 12–24 mm in length, and has deeply notched lobes. *Nolana linearifolia* also occurs around Antofagasta, and Johnston related it to *N. mollis*, *N. patula* and *N. tarapacana*, but its deeply notched corolla lobes readily distinguish it from those species. It is notable that two species were collected by A. A. Beetle from the same geographic area, *N. linearifolia* (*#26180*) and another *N. inconspicua* (*#26184*) from a nearby the locality.

Nolana deflexa is reduced to synonymy with *N. linearifolia*, after examining many collections and comparing it to the fragmentary collection made at Carrizalillo by J. E. Harding from an interior locality some 50 km northeast of Chañaral and directly east of Caleta de Pan de Azúcar. It is characterized by very slender leaves, slender attenuate calyx lobes, and conspicuously deflexed fruiting pedicels, a character shared by many *Nolana* species, including *N. linearifolia*. Furthermore, the type locality of *N. linearifolia*, Sierra Esmeralda, and that of *N. deflexa*, Carrizalillo, are separated by no more than 20 km. A series of collections were determined as *N. deflexa* in SGO; however, these collections have characters suggesting they are best treated as *N. clivicola*, and the following were moved to that species: *M. R. Espinosa s.n.*, SGO 139536, SGO 139544, and SGO 143276).

Additional specimens examined: CHILE. **Antofagasta**: Cordillera Costa, quebrada paralela a la Costa, 8 km al interior, frente a Caleta Coloso, *J. Anabalón s.n.* (SGO 126926), *s.n.* (SGO 126925), s.n. (SGO 126927); Quebrada La Chimba, 23°32'01"S, 70°21'02"W, 541 m.a.s.l., 19 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 1* (E00230522); 4 km S of Botija, 24°32'13"S, 70°34'17"W, 83 m.a.s.l., 20 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 13* (E00420135); 8 km SE of Antofagasta, 50 m.a.s.l., 27 February 1939, *A. A. Beetle 26180* (GH, K); Tocopilla, *O. Berninger 441* (GH); Quebrada Blanco Encalada, *W. Biese 3129* (SGO 696734); Taltal–Paposo, Quebrada Bandurrias, 17 January 1991, *A. Brinck s.n.* (SGO 122833); Quebrada de La Chimba, ca. 10 km NNE of Antofagasta, 23°33'S, 70°22'W, 300–350 m.a.s.l., 17 December 1987, *M. O. Dillon & S. Teillier 5340* (F 2010917); Quebrada Botija, ca. 11 km N of Miguel Díaz, 24°31'S, 70°33'W, 18 December 1987 *M. O. Dillon 5356* (F 2010903); Quebrada Paposo, 350–950 m.a.s.l., 28 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5552* (CONC, E, F 2010229, GH); Quebrada above Playa de los Hornos, just N of Punta Hornos, 26 km S of Caleta Michilla, 51 km N of Tropic of Capricorn, 22°55'S, 70°15'W, 300–350 m.a.s.l., 20 October 1988, *M. O. Dillon & D. Dillon 5727* (CONC, E, F 2045829, GH, K, NY, SGO, US); Quebrada La Negra, between Antofagasta and La Negra, 23°42'S, 70°23'W, 190 m.a.s.l., 12 November 1988, *M. O. Dillon & D. Dillon 5890* (CONC, E, F 2144388, GH, SGO, US); Quebrada Taltal, ca. 1.5 km E of Taltal, 25°25'S, 70°28'W, 90 m.a.s.l., 26 November 1997, *M. O. Dillon 8099* (CONC 149983, E, F 2182967, GH, K, SGO 143697); Quebrada Paposo, E of Caleta Paposo, 24°59'S, 70°25'W, 980 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo*

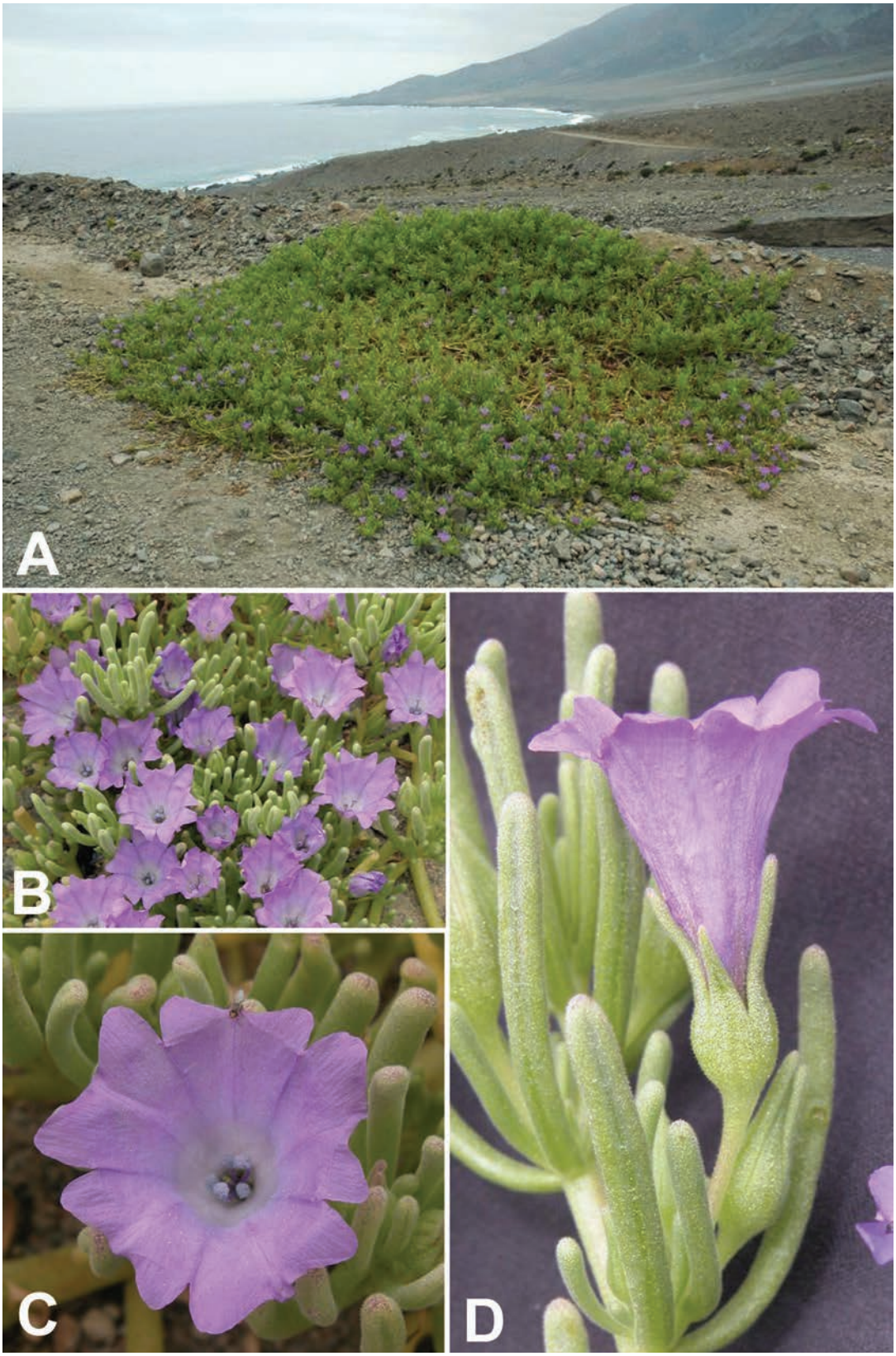


FIGURE 312. *Nolana linearifolia*. **A**, Spreading annuals in near-ocean habitats; **B**, Linear, erect leaves, and corollas; **C**, Each lobe is retuse to emarginate making it appear as ten lobes; **D**, Lateral view of flower with unequal calyx lobes.

C. 8035 (CONC 149994, E, F 2183335, GH, K, SGO 143696, US); Quebrada La Chimba, NE of Antofagasta, 23°33'S, 70°22'W, 380–480 m.a.s.l., 11 November 1988, *M. O. Dillon & D. Dillon 5879* (F 2144385); Quebrada de La Chimba, 23°32'16"S, 70°21'33"W, 500 m.a.s.l., 21 October 2004, *M. O. Dillon & M. Finger C. 8592* (F 2292816, SGO 158701); 15 km N of Paposo ThermoElectric plant, 24°52'58"S, 70°31'09"W, 90 m.a.s.l., 1 November 2004, *M. O. Dillon & M. Finger C. 8629* (F 2292827, SGO 158719); S of Antofagasta, Cerro Coloso–Cerro Jarón area, Quebrada del Buey, 3 km W of the coast on mining road towards Pozo Lombriz, 23°46'46"S, 70°27'25"W, 180 m.a.s.l., 17 February 1977, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2690* (B, CONC 138428, SGO 145885); 16 km N of Tocopilla on Ruta 1, 21°58'S, 70°10'W, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2840* (B, CONC 138510, SGO 146042); 56 km SW of Panamericana towards El Cobre, 4 km NE of El Cobre, 24°16'03"S, 70°31'05"W, 350 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2853* (B, CONC 138482, SGO 146066); Tocopilla, Cerro Rosario, *M. R. Espinosa s.n.* (SGO 143258); Quebrada de Los Barriles, *M. R. Espinosa s.n.* (SGO 143274, SGO 143275); Quebrada Mamilla, about 5 km N of Tocopilla, 22°00'32"S, 70°11'11"W, 12 November 1995, *K. Gengler 85* (SGO 137345); Antofagasta, 29 October 1930, *F. Jaffuel 1128* (GH); Antofagasta, 6 November 1931, *F. Jaffuel 2625a* (GH); Antofagasta, SE of La Chimba, 19 October 1925, *I. M. Johnston 3637* (GH); Aguada Panulcito, ca. 24°49'S, 5 December 1925, *I. M. Johnston 5461* (GH); Antofagasta, 6 November 1931, *F. Jaffuel 2626* (GH); Tocopilla, III Quebrada, 22°03'12"S, 70°10'22"W, 1748 m.a.s.l., 29 September 2005, *F. Luebert, N. García, & N. Schulz 2562/956* (F 2290728); camino bajando a Caleta El Cobre, 24°15'43"S, 70°31'00"W, 315 m.a.s.l., 4 October 2005, *F. Luebert & N. García 2616/1010* (F 2290710); Quebrada Matancilla, 25°06'45"S, 70°27'29"W, 170–400 m.a.s.l., 8 October 2005, *F. Luebert & N. García 2720/1114* (F 2290713); Quebrada Chapacase, 22°01'20"S, 70°10'28"W, 400–500 m.a.s.l., 22 October 2009, *F. Luebert & A. Moreira M. 2988* (SGO 158970); 18 km al norte Tocopilla por la Ruta 1, 21°56'S, 70°10'W, 100 m.a.s.l., 26, September 1996, *O. Matthei 471* (CONC 137075, SGO 152886); 18 km al norte de Tocopilla por la Ruta 1, 21°56'S, 70°10'W, 400 m.a.s.l., 26 September 1996, *O. Matthei 473* (CONC 137077, SGO 152806); camino de Tocopilla a Maria Elena, a 2 km de Tocopilla, 22°05'S, 70°10'W, 425 m.a.s.l., 26 September 1996, *O. Matthei 478* (CONC 137082, MA, SGO 152808); camino de Tocopilla a Antofagasta, Caleta Buena, 22°26'S, 70°15'W, 30 m.a.s.l., 27 September 1996, *O. Matthei 491* (CONC 137095, SGO 152805); Salida sur de Antofagasta, a 27 km de la ciudad, 23°44'S, 70°21'W, 340 m.a.s.l., 29 September 1996, *O. Matthei 522* (CONC 152823, SGO 152823); Ruta 5, entrada nueva a Taltal, 25°34'05"S, 70°21'42"W, 815 m.a.s.l., 29 September 2005, *M. Muñoz S. 4582* (SGO 153609); between Tocopilla and Antofagasta, 400 m.a.s.l., *M. Ono & T. Masuzawa s.n.* (MAK 274961); N of Antofagasta, *M. Ono & T. Masuzawa s.n.* (MAK 274952); N. of Antofagasta, *M. Ono & T. Masuzawa s.n.* (MAK 274956); Antofagasta, 23°39'S, 100–200 m.a.s.l., *F. W. Pennell 13021* (F 557496, GH); Antofagasta, 100–200 m.a.s.l., 3 April 1925, *F. W. Pennell 13027* (F 557500, GH, US 1343023); Tocopilla, Camino a Mina Mantos de La Luna, 22°23'S, 70°13'W, *M. Quezada & E. Ruiz 19* (CONC 121076; SGO 127878); Antofagasta–Calama, 23°37'S, 70°17'W, 501–600 m.a.s.l., *M. Ricardi 5505* (CONC 36172); Cuesta Barriles, *M. Ricardi 1075* (CONC 43020); Quebrada W de Las Bombas, 26°02'S, 70°27'W, 501–600 m.a.s.l., *M. Ricardi 5539* (CONC 56171); Quebrada Chacaya, 22°59'S, 70°20'W, *M. Ricardi 5517* (CONC 36173); Quebrada La Chimba, 23°32'S, 70°21'W, 11 November 1996, *R. Rodríguez 3089* (CONC 136609, SGO 151594); Antofagasta, Quebrada La Negra, 23°38'S, 70°24'W, 200 m.a.s.l., *S. Teillier 3411* (SGO 140916); Cuesta Barriles, camino Calama–Tocopilla, *S. Teillier 4791* (CONC 150941); Quebrada La Chimba, *E. Pisano V. & J. Venturelli E. 1671* (SGO 118043); Quebrada Guanillos, 25°03'S, 70°30'W, 1040 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2748* (SGO 129369); Quebrada de Taltal, 25°26'S, 70°35'W, 410 m.a.s.l., 17 September 1992, *S. Teillier, P. Rundel & P. García 2847* (F 2114614); Quebrada de Taltal, 2 km E, 25°26'S, 70°35'W, 130 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2886* (F 2114613, SGO 129368); Tocopilla, quebrada que va camino a Chuquicamata, *M. A. Trivelli s.n.* (SGO 144327); 10 km E of Antofagasta, ca. 200 m.a.s.l., 17 November 1935, *J. West 3860* (GH). **Atacama**: Prov. Chañaral, 21 km W of Pan Americana Hwy on northern route to Parque Nacional Pan de Azúcar, 26°08'S, 70°37'W, ca. 85 m.a.s.l., 30 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5603* (F 2012859, GH, US).

G13. ***Nolana mollis*** (Phil.) I.M. Johnst., Contrib. Gray Herb. 112: 61. 1936. Fig. 313–316.

Basionym: *Alona mollis* Phil., Fl Atac. 44 and Viage Des. Atac. 16, 24, 38, 218. 1860. TYPE: CHILE. Atacama: Cachinal de la Costa, *R. A. Philippi s.n.* (Holotype: SGO [55184]).

Digital image: Holotype of *Alona mollis* from Museo Nacional de Historia Natural, Santiago [SGO 55184]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004339

Homotypic synonyms: *Bargemontia mollis* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 109. 1929; *Nolana leptophylla* (Miers) subsp. *mollis* (Phil.) Mesa-M., Fl. Neotrop. Monogr. 26: 116. 1981.

Heterotypic synonym: *Dolia macrocalyx* Phil., Anal. Univ. Chile 91: 45. 1895. TYPE: CHILE. Antofagasta: Taltal, 1887, *A. Borchers s.n.* (Holotype: SGO [SGO 55171]). [fide Johnston, 1936: 66] Herzog, Meded. Rijks-Herb. 29: 22. 1916.

Shrubs, erect to decumbent, 1.0–1.5 m tall, 1–2 m in diam., densely branched, densely leafy. *Leaves* alternate, or appearing decussate, blades oblong to lance-oblong, 5–10 mm long, ca. 5 mm wide, curved, succulent, densely pubescent with long, capitate-glandular trichomes, abaxial surface grooved, margins revolute; petiole 2–3 mm long.

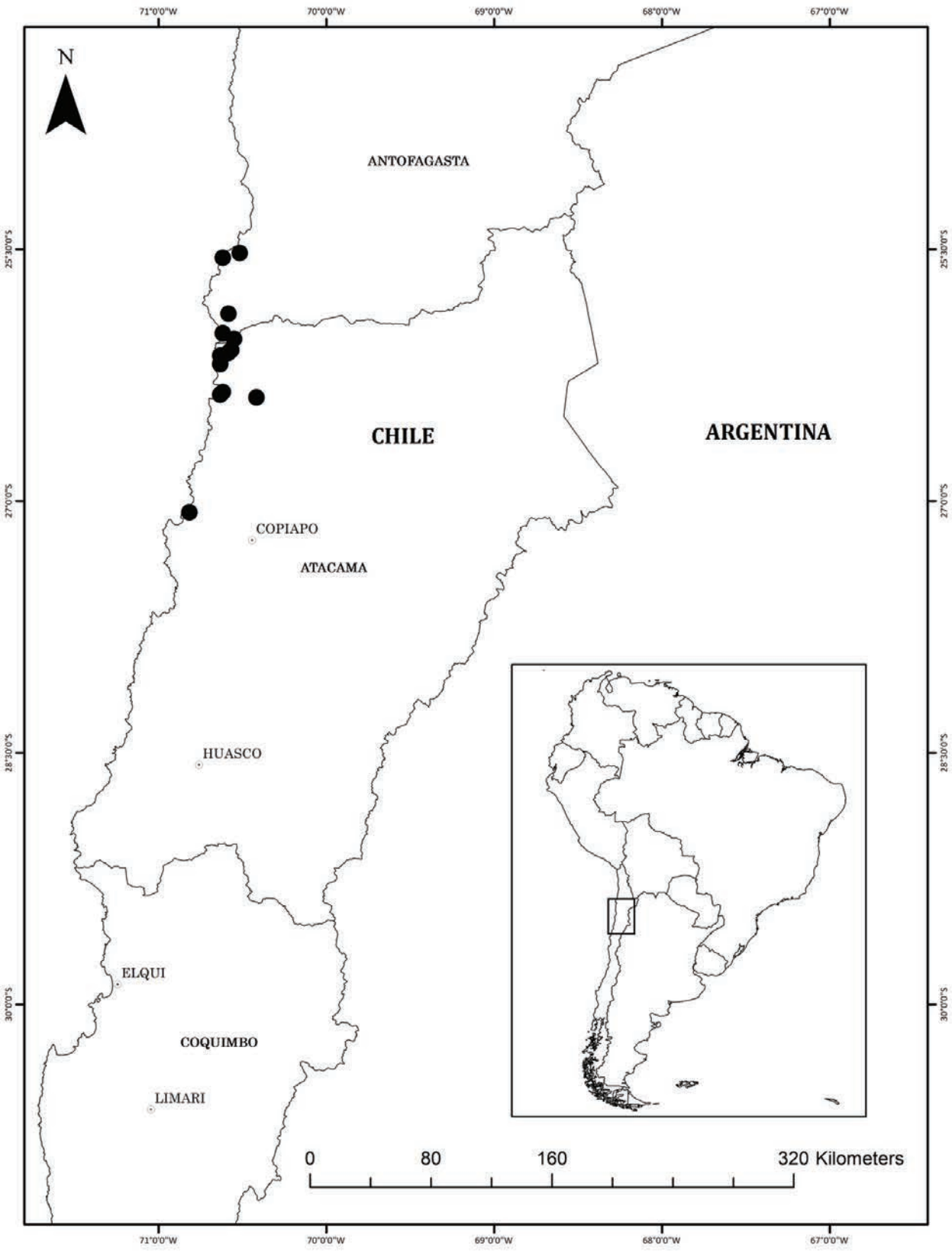


FIGURE 313. Distribution of *Nolana mollis* (Phil.) I.M. Johnst.

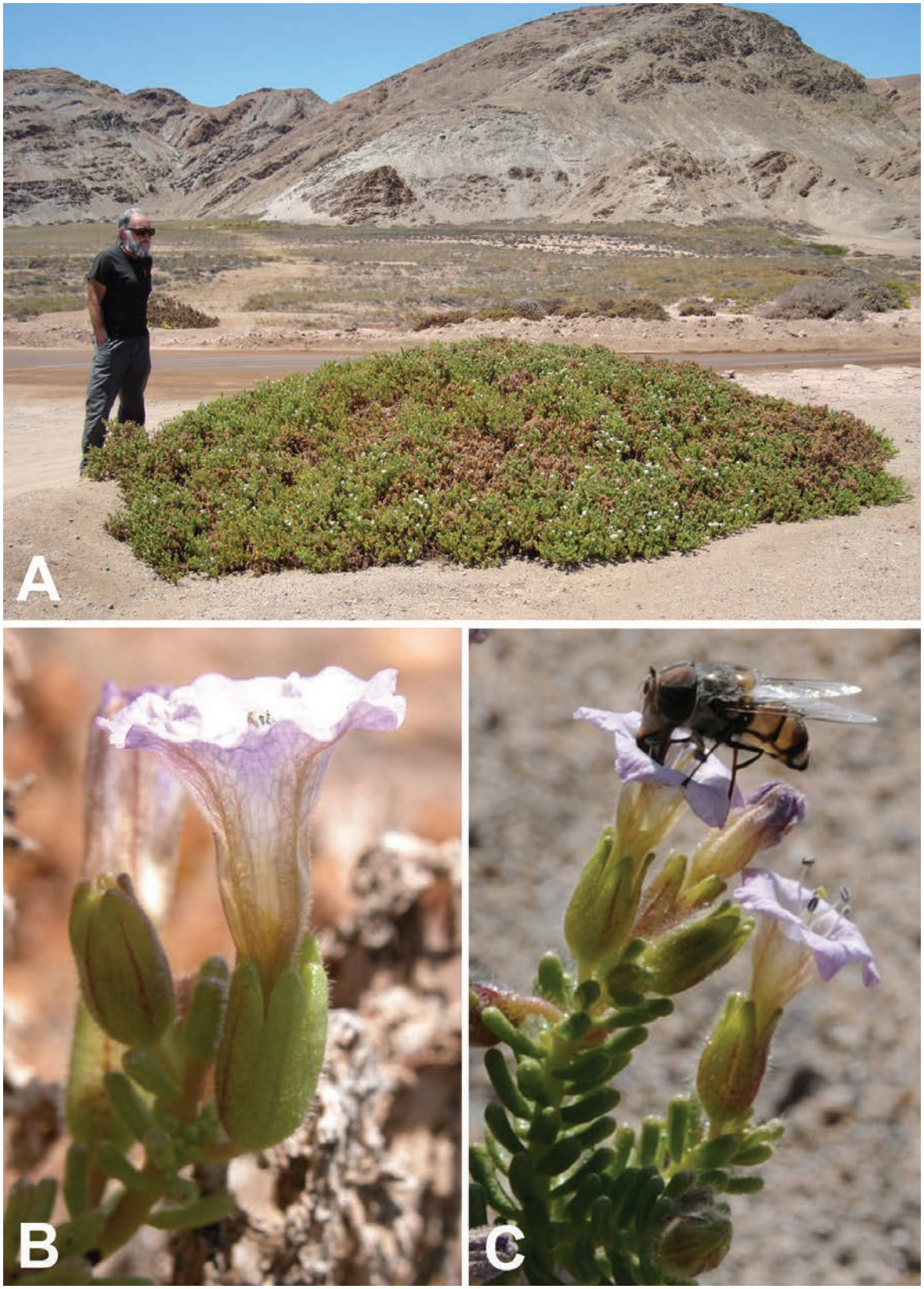


FIGURE 314. *Nolana mollis*. **A**, Large shrubs to six meters in diameter with Rudolf Schulz, *Copiapoa* expert; **B**, Lateral view of flower; **C**, Flowers visited by flower flies (Syrphidae).

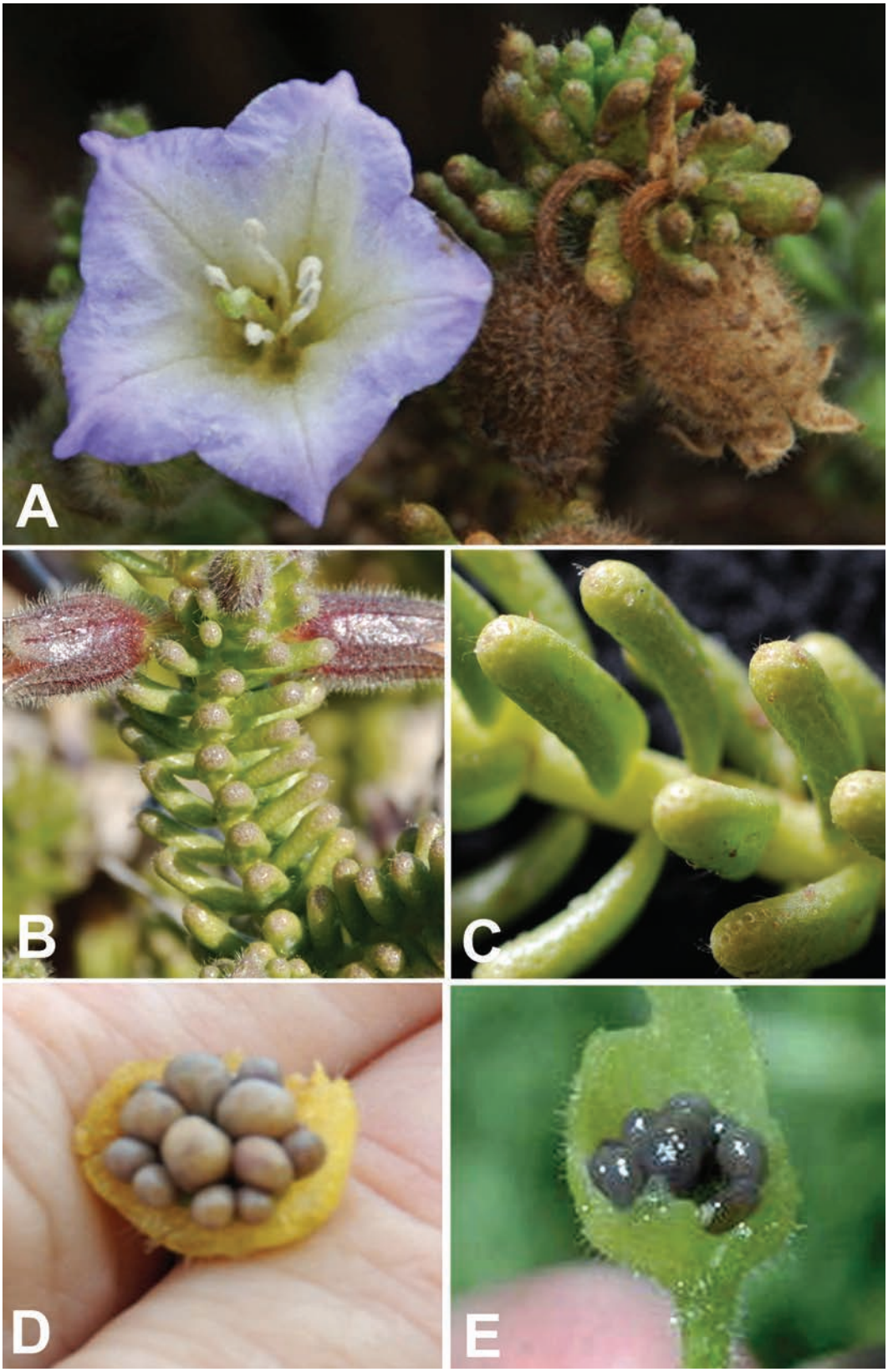


FIGURE 315. *Nolana mollis*. **A**, Frontal view of corolla with white anther thecae and pollen; **B–C**, Leaves densely set appearing decussate; **D–E**, Gynoecium with immature mericarps.

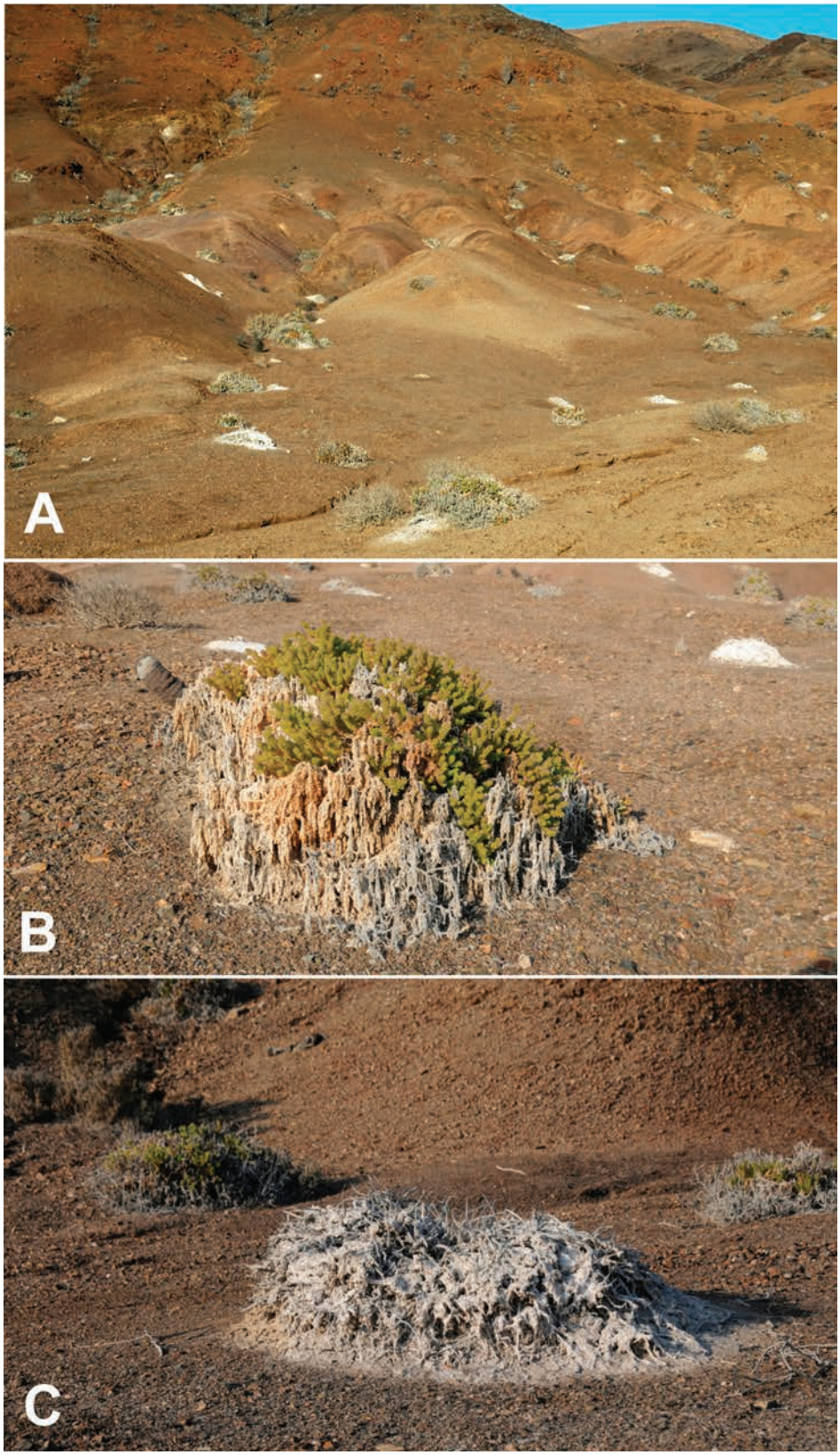


FIGURE 316. *Nolana mollis*. **A–C**, Plants end life cycle, senescence involves decomposing stems and leaves, leaving a white halo after disintegrating.

Inflorescences of solitary flowers, axillary or in lose scorpioid cymes; pedicels (8–)10–12 mm long, strongly reflexed. *Flowers* 5-merous; calyces campanulate, 4–10 mm long, 5-dentate, lobes equal, 2–3 mm long; corollas infundibularis, 8–20(–24) mm long, ca. 10 mm wide, white, violet to pale blue or lilac, lobes obtuse, apiculate, ca. 5 mm wide, ca. 5 mm long, reflexed in anthesis, the tubular basal portion pubescent; stamens unequal; anther filaments villous at the base; nectary disc patelliform; style ca. 15 mm long, as long as the shorter filaments, gynobasic; style capitate. *Mericarps* 8–10(4–5 large, 4–5 small), black, nitid; seeds 1–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is derived from the Latin, *mollis*, soft, pliant, and refers to the dense pubescence covering vegetative parts.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; 20–550 m.a.s.l. (Fig. 313). It is recorded from sandy soils at some distance from the coast, always within the influence of the fog.

Nolana mollis is typically a large shrub in the northern Chilean desert flora (Fig. 314A). It has a limited geographic distribution but is always within range of coastal fog. The shrubs have abundant, showy flowers (Fig. 314B–C, Fig 315A) that superficially resemble *Nicotiana* (cf. *N. alata* Link & Otto), with campanulate calyces with short lobes and trumpet-shaped tubular corollas with pointed lobes (Fig. 314B–C). Observations suggest the flowers are visited by flower flies (Syrphidae), that are putative pollinators (Fig. 314C).

The leaf orientation in some, but not all individuals, exhibits the densely set leaves that appear decussate (Fig. 314C) and are comparable to those of *Nolana pallida* (Fig. 245A). *Nolana mollis* has 8–10 round mericarps (Fig. 315D–E), which is the upper limit for the total number of mericarps in shrubby Chilean species. The outer surfaces of the mericarps often develop an orange-colored material that may be an elaiosome (Fig. 15F). *Nolana mollis* is one of the species that exhibit auto-combustion (Fig. 21); as the plants end their life cycle, their senescence involves decomposing stems and leaves, which leave a white halo on the ground after they disintegrate (Fig. 316A–C). This residual ash contains up to 40% dry weight in salts (Rundel et al., 1991).

Johnston (1929: 109) described this species as a succulent shrub with a slimy indumentum of long, simple trichomes. It forms globose shrubs 1.0–1.5 m tall, or the stems can be more decumbent and appear as sprawling masses 3–6 dm tall and 6–12 dm broad. The large corollas are violet or very pale bluish, and the base of the filaments densely villous. He went on to say that it is a very distinct species and is probably most closely related to *N. patula* (as *N. flaccida*), with which it shares cylindrical and merely toothed calyces and large corollas.

Nolana mollis has been involved in studies of salt glands on leaf surfaces; the glands exude salt that becomes hydrated during diurnal fog periods (hygroscopic effect), and this "salty dew" condenses back onto the plant (Mooney et al. 1980). The publication by Mooney et al. (1980) specifically mentioned *Nolana mollis* as the species with salty dew condensed on the leaf surfaces. Given the leaf pubescence of *N. mollis*, it is highly unlikely that such a phenomenon would occur, and no plant vouchers were ever cited. Thompson et al. (1998) suggested an alternative hypothesis, where the species involved is *Nolana patula* (as *N. flaccida*), a glabrous species on which it is possible to observe the salty water coating the leaves acting as a means for inhibiting transpiration.

Additional specimens examined: CHILE. **Antofagasta**. Prov. Antofagasta, Dept. Taltal, Quebrada Cachina, 200 m.a.s.l., 3 February 1947, *W. Biese 2256* (SGO 74484); Aguada Isla, *W. Biese 3219* (SGO 96822); Quebrada Guanillos, 10 km al N del Cachinal de la Costa, *W. Biese 3348* (SGO 75220); Aguada Cachina (Cachinal de La Costa), *W. Biese 3265* (SGO 696870); Quebrada to Bahia Tórtolas, S side of Cerro San Pedro, 25°33'S, 70°37'W, 20–70 m.a.s.l., 12 October 1988, *M. O. Dillon & D. Dillon 5681* (E, F 2014387, GH); ca. 60 km S of Taltal, near mouth of Quebrada de La Cachina, 26°00'S, 70°37'W, 50–100 m.a.s.l., 28 November 1988, *M. O. Dillon & D. Dillon 6043* (F 2144369); Taltal, *F. Jaffuel 2595* (CONC 68828, GH); Aguada Cachina, ca. 6 km inland from Caleta Esmeralda, Aguada Cachina, ca. 25°53'S, 14–15 December 1925, *I. M. Johnston 5695* (GH, K); La Tórtolas, Sierra de San Pedro, 25°34'S, 70°36'W, 170 m.a.s.l., 12 October 2005, *F. Luebert & N. García 2757* (SGO 159453); Taltal, Quebrada Los Changos, 125 m.a.s.l., 10 September 1936, *G. Montero O. 2955* (GH); Taltal, Chépica, 17 September 1954, *M. Ricardi S. 3077* (CONC 18310, F 2048623); Quebrada Cachina, camino a Esmeralda, 14 September 1958, *M. Ricardi & C. Marticorena 4624/1009* (CONC 25414); Quebrada Taltal, 2 km E, 26°26'S, 70°35'W, 130 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2879* (F 2114619, SGO 129375); end of Cifuncho road S of Taltal, ca. 5 km from ocean near junction of road and Quebrada Cifuncho, 30 m.a.s.l., 15 October 1938, *C. R. Worth & J. L. Morrison 16124* (GH, K). **Atacama**: Parque Nacional Pan de Azúcar, Quebrada del Castillo, 26°12'03"S, 70°37'02"W, 250 m.a.s.l., 24 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 119* (E00230463); Entre Vallenar y Copiapó, 11 October 1987, *Ch von Bohlen 269* (E00719010); Prov. Chañaral, 6–9 km SW of Pan-Americana Hwy 5 on northern route to Parque Nacional Pan de Azúcar, 220–550 m.a.s.l., 5 December 1987, *M. O. Dillon & J. T. S. Teillier 5065* (CONC, E, F 2010288, GH, SGO); 21 km W of Pan-Americana Hwy 5, 26°08'S, 70°37'W, 85 m.a.s.l., 30 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5604* (CONC, E, F 2012858, GH); Parque Nacional Pan de Azúcar, Las Lomitas, 6 km E of coast, 26°02'S, 70°33'W, 560 m.a.s.l., 12 November 1997, *M. O. Dillon & C. Trujillo C. 8015* (CONC 149967, E, F 2183317, GH, K, SGO 143691); Parque Nacional Pan de Azúcar, 26°07'S, 70°35'W, 200 m.a.s.l., 1 December 1997, *M. O. Dillon 8150* (F 2182956); Parque Nacional Pan de Azúcar, 26°11'S, 70°38'W, 320 m.a.s.l., 1 December 1997, *M. O. Dillon 8158* (CONC 150044, F 2182950, HG, SGO 143705); ca. 7 SW of Chañaral, 26°23'02"S, 70°39'49"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9080*

(CONC, SGO); Puerto de Chañaral, El Barquito, 26°23'S, 28–29 October 1925, *I. M. Johnston 4771* (GH); caleta Pan de Azúcar, 26°7'S, 18 December 1925, *I. M. Johnston 5835* (GH); Panamericana, a 16 km al S de Chañaral, 19 September 1966, *E. M. L. Kausel 5063* (SGO 79438); Playa al Sur de Chañaral, 13 September 1965, *A. Kohler 101* (CONC 36058); Camino de Chañaral a El Salado, Km 16, 160 m.a.s.l., 25 October 1971, *C. Marticorena, R. Rodríguez, & E. Weldt 1898* (CONC 36792); Parque Nacional Pan de Azúcar, 10 km despues del cruce a Chinquihue hacia la Plataforma, *M. Muñoz S. & I. Meza P. 2306* (SGO 137728); PNPA, Quebrada de Coquimbo, 26°08'S, 70°38'W, 31 October 1991, *M. Muñoz, S. Teillier, & I. Meza P. 2847* (SGO 125141); Parque Nacional Pan de Azúcar, *S. Teillier, P. Rundel, & P. García 2728* (SGO 129374).

G14. ***Nolana onoana*** M.O. Dillon & M. Nakaz., Arnaldoa 14(2): 199. 2007. TYPE: CHILE. Antofagasta: Prov. Antofagasta, 15–17 km S of La Negra near southern end of Quebrada de Mateo, ca. 32 km SSE of Antofagasta, 23°54'S, 70°18'W, ca. 600 m, 20 October 1988, *M. O. Dillon & D. Dillon 5729* (Holotype: SGO; Isotypes: E, F [F 2045821], GH, US). Fig. 317–322.

Digital image: Isotype of *Nolana onoana* from the Field Museum, Chicago [F 2045821]. https://collections-botany.fieldmuseum.org/catalogue/365184

Robust, tap-rooted, annual *herbs* to ca. 1 m tall; stems erect to ascending, but decumbent when densely leafy. *Leaves* alternate, fasciculate, blades linear to narrowly oblanceolate, 10–15 mm long, 3–5 mm wide, sessile, strongly revolute, terete, densely pubescent with stout, capitate-glandular trichomes. *Inflorescence* of solitary flowers in the densely crowded, upper leaf axils, sessile. *Flowers* 5-merous; calyces narrowly campanulate, 5–7 mm long, tube 3–5 mm long, ca. 5 mm wide, 5-lobed, lobes lanceolate, 2–3 mm long, ca. 1 mm wide, equal; corollas infundibularis, 18–24 mm long, 8–12 mm wide distally, lavender to light blue, pubescent with capitate-glandular trichomes, 5-lobed, zygomorphic, lobes obtuse, the largest 3–4 mm wide tubular, 3–4 mm long, rounded to obtuse; stamens 5, included, unequal, 3 long, 2 short; ovary glabrous, basal nectary, 5-carpels; style included, stigma capitate, green. *Mericarps* (4–)6–7, spherical to ovoid, 2–3 mm in diam.; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Mikio Ono (b. 1932–d. 2014), a Japanese plant systematist, biogeographer, and the first collector of this taxon. He was a professor and head of the Makino Herbarium, Botany Section at Tokyo Metropolitan University (TMU). Dra. Miyuki Nakazawa (M. Nakaz.) received her PhD under his direction at TMU and conducted the first extensive DNA studies on *Nolana* (Tago, 1999; Tago-Nakawaza and Dillon, 1999).

Distribution and Ecology: Chile, Region of Antofagasta, ranging ca. 100 km; (100–)500–600(–1200) m.a.s.l. (Fig. 317). It is recorded from a few localities in sandy soils; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana onoana is essentially an annual herb that can reach over one meter tall with densely crowded leaves and small flowers. The type locality is a roadside depression ca. 32 km south of Antofagasta, where moisture from the El Niño rains had gathered and evaporated over a period of several months. The material that ultimately became the type specimen was collected in October of 1988, where the water had evaporated and the ground was quite dry and cracked (Fig. 319). When the site was visited in 2015, many flowering individuals were found under the same condition of the drying out of the *pozo* (Fig. 320A–C). In subsequent years, another population of this species was encountered to the southeast of the type locality at slightly higher elevations in nearby quebradas (Fig. 321A). These sites are interior environments east of the coastal fog on the other side of the coastal mountains. Depending upon the amount of available moisture, robust annuals can take on various forms. When moisture is not limiting, the plants can reach very large proportions, as in the type individual; however, when water is limited, the plants grow as spikes with little branching (Fig. 321B). Other collections of this species were made north of Antofagasta and west of the coastal range near Bahía de los Tres Compadres, *Dillon & Dillon 5724*. In 1991, Ono and Masuzawa made a series of collections north of Antofagasta as well.

The corollas initially suggest *N. aplocaryoides*, but the wider leaves and the number of mericarps (3–5) of that species makes it distinct. Using the GBSSI waxy marker (Dillon et al., 2007c), *N. onoana* was not related to *N. aplocaryoides*. In that study, *N. onoana* was retrieved in a clade that includes *N. villosa, N. peruviana,* and *N. sphaerophylla,* all species with very different habits, leaves, and floral morphologies than *N. onoana*.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Quebrada La Negra, April 1958, *O. Astrudillo s.n.* (CONC 12975); Península Moreno, cerros al O de Juan López, 23°30'S, 70°33'W, 150 m.a.s.l., 18 October 1992, *G. Baumann 1* (CONC 122441); Bahía de los Tres Compadres, ca. 64 km N of Tropic of Capricorn, 32 km S of Michilla, 22°52'S, 70°16'W, ca. 100 m.a.s.l., 20 October 1988, *M. O. Dillon & D. Dillon 5724* (CONC, E, F 2045832, G, GH, HSP, US); ca. 5 km S of Fundición Alto Norte, 23°51'44"S, 70°18'41"W, ca. 600 m.a.s.l., 29 October 2007, *M. O. Dillon 9050* (CONC 179084, E, F 2329904, GH, SGO 158736); ca. 60 km S of Antofagasta; ca. 2 km E of Posada Las Primas off Ruta B-55, 24°05'32"S, 70°10'20"W, ca. 1118 m.a.s.l., 27 November 2011, *M. O. Dillon 9219* (SGO); ca. 60 km S of Antofagasta; ca. 2 km E of Posada Las Primas off Ruta B-55, 24°05'19"S, 70°10'08"W, ca. 1103 m.a.s.l., 27 November 2011, *M. O. Dillon 9220* (CONC, SGO), *9221* (SGO), *9222* (SGO); *9223* (CONC, SGO), *9224* (SGO); *9225* (CONC, SGO); Mejillones, 23°06'S, 70°24'W, 50 m.a.s.l., 29 September 1996, *O. Matthei 494* (CONC 137098, MA, SGO 152875); 16 km al norte de Antofagasta, camino a Tocopilla, 23°29'S, 70°25'W, 100 m.a.s.l., 29 September 1966, *O. Matthei 503* (CONC 137107); Salida N de Antofagasta, a 8 km de la ciudad, 23°37'S, 70°10'W, 560 m.a.s.l., 29 September 1996, *O. Matthei 527* (CONC 137131, SGO 152874); between

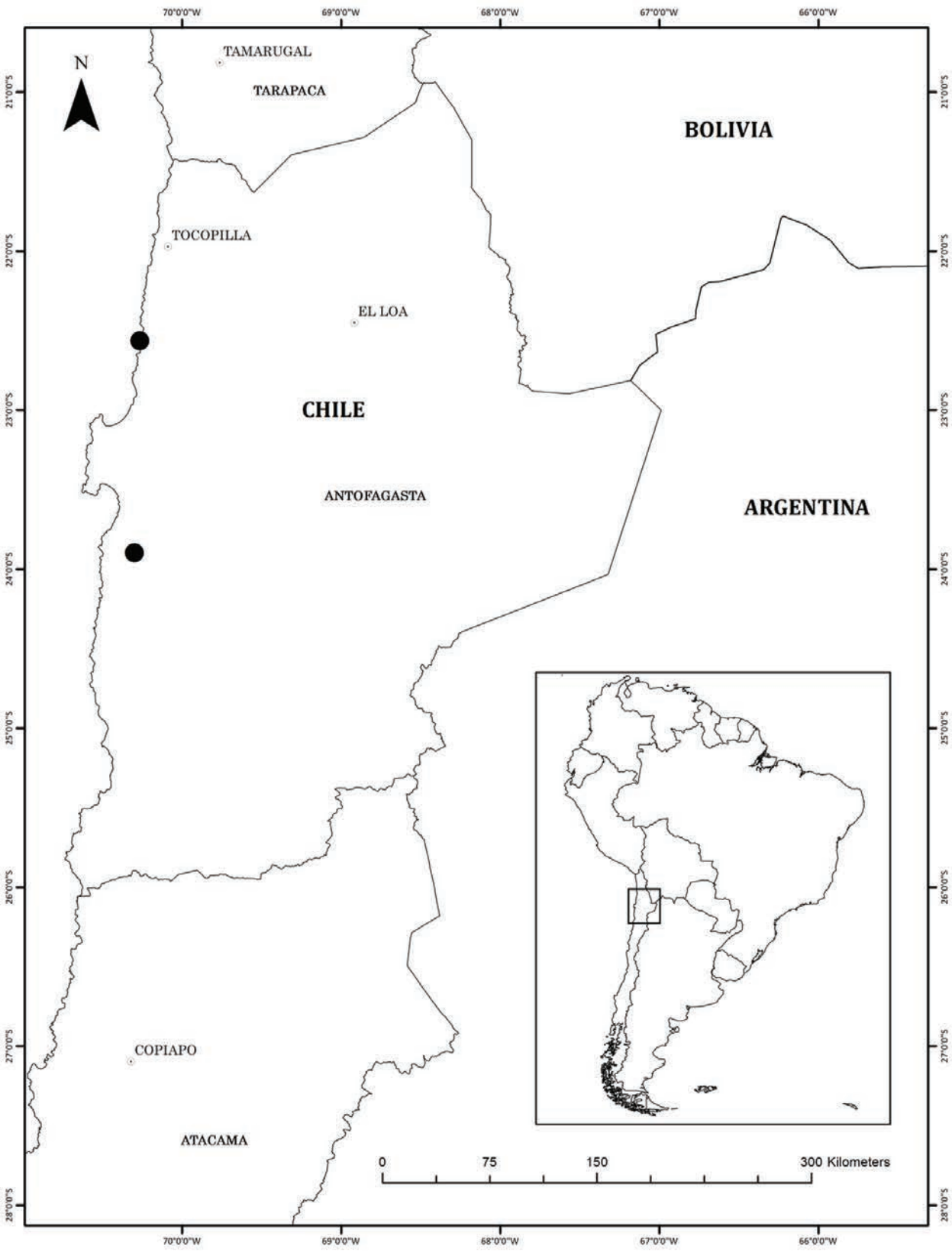


FIGURE 317. Distribution of *Nolana onoana* M.O. Dillon & Nakazawa.

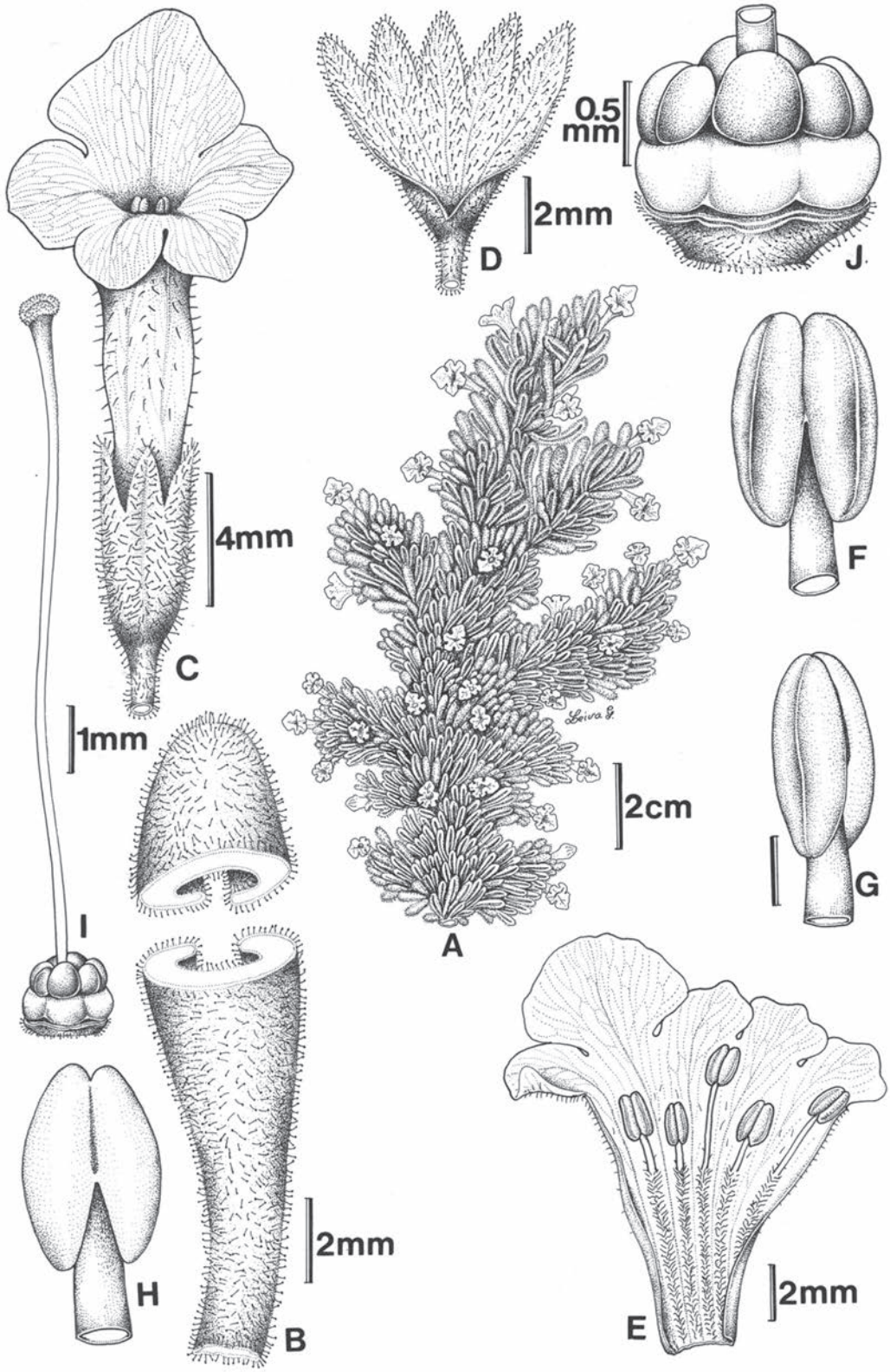


FIGURE 318. Illustration of *Nolana onoana*. **A**, Flowering branch; **B**, Leaf with dissected blade to illustrate revolute margins; **C**, Flower; **D**, Dissected calyx; **E**, Dissected corolla; **F**, Anther dorsal view; **G**, Anther lateral view; **H**. Anther ventral view; **I,** Gynoecium. Drawn by Segundo Leiva Gonzáles.

FIGURE 319. *Nolana onoana*. Type specimen was seen in October of 1988 in an evaporating pool south of Antofagasta, Chile.

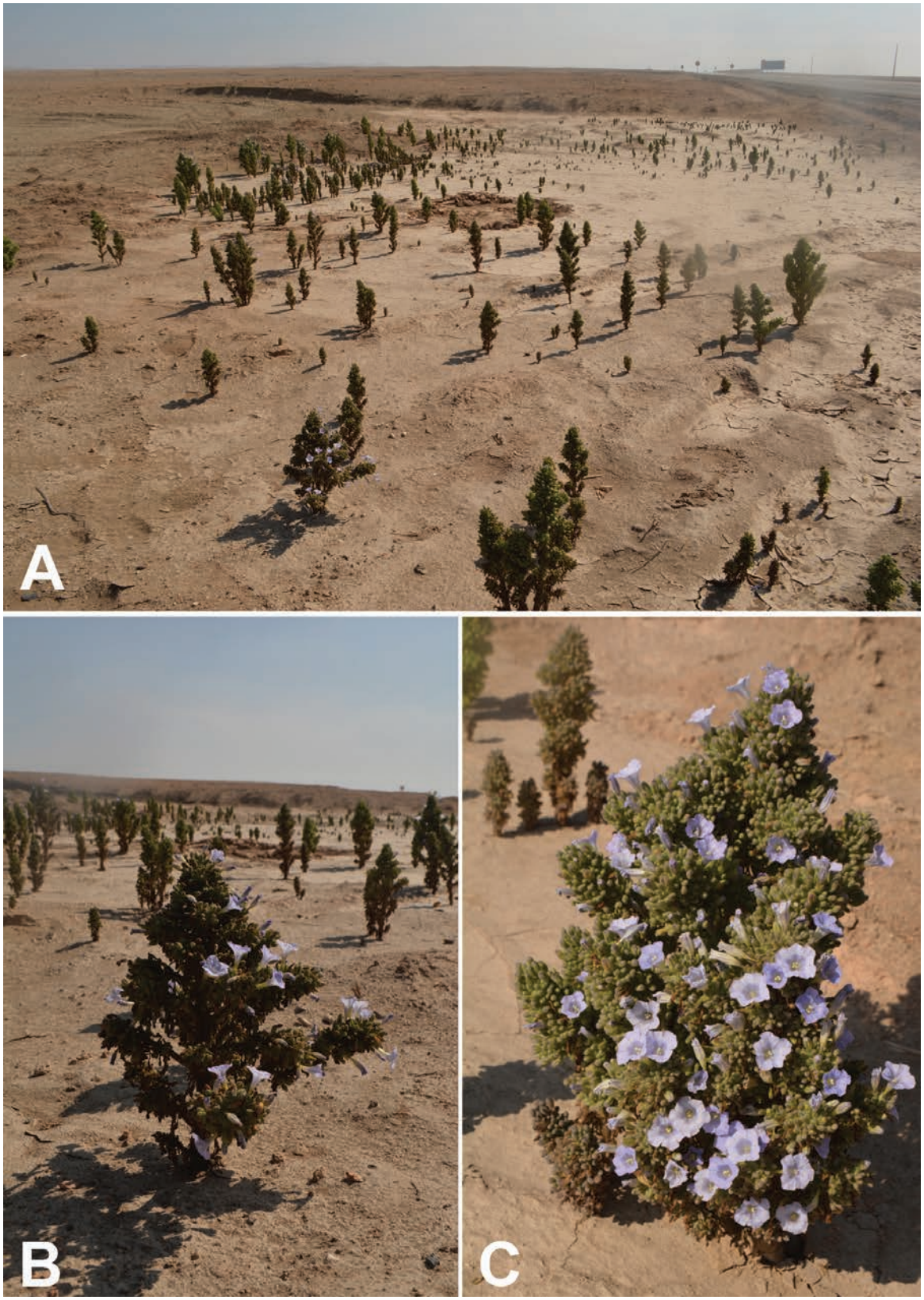


FIGURE 320. *Nolana onoana*. **A–C**, Site south of Antofagasta, Chile in 2015 with a population germinating from the *pozo*, or runoff pond, where the type was collected in 1988.

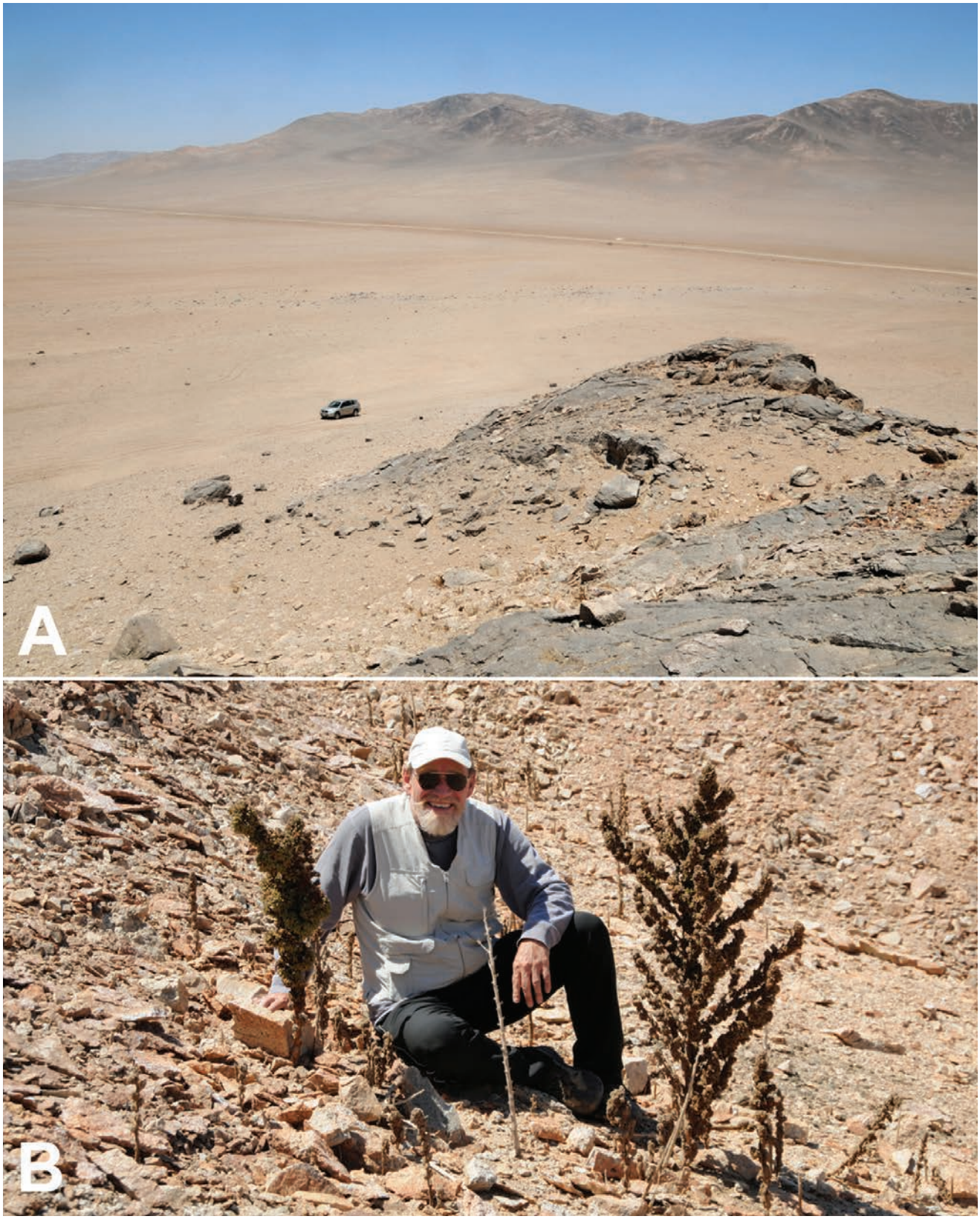


FIGURE 321. *Nolana onoana*. **A**, Locality east of the coastal fog approaching absolute desert; **B**, Erect habit with flowering and fruiting stems.

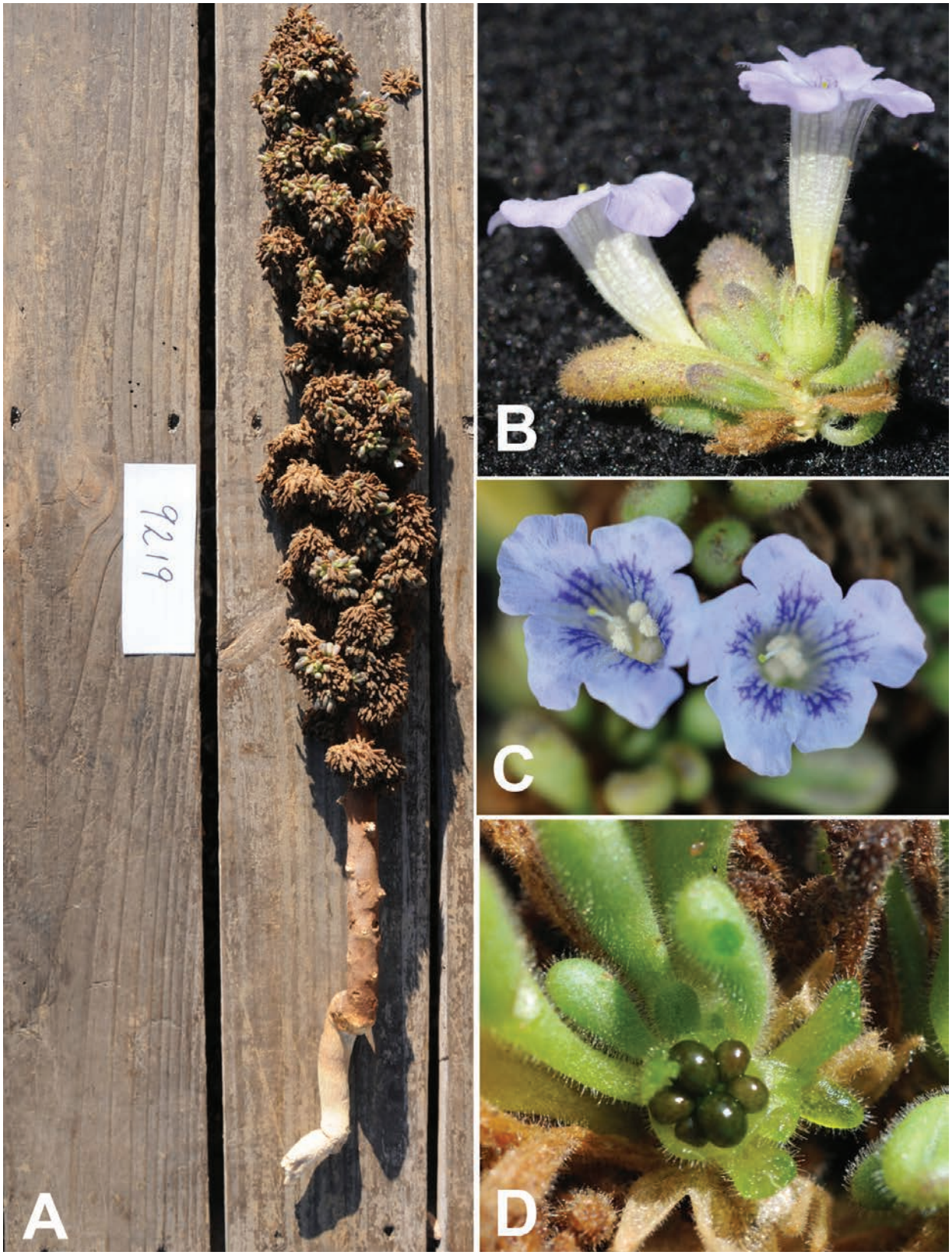


FIGURE 322. *Nolana onoana*. **A**, Annual individual with flowers and fruits; **B**, Flowers and apical leaves; **C**, Frontal view of corollas with purple guides, white anther thecae and pollen; **D**, Gynoecium with immature mericarps.

Tocopilla and Antofagasta, 8 November 1991, *M. Ono & T. Masuzawa s.n.* (MAK 274958), *s.n.* (MAK 274959), *s.n.* (MAK 274960); N of Antofagasta, 9 November 1991, *M. Ono & T. Masuzawa s.n.* (MAK 274950), *s.n.* (MAK 274953); Península Moreno, cerros frente a Juan López, 23°30'S, 70°33'W, 500 m.a.s.l., 29 September 1991, *M. Quezada y E. Ruíz 65* (CONC 121072); Quebrada frente a Juan López, 23°30'S, 70°32'W, 150 m.a.s.l., 10 November 1966, *R. Rodríguez 3081* (CONC 136601); pie de Monte de Morro Moreno, 23°30'S, 70°32'W, 50 m.a.s.l., 30 October 1985, *F. Schlegel 7782* (CONC 115575); entre Mejillones y Mantos Blancos, 23°12'S, 70°10'W, 500 m.a.s.l., 25 January 1995, *S. Teillier 3410* (SGO 140915); Quebrada La Negra, 10 km E de Antofagasta, 23°38'S, 70°24'W, 100 m.a.s.l., 25 January 1995, *S. Teillier 3413* (SGO 140914).

G15. ***Nolana patachensis*** J. Hepp & M.O. Dillon, Arnaldoa. 25(2): 325. 2018. TYPE: CHILE. Tarapacá: Prov. Iquique, Alto Punta Patache, 20°49'S, 70°09'W, 1 November 1997, *W. Sielfeld 32* (Holotype: SGO [143057]). Fig. 323–326.

Digital image: No image is currently available via the internet; the holotype image of *Nolana patachensis* (Fig. 324) was provided by Museo Nacional de Historia Natural, Santiago [SGO 143057].

Taprooted annual *herbs* to ca. 50 cm in diam., 10–20 cm tall, basally branched; stems prostrate to decumbent, to ca. 15 cm long, densely pubescent with capitate-glandular trichomes. *Leaves* alternate, blades linear-oblong or cylindrical, 10–20 mm long, 3–4 mm wide, terete, erect or perpendicular orientation, succulent, apically rounded, bases rounded, densely pubescence with stout, capitate-glandular trichomes; sessile. *Inflorescences* of solitary flowers in upper leaf axils; pedicels cylindrical, densely pubescent, 2–7(–10) mm long. *Flowers* 5-merous; calyces narrowly campanulate, 5–7 mm wide at anthesis, densely pubescent with capitate-glandular trichomes, 5-lobed, tube 3–5 mm long, ca. 5 mm wide, lobes lanceolate, unequal, 2–3 mm long, ca. 1 mm wide, apices obtuse or rounded; corollas zygomorphic, infundibuliform, 18–24 mm long, 8–12 mm wide at anthesis, distally lavender to light blue, the throat clear, externally and internally glabrous, lobes obtuse; stamens 5, included, filaments inserted on lower third of corolla, unequal, 3 long, 2 short, anther thecae purple, ca. 1.2 mm long, ca. 1 mm wide, glabrous; ovary glabrous, basal nectary ca. 1 mm wide, carpels 5, style included, stigma green. *Mericarps* 5, 1-seriate, oval to elliptic, black, 2–3 mm long, 1.5–2.0 mm wide, adaxial surfaces minutely bullate; seeds (1–)2–3(–4) per mericarp. Chromosome number: unknown.

Etymology: The species epithet is the latinisation of the geographic locality of the type collection, Alto Patache fog oasis, or *lomas* formation, located in the Region of Tarapacá in northern Chile. As with many place names, the origins remain obscure, but it may have its origins in *Pukina*, a language distantly related to *Quechua*. It is not associated directly with either *Quechua* or *Aymara*.

Distribution and Ecology: Chile, Region of Tarapacá and Antofagasta; ca. 800 m.a.s.l. (Fig. 323). It is confined to southwest oriented slopes exposed to fog; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana patachensis is a low spreading annual (Fig. 325A–B) with a narrow distribution in a few isolated *lomas* formations. The corollas are slightly zygomorphic, with one slightly enlarged lobe, and are lavender or pale blue with no internal guides (Fig. 326A). Leaves are erect, as are the flowers, and the capitate-glandular trichomes capture blowing sand and dust (Fig. 326B). Butterflies are the putative pollinators, and the one in Figure 326B is identified as *Pyrgus bocchoris trisignatus* (Lepidoptera: Hespercidae).

The flowers of *Nolana patachensis* most closely resemble those of *N. onoana*; however, they differ in the spreading, prostrate habit, and erect, terete leaves. Furthermore, the elliptic or oval mericarps of *N. patachensis*, with (1–)2–3 (–4) seeds and finely bullate surfaces, are essentially unique within its congeners in northern Chile. The mericarps in *N. patachensis* also differ from mericarps in *N. onoana*, which are round or spherical, with a finely reticulate or alveolate surfaces. Another annual, tap-rooted species, *N. aplocaryoides*, has much wider leaves with long, villous trichomes, and round or spherical mericarps, and *N. gracillima* has glabrescent to pilose pubescent leaves, shorter corollas, and pyriform mericarps.

The Alto Patache fog oasis has been recognized as a priority area for conservation since 2007 and is currently protected in a concession granted by the Ministry of National Assets to Pontificia Universidad Católica de Chile, through the Atacama Desert Center (Osses et al., 2017). It supports an endemic biota, including endemic lichens (Vargas et al., 2017), several of which are common to the Atacama Desert. The flora at Alto Patache contains about 42 vascular plants (Pliscoff et al., 2017), including one of the few populations of *Alstroemeria lutea* Muñoz-Schick (Muñoz-Schick, 2000). The arthropod fauna includes two endemic Coleoptera, *Scotobius patachensis* and *Scotobius larraini* (Sagredo et al., 2002), and two bees, *Penapis larraini* (Hymenoptera: Halictidae: Rophitinae) (Packer, 2012) and *Neofidelia submersa* (Hymenoptera: Apoidea: Megachilidae) (Dumesh and Packer, 2013). The first record in Chile of a noctuid moth, *Hemieuxoa polymorpha* Forbes, was a collection of adults at Alto Patache in 1999 (Angulo and Olivares, 2005). Alto Punta Lobos is located approximately 25 km south of Alto Patache and harbors 20 endemics in a flora of 40 species (Muñoz-Schick et al., 2001).

While *Nolana patachensis* has not been included in any DNA analysis, overall morphological similarity suggests that it is related to *Nolana onoana* and a group of northern Chilean species of small to large annuals, all with small leaves, (1–)10–20(–40) mm long and (1–)2–5(–7) mm wide.

The first herbarium material of this taxon was labelled as *Nolana aplocaryoides*, another tap-rooted annual species typically recorded from farther to the south and with different leaves, pubescence and corollas. At that time, I believed the sheets would be better treated as *N. gracillima*, a species originally described from southern Peru with populations in northern Chile. In 2018, I examined photographs of living plants with flowers taken by Josephina Hepp on a field trip to Alto Patache in 2015, after the abundant August rains in the region. The photographs confirmed that the taxon was neither *Nolana aplocaryoides* nor *N. gracillima*, but something entirely different.

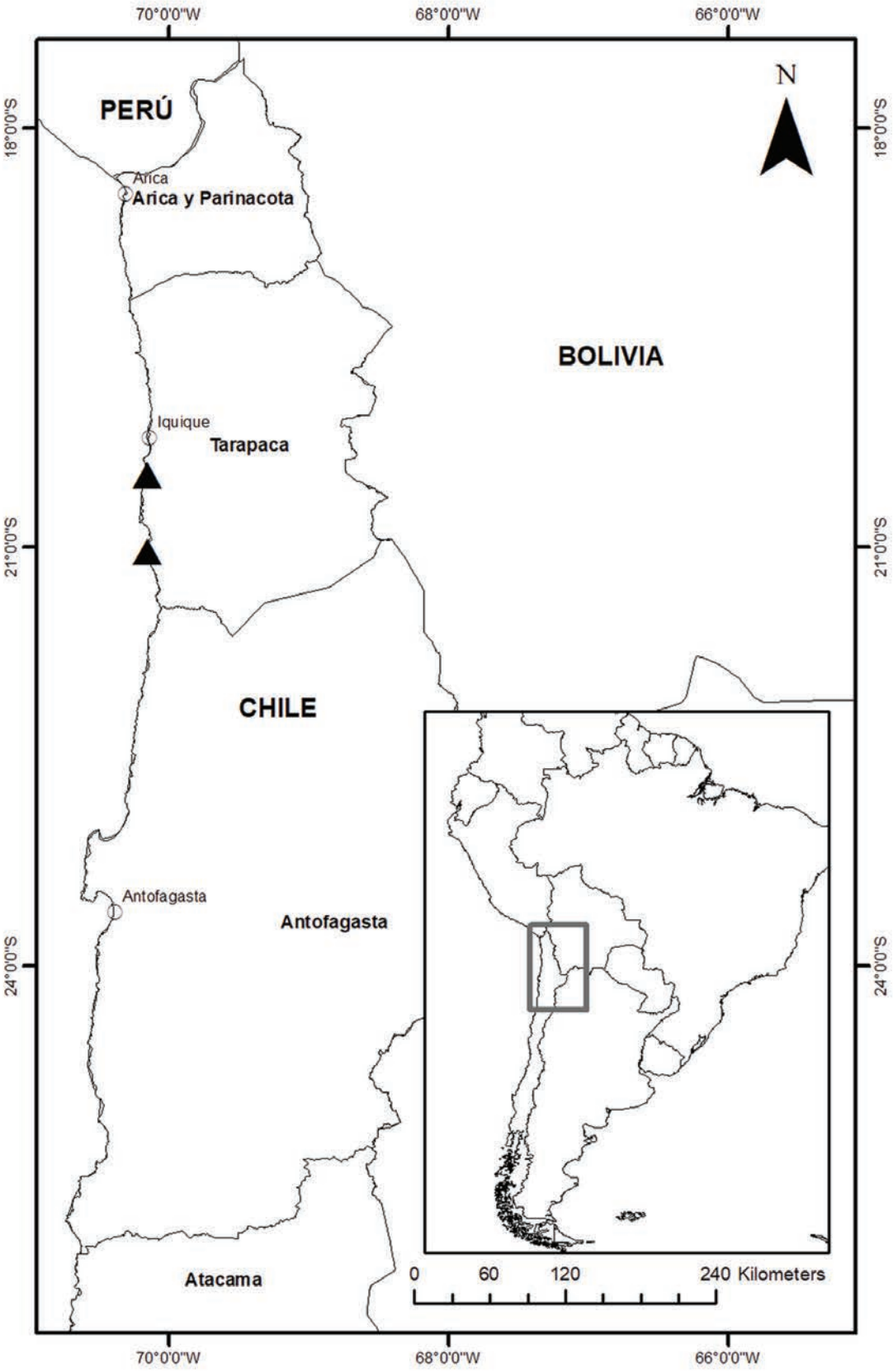


FIGURE 323. Distribution of *Nolana patachensis* J. Hepp & M.O. Dillon.

FIGURE 324. Holotype of *Nolana patachensis* J. Hepp & M.O. Dillon housed at SGO. No digital image is available via the internet.

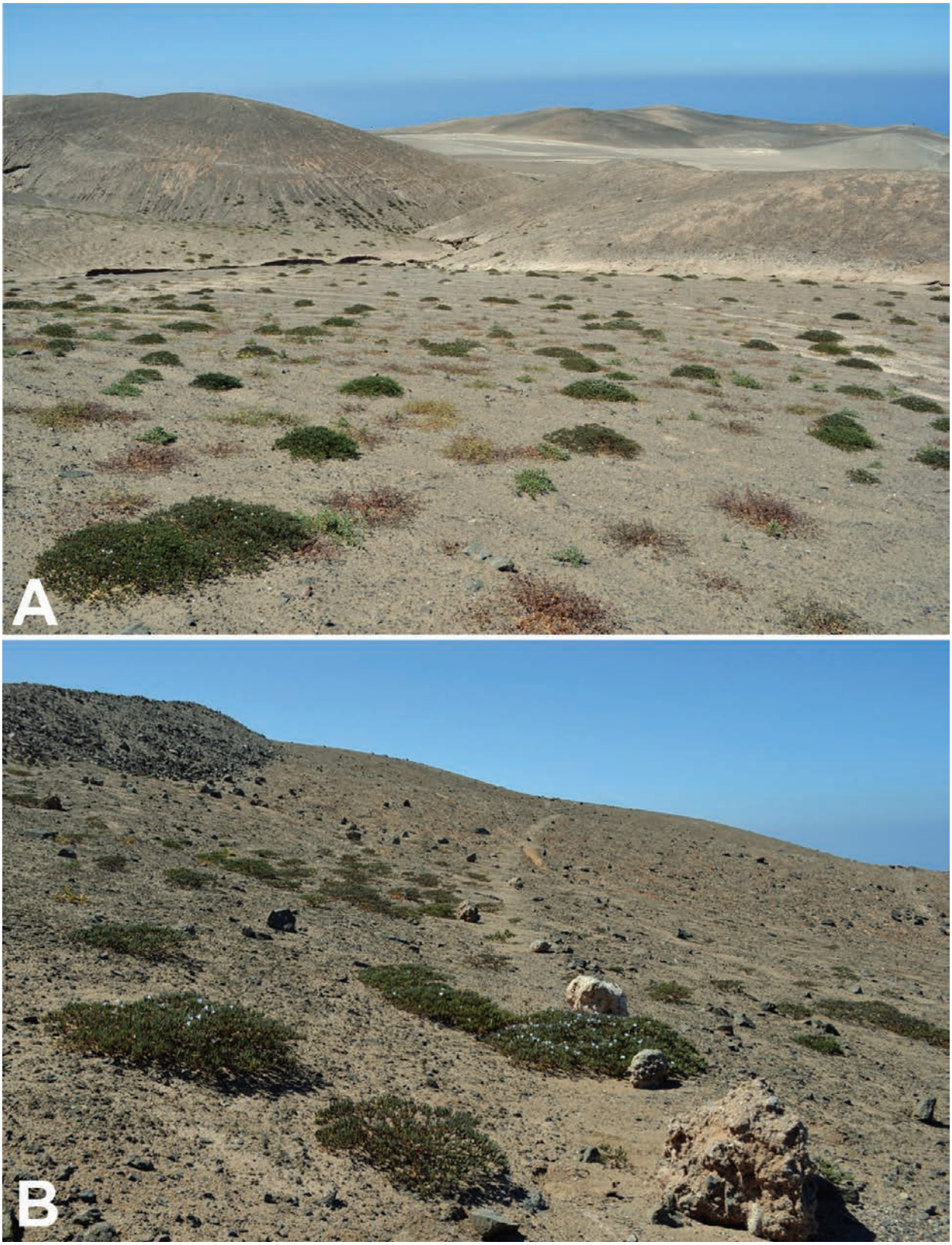


FIGURE 325. *Nolana patachensis* habitats. **A**, Individuals of *Nolana patachensis* growing together with *N. jaffuelii*, *N. intonsa* and *Cristaria molinae* in December 2015, at the hills and inner plateau of Alto Patache oasis, Chile, which, in dry years, are devoid of plants; **B**, Prostrate growth habit of *N. patachensis*. Photographs by Josefina Hepp.

FIGURE 326. *Nolana patachensis*. **A**, Close-up of flowers showing light blue color on the edge of the corolla; **B**, Lepidoptera (Family Hesperiidae–Skippers) pollinating the flowers available in the oasis, December 2015, trichomes visible on erect leaves. Photographs by Josefina Hepp.

Additional specimens examined: CHILE. **Antofagasta:** 20 km al Norte de Tocopilla, camino costero, 16 October 1991, *A. Brinck s.n.* (SGO 122819). **Tarapacá**: Prov. Iquique, Alto Patache, 20°49'S, 70°09'W, 800 m.a.s.l., 23 November 1997, *E. Belmonte 97-770* (CONC 143484), Alto Punta Patache, 20°49'S, 70°09'W, 800 m.a.s.l., 8 November 1997, *R. Pinto s.n.* (SGO 142975); Alto Punta Lobos, 21°02'S, 70°09'W, 800 m.a.s.l., 17 January 1998, *R. Pinto s.n.* (SGO 142976).

G16. ***Nolana patula*** (Phil.) Mesa ex M.O. Dillon, Gayana Bot. 66: 294. 2009. Fig. 327–329.

Basionym: *Alona patula* Phil., Anal. Univ. Chile 91. 39. 1895. TYPE: CHILE. Antofagasta: Juncal, [25°45'S, 69°27'W], 1884–1885, *F. J. San Román s.n.* (Lectotype designated by Mesa-M., 1981: SGO [42657]; Isolectotype: SGO [SGO 55080]).

Digital image: Lectotype for *Alona patula* from Museo Nacional de Historia Natural, Santiago [SGO 42657]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004340

Erect to decumbent *shrubs*, to ca. 50 cm tall, stems glabrous. *Leaves* alternate, blades oblong, 5–11 mm long, ca. 3 mm wide, succulent, nearly terete, apices rounded, abaxial surface grooved, glabrous, pockmarked with salt glands, appearing shiny. *Inflorescences* of solitary flowers, terminal and axillary, pedicels 5–10 mm long. *Flowers* 5-merous; calyces campanulate to cylindrical, succulent, ca. 10 mm long, lobes equal, deltoid to lanceolate, apically rounded, margins slightly revolute; corollas infundibularis, weakly zygomorphic, 20–30 mm long, ca. 20 mm wide at mouth, pale lilac to white, lobes rounded; anther filaments unequal, bases densely villous, thecae white to lavender. *Mericarps* (3–)5(–6), black; seeds 1–3 per mericarp. Chromosome number: unknown

Etymology: The species epithet is from the Latin, *patula*, spreading, and refers to the typical spreading habit of this species.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; (85–)200–750 m.a.s.l. (Fig. 327). Recorded from habits far removed from the coast, but still within the influence of coastal fog, Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana patula is variable in stature with individuals flowering at a height of only a few centimeters, or if water is unlimited, they can mature to much-branched, semi-woody shrubs of several meters in diameter and persist for undetermined periods (Fig. 328A). The corollas are invariably white with pale lilac to white anthers and pollen (Fig. 328B). The anther filaments are pink and densely pubescent at the bases (Fig. 329A), and the calyces are cylindrical with triangular lobes (Fig. 329A–C). The mericarps are basally attached with a pronounced nectary (Fig. 329D).

Johnston (1936) applied the name *Nolana flaccida* to taxa with glabrous stems and leaves. He described the plant as, "A loosely and very widely branched, prostrate, pale green shrub 1.5–3.0 dm tall and 10–20 dm broad, growing on the sandy floor of the quebrada-mouth at Caleta de Pan de Azúcar (*Johnston 5834*). The plant has glabrous stems and leaves, although occasionally a very few simple hairs are to be observed on the calyces and growing parts of the stems. The conspicuous pale lilac corollas are villous towards the base within as are also the base of the filaments."

In 1860, R. A. Philippi published a series of new species, including *Alona sphaerophylla* Phil. (Fl. Atacam. 44. 1860), based upon one of his collections made near Las Animas Atacama during his 1853–1854 expedition to the Atacama Desert. Johnston (1929: 107) placed *A. sphaerophylla* into synonymy with *Bargemontia clavata* (Miers) I.M. Johnst., a species he later reduced to synonymy with *Nolana divaricata* (Johnston 1936: 65). In 1895, R. A. Philippi described additional *Alona* species, including *Alona flaccida* Phil., from a collection by San Román near Salado Atacama, and *Alona patula* Phil., from another collection by San Román near Juncal Antofagasta. Johnston (1929) transferred *A. flaccida* to *Bargemontia* and placed *A. patula* into synonymy with that species. This established priority of the epithet '*flaccida*' over '*patula*' when the two names were considered synonymous (Art. 11.5). Later, Johnston (1936) transferred *B. flaccida* (Phil.) I.M. Johnst. to *Nolana* and listed *A. patula* as a synonym of that taxon. Johnston (1936) accepted *N. flaccida* (Phil.) I.M. Johnst., a species growing on the sandy floor of the quebrada mouth at Caleta de Pan de Azúcar (e.g., *Johnston 5834*).

Nolana patula has perhaps coevolved with the bee genus, *Xeromelissa* (Rozen and Wyman, 2015), which may be a strict specialist on that taxon (Fig. 329E). The relationship between pollinators and *Nolana* species is a topic that needs additional study (Laurence Packer, pers. comm.).

Mesa-M. (1981) placed *Alona flaccida*, *A. patula*, and *A. sphaerophylla* Phil. into synonymy with *Nolana leptophylla* (Miers) I.M. Johnst. ssp. *mollis* (Phil.) Mesa; however, in 1997, he revisited the group, removed the three names from synonymy, and, recognizing two taxa at the rank of species, published combinations in *Nolana* for *A. patula* and *A. sphaerophylla*. Unfortunately, Mesa failed to provide full and direct references to the basionym in *Alona*, therefore, the proposed combinations were not validly published, and this small error was rectified by Dillon (2009).

There is at least one mixed collection on the herbarium sheet, *Eggli et al. 2682*. The sheets at SGO (i.e., SGO 145879) and CONC (i.e., CONC 138420) are clearly *N. patula*, but on the Berlin duplicate sheet there is a small branch of *N. sphaerophylla* designated as *Eggli et al. 2682a* (B).

Additional specimens examined: CHILE. **Antofagasta**: 65 km S de Taltal, 3 February 1947, *W. Biese 2252* (SGO 74477); Km 1085, 900 m.a.s.l., 6 November 1969, *C. Jiles 5312* (CONC 92373); Trayecto Agua Verde–Chañaral, 1300 m.a.s.l., 26 February 2001, *C. Latorre, C. Villagrán, & A. Maldonado 244* (CONC 150970); Los Puentes, a la entrada de la carretera a Quebrada Breas, 25°30'S, 70°25'W, 490 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2748/1142* (F 2290735, SGO 159458); Sierra Cifuncho, 25°44'S, 70°33'W, 450 m.a.s.l., 12 October 2005, *F. Luebert*

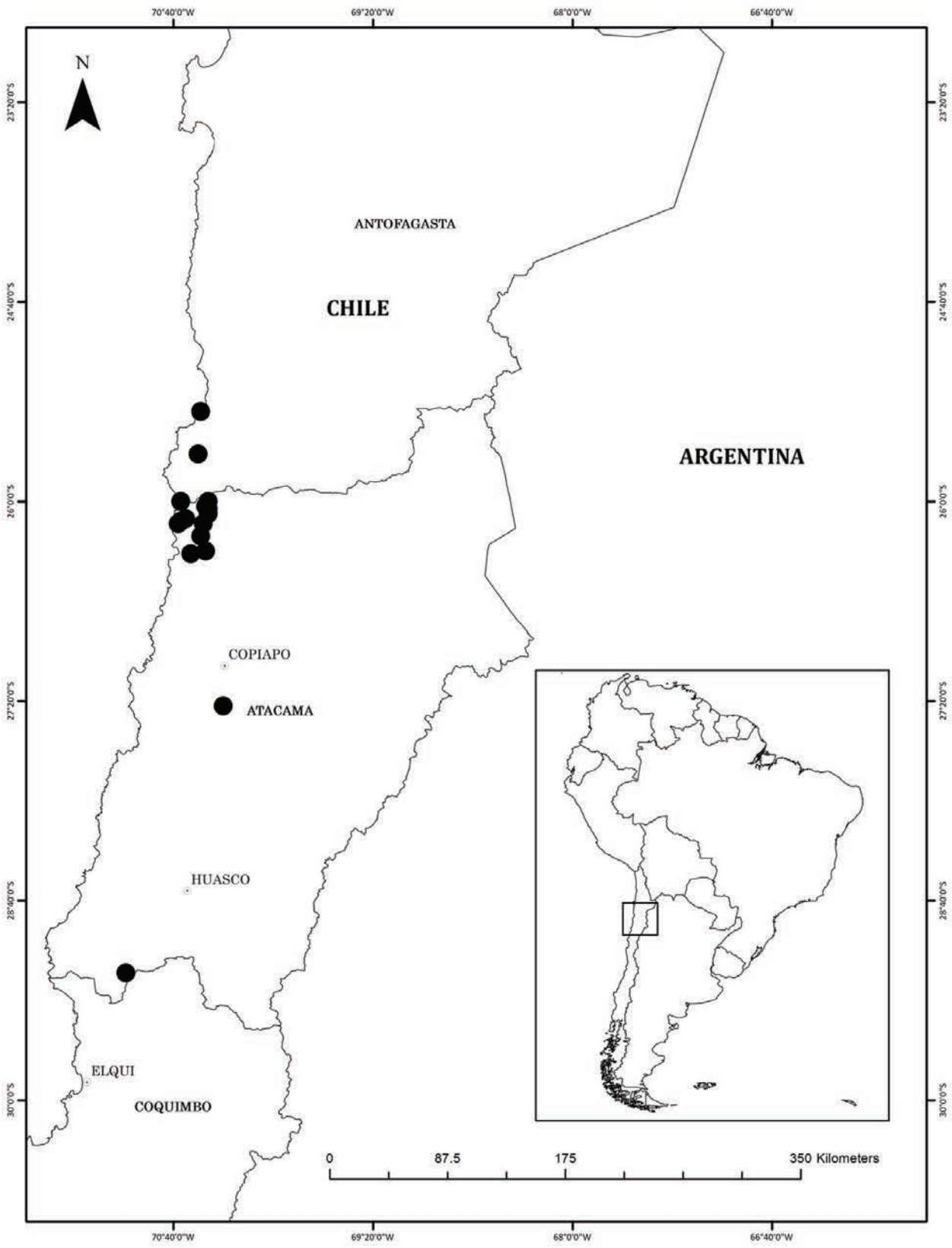


FIGURE 327. Distribution of *Nolana patula* (Phil.) Mesa ex M.O. Dillon.

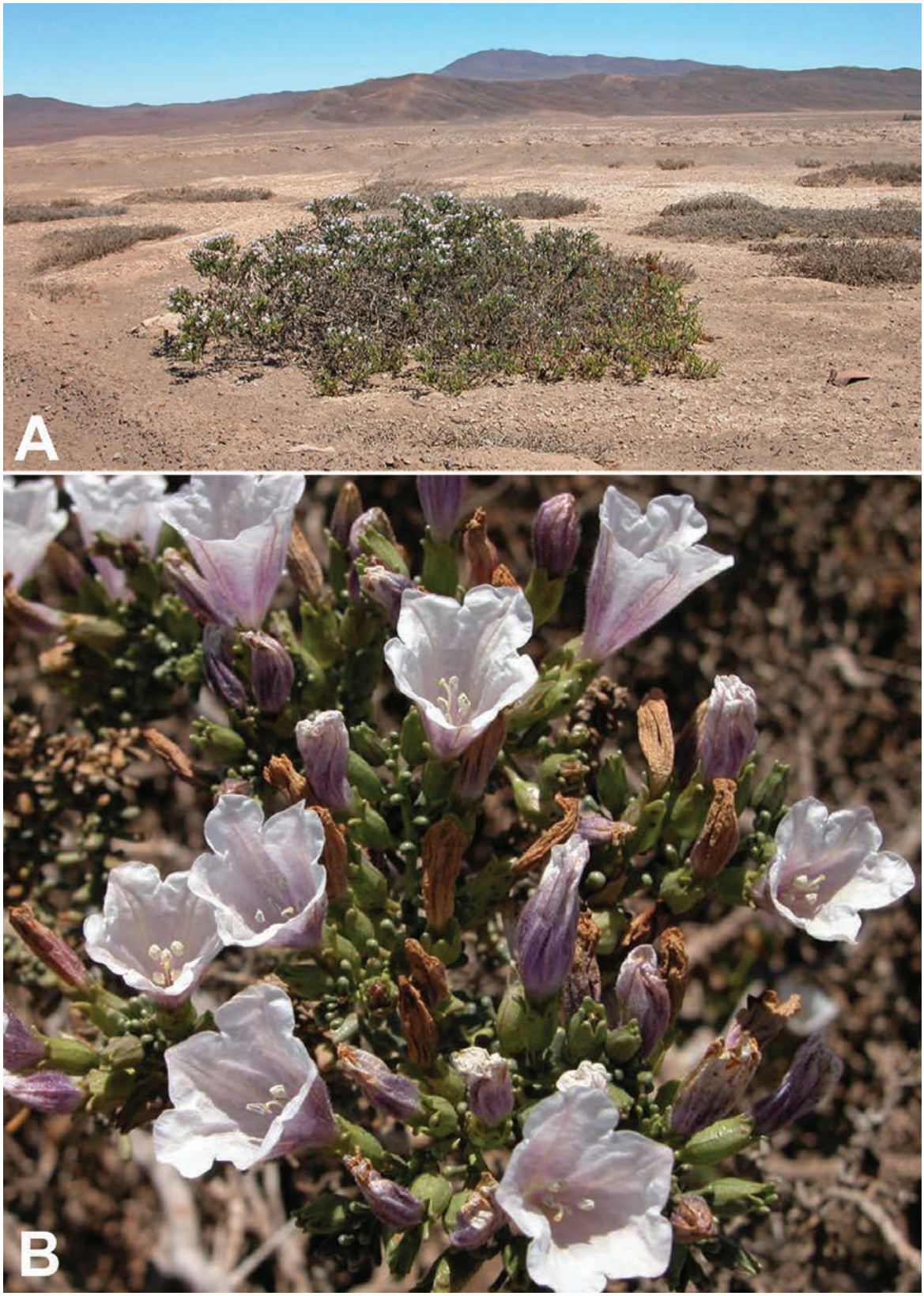


FIGURE 328. *Nolana patula*. **A**, Much-branched, semi-woody shrubs of several meters in diameter; **B,** Corollas white with pale lilac guides, white anther thecae and pollen.

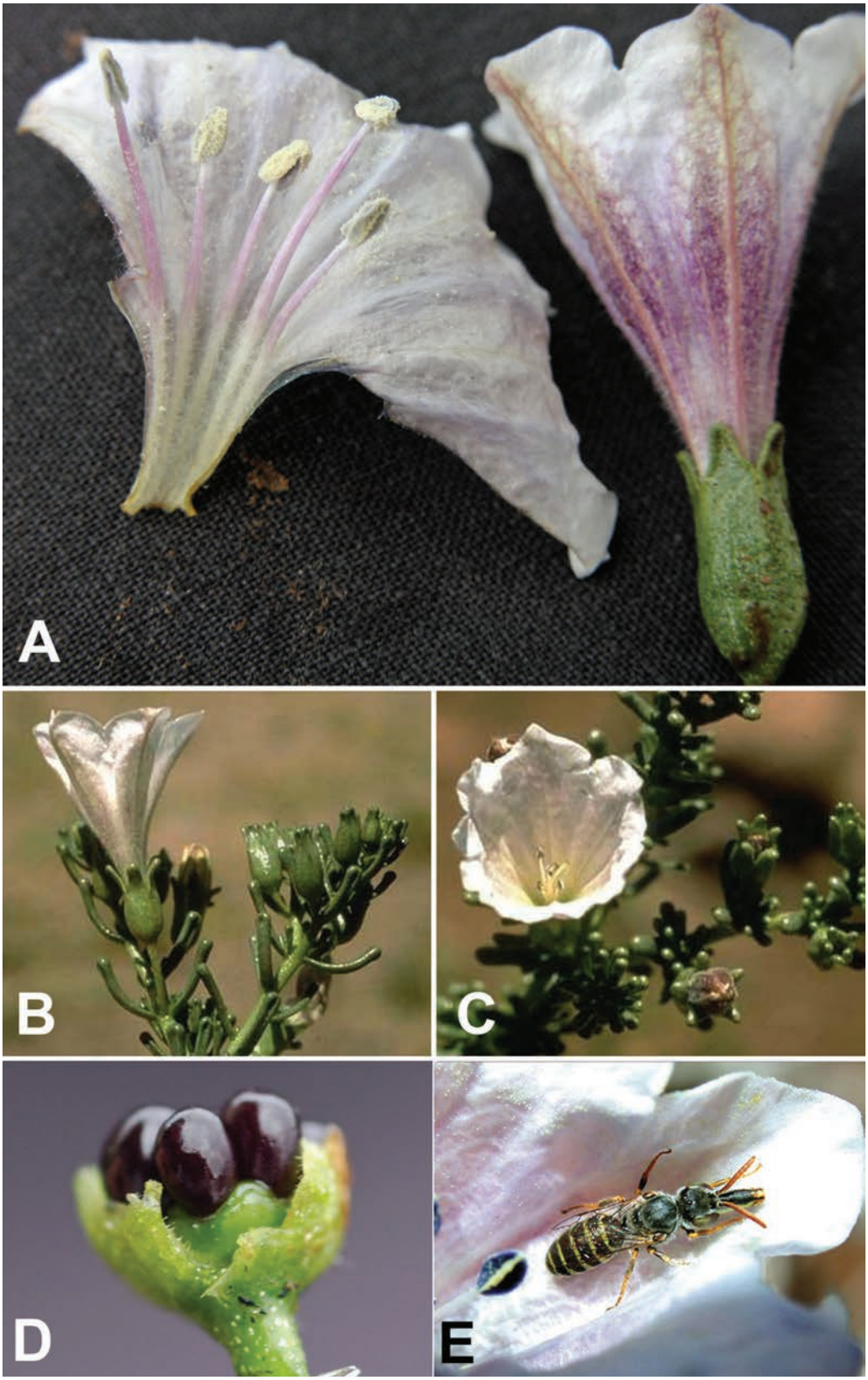


FIGURE 329. *Nolana patula*. **A**, Dissected corolla with pink anther filaments, densely pubescent at the base, calyx cylindrical with triangular lobes; **B**, Lateral view of flower, vegetative parts covered with salt glands; **C**, Frontal view of corolla, slightly zygomorphic; **D**, Gynoecium with mericarps attached basally, pronounced nectary; **E**, Bee, *Xeromelissa roseni*, in the mouth of the corolla.

& N. García 2776/1170 (F 2290687, SGO 159455); camino entre Esmeralda y Pan de Azúcar, cruce a Baritina San Luis, 25°59'10"S, 70°26'18"W, 720 m.a.s.l., 13 October 2005, *F. Luebert & N. García 2812/1206* (F 2290724); al Norte de Sierra Colorado, Km 1020, 27 October 1987, *M. Muñoz S. & I. Meza P. 2265* (SGO 137725); Pan de Azúcar, 600 m.a.s.l., *K. H. Rechinger & W. Rechinger 63498* (B); 8 km S Las Breas, 25°28'S, 70°51'W, 950 m.a.s.l., 15 September 1992, *S. Teillier, P. Rundel, & P. García 2711* (F 2114632, SGO 129360); Taltal, 16 September 1968, *O. Zöllner 2682* (CONC 129673). **Atacama**: Chañaral: Ruta Norte 5 at 3 km N of entrance to Parque Nacional de Pan de Azúcar, 680 m.a.s.l., *M. Acosta, M. F. Leon, & M. Narria 062* (K); Las Bombas, 500 m.a.s.l., 7 February 1960, *V. Behn s.n.* (CONC 31167); 7 km W of PanAmerican Hwy, 25 km from coast, 30–305 m.a.s.l., 9 November 1990, *O. F. Clarke 18-01* (CONC 158542); Ca. 43 km N of Chañaral along Pan-Americana Hwy 5, 26°09'S, 70°28'W, ca. 610 m.a.s.l., 3 December 1987, *M. O. Dillon & S. Teillier 5057* (CONC, E, F 2010280, GH, SGO, US); 21 km W of Pan-American Highway (#5) on northern route to Parque Nacional Pan de Azúcar; ca. 100 km S of Taltal, 26°08'S, 70°37'W, ca. 85 m.a.s.l., 30 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5608* (E, F 2012853, GH); Parque Nacional Pan de Azúcar, Las Lomitas, 6 km E of coast, 26°02'S, 70°33'W, ca. 560 m.a.s.l., 12 November 1997, *M. O. Dillon & C. Trujillo C. 8018* (CONC 150012, E, F 2183339, GH, SGO 143719, US); Central entrance to Parque Nacional Pan de Azúcar, ca. 95 km S of Taltal on Ruta 5, 26°09'S, 70°28'W, 630 m.a.s.l., 26 November 1997, *M. O. Dillon 8101* (CONC 149949, E, F 2182965, SGO 143715); Parque Nacional Pan de Azúcar, 26°07'S, 70°35'W, 200 m.a.s.l., 1 December 1997, *M. O. Dillon 8148* (F 2182958); 5 km E on road to Carrizalillo, 25°00'S, 70°23'W, 600 m.a.s.l., 25 October 2004, *M. O. Dillon & M. Finger C. 8603* (CONC 179072, F 2292814, SGO 158699); Cuesta Portezuelo Blanco on Ruta 5, 26°19'39"S, 70°26'01"W, 450 m.a.s.l., 5 November 2007, *M. O. Dillon & R. Schulz 9058* (F 2292844, SGO 158734); ca. 20 km E of Chañaral along Hwy 5, 26°19'15"S, 70°25'56"W, 426 m.a.s.l., 14 November 2009, *M. O. Dillon & A. Casareggio M. 9102* (CONC, F 2293466, SGO); 95 km S of Taltal, 70 km S on Panamericana from junction with Taltal, 750 m.a.s.l., 26 November 1991, *U. Eggli & B. E. Leuenberger 1778* (B, SGO 145719); 25 km NE of Chañaral long Panamericana (Km 998), 26°18'24"S, 70°26'36"W, 550 m.a.s.l., 16 February 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2682* (B, CONC 138420, SGO 145879); Charrizalillo, ca. 50 km NE of Port of Chañaral, 1921, *J. E. Harding 3* (GH); Km 1000, 800 m.a.s.l., 6 September 1966, *C. Jiles 4944-A* (CONC 34625, CONC 103760); Las Bombas, Km 1015, 750 m.a.s.l., 6 November 1969, *C. Jiles 5310* (CONC 92371); Chañaral, Las Bombas a Pan de Azúcar, 400 m.a.s.l., 9 February 2012, *I. Jimenez & M. Rosas 1228 [Rosas 7932]* (K); Taltal, 5 February 2013, 560 m.a.s.l., *I. Jimenez & M. Rosas 1298 [Rosas 8337]* (K); Dept. Chañaral, Vicinity of Caleta Pan de Azúcar, 18 December 1925, *I. M. Johnston 5834* (GH, K); 10 km N Cruce a Las Bombas, 500 m.a.s.l., 14 September 1994, *L. Loyola 94-2* (CONC 132942); al N de Chañaral en el Km 990, 27 October 1987, *M. Muñoz S. & I. Meza P. 2246* (SGO 137714); between Caldera and Chañaral, 10 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274050); 10 km N of Pan de Azúcar, 15 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274043); límite N Prov. Atacama, 26 January 1950, *A. Pfister s.n.* (CONC 9546); Chañaral, Barquito, 150 m.a.s.l., 26 October 1941, *E. Pisano V. & R. Bravo F. 516* (CONC 144530, SGO 156442); Quebrada 10 km al N del camino Chañaral–Taltal, 10 February1968, *M. Ricardi 5496* (CONC 36122); Quebrada al occidente de Las Bombas, 600 m.a.s.l., 15 February 1968, *M. Ricardi 5540* (CONC 36109); Quebrada detrás de las Bombas, 500 m.a.s.l., 30 April 1972, *M. Ricardi, E. Weldt, & M. Quezada 15* (CONC 36311); carretera Panamericana, al norte de Copiapó, 19 March 1961, *M. Ricardi, C. Marticorena, & O. Matthei 17* (CONC 27490); a 60 km N de Chañaral, 22 February 1969, *M. Ricardi & O. Parra 87* (CONC 33015); camino de Chañaral a Caldera, Km 13, *M. Ricardi, C. Marticorena, & O. Matthei 1092* (CONC 36179); Carretera Panamericana, Las Bombas, 17 February 1970, *R. Rodríguez & P. Rivera 35* (CONC 34911); Parque Nacional Pan de Azúcar, 100 m.a.s.l., *F. Schlegel 8104* (CONC 115652); Rt. 5 ca. 20 km S of entrance to Taltal, 500 m.a.s.l., 13 April 1994, *C. M. Taylor & A. Pool 11597* (CONC 143573); Chañaral, 20 km E Cerro Vetado, 26°20'S, 70°27'W, 4 October 1987, *S. Teillier 660* (CONC 143323, SGO 141771); 20 km a S de Chañaral, 1 July 1970, *E. Weldt 457* (CONC 33571); Caldera, 16 September 1967, *O. Zöllner 1734* (CONC 129672); Pan de Azúcar, 19 September 1979, *O. Zöllner 10501* (CONC 129583).

G17. ***Nolana peruviana*** (Gaudich.) I.M. Johnst., Contrib. Gray Herb. 112: 66. 1936. Fig 330–333.

Bargemontia peruviana Gaudich., Voy. Bonite pl. 8. 1841. TYPE: CHILE. Antofagasta: Cobija, 1–3 July 1836, [Bolivia], *C. Gaudichaud 8* (Lectotype designated by Mesa-M., 1981: P [00605860]; Isolectotypes: F [F 680791, F 976539], FI [FI 132656, FI009584], G [G00383948, G00383961, G00383964], P [P00605861, P00605862]).

Digital image: Lectotype of *Bargemontia peruviana* from the National Museum of Natural History, Paris [P00605860]. http://mediaphoto.mnhn.fr/media/1442764935349SRehMEhKpfbGmgbM

Spreading *shrubs* to ca. 1.5 m tall, 1–2 m in diam.; stems erect to decumbent, pubescent with short, capitate-glandular to branched-eglandular trichomes. *Leaves* alternate to fasciculate, blades broadly clavate to globular-obovate, 5–10 mm long, 1.0–1.5 mm wide, gray green, densely pubescent with stout, dendritic to unbranched trichomes, rarely glabrous, succulent, margins revolute or not; petioles indistinct with attenuate bases. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 3–12 mm long, densely pubescent. *Flowers* 5-merous; calyces 5–7 mm long, campanulate, enlarging in fruit, 5-dentate, teeth unequal, erect, linear-acuminate, teeth less than 1/2 of total calyx length; corollas suburceolate, 6–9 mm long, weakly

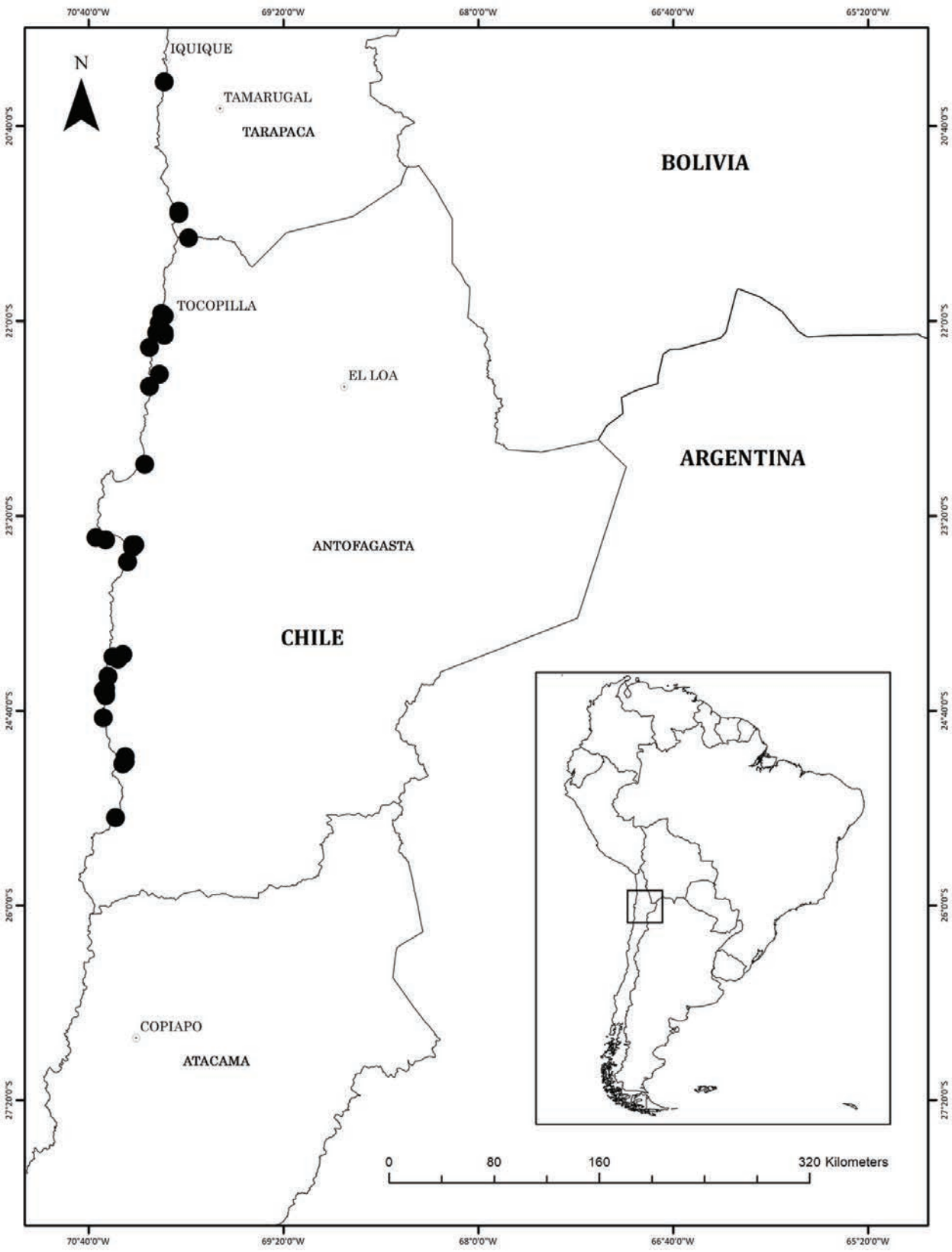


FIGURE 330. Distribution of *Nolana peruviana* (Gaudich.) I.M. Johnst.

zygomorphic to sub-regular, whitish, greenish-white to, rarely, lilac; stamens unequal, 2 longer and 3 shorter; filaments widened at the base, pubescent or not; nectary disc crateriform, margin sinuate; style as long as the shorter filaments, gynobasic; stigma capitate or lobate. *Mericarps* 3–5, unequal; seeds 2–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet refers to the geographic locality of the type when the species was first discovered and described; however, at the time of the first collection, said to be Cobija, the region was under Bolivian control. After the War of the Pacific (1879–1883), the boundaries were redrawn, and Chile occupied both Bolivia's Pacific coastal territory and Peru, north to its current border between Arica and Tacna.

Distribution and Ecology: Chile, Regions of Arica y Parinacota, Tarapacá and Antofagasta; (0–)200–800(–1600) m.a.s.l. (Fig. 330). It is recorded from a wide variety of habitats in sandy soils; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Illustration: Fig. 331. Illustration of *Nolana peruviana*. Plate 8. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana peruviana is a distinctive spreading shrub with broadly clavate to globular-obovate leaf blades, seldom larger than ca. 10 mm long and ca. 1.5 mm wide, densely covered with dendritic trichomes, that make the entire plant look canescent or light gray (Fig. 332A). The suburceolate, yellowish corollas with small lobes are unique in the genus; no other species exhibits corollas in this shape or size (Fig. 332B–C). *Nolana peruviana* can grow sympatrically with several different species, such as *N. ramosissima* (Fig. 333A). Young stems have more elongate leaves with attenuate bases (Fig. 333B). This species is also infested by parasitic wasps that lay their eggs in the developing galls on the stems (Fig. 333C).

One glabrous collection from Alto Huanillo (Iquique, *Pinto s.n.*, SGO 142981) has a leaf morphology that compares favorably with typical collections of *Nolana peruviana*. This may indicate that the presence or absence of pubescence is determined by a few genes.

Additional specimens examined: CHILE. **Arica y Parinacota**: Prov. de Arica, Punta Madrid, 1000 m.a.s.l., 22 September 2002, *R. Pinto 182* (SGO). **Tarapacá**: Iquique, Alto Huanillo, 21°15'S, 70°03'W, 27 January 1998, *R. Pinto s.n.* (SGO 142981); Alto Chipana, 21°16'S, 70°03'W, 800 m.a.s.l., 31 January 1998, *R. Pinto s.n.* (SGO 142970); Alto Punta Gruesa, 20°22'S, 70°09'W, 14 December 1997, *R. Pinto s.n.* (SGO 142971); Alto Chipana, 21°16'S, 70°03'W, 15 October 1997, *W. Sielfeld 8* (SGO 143055). **Antofagasta**: Antofagasta, Quebrada de la Plata, 40.9 km N of Paposo, 191 m.a.s.l., 17 November 2005, *M. Acosta, P. Guerrero, & M. Rosas 434* (K); Quebrada La Chimba, *C. Aedo 7017* (CONC 161676, MA); Cordillera Costa, quebrada paralela a la Costa, 8 km al interior, frente a Caleta Coloso, 150–650 m.a.s.l., April 1992, *J. Anabalón s.n.* (SGO 126922); Quebrada La Chimba, 23°32'15"S, 70°21'33"W, 430 m.a.s.l., 19 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 3* (E 00230523); Península Moreno, cerros al O de Juan López, 23°30'S, 70°33'W, 200 m.a.s.l., 18 October 1992, *G. Baumann 2* (CONC 122468, SGO 127836); Cerro Cerisso, road to airport SE of Antofagasta, 100 m.a.s.l., 27 February 1939, *A. A. Beetle 26185* (GH, K); Quebrada al norte de la ciudad de Antofagasta, *F. Behn s.n.* (CONC 36159); Cobija, Quebrada Aguada Caña, 500–800 m.a.s.l., 16 October 1949, *W. Biese 2799* (SGO 97252); Cobija, Quebrada Aguada Cañas, 500–800 m.a.s.l., 16 October 1949, *W. Biese 2801* (SGO 96620); Quebrada Blanco Encalada, 50–250 m.a.s.l., 11 December 1949, *W. Biese 3141* (SGO 96745); 10 km al Sur de Caleta Blanco Encalada, 200–800 m.a.s.l., 11 December 1949, *W. Biese 3149* (SGO 96752); Quebrada La Chimba, *Buchanan s.n.* (CONC 36954); Quebrada La Chimba, 27 September 1953, *A. Cabrera 11358* (SGO 126669); Quebrada La Chimba, 27 September 1953, *A. Cabrera 11360* (SGO 126671); Quebrada La Chimba, *A. Cabrera 11358* (CONC 24176); Vicinity of Miguel Díaz, directly N of Quebrada Iscuña, 24°33'S, 70°33'W, 100–350 m.a.s.l., 15 December 1987, *M. O. Dillon & S. Teillier 5303* (F 2010885); Quebrada La Chimba, 23°33'S, 70°22'W, 300–550 m.a.s.l., 17 December 1987, *M. O. Dillon & S. Teillier 5346* (F 2010910); near Quebrada Botija, ca. 11 km N of Miguel Díaz, 24°31'S, 70°33'W, 18 December 1987, *M. O. Dillon 5354* (F 2010904); Quebrada Paposo, 25°01'S, 70°25'W, 350–950 m.a.s.l., 28 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5545* (F 2010224); ca. 15 km E (by road) of Caleta El Cobre, below the mirador, 24°17'S, 74°26'W, 600–660 m.a.s.l., 4 October 1988, *M. O. Dillon & D. Dillon 5622* (CONC, E, F 2013668, GH, SGO, US); Aguada directly W of Quebrada de Iscuña, ca. 46 km S of Caleta El Cobre, 24°34'S, 70°33'W, 20–30 m.a.s.l., 4 October 1988, *M. O. Dillon & D. Dillon 5634* (CONC, F 2013657, GH); Tocopilla, near Punta Grande, ca. 8 km N of Gático, just S of Caleta Buena, 22°27'S, 70°15'W, ca. 5 m.a.s.l., 14 October 1988, *M. O. Dillon & D. Dillon 5695* (E, F 2014379, US 3470036); Quebrada ca. 15 km E of Tocopilla, 22°05'S, 70°09'W, 520–550 m.a.s.l., 18 October 1988, *M. O. Dillon & D. Dillon 5708* (E, F 2014372, GH); Quebrada 2–3 km N of Tocopilla, 22°05'S, 70°11'W, 150–250 m.a.s.l., 18 October 1988, *M. O. Dillon & D. Dillon 5722* (E, F 2045833, GH); Quebrada La Chimba, 23°33'S, 70°22'W, 380–480 m.a.s.l., 11 November 1988, *M. O. Dillon & D. Dillon 5880* (F 2144386); north side of Punta Dos Reyes, ca. 39 km S of Quebrada El Cobre, 5–10 m.a.s.l., 13 November 1988, *M. O. Dillon & D. Dillon 5901* (F 2144374); Quebrada Paposo, 24°59'S, 70°25'W, 880 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8037* (CONC 149992, E, F 2183333, GH, K, SGO 143710); near mouth of Quebrada Punta Plata, 24°43'S, 70°34'W, 30 m.a.s.l., 23 November 1997, *M. O. Dillon, C. Trujillo C., & M. Villarroel O. 8091* (F 2183352); Quebrada de La Chimba, 23°32'16"S, 70°21'33"W, 500 m.a.s.l., 21 October 2004, *M. O. Dillon & M. Finger C. 8593* (CONC 179071, F 2292815, SGO 158700); ca. 36 km N of Paposo, 24°41'05"S, 70°33'52"W, 100 m.a.s.l., 1

FIGURE 331. Illustration of *Nolana peruviana*. Plate 8. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

FIGURE 332. *Nolana peruviana*. **A**, Spreading shrubs; **B**, Clavate to globular-obovate leaf blades; **C**, Suburceolate, yellowish corollas with small lobes.

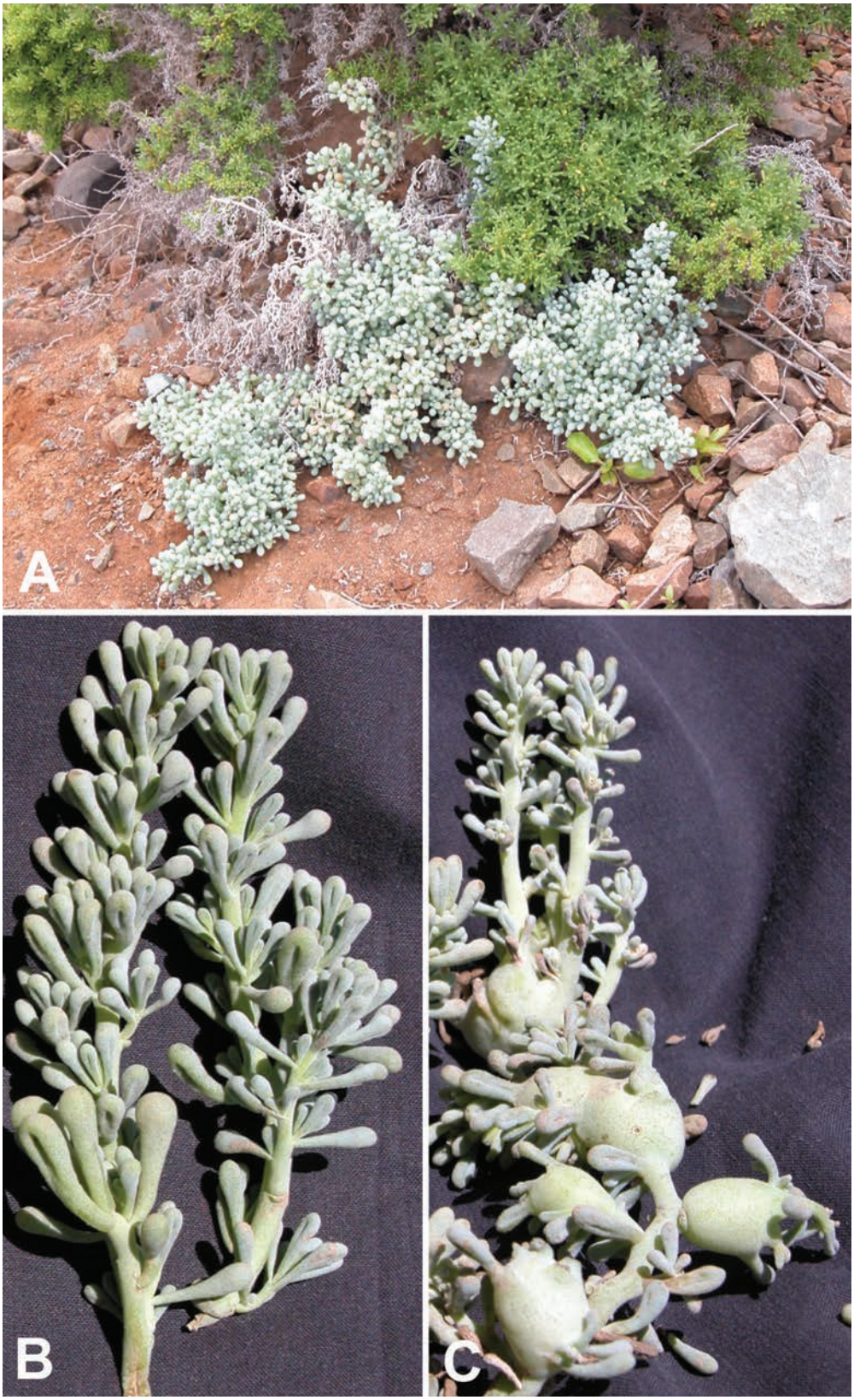


FIGURE 333. *Nolana peruviana*. **A**, Growing sympatrically with *N. ramosissima*; **B**, Young stems with elongate leaves; **C**, Galls developing due to parasitic wasps laying eggs in the developing tissues.

November 2004, *M. O. Dillon & M. Finger C. 8638* (F 2292829, SGO 158716); ca. 34 km N of Paposo, N of Punta Plata, 24°42'54"S, 70°34'13"W, 100 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8681* (CONC 179107, F 2292794, SGO 158924); ca. 27 km N of Taltal, 25°10'07"S, 70°26'44"W, 26 September 2010, *M. Dillon 9123* (CONC, F 2331756, SGO); Peninsula Moreno, SW flank of Morro Moreno above Caleta Errázuriz, 23°28'57"S, 70°36'43"W, 20 m.a.s.l., 18 February 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2698* (B, CONC 138564, SGO 145881); 50 km SW of Panamericana towards El Cobre, 10 km NE of El Cobre, 24°17'51"S, 70°29'38"W, 800 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2849* (B, CONC 138508, SGO 146075); 22 km S of El Cobre towards Paposo, 78 km N of Paposo, 24°25'38"S, 70°31'57"W, 100 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2857* (B, CONC 138486, SGO 146070); 43 km SW of the Panamericana towards El Cobre, 17 km NE of El Cobre at Km marker 45, 24°19'01"S, 70°27'19"W, 1020 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2845* (B, CONC 138512, SGO 146074); 16 km N of Tocopilla on Ruta 1 towards Iquique, 21°58'00"S, 70°10'29"W, 100 m.a.s.l., 6 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2841* (B, CONC 138511, SGO 146041); 30 km S of Tocopilla on Ruta 1 towards Antofagasta, 22°20'17"S, 70°14'46"W, 60–100 m.a.s.l., 7 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2842* (B, CONC 138524, SGO 146071); Tocopilla, Cerro Rosario, 1 November 1941, *M. R. Espinosa s.n.* (SGO 139551); falda NE Quebrada Rosario, 12 November 1941, *M. R. Espinosa s.n.* (SGO 139550); close to Campa Indigena, 40 km before Tocopilla, 0 m.a.s.l., 12 November 1995, *K. Gengler 84* (SGO 137346); Tocopilla, *Gülland s.n.* (CONC 129668); Tocopilla, *G. Hartmann s.n.* (CONC 32322); Quebrada La Chimba, *A. Hoffmann & R. Rodríguez 15* (CONC 99204); Tocopilla, *F. Jaffuel 1043* (CONC 129669, GH); Antofagasta, 29 October 1930, *F. Jaffuel 1118* (GH); Tocopilla, *F. Jaffuel 2517* (GH);Taltal, *F. Jaffuel 2594* (CONC 68826, GH); Antofagasta, 6 November 1931, *F. Jaffuel 2620* (GH); Tocopilla, ladera cerca de Mina Magali, 450 m.a.s.l., 28 September 2005, *F. Luebert & N. García 2559/953* (F 2290734); Tocopilla, 22°03'12"S, 70°10'29"W, 275 m.a.s.l., 29 September 2005, *F. Luebert, N. García, & N. Schulz 2563/957* (F 2290684); Cerro Moreno, 23°29'06"S, 70°35'30"W, 570 m.a.s.l., 2 October 2005, *F. Luebert & N. García 2606/1000* (F 2290741); Camino entre Ruta 5 y Caleta El Cobre, 24°18'49"S, 70°27'11"W, 1020 m.a.s.l., 4 October 2005, *F. Luebert & N. García 2613/1007* (F 2290681); Tocopilla, Quebrada Chapacase, 22°01'20"S, 70°10'15"W, 500–600 m.a.s.l., 21 October 2009, *F. Luebert & A. Moreira M. 2986* (SGO 158968); Quebrada del Río Loa, 8 km al interior desde la desembocadura, 21°26'S, 69°59'W, 20–30 m.a.s.l., 26 September 1996, *O. Matthei 469* (CONC 137073, SGO 152872); 18 km al norte de Tocopilla por la Ruta 1, 21°56'S, 70°10'W, 400 m.a.s.l., 26 September 1996, *O. Matthei 472* (CONC 137076, SGO 152876); Camino de Tocopilla a María Elena, a 2 km de Tocopilla, 22°05'S, 70°10'W, 320 m.a.s.l., 26 September 1996, *O. Matthei 476* (CONC 137080, MA, SGO 152871); Camino de Tocopilla a Antofagasta, 29 km al sur de Tocopilla, 22°21'S, 70°15'W, 60 m.a.s.l., 27 September 1996, *O. Matthei 485* (CONC 137089, SGO 152873); Quebrada de La Chimba, a 16 km al NO de Antofagasta, 500 m.a.s.l., 16 December 1942, *C. Muñoz P. 3643* (SGO 119111); 20 km N Paposo, Quebrada de Médano, 1000–1600 m.a.s.l., April 1985, *H. Niemeyer F. s.n.* (F 2065893); N of Antofagasta, 9 November 1991, *M. Ono & T. Masuzawa s.n.* (MAK 274955); Cobija, *R. Pearce s.n.* (K); Antofagasta, 100–300 m.a.s.l., 3 April 1925, *F. W. Pennell 13017* (F 557493, GH, K, US 1343020); Tocopilla, *E. Perry 4378* (CONC); camino de Tocopilla a Antofagasta, *E. Perry 6076* (CONC), *6974* (CONC); Quebrada Barriles, *E. Perry 6981* (CONC); Quebrada Paposo, *A. Pfister 9520* (CONC); Quebrada Chapacase, 7 km al N de Tocopilla, *M. Quezada & E. Ruiz 11* (CONC 121069); Camino de Tocopilla a la Quebrada de Mamilla, *M. Ricardi, C. Marticorena, & O. Matthei 1066* (CONC 30068); Cuesta Barriles, *M. Ricardi 3025* (CONC 18258); Quebrada La Chimba, 23°32'S, 70°21'W, 11 November 1996, *R. Rodríguez 3088* (CONC 136608; SGO 152925); Vicinity of Antofagasta, 31 October 1914, *Mr. & Mrs. J. N. Rose 19420* (US 761948). Tocopilla, Quebrada Mamilla, *F. Schlegel 7709* (CONC 99804); Tocopilla, Quebrada Mina Indiana, al N de Paso Malo, *F. Schlegel 7715* (CONC 99797); Cuesta Barriles, camino Calama–Tocopilla, *S. Teillier 4790* (CONC 150940); 10 km al sur de Tocopilla, *E. Weldt 454* (CONC 33624); 10 km SE of Antofagasta, ca. 200 m.a.s.l., 17 November 1935, *J. West 3861* (GH).

G18. ***Nolana philippiana*** M.O. Dillon & Luebert, Arnaldoa 14(2): 203. 2007. TYPE: CHILE. Antofagasta: Prov. Antofagasta, ca. 15 km SE of Caleta El Cobre, below the mirador, 24°20'S, 70°26'W, 700 m, 4 October 1988, *M. O. Dillon & D. Dillon 5625* (Holotype: SGO; Isotypes: E, F [F 2013665], G, GH, HSP, US). Fig. 334–336.

Digital image: Isotype of *Nolana philippiana* from the Field Museum, Chicago [F 2013665]. https://collections-botany.fieldmuseum.org/catalogue/365168

Annual to short-lived, perennial *herbs*, to ca. 30 cm tall; stems prostrate to strongly decumbent to procumbent, ca. 50 cm long, much-branched, purplish, villous. *Leaves* alternate, blades oblong to oblanceolate, 20–30 mm long, 5–7 mm wide, strongly concave adaxially, succulent, villous with capitate-glandular trichomes, apically rounded, basally cuneate, sessile, margins strongly revolute. *Inflorescences* of solitary flowers, terminal and axillary; pedicels filiform, glabrous, (5–) 9–13 mm long. *Flowers* 5-merous; calyces campanulate, 4.0–4.5 mm wide at anthesis, glabrous, tube 4.0–4.5 mm long, 5–6 mm wide; 5-lobed, lobes lanceolate, equal, 6–7 mm long, 3.5–4.5 mm wide; corollas infundibularis, 35–40 mm long, 30–40 mm wide distally, pale lavender, inner throat white, without guides, externally pubescent, trichomes uniseriate and glandular, tube ca. 30 mm long, 5-lobed, lobes obtuse, ca. 10 cm wide; stamens

FIGURE 334. Distribution of *Nolana philippiana* M.O. Dillon & Luebert.

FIGURE 335. *Nolana philippiana*. Robust flowering plants growing in the type locality in 1988.

FIGURE 336. *Nolana philippiana*. **A–B**, Close-up of procumbent stem apices and corollas.

5, included, filaments inserted on lower third of corolla, unequal, three 6–7 mm long, two 7–10 mm long, pilose at the bases; anther thecae white, pollen white; ovary glabrous, basal nectary, carpels 5, style included, stigma capitate, green. *Mericarps* 6–10, spherical, 2–4 mm in diam., included within the expanding calyx; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Rudolph Amandus Philippi (b. 1808–d. 1904), a doctor by training but a naturalist by inclination. R. A. Philippi began his career as a Professor of Botany and Zoology at the Universidad de Chile, and, in 1853, was named Director of the Museo Nacional de Historia Natural, a job he held until 1897. His wide-ranging interests in natural history have had an enduring influence on the disciplines of archaeology, anthropology, botany, malacology, paleontology, and zoology in Chile. Philippi collected throughout Chile, and his work resulted in the publication of over 3000 named species of plants, including over 50 *Nolana* species of which ten are currently recognized. Perhaps one of his most important efforts was the publication of his observations and the plants he encountered during an extended trip into the northern Atacama Desert (Philippi, 1860). The plants described by R. A. Philippi have been the focus of important publications by C. Muñoz P. (1960), M. Muñoz S. (1973), and Taylor and Muñoz S. (1994).

Distribution and Ecology: Chile, Region of Antofagasta; 300–700 m.a.s.l. (Fig. 334). It is recorded from sandy soils in only a few localities within reach of coastal fog; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana philippiana is a distinctive annual to perennating herb (Fig. 335). In 1988, large individuals were encountered near Caleta El Cobre at ca. 700 m.a.s.l. along the road that turns southeast at the mine headquarters and abruptly climbs up to over 1600 m.a.s.l. These plants had showy, pale lavender corollas with clear white throats that were absent of guides (Fig. 336A–B). Collections from this area were initially identified as morphological variants of *Nolana aplocaryoides*; however, with increased knowledge of the variation exhibited by that taxon, they were recognized as distinct.

The only other plants recorded from this locality were *Copiapoa solaris* Ritter (Cactaceae). During the 1987–1988 El Niño event, additional precipitation stimulated an unprecedented blooming event. This taxon has not been collected by me since that time, despite repeated visits to the type locality. A second collection, *Dillon & Dillon 5624*, was made just below the type locality at 600–660 m.a.s.l.; field notes indicate that it was considered the same as *Dillon & Dillon 5625*, but with shorter, white corollas. Data from molecular studies is not available.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, ca. 15 km E of Caleta El Cobre, below the mirador, 24°20'S, 70°26'W, 600–660 m.a.s.l., 4 October 1998, *M. O. Dillon & D. Dillon 5624* (E, F 2013666, GH); Quebrada del Cobre, 24°14'S, 70°31'W, 300 m.a.s.l., 2 October 1991, *M. Quezada y E. Ruiz 132* (CONC 121188, SGO 127899); Camino Caleta El Cobre–Blanco Encaldad, 24°15'S, 70°33'W, 1 October 1987, *S. Teillier 483* (CONC 138406, SGO 141651).

G19. ***Nolana ramosissima*** I.M. Johnst., Contrib. Gray Herb. 112: 72. 1936. TYPE: CHILE. Antofagasta: about dry rocky slope at mouth of Quebrada de Guanillos near Paposo, ca. lat. 25°02'S, a dense succulent globose bush 9–12 dm tall, flowers blue, 8 December 1925, *I. M. Johnston 5590* (Holotype: GH [00282377]). Fig. 337–340.

Digital image: Holotype of *Nolana ramosissima* from Harvard University Herbaria, Cambridge [GH00282377]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00282377

Homotypic synonyms: *Nolana peruviana* (Gaudich.) I.M. Johnst. subsp. *divaricata* (Lindl.) Mesa, Fl. Neotropica 26: 81. 1981; *Dolia salsoloides* Lindl. auct. Gaudich., Voy. Bonite, pl. 113. 1851, non Lindl., 1844.

Erect to spreading *shrubs*, 1–3 m tall, 1–2 m in diam.; stems intricately branched, densely leafy, glandular-pubescent with capitate-glandular trichomes, and/or longer crooked trichomes without capitate-glandular apices. *Leaves* alternate to fasciculate, blades linear, 5–13 mm long, 0.5–1.1 mm wide, pubescent with capitate-glandular trichomes, margins revolute, strongly concave adaxially, basally attenuate, apically rounded. *Inflorescences* of solitary flowers, terminal and axillary; pedicels 1–5 mm long, erect to ascending. *Flowers* 5-merous; calyces narrowly campanulate to cupulate, 8–10 mm long, tube 1.5–2.0 mm long, lobes deeply cut to the bottom of the cup, subequal, strongly reflexed in fruit; corollas 12–14 mm long, narrowly tubular, light blue; nectary well-developed. *Mericarps* 3–8, ovoid-elongate, attached at base, shiny, smooth, 2–3 mm long, seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet refers to the Latin, *rami-*, and *ramossisimus*, meaning very much branched, and typifies the densely branching habit of this compact shrub.

Distribution and Ecology: Chile, Region of Antofagasta; sea level to 1100 m.a.s.l. (Fig. 337). It is reported from several near-ocean localities; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana ramosissima is one of the largest shrubs in the genus, with older individuals reaching 3–4 m tall and similar in width (Fig. 338). The trunks are well-developed (Fig. 338B), and the plants occur where recurrent moisture is available. Younger individuals are smaller but very compact, much-branched shrubs. The corollas are blue to violet (Fig. 339A), and some white morphs occur. They have slender calyx lobes which are cut nearly to the base of the calyx tube (Fig. 339B). The corollas are clearly zygomorphic with an enlarged dorsal lobe (Fig. 339C, 340A), and the corolla just surpasses the unequal calyx lobes (Fig. 340B). The mericarps are oblong and basally affixed (Fig. 340C–D).

Two collections tentatively placed under *N. ramosissima* may represent an undescribed species: *C. Jiles 4975* and *S. Teillier 585*. They are small shrubs, 10–30 cm tall, with succulent leaves and white flowers; both are recorded from between Taltal and Paposo at or near sea level.

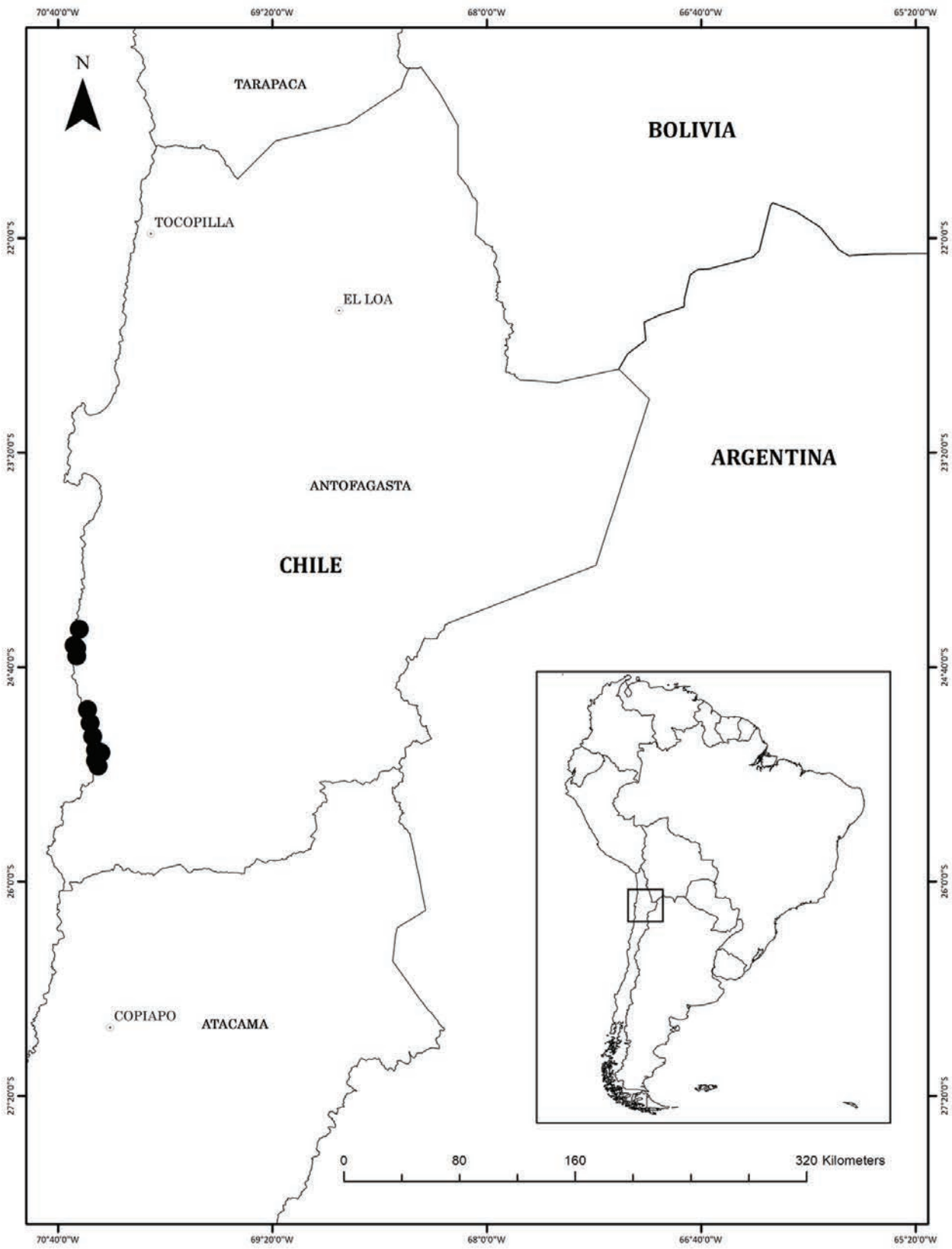


FIGURE 337. Distribution of *Nolana ramosissima* I.M. Johnst.

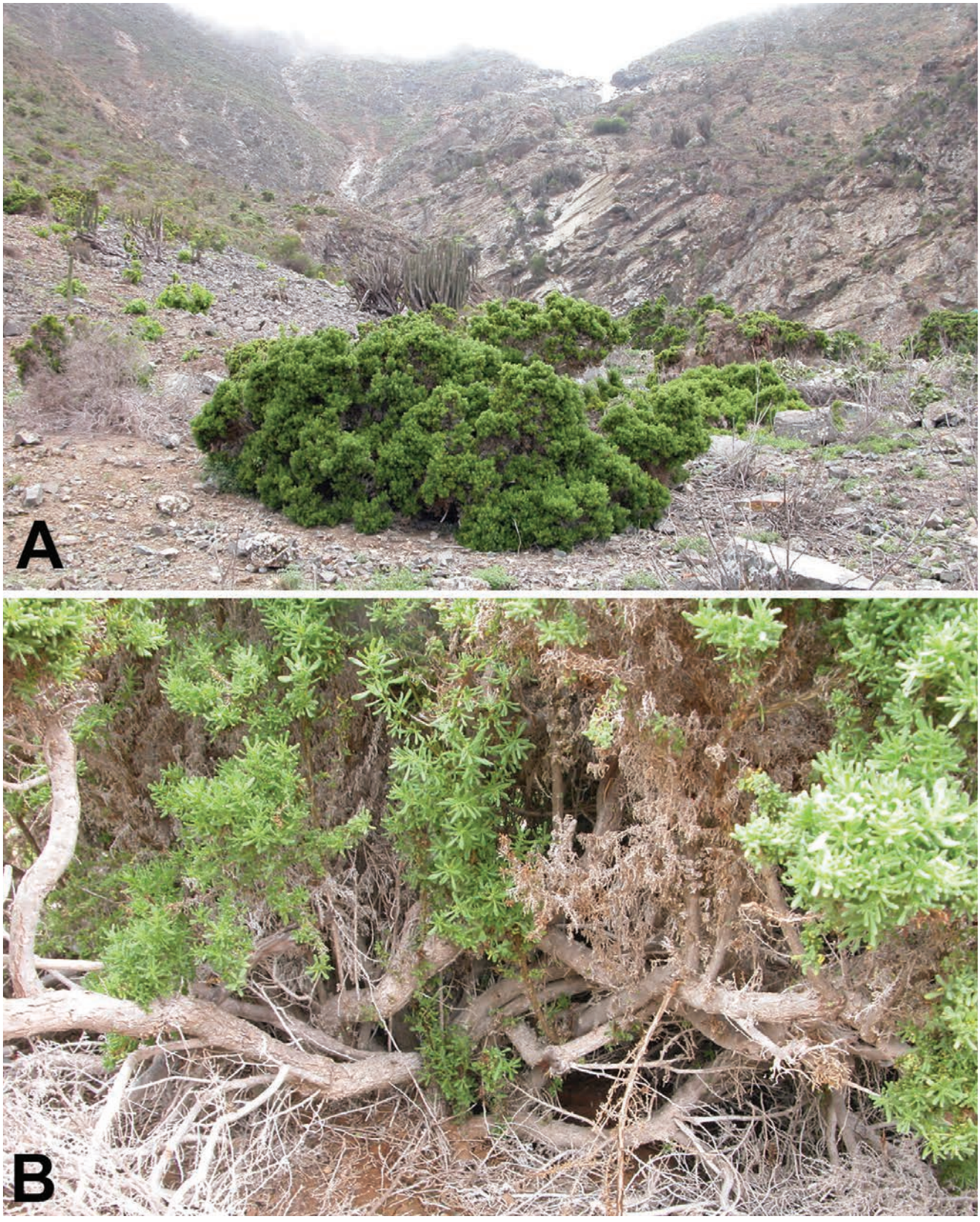


FIGURE 338. *Nolana ramosissima*. **A**, Large, spreading shrubs three to four meters in width; **B**, Thick woody stems with bark.

FIGURE 339. *Nolana ramosissima*. **A**, White and blue to violet corollas; **B**, Slender calyx lobes cut to the base; **C**, Corollas zygomorphic with enlarged dorsal lobe.

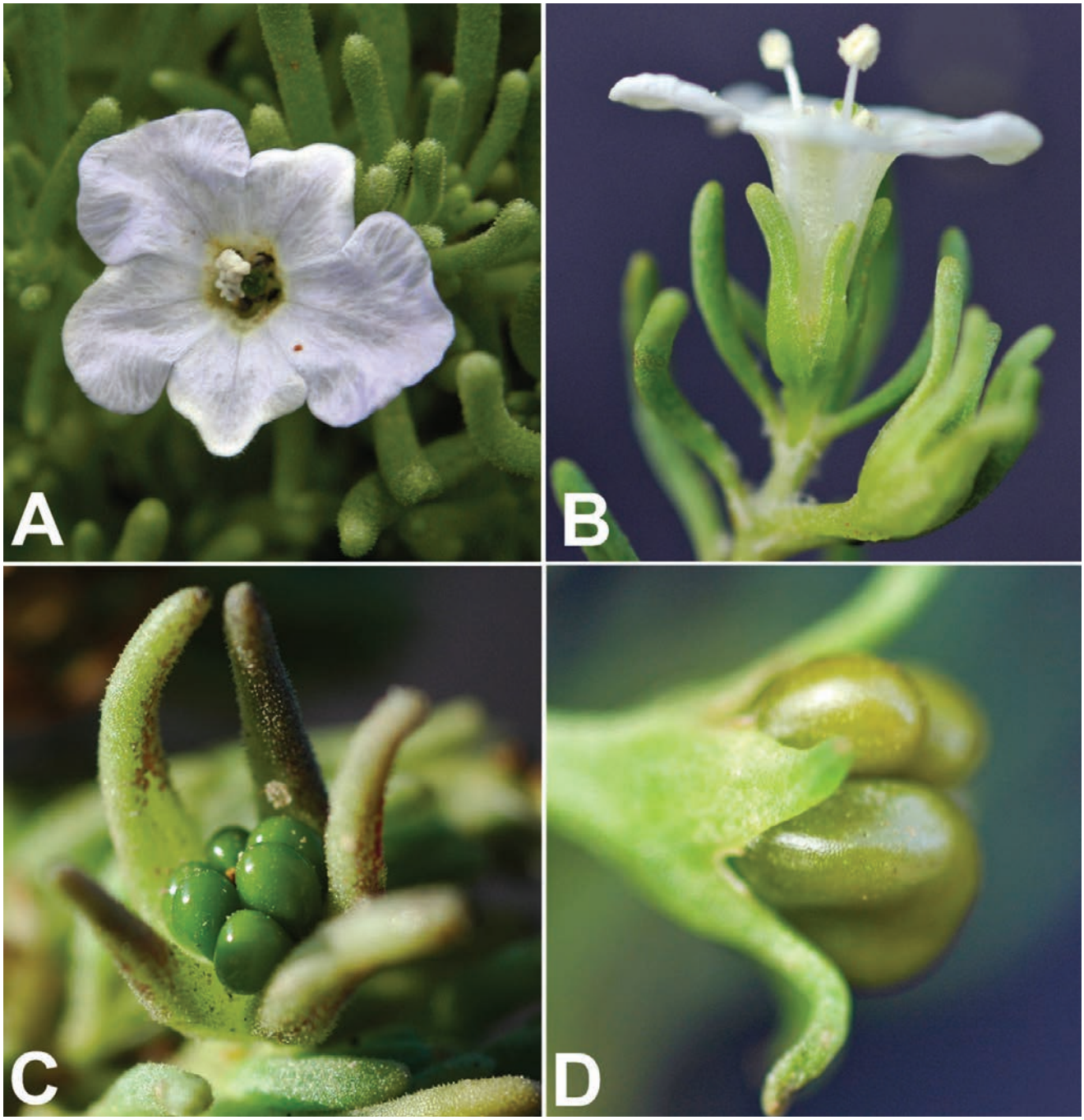


FIGURE 340. *Nolana ramosissima*. **A**, Zygomorphic corolla; **B,** Corolla surpasses the unequal calyx lobes; **C–D**, Mericarps oblong and affixed basally.

In 1929, under a discussion of *Bargemontia salsoloides*, Johnston described a pair of his collections from northern Chile: "A dense light-green succulent globose bush 1.0–1.5 m tall. It was collected on a seaward slope at the mouth of Quebrada San Ramon near Taltal (*Johnston 5167*) and near the mouth of Quebrada Guanillo near Paposo (*Johnston 5590*). The elongate corollas are bluish and are glabrous within. The only other material I have seen that is conspecific is a collection made near Paposo by Philippi."

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Quebrada Chinchilla, 22.6 km N of Caleta Paposo, 290 m.a.s.l., 15 January 2003, *M. Acosta, M. F. Leon, & M. Vargas 057* (K); Quebrada Peralito, Cuesta Paposo, 25°01'18"S, 70°26'39"W, 488 m.a.s.l., *M. Acosta, P. Guerrero, & M. Rosas 423* (K); 4 km S of Botija, 24°32'13"S, 70°34'17"W, 83 m.a.s.l., 20 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 11* (E 00230546); 4 km S of Botija, 24°32'13"S,

70°34'17"W, 83 m.a.s.l., 20 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 12* (E00420134); 10 km al Sur de Caleta Blanco, *W. Biese 3205* (SGO 96808); Quebrada Guanillos, 10 km al N del Cachinal de La Costa, *W. Biese 3342* (SGO 75175); near Quebrada Botija, ca. 11 km N of Miguel Díaz, ca. 60 km N of Paposo, 24°31'S, 70°33'W, 18 December 1987, *M. O. Dillon 5355A* (F 2010901); N side of Punta Dos Reyes, ca. 39 km S of Quebrada El Cobre, 24°32'S, 70°34'W, 5–10 m.a.s.l., 13 November 1998, *M. O. Dillon & D. Dillon 5897* (E, F 2144372, GH), Quebrada Agua de Cascabeles, ca. 15 km N of Taltal, 25°17'S, 70°25'W, 30–150 m.a.s.l., *M. O. Dillon & D. Dillon 5846* (E, F 2144384, GH, US); Ridge E of Punta Dos Reyes, 24°36'S, 70°33'W, 500–950 m.a.s.l., 15 November 1988, *M. O. Dillon & D. Dillon 5955* (F 2144377, GH); N side of Punta Dos Reyes, ca. 39 km S Quebrada El Cobre, 24°32'S, 70°34'W, 5–10 m.a.s.l., 13 November 1988, *M. O. Dillon & D. Dillon 5899* (F 2144373); Quebrada Paposo, 25°00'51"S, 70°26'43"W, 650 m.a.s.l., 15 October 2004, *M. O. Dillon & M. Finger C. 8572* (CONC 179085, SGO 158703); 5 km N of Paposo, 24°58'06"S, 70°28'18"W, 10 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8623* (SGO 158720); 36 km N of Paposo, ThermoElectric plant, 24°41'05"S, 70°33'52"W, 100 m.a.s.l., 1 November 2004, *M. O. Dillon & M. Finger C. 8636* (SGO 158718); mirador above ThermoElectric plant, 2.4 km ESE, 25°00'06"S, 70°26'48"W, 720 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8668* (SGO 158937); Mirador above the ThermoElectric plant below Quebrada Paposo; ca. 2.4 km ESE from ThermoElectric plant, ca. 720 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8669* (SGO 158936); 20 km N of ThermoElectric plant N of Paposo, in front of Quebrada Médano, 24°50'40"S, 70°32'06"W, 100 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8679* (CONC 179105, SGO 158926); ca. 20 km N of Paposo, in front of Quebrada Panul, 24°46'04"S, 70°32'47"W, 50 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9066* (SGO 158724); above Caleta Cobre, 24°16'49"S, 70°30'59"W, 440 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9068* (SGO 158727); Quebrada Paposo, 24°59'S, 70°25'W, 620 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8038* (CONC 149953, E, F 2183332, GH, K, SGO 143709); Quebrada La Rinconada, ca. 5 km N of Paposo, 24°56'S, 70°29'W, 410–500 m.a.s.l., 18 November 1997, *M. O. Dillon, C. Trujillo C., & M. Villarroel O. 8055* (CONC 149982, E, F 2183325, GH, K, SGO 143711); Quebrada de Miguel Díaz, 24°33'S, 70°33'W, 420–470 m.a.s.l., 22 November 1997, *M. O. Dillon, C. Trujillo C., & M. Villarroel O. 8078* (E, F 2183313, GH); Quebrada de Miguel Díaz, 24°33'S, 70°33'W, 700–930 m.a.s.l., 22 November 1997, *M. O. Dillon, C. Trujillo C., & M. Villarroel O. 8085* (CONC 149942, E, F 2183312, GH, K, SGO 143700); Quebrada Matancilla, 25°06'S, 70°27'W, 150–500 m.a.s.l., 27 November 1997, *M. O. Dillon & M. Villarroel O. 8115* (CONC 149935, E, F 2182963, GH, K, SGO 143703); Quebrada San Miguel, immediately south of Quebrada Rinconada, ca. 10 km north of Paposo, 24°56'00"S, 70°28'35"W, ca. 400 m, 2 November 2010, *M. O. Dillon & A. Casareggio M. 9179* (CONC, F 2331764, SGO); Quebrada Médano, ca. 21 km N of Paposo, 24°50'26"S, 70°31'58"W, ca. 102 m.a.s.l., 19 November 2011, *M. O. Dillon 9214* (CONC, SGO); aluvión frente a Miguel Díaz, 24°33'S, 70°33'W, 200 m.a.s.l., 5 October 2005, *F. Luebert & N. García 2630/1024* (SGO 159463); Quebrada Matancilla, 25°07'S, 70°27'W, 170–400 m.a.s.l., 8 October 2005, *F. Luebert & N. García 2721/1115* (SGO 159466); Sierra Esmeralda, cerca de Caleta Guanillos, 25°53'S, 70°39'W, 200 m.a.s.l., 13 October 2005, *F. Luebert & N. García 2798/1192* (SGO 159474); Miguel Díaz, 2nd loma desde Punta Dos Reyes al sur, 24°32'10"S, 70°32'48"W, 1000–1100 m.a.s.l., 25 October 2009, *F. Luebert & A. Moreira 3011* (SGO 158992); 22 km S of El Cobre towards Paposo, 24°25'38"S, 79°31'57"W, 100 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2860* (B, CONC 138489, SGO 146069); Quebrada de Paposo, *C. Fernández & H. Niemeyer F. 91-140* (SGO 127510); entre quebrada de Paposo y quebrada de Taltal, *C. Jiles 4975* (CONC 103522); Quebrada de San Ramon, N of Taltal, 25°21'–24'S, 28 November 1925, *I. M. Johnston 5167* (GH, K); 10.4 km N of Paposo, La Rincoñada, 24°54'S, 70°30'W, 200 m.a.s.l., 15 September 1991, *L. R. Landrum et al. 7484* (F 2116618). Quebrada Paposo, ca. 200 m.a.s.l., 13 January 1971, *A. Lourteig 2565* (US 3304987); Paposo, *L. Loyola 19* (CONC 224328); El Rincón, *C. Muñoz P. & G. T. Johnson 2880* (SGO 118372); Quebrada Paposo, *A. Pfister s.n.* (CONC 9540); Paposo, December 1853, *R. A. Philippi s.n.* (SGO 55170); camino Taltal–Paposo, Sector Bandurrias, Quebrada Anchuña, 25°11'S, 70°26'W, 90 m.a.s.l., 14 November 1996, *R. Rodríguez 3115* (CONC 136635, SGO 152936); Quebrada El Médano, 24°49'44"S, 70°31'10"W, 450 m.a.s.l., 9 January 2011, *M. Rosas 7189* (K); Quebrada Bandurrias, *F. Schlegel 7852* (CONC 99945); Matancilla, *N. Schulz 6* (SGO 154761); Quebrada Guanillos, *S. Teillier, P. Rundel, & P. García 2787* (SGO 129362); Paposo, Punta Grande, 25°03'S, 70°30'W, *S. Teillier 565* (SGO 141657); camino a Paposo, Km 25, *S. Teillier 585* (CONC 138393).

G20. ***Nolana salsoloides*** (Lindl.) I.M. Johnst., Contrib. Gray Herb. 112: 62. 1936. Fig. 341–344.

Basionym: *Dolia salsoloides* Lindl., Bot. Reg. 30, tab. 46. 1844. TYPE: CHILE. Coquimbo: *J. Macrae 16* (Holotype: CGE, not seen; Isotypes: G [G00383950], F [F neg. 23245], K [K000532198].

Digital image: Isotype of *Dolia salsoloides* from Conservatoire et Jardin botaniques de la Ville de Genève, Geneva [G00383950]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.g00383950

Homotypic synonym: *Nolana peruviana* (Gaudich.) I.M. Johnst. subsp. *divaricata* (Lindl.) Mesa, Fl. Neotrop. Mongr. 26: 81. 1981.

Heterotypic synonyms: *Alona micrantha* Phil., Fl. Atac. 44: 307. 1860. TYPE: CHILE. Atacama: Chañaral, Cachinal de la Costa, *R. A. Philippi s.n.* (Holotype: SGO [55169]); *Dolia puberula* Phil, Ann. Univ. Chile 91: 43. 1895. TYPE: CHILE. Atacama: Copiapó, Chañarcillo, 1885, *F. Philippi s.n.* (Holotype: SGO [55166]). *Dolia clavata* Miers var. *puberula* (Phil.) Reiche. **Paratype**: Copiapó, September 1885, *F.*

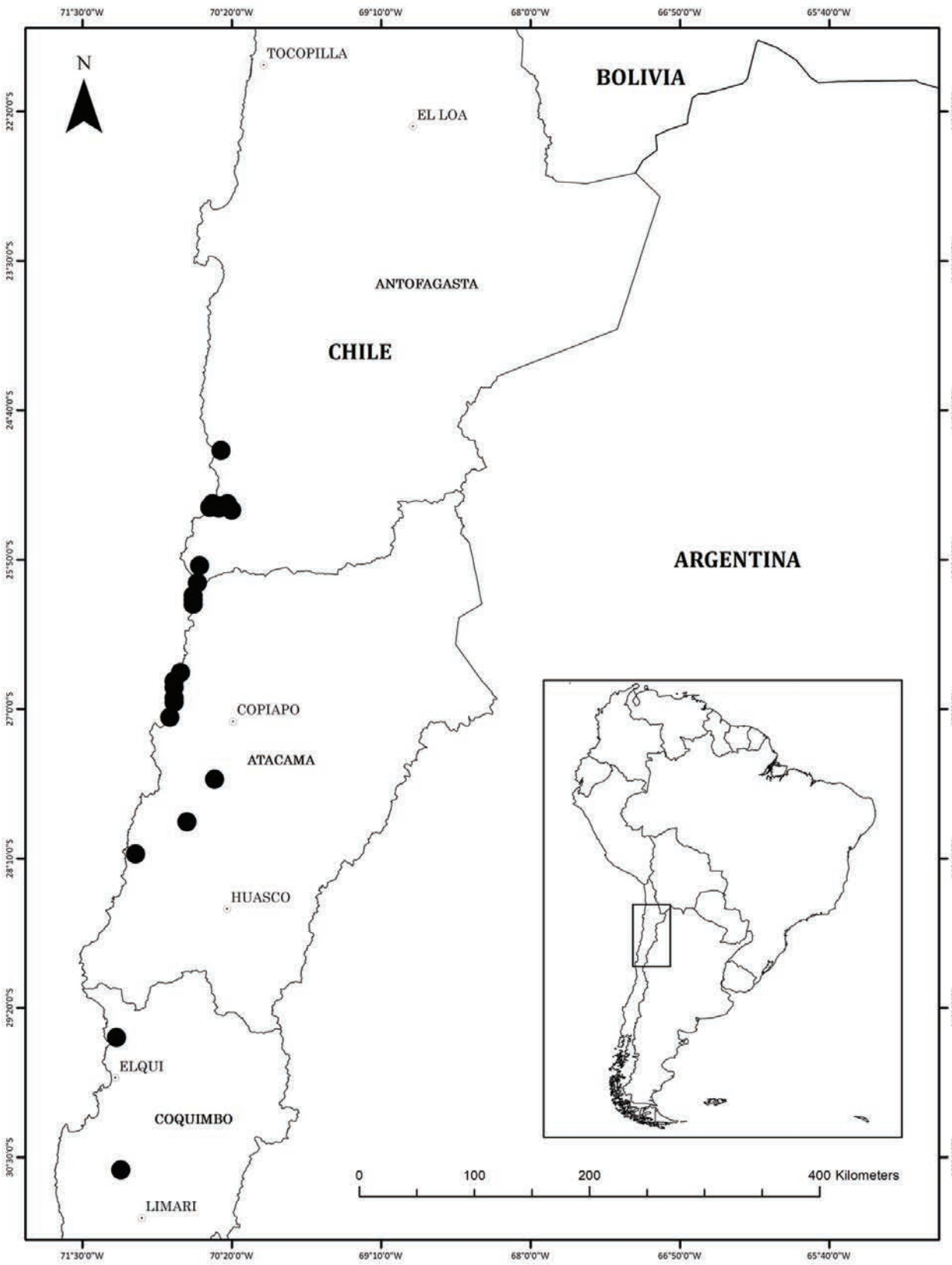


FIGURE 341. Distribution of *Nolana salsoloides* (Lindl.) I.M. Johnst.

Philippi s.n. (Paratype: SGO [42683]). *Osteocarpus spathulatus* Phil., Anal. Univ. Chile 91: 41. 1895. TYPE: CHILE. Atacama: Copiapó, Morro de Caldera, 1886, *G. Geisse s.n.* (Holotype: SGO [55129, SGO000004394]). *Alona xerophylla* Phil., Fl. Atac. 44. 1860. TYPE: CHILE. Antofagasta: Antofagasta, Cachiyuyal, [25°46'S]. *R. A. Philippi s.n.* (Holotype: SGO [55196]. *Alona rigida* Phil., Anal Univ. Chile 91: 38. 1895. TYPE: CHILE. Atacama: Sierra Esmeralda, (1885), *F. J. San Román s.n.* (Holotype: SGO [55197, SGO000004344]). *Dolia hirsutula* Phil., Anal. Univ. Chile 93: 46. 1895. TYPE: CHILE. Atacama: Breas, *D. Alamirano Larrañaga s.n.* (Holotype: SGO [55167, SGO000004355]).

Shrubs, globose 1.0–1.5 m tall, 0.5–2.0 m in diam.; stems woody, fragile. *Leaves* alternate to fasciculate, blades spathulate to clavate, 8–10 mm long, 1.0–1.5 mm wide, densely pubescent with capitate-glandular trichomes, terete, margins revolute with hyaline margin when dry, bases sclerified, persistent, with long, shaggy pubescence. *Inflorescences* of solitary flowers in upper leaf axils. *Flowers* 5-merous; calyces campanulate, ca. 6 mm long, pubescent with capitate-glandular trichomes, lobes ca. 4 mm long, succulent, pale green, apically swollen; corollas infundibularis, tube ca. 6 mm long, limb spreading, petals 4–5 mm long, pale blue to lavender; filaments surpassing corolla tube; anthers and pollen are recorded as white. *Mericarps* 3–5, reniform, 3–4 mm long, black, connate; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet suggests a resemblance to *Salsola vermiculata* L. (Amaranthaceae), a shrub in saline habitats with small succulent terete leaves and exemplifies the general gestalt of this species.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; ranging over 1000 km, (40–)100–600(–850) m.a.s.l. (Fig. 341). It is recorded from a wide variety of environments; Matorral Desértico Tropical Costero and Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Discussion: *Nolana salsoloides* is a conspicuous shrub in the coastal desert of north central Chile (Fig. 342A–B). It is recognized by a combination of characters, including spathulate to clavate leaves with cylindrical or terete blades that are densely pubescent with capitate-glandular trichomes. The corollas are invariably blue to lavender with a white central throat (Fig. 343A–B). In the dried state, *N. salsoloides* is most easily confused with *N. divaricata*, a completely glabrous species with succulent leaves (Fig. 344). Interestingly, these two species do not appear closely related as reflected by molecular studies (Dillon et al., 2007c, 2009; Tu et al., 2008). In those studies, *Nolana salsoloides* is recovered with *N. diffusa* and *N. ramosissima*, two pubescent species with small blue flowers from northern Chile.

Johnston investigated the exact locality where James Macrae collected the material chosen for the type of Lindley's *Dolia salsoloides*. Macrae was a Scottish botanist assigned by the Royal Horticultural Society to accompany the *H.M.S. Blonde* during its voyage to Hawaii in 1824. The *H.M.S. Blonde* departed England in September 1824 with the bodies of King Kamehameha II and Queen Kamāmala of the Kingdom of Hawaii, who had died while trying to visit King George. The ship overwintered in Brazil and reached Chile by late 1825.

In 1936, Johnston (p. 63) remarked: "The type of *N. salsoloides* was collected by [James] Macrae during the ten days that the *Blonde* lay at anchor in Coquimbo Bay early in December 1825. The type is not representative of the common form of the species as here defined. I have seen no material like it from the province of Coquimbo. A party from the *Blonde*, however, did visit Arqueros, a mining district northeast of Coquimbo. It seems most probable, therefore, that the type of *N. salsoloides* may have come from that locality, especially since many plants of Arqueros do have their closest affinities in western Atacama, the very region in which some forms suggesting the type of *N. salsoloides* have been found."

In 1929, Johnston (p. 111) discussed some of his 1925 collections under *Bargemontia salsoloides*, which were ultimately described as *Nolana ramosissima* (1936: 72). Furthermore, Johnston recognized *Bargemontia micrantha* and related it and *Dolia hirsutula* to *B. divaricata*. Those plants are densely pubescent with erect, unbranched capitate-glandular trichomes and are treated here as *N. salsoloides*. *Dolia puberula,* described from the Copiapó region, has densely pubescent stems covered with capitate-glandular trichomes, but is treated here as a synonym of *Nolana salsoloides*.

Johnston (1936) discussed a xerophytic shrub from Sierra Esmeralda that was growing in a dry gravelly bed of the quebrada just north of Portezuelo de Mina Carola (*I. M. Johnston 5675*, GH). It was described as a stiff shrub 4–10 dm tall and was clearly conspecific with material collected at Cachiyuyal (the type locality for *Alona xerophila* Philippi) and in the Sierra Esmeralda (the type locality for San Román's collection of *Alona rigida* Philippi). Philippi's type collection of *Alona xerophila* has persistent leaf bases; stems with both spreading, elongate capitate-glandular trichomes; and a spreading calyx in fruit that is densely pubescent with capitate-glandular trichomes inside. I originally determined the collections at B and SGO as *Nolana divaricata*; however, after examining the collection at CONC, the presence of pubescence is more indicative of *N. salsoloides*. Further studies will be necessary to access the taxonomic utility of pubescent morphs in *N. divaricata* and *N. salsoloides*. Two collections of *Nolana salsoloides* attributed to Coquimbo are outside of the typical distributional range (i.e., *F. Behn s.n.,* CONC 8594; *B. Collantes T. s.n.*, CONC 21947), and the collection by J. Kummerow from Fray Jorge (i.e., *J. Kummerow s.n.*, CONC 42633) must be examined further.

Although Johnston annotated Gaudichaud's illustration, Bot. Atlas (1841–1852), Plate 113, *Dolia salsoloides* as *Nolana ramosissima*, an examination of the type material shows it to be better treated as *N. clivicola*, and it is discussed under that species.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Dept. Taltal, Lomas de Taltal, *M. Ackermann 466* (SGO 150950); Taltal, cumbre del Cerro Perales, 25°25'10"S, 70°25'33"W, 1032 m.a.s.l., 23

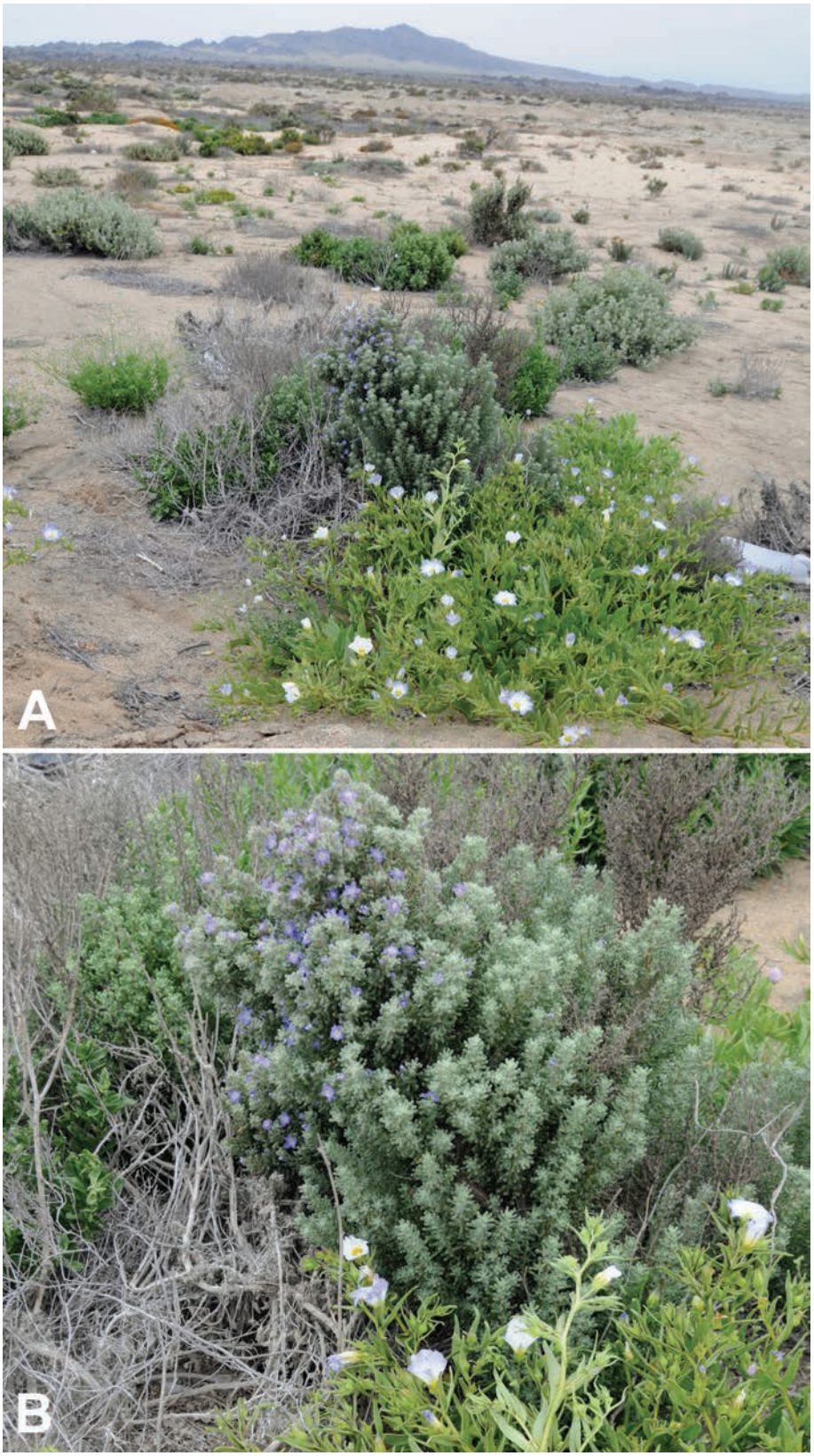


FIGURE 342. *Nolana salsoloides*. **A**, Shrubs occurring with *N. acuminata*; **B**, Flowering individuals with blue to lavender flowers.

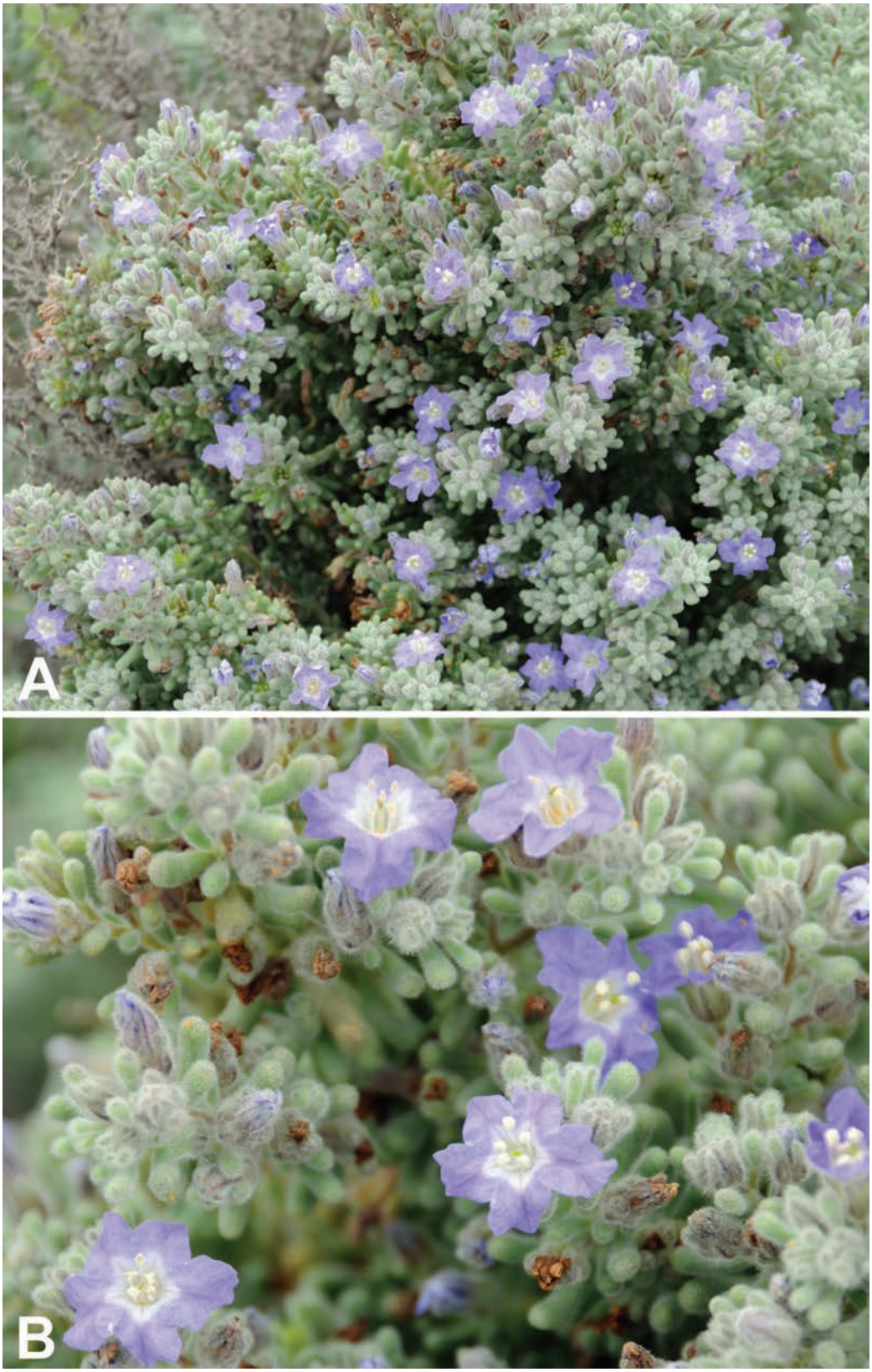


FIGURE 343. *Nolana salsoloides*. **A**, Leaves densely pubescent, corollas blue to lavender with a white central throat; **B**, Central white throat, white anther thecae and pollen.

FIGURE 344. *Nolana salsoloides*. Compare pubescent *N. salsoloides* (left) with glabrous *N. divaricata* (right).

November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 94* (CONC 176969, E 00230491); Playa, 40 km S de Paposo, 2 September 1947, *W. Biese 2277* (SGO 74197); Cerro Perales, ca. 5 km E of Taltal, 25°25'S, 70°25'W, 600–850 m.a.s.l., 21 December 1987, *M. O. Dillon 5367* (F 2010974); Quebrada de La Cortadera, 25°26'S, 70°24'W, 350–400 m.a.s.l., 30 October 1988, *M. O. Dillon & D. Dillon 5816* (E, F 2330873, GH); Cerro Perales, E of Taltal, 25°26'S, 70°26'W, 890 m.a.s.l., 16 November 1997, *M. O. Dillon & C. Trujillo C. 8047* (CONC 150028, E, F 2183328, GH, SGO 143702); road to Cifuncho, 25°31'41"S, 70°25'43"W, ca. 90 m.a.s.l., 7 October 2005, *M. O. Dillon & A. Casareggio M. 8701* (E, F 2294694, GH, SGO); Cerro Perales, 25°25'41"S, 70°26'12"W, 860 m.a.s.l., 9 October 2005, *M. O. Dillon, M. Finger C., & A. Casareggio M. 8703* (F 2330870, SGO); Cerro Perales, 9 October 2005, *M. O. Dillon, M. Finger C., & A. Casareggio M. 8708* (F 2330871, GH, SGO); Cerro Perales, 25°25'41"S, 70°26'11"W, ca. 580 m.a.s.l., 15 October 2005, *M. O. Dillon, E. Kamps E., P. Ossa Z., T. Vega Z., & M. Finger C. 8711* (E, F 2294684, GH, SGO, US); Cerro Perales, 25°25'41"S, 70°26'11"W, ca. 580 m.a.s.l., 15 October 2005, *M. O. Dillon, E. Kamps E., P. Ossa Z., T. Vega Z., & M. Finger C. 8715* (F 2330872, GH, US); Quebrada Changos, *M. Ricardi 2569* (CONC 14362); Quebrada La Cachina, *M. Ricardi 2493* (CONC 14286); Agua del Loro, *M. Ricardi 3084* (CONC 18317); Quebrada Bandurrias, 40 m.a.s.l., 5 November 1985, *F. Schlegel 7850* (SGO 105231); Quebrada Taltal, Km 15, 25°26'S, 70°35'W, 570 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García 2666* (SGO 129364); Quebrada Taltal, Km 15, 25°26'S, 70°35'W, 570 m.a.s.l., *S. Teillier, P. Rundel, & P. García 2667* (F 2114630); Quebrada de Taltal, 25°26'S, 70°35'W, 410 m.a.s.l., 17 September 1992, *S. Teillier, P. Rundel, & P. García 2836* (F 2114629, SGO 129365); Taltal, Morro Colorado, 25°23'S, 70°27'W, 120 m.a.s.l., 4 December 2002, S. Teillier 6005 (CONC 170821); ca. 10 km E of Taltal, 50–300 m.a.s.l., 12 October 1938, *C. R. Worth & J. L. Morrison 15787* (GH, K). **Atacama**: Prov. Atacama, Huasco, 16 September 1971, *K. Beckett, M. Cheese, & J. Watson 4694* (SGO 110037), *4695* (SGO 110036); Caldera a Chañaral, *F. Behn s.n.* (CONC 30873). Prov. Chañaral, 11 km W of Panamericana Hwy on road to Pan de Azúcar, *O. F. Clarke 18.5-01* (CONC 158483); Parque Nacional Pan de Azúcar, Quebrada Coquimbo, 26°09'S, 70°39'W, 160–200 m.a.s.l., 5 December 1987, *M. O. Dillon & J. T. S. Teillier 5084* (CONC, E, F 1994738, GH, SGO); Parque Nacional Pan de Azúcar, Las Lomitas, 26°01'S, 70°36'W, 720–780 m.a.s.l., 11 November 1997, *M. O. Dillon & C. Trujillo*

8012 (CONC 150032, E, F 2183319, GH, K, SGO 143716, US); Parque Nacional Pan de Azúcar, 26°11'S, 70°38'W, 320 m.a.s.l., 1 December 1997, *M. O. Dillon 8156* (F 2182952); Mirador, Parque Nacional Pan de Azúcar, 26°07'S, 70°39'W, 320 m.a.s.l., 3 December 1997, *M. O. Dillon 8176* (CONC 149972, F 2183341, GH, SGO 143713); ca. 44 km N of Caldera, *M. O. Dillon 8094* (CONC 150019, E, F 2183310, GH, K, SGO 143693); Carrizal Bajo, 28°04'54"S, 71°08'48"W, 0–5 m.a.s.l., 28 October 2004, *M. O. Dillon & M. Finger C. 8618* (F 2330859, SGO 158723); Huasco/Copiapó, W of Ruta 5 towards Carrizal Bajo, 28°06'30"S, 71°06'12"W, 150 m.a.s.l., 29 November 2004, *M. O. Dillon 8662* (SGO 158947); Gruta Padre Negro, ca. 78 km NW of Copiapó, 26°47'48"S, 70°46'34"W, 24 m.a.s.l., 29 October 2009, *M. O. Dillon & R. Concha 9096* (CONC, SGO); Quebrada de León, ca. 17 km NNE of Caldera, 26°56'00"S, 70°44'30"W, 326 m.a.s.l., 2 October 2010, *M. O. Dillon 9151* (CONC, SGO); 41 km S of Copiapó towards Vallenar, 27°41'22"S, 70°28'51"W, 650 m.a.s.l., 9 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2872* (SGO 146036); vicinity of Caldera, *E. E. Gigoux 39* (GH); vicinity of Caldera, *E. E. Gigoux 56* (GH); Estancia Castilla, *G. Gleisner 39* (CONC 34994); Caldera, *C. Jiles 5295* (CONC 92372); Obispito, 10 October 1971, *E. M. L. Kausel 5492* (SGO 80555); Pan de Azúcar, Las Lomitas, 26°00'S, 70°36'W, 820 m.a.s.l., 14 October 2005, *F. Luebert & N. García 2817/1211* (SGO 159445); Quebrada El León, 26°57'S, 70°44'W, 240 m.a.s.l., 16 October 2005, *F. Luebert & C. Becker 2849* (SGO 159443); Sierra de Los Sapos, 28°03'S, 70°25'W, 840 m.a.s.l., 17 September 2005, *F. Luebert & N. García 2500/894* (SGO 159470); Caldera a Chañaral, Km 17, frente a Barranquilla, *C. Marticorena, R. Rodríguez, & E. Weldt 1877* (CONC 36254); Caldera, 15 May 1973, *A. Richardson 2177* (SGO 85498). Dept. Copiapó, Pampa Caracoles, ca. 17 km N of Caldera, 26°57'S, 70°47'W, 100 m.a.s.l., 24 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5485* (E, F 2011632, GH, SGO); Piedra Colgada, cerca de Copiapó, 22 September 1941, *C. Muñoz P. & G. T. Johnson 2057* (SGO 112244); Bahía Inglesa, 26°53'56"S, 70°47'34"W, 86 m.a.s.l., 29 September 2005, *M. Muñoz S. 4573* (E00936020, SGO 153600); between Caldera and Chañaral, 24 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274039); between Caldera and Chañaral, 10 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274041); 24 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274042); 13 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274038); entre Caldera y Chañaral, Km 18, *M. Ricardi, C. Marticorena, & O. Matthei 1280* (CONC 36180); Travesía, *E. Saá s.n.* (CONC 129677); Prov. Copiapó, Rt. 1 N of Caldera, 26°50'S, 70°45'W, 4 October 1991, *C. M. Taylor, C. von Bohlen, & A. Marticorena 10693* (F 2116661); along Ruta 5, 28°20'S, 70°40'W, 500 m.a.s.l., 8 April 1994, *C. Taylor & A. Pool 11525* (SGO 147809); Quebrada de León, ca. 20 km N of Caldera, 150 m.a.s.l., 20 October 1938, *C. R. Worth & J. L. Morrison 16155* (K); Carrizal Bajo, *O. Zöllner 2807* (CONC 129576). **No exact locality**: Desert of Atacama, September–October 1890, *T. Morong 1247* (F 166475, GH, K, US 1417077).

G21. ***Nolana sedifolia*** Poepp., Froriep., Notizen 23: 276. 1829; Not. Natur- Heilk. 23: 276. 1829. TYPE: CHILE. Valparaíso: "in rupibus maritus ubique prope Concón", *E. F. Poeppig 68* (Lectotype designated by Dillon and Quipuscoa, 2023: W [1889-0301807]; Isolectotypes: BM [BM000941358], F [F 870466], GH [GH00282361], HAL [HAL 115091], K [K000532209], W [W0075450]. Fig. 345–348.

Digital image: Lectotype of *Nolana sedifolia* from Institute of Botany, University of Vienna, Vienna [W1889-0301807]. https://herbarium.univie.ac.at/database/detail.php?ID=1103927

Homotypic synonym: *Bargemontia sedifolia* (Poepp.) I.M. Johnst., Contrib. Gray Herb. 85: 110. 1929.

Heterotypic synonyms: *Alibrexia brevifolia* Phil., Linnaea 33: 208. 1864–1865. TYPE: CHILE. Valparaíso: Prov. Aconcagua, Los Mollis, November 1862, *C. L. Landbeck s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 55127]; Isolectotypes: K, SGO [SGO 42661]; Photoisolectotype: W, not seen, F neg. 33144); *Dolia brevifolia* (Phil.) Phil. *ex* Wettst., Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 4. 1891; *Fabiana lanuginosa* Hook. & Arn., Bot. Beechey Voy. 1: 35. 1830. TYPE: CHILE. Coquimbo: Coquimbo, Capt. F. W. Beechey Voyage, *A. Collie & G. T. Lay* s.n. (Lectotype designated by Dillon and Quipuscoa, 2023: (E [00369176]); *Dolia vermiculata* Lindl., Bot. Reg. 30. tab. 46. 1844. TYPE: CHILE. Coquimbo: Coquimbo, 1831, *H. Cuming 893* (Lectotype designated by Mesa-M., 1981: K [K000532208]; Isolectotype: E [E00130934], SGO [SGO 55172]). *Salsola glomerulata* Meyen, Observ. Bot. 1: 375. 1834. (no type designated). **Paratype**: CHILE. Coquimbo: Coquimbo, 1842, *T. Bridges 1331* [notebook–*1330*], (Lectotype designated by Mesa-M., 1981: K [000532207]; Isolectotypes: K [K000532205], E [E00130935], FI).

Subshrubs, occasionally flowering in the first year, 5–120 cm tall; branches erect or, more rarely, decumbent, densely foliose, slender divaricate, becoming woody, arachnoid-tomentose, with eglandular long, simple, curly, or, more rarely, capitate-glandular trichomes. *Leaves* alternate to fasciculate, blades clavate to globular, 1–2(–5) mm long, ca. 2 mm wide, margins revolute, pubescent with curly, arachnoid-tomentose trichomes. *Inflorescences* of solitary flowers, terminal and axillary, sessile. *Flowers* 5-merous: calyces 3–4 mm long, enlarging in fruit, teeth nearly 1/2 of total calyx length, unequal, erect, apically bulbous; corollas hypocrateriformis, zygomorphic, 6–9(–12) mm long, 8–10 mm wide, white or, rarely, bluish, 2–3 times as long as the calyx; stamens 2 longer and 3 shorter or all subequal; filaments not widened at the base and rarely pubescent; nectary disc patelliform, margin sinuous; style as long as the filaments, gynobasic; stigma capitate or capitate-lobate. *Mericarps* (4–)6–8, ovoid, unequal, 2–3 mm long, 1–2 mm wide; seeds 1–2 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Greek, *sarkodes*, fleshy, or from the Latin, *sedi-*, fleshy and *-folia*, foliage, and refers to the succulent leaves.

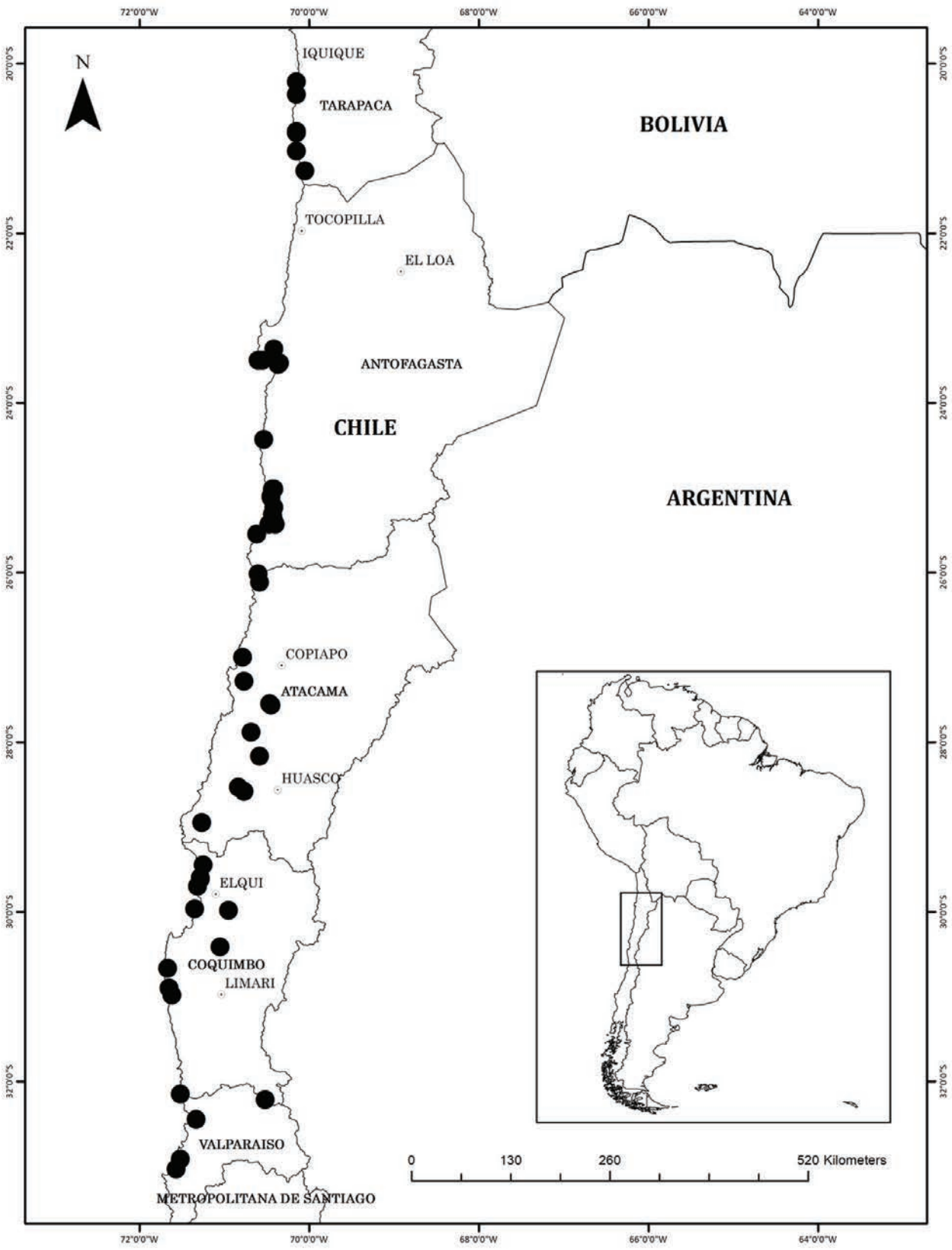


FIGURE 345. Distribution of *Nolana sedifolia* Poepp.

Distribution and Ecology: Chile, Regions of Arica y Parinacota**,** Tarapacá, Antofagasta, Atacama, Coquimbo and Valparaíso; (10–)100–800(–1000) m.a.s.l. (Fig. 345). It is recorded over a vast area with populations spanning over 1800 km; dry, rocky places from near the ocean to inland sites at higher elevations to 1000 m.a.s.l. (Pinto and Luebert, 2009); Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Common name: *Sosa brava hoja chica*.

Illustration: Fig. 346. Illustration of *Nolana sedifolia* as *Dolia vermiculata* Lindl., Plate 12. Miers, *Illustrations of South American plants* (vol. 1. 1850). Fig. 347. Illustration of *Nolana sedifolia* as *Dolia vermiculata* Lindl., Plate 112. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852). No text was published by the author. Regarding dates of publication, see Table 3 adapted from Johnston (1944).

Nolana sedifolia is a small shrub (Fig. 348 A) with small white, tubular flowers (Fig. 348B–C). The stems are pubescent with curly, arachnoid-tomentose trichomes, as are the leaves (Fig. 348C). The calyces have five, unequal succulent lobes (Fig. 348B–D), and the mericarps are enveloped by the calyx (Fig. 348D). When dried, the differences between *N. sedifolia*, *N. diffusa*, and *N. tocopillensis* are sometimes difficult to discern, but the corolla size, shape and coloration pattern are used for separating these species.

Johnston (1929: 110) described *Nolana sedifolia* as an erect globose shrub 5–12 dm tall. He collected it on a rocky hillside near the crest of the hills behind Barquito (*I. M. Johnston 4767*), in dry, rocky places near the crest of Cerro Yumbes near Paposo (*I. M. Johnston 5551*), and on the rocky floor of the gulch just below Ag. Panul (*I. M. Johnston 5435*). Its corollas are almost always white and glabrous within.

Two Pfister collections are from a quebrada 20 km south of Cobija; they are somewhat aberrant with densely crowded, longer leaves (i.e., *A. Pfister s.n.*, CONC 9513 and *A. Pfister s.n.*, CONC 117896). A collection from near Cobija (*M. Ricardi 3033*) was initially considered to be *N. tocopillensis*, due to its abundant capitate-glandular trichomes and sparse, curly leaf pubescence; however, the overall morphology suggests it to be within the bounds of variation exhibited by *N. sedifolia*. Furthermore, material collected from around Taltal is here treated as a morph of *N. sedifolia*, including a collection from El Rincón (*M. Ricardi 3555*) and a collection from Quebrada Taltal (*R. Montero 2902*).

Two collections from south of El Cobre, *Eggli et al. 2858* and *2859*, were initially placed under *N. sedifolia*, and *N. diffusa*; both collections are here treated as *N. sedifolia*. Another collection from Quebrada Caracoles, "E of Antofagasta on Ruta 26," *Eggli et al. 2699*, was initially placed in *N. diffusa*; however, it is best referred to as *N. sedifolia*. After detailed examination, a collection from Aconcagua (*M. Ricardi 5249*) is attributed to *N. sedifolia*. Initially, its unusually long leaves appeared to be within the size range of *N. salsoloides*.

As discussed in the *Phytochemistry* section, Vio-Michaelis et al. (2012) examined the antifungal effect of a complete methanolic extract of *Nolana sedifolia*, which was tested for antifungal activity on mycelial growth.

Additional specimens examined: CHILE. **Arica y Parinacota**: Prov. Arica, Cerro Camaraca, 900 m.a.s.l., 14 September 2002, *R. Pinto 136* (SGO); Punta Madrid, 1000 m.a.s.l., 22 September 2002, *R. Pinto 181* (SGO). **Tarapacá**: Prov. Iquique, Alto Patache, 800 m.a.s.l., *E. Belmonte 97-710* (SGO 149103); Iquique, *F. Jaffuel 261* (CONC 45987); Punta Gruesa, 20°21'50"S, 70°09'00"W, 840 m.a.s.l., 26 September 2005, *F. Luebert & N. García 2544/938* (F 2290683); Alto Punta Lobos, *R. Pinto s.n.* (SGO 142979), *R. Pinto s.n.* (SGO 142980); Alto Punta Patache, *R. Pinto s.n.* (SGO 142967); Alto Chipana, *W. Sielfeld 9* (SGO 143053); Cerro Tarapacá, 20°20'S, 70°07'W, 700 m.a.s.l., 3 September 1993, *W. Sielfeld 38* (SGO 144339). **Antofagasta**: Prov. Antofagasta, S of Taltal, 340 m.a.s.l., 25°27'08"S, 70°29'00"W, *M. Acosta, P. Guerrero, & M. Rosas 418* (K); La Chimba, 13 September 1957, *G. Arias & J. Alvarez s.n.* (SGO 135546); Paposo, Quebrada la Rinconada, 24°55'50"S, 70°20'05"W, 390 m.a.s.l., 22 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 67* (E00230449); Salar del Carmen, 24 September 1940, *E. Barros 5591* (US 2168168); Península Moreno, cerros al lado Oeste de Juan López, 23°30'S, 70°34'W, 830 m.a.s.l., 1 August 1992, *G. Baumann 8* (SGO 127839); Antofagasta–Taltal, *F. Behn s.n.* (CONC 22593); Punta Gualaguala, 16 October 1949, *W. Biese 2774* (SGO 97233); Taltal, *W. Biese 530* (CONC 11437); Quebrada Blanco Encalada, *W. Biese 3143* (SGO 696747); Tocopilla, Cobija, Quebrada Aguada Cañas, *W. Biese 2800* (SGO 97055); Cobija, 1982, *T. Bridges s.n.* (K); Taltal, Quebrada Anchuña, *W. Biese 2480* (SGO 696508); Quebrada Mantancilla; ca. 5 km S of Punta Grande, ca. 35 km N of Taltal, 25°07'S, 70°27'W, 170–350 m.a.s.l., 27 October 1988, *M. O. Dillon & D. Dillon 5780* (CONC, E, F 2330866, GH, SGO, US); Quebrada de La Cortadera, 25°26'S, 70°24'W, 350–400 m.a.s.l., 30 October 1988, *M. O. Dillon & D. Dillon 5819* (E, F 2144379, GH, US); Quebrada La Chimba, NE of Antofagasta, 23°33'S, 70°22'W, 380–480 m.a.s.l., 11 November 1988, *M. O. Dillon & D. Dillon 5882* (F 2144387); Quebrada Paposo, ca. 5–12 km E of Caleta Paposo, 25°01'S, 70°25'W, 350–950 m.a.s.l., 28 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5547* (CONC, E, F 2010226, GH, SGO). Quebrada Paposo, ca. 12 km E of Caleta Paposo, 25°01'S, 70°25'W, 910 m.a.s.l., 7 December 1987, *M. O. Dillon & S. Teillier 5135* (E, F 2010720, GH); Quebrada de La Chimba, ca. 10 km NNE of Antofagasta, 23°33'S, 70°22'W, 300–550 m.a.s.l., 17 December 1987, *M. O. Dillon & S. Teillier 5345* (CONC, F 2010911); Quebrada to Bahía Tórtolas, S side of Cerro San Pedro, ca. 22 (air) SW of Taltal; ca. 13 km N of Cifuncho, 25°33'S, 70°37'W, 20–70 m.a.s.l., 12 October 1988, *M. O. Dillon & D. Dillon 5674* (F 2014392); ca. 10 km N of Paposo, 24°55'43"S, 70°30'55"W, ca. 70 m.a.s.l., 1 December 2004, *M. O. Dillon & M. Finger C. 8682* (CONC 179108, F 2292793, SGO 158923); Cerro Perales, 25°25'41"S, 70°26'12"W, ca. 860 m.a.s.l., 9 October 2005,

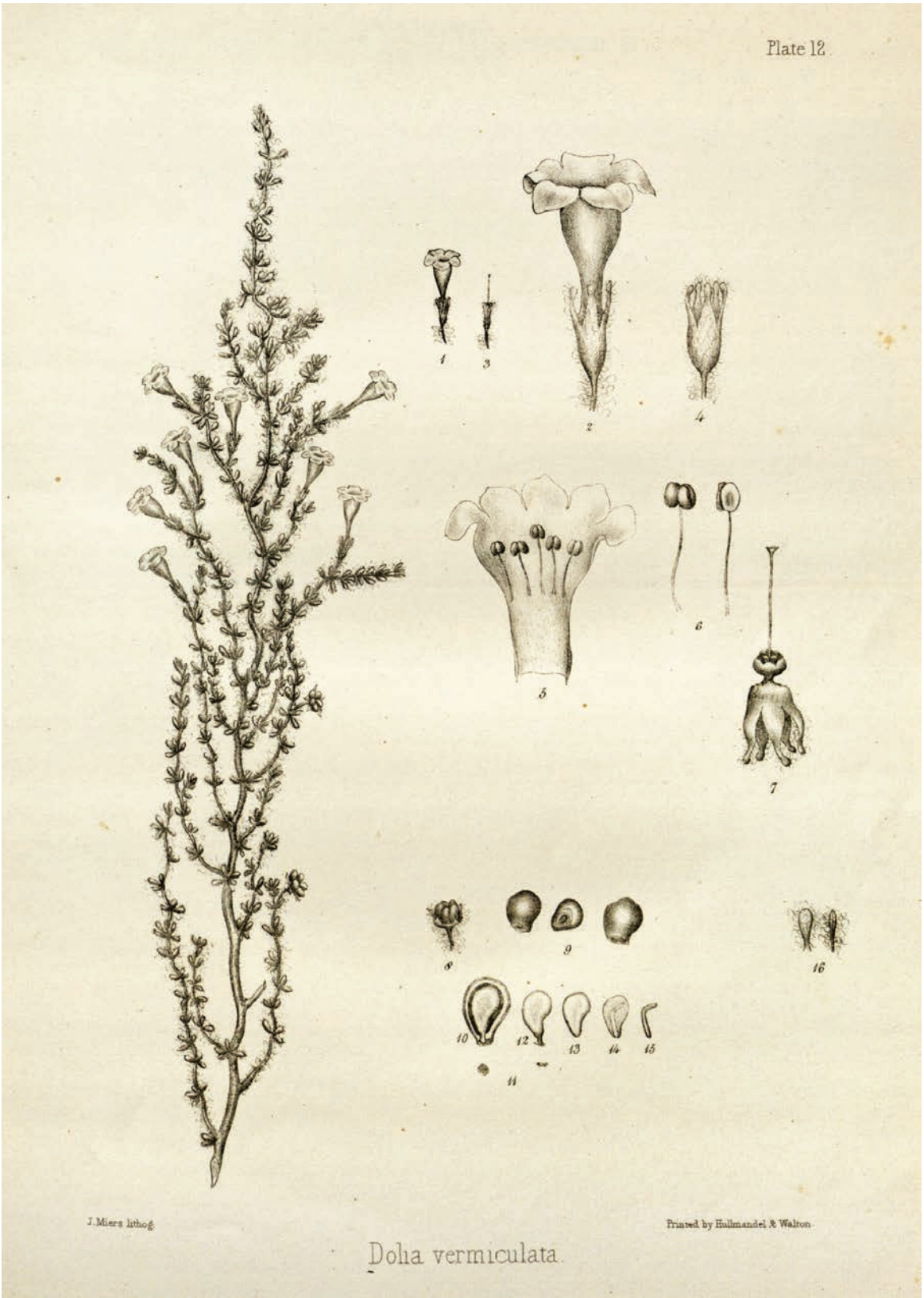


FIGURE 346. Illustration of *Nolana sedifolia* as *Dolia vermiculata* Lindl., Plate 12. Miers, Illustrations of South American plants (1850).

FIGURE 347. Illustration of *Nolana sedifolia* as *Dolia vermiculata* Lindl., Plate 112. Gaudichaud, Voyage autour du monde sur la corvette La Bonite, Bot. Atlas (1841–1852).

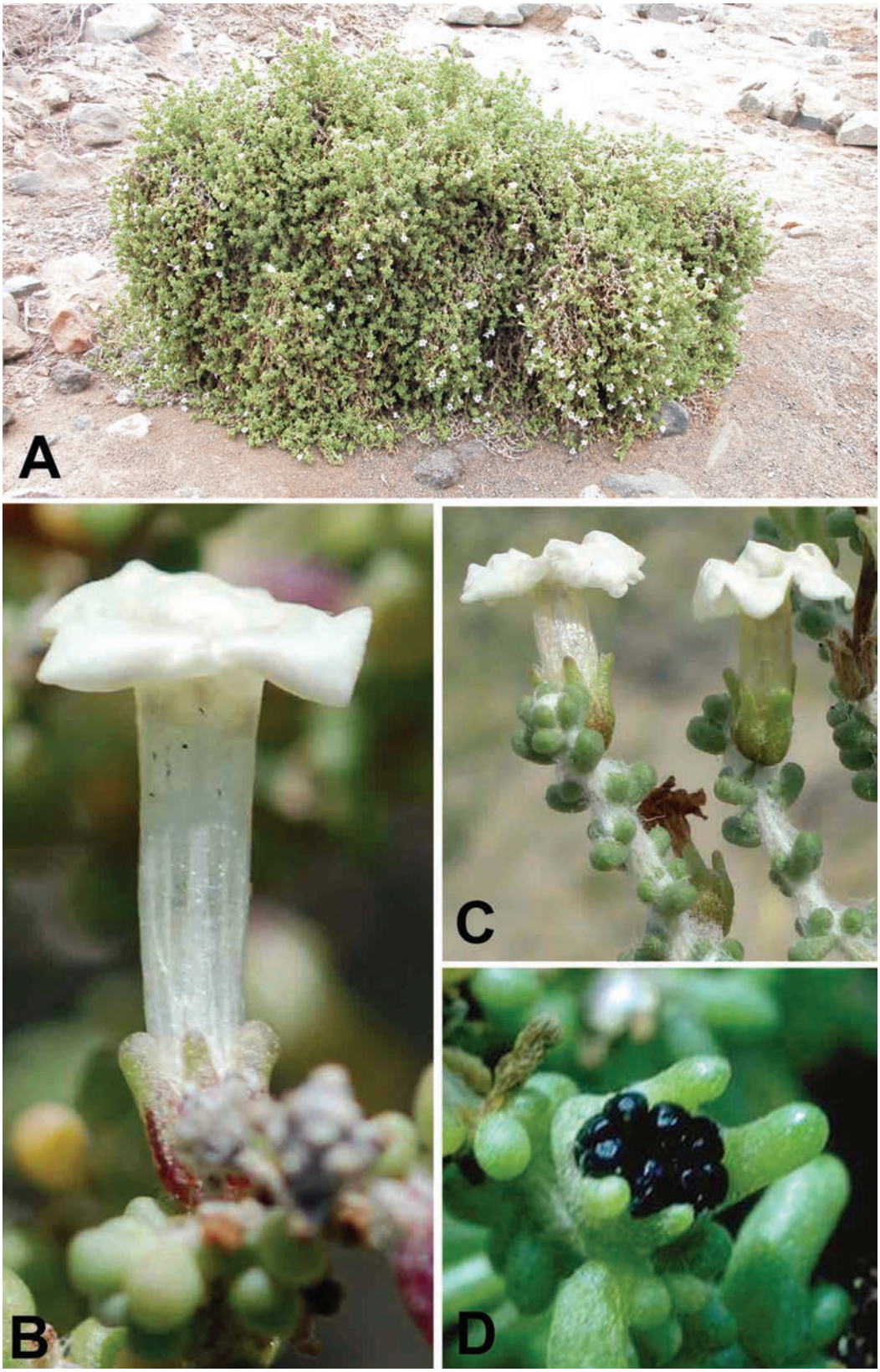


FIGURE 348. *Nolana sedifolia*. **A**, Compact, erect shrubs; **B,** White, tubular flowers; **C**, Stems and leaves pubescent with curly, arachnoid-tomentose pubescence; **D**, Calyces with five, unequal succulent lobes, mericarps are enveloped by the calyx.

M. O. Dillon, A. Casareggio M., & M. Finger C. 8706 (F 2294689, SGO); Punta Plata, 24°33'47"S, 70°31'33"W, ca. 50 m.a.s.l., 7 November 2007, *M. O. Dillon & M. Finger C. 9063* (F 2292852, SGO 158739); Peninsula Moreno, SW flank of Morro Moreno above Caleta Errázuriz, 23°29'17"S, 70°35'59"W, 500–550 m.a.s.l., *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2696* (B, CONC 138562, SGO 145883); Quebrada Caracoles E of Antofagasta on Ruta 26, N access from Antofagasta to Panamericana, 5 km E of town, 23°37'07"S, 70°19'58"W, 520–650 m.a.s.l., 18 February 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2699* (B, CONC 138565, SGO 145880); Prov. Tocopilla, 16 km N of Tocopilla on Ruta 1 towards Iquique, 21°58'00"S, 70°10'29"W, 100 m.a.s.l., 6 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2838* (B); 22 km S of El Cobre toward Paposo on coastal gravel road (78 km N of Paposo), *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2858* (B, CONC 138487, SGO 146065), *2861* (B, SGO 146067); 24°25'38"S, 70°31'57"W, 100 m.a.s.l., 8 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2859* (CONC 138488, SGO 146068); 14 km above (E) Taltal towards Panamericana, just below the turnoff to Cifuncho, 540–580 m.a.s.l., 26 November 1991, *U. Eggli & B. E. Leuenberger 1775* (B, SGO 141301); Bandurrias, *G. Geisse 7997* (CONC 129619); Quebrada de La Chimba, *A. Hoffmann & R. Rodríguez 12* (CONC 99075); Antofagasta, 29 October 1930, *F. Jaffuel 1152* (GH); Taltal, *F. Jaffuel 2598* (CONC 45985); Taltal, Aguada del Panul, 24°47'S, 4 December 1925, *I. M. Johnston 5435* (GH, K, US 1473987); vicinity of Paposo, Cerro Yumbes, ridge E of Paposo, 8 December 1925, *I. M. Johnston 5551* (GH, K); Tocopilla, III Quebrada, 22°03'06"S, 70°10'35"W, 150 m.a.s.l., 29 September 2005, *F. Luebert, N. García, & N. Schulz 2567/961* (F 2290727); Cerro Moreno, 23°29'19"S, 70°35'31"W, 590–670 m.a.s.l., 2 October 2005, *F. Luebert & N. García 2576/970* (F 2290742); Panul, 24°47'42"S, 70°31'50"W, 7 October 2005, *F. Luebert & N. García 2674/1068* (F 2290737); Breas, 25°29'56"S, 70°24'03"W, 570 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2738/1132* (F 2290693); Quebrada Cascabeles, 10 m.a.s.l., 16 September 1941, *C. Muñoz P. & G. T. Johnson 2849* (SGO 118310); Quebrada La Chimba, 500 m.a.s.l., 16 December 1943, *C. Muñoz P. 3640* (SGO 119108); Antofagasta, 100–300 m.a.s.l., 3 April 1925, *F. W. Pennell 13035* (GH); Quebrada 20 km S de Cobija, *A. Pfister s.n.* (CONC 9513, CONC 117896); Quebrada Paposo, *A. Pfister s.n.* (CONC 9525); Península Moreno, cerros frente a Juan López, *M. Quezada & E. Ruiz 60* (CONC 121077); Quebrada La Chimba, *M. Quezada & E. Ruiz 86* (CONC 121180); Quebrada Paposo, *M. Quezada & E. Ruiz 191* (CONC 121154); Quebrada Taltal, *R. Montero 2902* (CONC 112946); Cerro Moreno, *M. Ricardi, C. Marticorena, & O. Matthei 1410* (CONC 31165); Quebrada La Chimba, *M. Ricardi 3055* (CONC 18288, GH); El Rincón, *M. Ricardi 3555* (CONC 19498); La Chimba, *F. Schlegel 7742* (CONC 115615); Quebrada Matancilla, *F. Schlegel 7904* (CONC 99962); Quebrada de La Chimba, *S. Teillier 459* (CONC 138394, SGO 141655); Quebrada de Taltal, Km 15, 25°26'S, 70°35'W, 570 m.a.s.l., 14 September 1992, *S. Teillier, P. Rundel, & P. García 2672* (F 2114616, SGO 129356); Sector El Gaucho, 25°26'S, 70°35'W, 50 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2902* (F 2114618); Sector El Gaucho, 25°26'S, 70°35'W, 50 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2905* (F 2114617); Sector El Gaucho, 25°26'S, 70°35'W, 50 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2921* (SGO 129371); Hueso Parado, *O. Zöllner 1850* (CONC 129609); Cerro Moreno, *O. Zöllner 3528* (CONC 129616). **Atacama**: Caleta Carrizalillo, 29°06'56"S, 71°28'06"W, 7 m.a.s.l., *L. Arriagada 226* (K); Totoralillo, falda Este del Valle Copiapó, 700–800 m.a.s.l., 13 October 1949, *W. Biese 2676* (SGO 96595); Vallenar, October1927, *Bro. Claude-Joseph 5028* (US 1422140). Prov. Chañaral, Parque Nacional Pan de Azúcar, Las Lomitas, 26°01'S, 70°36'W, 720–780 m.a.s.l., 11 November 1997, *M. O. Dillon & C. Trujillo C. 8007* (CONC 150015, E, F 2183321, GH, K, SGO 143717), Parque Nacional Pan de Azúcar, 26°07'S, 70°35'W, 200 m.a.s.l., 1 December 1997, *M. O. Dillon 8152* (F 2182955); Quebrada de León, ca. 17 km NNE of Caldera, 26°56'00"S, 70°44'30"W, 326 m.a.s.l., 2 October 2010, *M. O. Dillon 9150* (CONC, SGO); Huasco, ca. 18 km E of Huasco, 28°30'21"S, 71°07'33"W, ca. 200 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8651* (F 2292788, SGO 158918); Huasco, 2 November 1930, *F. Jaffuel 1170* (GH); vicinity of Caldera, September 1894, *E. E. Gigoux 41* (GH); vicinity of Caldera, 1922, *E. E. Gigoux s.n.* (GH); Copiapó, Estancia Castilla, *G. Gleisner 56* (CONC 34541); Huasco a Vallenar, *G. Hartmann s.n.* (CONC 31174); Copiapó, *C. Jiles 2080* (CONC 36118); Dept. Chañaral, Falda Verde, slopes of Cerro Chañaral 4–5 km N of Chañaral, *U. Eggli 2895* (B, SGO 146125); Vicinity of Puerto de Chañaral, hills back of El Barquito, 26°23'S, 28–29 October 1925, *I. M. Johnston 4767* (GH, K, US 1473984); Quebrada El León, 26°57'18"S, 70°44'07"W, 240 m.a.s.l., 16 October 2005, *F. Luebert & C. Becker 2848* (F 2290738); Cerro NE de Copiapó, *G. Montero O. 2996* (CONC 114945, GH); Vallenar, *R. Montero 7687* (CONC 112947); Nantoco, a 25 km de Copiapó, 20 September 1941, *C. Muñoz P. & G. T. Johnson 1869* (SGO 112626); between Caldera and Chañaral, 10 October 1993, *M. Ono & K. Suzuki s.n.* (MAK 274061), *s.n.* (MAK 274063), *s.n.* (MAK 274062); Chañarcillo, *R. A. Philippi s.n.* (US 1336140); entre Caldera y Chañaral, Km 8, *M. Ricardi, C. Marticorena, & O. Matthei 1051* (CONC 31168); Copiapó, Travesía, *E. Saá s.n.* (CONC 129613); Caldera, Quebrada León, 30 m.a.s.l., October 1924, *E. Werdermann 440* (A, B, BM000941354, CONC 56025, F 565262, K, US 1516918); Caldera, 10 m.a.s.l., September 1924, *E. Werdermann 387* (A, BM000941359, CONC 68831, F 565209, K, US 1444744); sur de Copiapó, *O. Zöllner 8862* (CONC 129618). Dept. Freirina. Quebrada El Morado, 1 km SO de la junta del camino Carrizalillo–El Morado, *C. Marticorena, R. Rodríguez, & E. Weldt 1796* (CONC 36156); 5 km al sur de Vallenar, *M. Ricardi & C. Marticorena 4850/1235* (CONC 25644). **Coquimbo**: Prov. Aconcagua, 4 km S of Los Molles, 17 December 1971, *K. Beckett, M. Cheese, & J.*

Watson 4568 (SGO 110670); Aconcagua–Papudo, *F. Behn s.n.* (CONC 22591); entre Papudo y Zapallar, 23 February 1965, *M. Ricardi 5249* (CONC 30023); Zapallar, Cerro de la Cruz 20 m.a.s.l., 10 October 1948, *G. Looser 5527* (GH). Prov. Choapa, Mun. Mincha, Caleta Oscuro, 3 km W of Puerto Oscuro, 31°25'S, 71°36'W, 2 February 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 3089b* (B). Prov. Coquimbo, Coquimbo, August 1890, *J. Ball s.n.* (K); Coquimbo–Cruz Grande, *F. Behn s.n.* (CONC 22592); Guayacán, *A. Cabrera 11383* (SGO 126632); La Serena, *A. Cabrera 11385* (CONC 24179); Coquimbo, 1929–1930, *C. Elliot 522* (GH, K [2 sheets]); Coquimbo, 1839, *C. Gay s.n.* (F 977012 ex P; G-DC, G00137949); Coquimbo, *C. Grandjot 987* (SGO 116576); Coquimbo, 1917, *C. J. F. Skottsberg & I. Skottsberg 718* (F 737406); Coquimbo, 25 December 1902, *A. W. Hill 341* (K). Prov. Elqui, road to Agua Grande at 45.2 km SE of La Serena, *M. Acosta, et al. 085* (K); Punta Arrayán, ca. 20 km N of La Serena, 29°42'S, 71°19'W, 140–150 m.a.s.l., 22–23 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5434* (CONC, E, F 2011543, GH); Cerros de La Herradura, 12 September 1991, *C. Fernández & H. Niemeyer F. 91-130* (SGO 127500); Quebrada Honda, *C. Jiles 4003* (CONC 126616); Zona de El Molle, *C. Jiles 4920* (CONC 103579, CONC 34613); Punta Tortuga, 25 m.a.s.l., 31 October 1990, *T. G. Lammers, C. M. Baeza P., & P. Peñailillo B. 7634* (CONC 113431, F 2055115); Playa Las Estacas, entre Coquimbo y Guanaqueros, *A. Landero 507* (CONC 115506); Quebrada Honda, C. Marticorena, O. Matthei, & R. Rodríguez 381 (CONC 186471); La Pampilla, *A. M. Mora s.n.* (SGO 131743); Punta Choros, 5 km hacia Carrizalillo, *A. Moreira 709* (SGO 149922); Punta de Teatinos, *C. Muñoz P. 3268* (SGO 118637); El Faro, puerto de Coquimbo, *C. Muñoz P. & G. T. Johnson 2783* (SGO 118275); La Serena, 1888, *F. Philippi s.n.* [1904] (BM000941363); Cuesta de Buenos Aires, Rt. 5–2 km N of Los Hornos, 29°36'51"S, 71°16'39"W, 280 m.a.s.l., 5 November 2006, *E. J. Tepe, A. Marticorena, & P. B. Pelser 1772* (F 2282503). Prov. Huasco, Algarrobal, *C. Jiles 5268* (CONC 68830). Prov. Illapel. Pichidangui, *O. Correa F. s.n.* (K); Pichidangui, *R. Montero 10821* (CONC 112948); Pichidangui, *J. Petersen s.n.* (CONC 42599). Prov. Ovalle. Fray Jorge, *J. Ibáñez, & G. Kuschel s.n.* (SGO 130624); Estancia Talca, *C. Jiles 1419* (CONC 36160); Estancia corral Quemado, *C. Jiles 2050* (CONC 36176); Tongoy, *C. Jiles 4365* (CONC 36119); Fray Jorge, *J. Kummerow s.n.* (CONC 42637); Tres Cruces, Estación Junta de Chingoles, 29°22'W, 14 September 1935, *C. Muñoz P. B-51* (GH); Fray Jorge, 30°40'S, 25 September 1935, *C. Muñoz P. B-62* (GH); Fray Jorge, *C. Muñoz P. 19634* (CONC 129611); Quebrada Teniente, *M. Ricardi 2049* (CONC 12704); Fray Jorge, Boca del Rio Limarí, *B. Sparre 2990* (SGO 98486). **Valparaíso**: Prov. Petorca, Zapallar, 19 September 1923, *F. Behn s.n.* (F 694345); 21 km N along Panamericana from turnoff to Papudo towards Los Vilos, 0–20 m, 10 November 1991, *U. Eggli & B. E. Leuenberger 1660* (B, SGO 145674); Concón, *L. H. Gunckel 21390* (CONC 129614); Ritoque, *L. H. Gunckel 43252* (CONC 129610). Prov. Petorca. 1.3 km N of road to Zapallar, 55 m.a.s.l., 1 November 1990, *T. G. Lammers, C. M. Baeza P., & P. Peñailillo B. 7717* (CONC 113183, F 2058926); 13 km al norte de Puente Guaquén, *C. Marticorena, R. Rodríguez, & E. Weldt 1321* (CONC 43001); Los Molles, *M. Muñoz S. & I. Meza P. 2192* (SGO 137720); Los Molles, *Petersen s.n.* (CONC 42573); Camino entre Papudo and Zapallar, *G. L. Stebbins 8585* (SGO 139705); Quintero, *A. Torres E. s.n.* (CONC 25159). Prov. Valparaíso, 1828, *E. F. Poeppig 144* (G00137859). **No exact locality**: CHILE. Desert of Atacama, September–October 1890, *T. Morong 1186* (F 18024, F 166459, GH, US 1417067).

G22. ***Nolana sphaerophylla*** (Phil.) Mesa ex M.O. Dillon, Darwiniana 45(2): 239. 2007. Fig. 349–352.

Basionym: *Alona sphaerophylla* Phil., Fl. Atac. 44. 1860. TYPE: CHILE. Atacama: Los Animas, [26°23'S, 70°44'W], (1853–1854) *R. A. Philippi s.n.* (Holotype: SGO [55082]).

Heterotypic synonyms: *Alona flaccida* Phil., Anal. Univ. Chile 91: 39. 1895. TYPE: CHILE. Atacama: [Valle] Salado [26°25'S, 69°35'W], 1884, *F. J. San Román s.n.* (Lectotype designated by Mesa-M., 1981: SGO [SGO 042659]; Isolectotype: SGO [SGO 055081]). *Bargemontia flaccida* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 109. 1929; *Nolana flaccida* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 109. 1929.

Digital image: Holotype of *Alona sphaerophylla* from Museo Nacional de Historia Natural, Santiago [SGO 55082]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004346

Homotypic synonym: *Nolana leptophylla* (Miers) I.M. Johnst. ssp. *mollis* (Phil.) Mesa, Fl. Neotrop. Monogr. 26: 116. 1981.

Shrubs to ca. 50 cm tall, ca. 1 m in diam.; stems much-branched, glabrous, stramineous, brittle or delicate. *Leaves* alternate, blades clavate, 2–3 mm long, ca. 2 mm wide, terete, salt glands appearing oily, apically rounded, basally abruptly cuneate, strongly concave adaxially, base with 4–6 apiculate, uniseriate, multicellular trichomes at each side, 0.8–1.2 mm long. *Inflorescences* of solitary flowers from subapical leaf axis; pedicels 8–12 mm long, glabrous, pendant in fruit. *Flowers* 5-merous; calyces campanulate to urceolate, 8–10(–15) mm long, ca. 5 mm wide, green, glabrous; maturing calyx urceolate, appearing inflated, 10–12 mm long, ca. 6 mm wide, lobes triangular, ca. 2 mm long, ca. 2 mm wide, margins thickened, slightly revolute, the interior subglabrous and shiny, with occasional trichomes near the base; corollas infundibularis, white or, more rarely, light blue, ca. 20 mm long, tube pale blue-white; receptacle subtended by lobed, stramineous nectary; receptacle deeply alveolate; style ca. 11 mm long. *Mericarps* (3–)4–5, spherical, 2.5–3.0 mm in diam., five minor ca. 1.5 in diam., nitid; seeds 2–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is derived from the Latin, *sphaericus*, and the Greek, *-phyllus*, and refers to the globose or spherical leaves distinctive in this taxon.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; 20–750 m.a.s.l. (Fig. 349). It is recorded from a few localities in alluvial, sandy soils; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

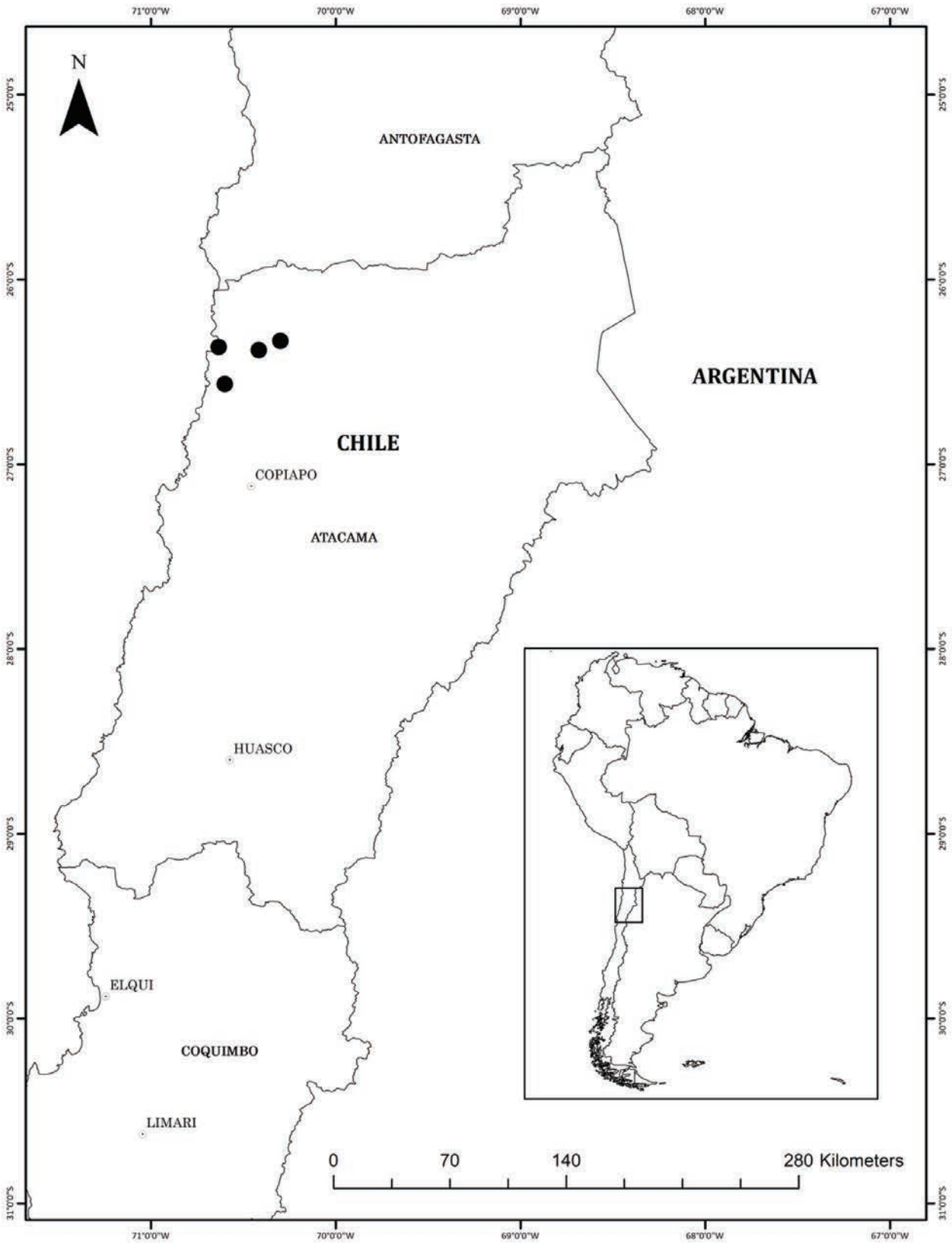


FIGURE 349. Distribution of *Nolana sphaerophylla* (Phil.) Mesa ex M.O. Dillon.

FIGURE 350. *Nolana sphaerophylla*. Low, spreading shrubs several meters in diameter, north of Chañaral, Chile, November 2007.

Nolana sphaerophylla is a small to large, low spreading shrub that can be several meters in diameter (Fig. 350). The leaves are much reduced and, like the calyces, are covered with salt glands (Fig. 351A–B) that can be seen clearly as pits on the leaf surfaces (Fig. 351B). The calyces are very similar to those in *Nolana patula* with deltoid or triangular lobes (Fig. 351C). The corollas are typically five lobed, but, rarely, individual flowers have only 4-lobes and the corollas have a square outline (Fig. 352A–B). The calyces are equally five-lobed, and the margins tend to be slightly revolute (Fig. 352C). The mericarps are rounded, basifixed and in two very unequal series (Fig. 352D). One interesting observation is the presence of three to eight multicellular trichomes, at least 1 mm long, on both sides of the petiole (Fig. 352E).

An examination of the type of *Alona flaccida* showed it to be conspecific with *N. sphaerophylla*, both of which share the unique character of small leaves with a few lateral trichomes on the leaf bases. Mesa-M. (1998) transferred *A. flaccida* to *Nolana*, but his publication did not meet all the requirements for a valid transfer, necessitating the transfer by Dillon (2009). Johnston (1936: 65) placed *Nolana* (*Bargemontia*) *sphaerophylla* in synonymy with *N. divaricata* and, as previously stated (Johnston, 1929: 107), he believed it was related to *Nolana* (*Bargemontia*) *clavata* (= *N. divaricata*) and *Nolana* (*Bargemontia*) *glauca*.

The collection in Berlin of *Eggli et al. 2682* is mixed, with a small branch of *N. sphaerophylla* (*Eggli et al. 2682a*) along with at least two branches of *N. patula* (as *N. flaccida*) under *Eggli et al. 2682*.

Additional specimens examined: CHILE. **Antofagasta**. Prov. Antofagasta, cercanías de Paposo, 25°00'34"S, 70°27'57"W, 20 June 2015, *K. Bull H. 675* (SGO 166634); Lavaderos de Cobre, ca. Taltal, Km 1008 camino Santiago–Arica, 29 February 1972, *G. Mohamedov s.n.* (SGO 116981). **Atacama**: Chañaral, 23 February 1939, 5 m.a.s.l., *A. A. Beetle 26161* (K); Bahía Flamenco, 26.5 km S of Chañaral, 26°34'28"S, 70°41'00"W, 50 m.a.s.l., 27 October 2004, *M. O. Dillon & M. Finger C. 8607* (CONC 179074, SGO 158697); 30 km E of Chañaral, Quebrada Saladito, 9.5 km N of El Salado, 26°23'05"S, 70°19'04"W, 750 m.a.s.l., 4 November 2004, *M. O. Dillon & M. Finger C. 8641* (CONC 179080, E, F 2329902, SGO 158713); 2nd individual for DNA, *8641B* (CONC 179080, SGO 158712); S of Chañaral, 26°20'24"S, 70°26'52"W, 350 m.a.s.l., 5 November 2007, *M. O. Dillon & R. Schulz 9057* (SGO 158735); ca. 7 km SW of Chañaral, 26°23'02"S, 70°39'49"W, 15 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9081* (CONC,

FIGURE 351. *Nolana sphaerophylla*. **A**, Leaves and calyces covered with salt glands; **B**, Salt glands in pits on the leaf surfaces; **C**, Calyces like *N. patula* with deltoid or triangular lobes.

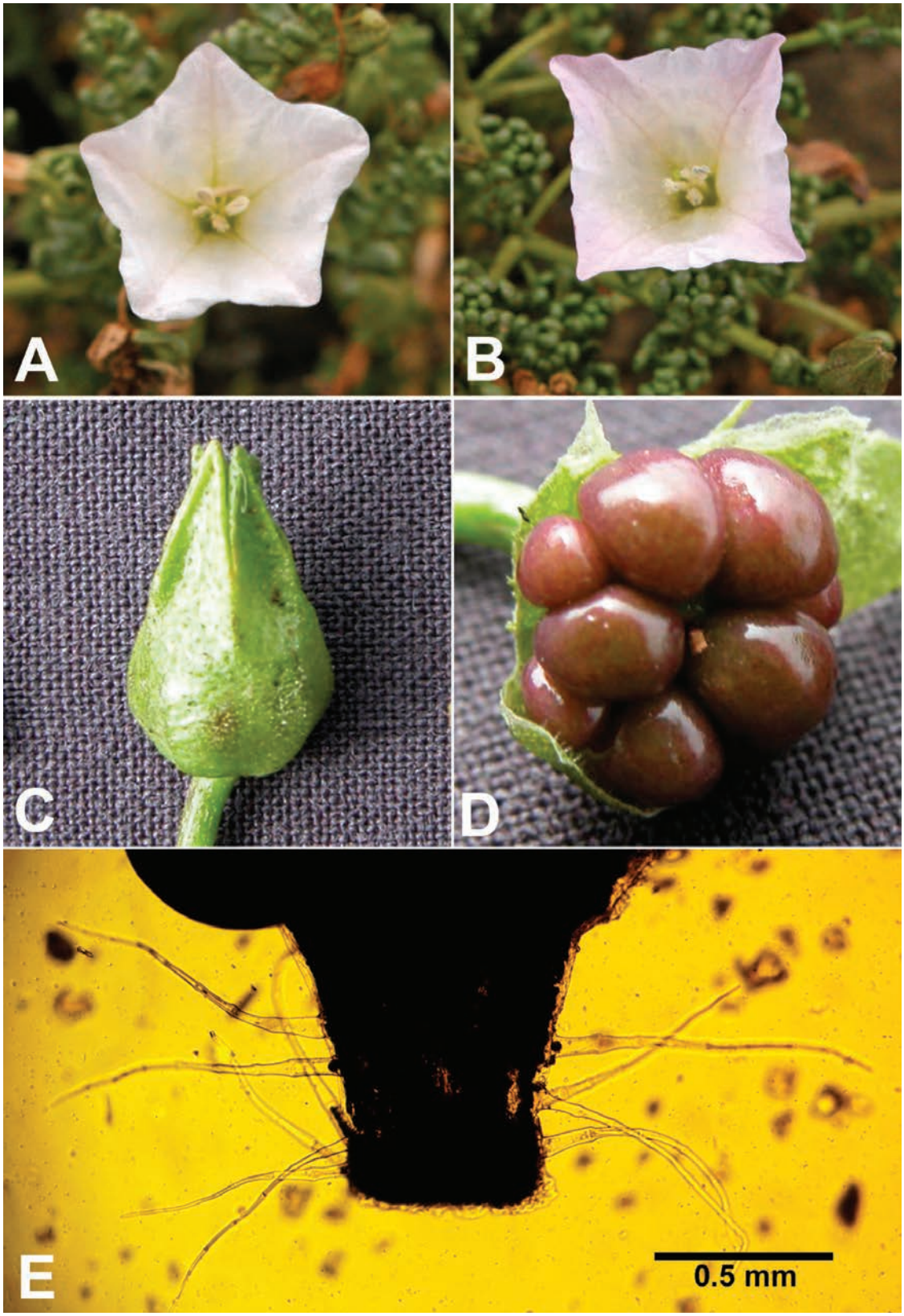


FIGURE 352. *Nolana sphaerophylla*. **A**, Five-lobed corollas with white anther thecae and pollen; **B**, Four-lobed, or square, corolla; **C**, Calyces equally five-lobed with slightly revolute margins; **D**, Rounded mericarps, basifixed, two unequal series; **E,** Three to eight multicellular trichomes, more than 1 mm long on margins of petiole.

SGO); ca. 6 km E of Ruta 5 on road to Mina Manto Verde, 26°27'29"S, 70°40'57"W, 133 m.a.s.l., 28 October 2009, *M. O. Dillon & R. Concha 9090* (CONC, SGO); Quebrada Flamenco, 7 km E of PanAmerican toward Manto Verde and Cerro Pinto, in broad gravely-sandy river bed, 26°34'20"S, 70°36'20"W, 200 m.a.s.l., 12 December 1994, *U. Eggli & B. E. Leuenberger 2632* (B, CONC 132096, SGO 145781); 25 km NE of Chañaral along Panamericana (Km 998), *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2682a* (B, CONC 163570); Flamenco, 26°34'S, 70°41'W, 15 October 2005, *F. Luebert & C. Becker 2840* (SGO 159444); Camino de El Salvador a Chañaral, Quebrada El Salado, 12 km al O de El Salado, 26°23'S, 70°25'W, 9 February 1988, *C. Marticorena, T. Stuessy, & C. M. Baeza P. 9893* (CONC 136257); Chañaral. 9 km al norte de Salado, 14 September 1958, 300 m.a.s.l., *M. Ricardi & C. Marticorena 4613/998* (CONC 25403); Camino de Chañaral a El Salado, Km 16, *C. Marticorena, R. Rodríguez, & E. Wendt 1897* (CONC 36117); al Norte de Chañaral en el Km 990, *M. Muñoz S. & I. Meza P. 2255* (SGO 137721); Poniente de El Salado más o menos 35 km desde Diego de Almagro, 26°24'S, 70°19'W, 490 m.a.s.l., 30 October 1991, *M. Muñoz S., S. Teillier, & I. Meza P. 2787* (SGO 126133); Playa Puerto Fino, Posada San Ramón, 26°30'59"S, 70°41'43"W, 22 m.a.s.l., *M. Muñoz S. 4579* (SGO 153606); Chañaral, Barquito, cerca de la playa, 10 m.a.s.l., 26 October 1941, *E. Pisano V. & R. Bravo F. 515* (CONC 144427, SGO 156441); Chañaral, September 1909, *C. Reiche s.n.* (SGO 61464); Flamenco, September 1909, *C. Reiche s.n.* (SGO 61463); ca. 63 km N of Caldera, ca. 7 km E of Flamenco, 26°34'S, 70°37'W, 180–200 m.a.s.l., 26 October 2000, *S. Teillier & M. O. Dillon 4924* (F 2331767).

G23. ***Nolana tocopillensis*** (I.M. Johnst.) I.M. Johnst., Contrib. Gray Herb 112: 78. 1936. Fig. 353–354.

Basonym: *Bargemontia tocopillensis* I.M. Johnst., Contrib. Gray Herb. 85: 158. 1929. TYPE: CHILE. Antofagasta: Tocopilla, steep hillside ca. 6 km N of port and about opposite Caleta Duendes, 18 October 1925, *I. M. Johnston 3603* (Holotype: GH [00282360]; Isotypes: K [K000532204], S [S04 2776], US [US 1473988, US00121976]).

Digital image: Holotype of *Bargemontia tocopillensis* from Harvard University Herbaria, Cambridge [GH00282360]. https://s3.amazonaws.com/huhwebimages/5F24E7C5F6D841C/type/full/282360.jpg

Homotypic synonym: *Nolana sedifolia* Poeppig ssp. *sedifolia* Mesa, Fl. Neotrop. Monogr. 26: 99. 1981.

Decumbent *subshrubs*, 30–100 cm tall, 30–50 cm in diam.; stems much-branched, pubescent with capitate-glandular trichomes, arachnoid-tomentose with flaccid, elongate, curly trichomes, internodes evident, (1–)4–6(–12) mm long. *Leaves* crowded, alternate to fasciculate, blades oblong, 2–6 mm long, 0.7–1.5 mm wide, inconspicuously pubescent with capitate-glandular trichomes, villous with flagelliform, elongate, curly trichomes, margins revolute. *Inflorescences* of solitary flowers in leaf axils; pedicels 2–4 mm long, densely villous with erect, capitate-glandular trichomes. *Flowers* 5-merous; calyces 5–6 mm long, laxly tomentose, tube ca. 2.5 mm long, ca. 2 mm wide, lobes linear, erect, unequal, ca. 3 mm long, densely pubescent with capitate-glandular trichomes within; corolla blue, 15–16 mm long, narrowly infundibuliform, tube ca. 1 mm wide, throat ca. 9 mm long; anthers 4–5 mm long, sparsely villous; style ca. 1 cm long. *Mericarps* 5; seeds unknown. Chromosome number: unknown.

Etymology: The species epithet refers to the geographic locality of the type, Tocopilla, and, in general, the entire distribution of this narrow endemic.

Distribution and Ecology: Chile, Region of Antofagasta; 100–300 m.a.s.l. (Fig. 353). It is recorded from a small area near Tocopilla, and possibly from historical records, from Cobija, ca. 50 km to the south; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana tocopillensis is a small shrub that rarely reaches one meter tall (Fig. 354). It most closely resembles *N. diffusa*, a species distributed in localities ca. 200 km to the south. Both species are low subshrubs with small, crowded leaves, lax tomentose, curly pubescence, and light blue corollas. Johnston (1929: 159) stated that it was a very distinct species characterized by its elongate corollas that are sparsely villous within, fasciculate leaves, depressed spreading habit, and sparse tomentose indumenta with intermixed copious inconspicuous glandular trichomes. He related it to *Nolana leptophylla*; however, he stated that the corolla in *N. tocopillensis* has an abruptly dilated campanulate throat, triangular calyx lobes, and leaves that are covered with a gray tomentum. Later, Johnston (1936: 78) mentioned that the leaves are glandular, thickened at the attachment, and slightly recurved beyond the middle, which makes the whole leaf look like a sigmoid curve in lateral outline.

The collections assigned to *N. tocopillensis* from Cobija present an interesting problem. It is not beyond the realm of possibility that *N. tocopillensis* (e.g., *Ricardi 3033*, CONC 18266) has been influenced by potential gene flow with such sympatric taxa as *N. clivicola*, and *N. sedifolia*, both recorded from the Cobija area.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Cobija, Aguada Caña, *W. Biese 3072* (SGO 696677); Tocopilla, Cerro Rosario, *M. R. Espinosa s.n.* (SGO 143263); Tocopilla, *F. Jaffuel 1022* (CONC 45986, GH); Tocopilla, September 1931, *F. Jaffuel 1040* (CONC 129678, GH); Tocopilla, September 1931, *F. Jaffuel 2526* (GH); Cobija, July 1836, *C. Gaudichaud s.n.* (GH); Cobija, *M. Ricardi 3033* (CONC 18266).

G24. ***Nolana villosa*** (Phil.) I.M. Johnst., Contrib. Gray Herb. 112: 70. 1936. Fig. 355–359.

Basionym: *Alibrexia villosa* Phil., Fl. Atac. 45. 1860. TYPE: CHILE. Atacama: Breadal, [25°31'S, 70°23'W], *R. A. Philippi s.n.* (Lectotype designated by Mesa-M., 1981: SGO [55125]; F [F neg. 33146]).

Digital image: Lectotype of *Alibrexia villosa* from Museo Nacional de Historia Natural, Santiago [SGO 55125]. http://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000004327

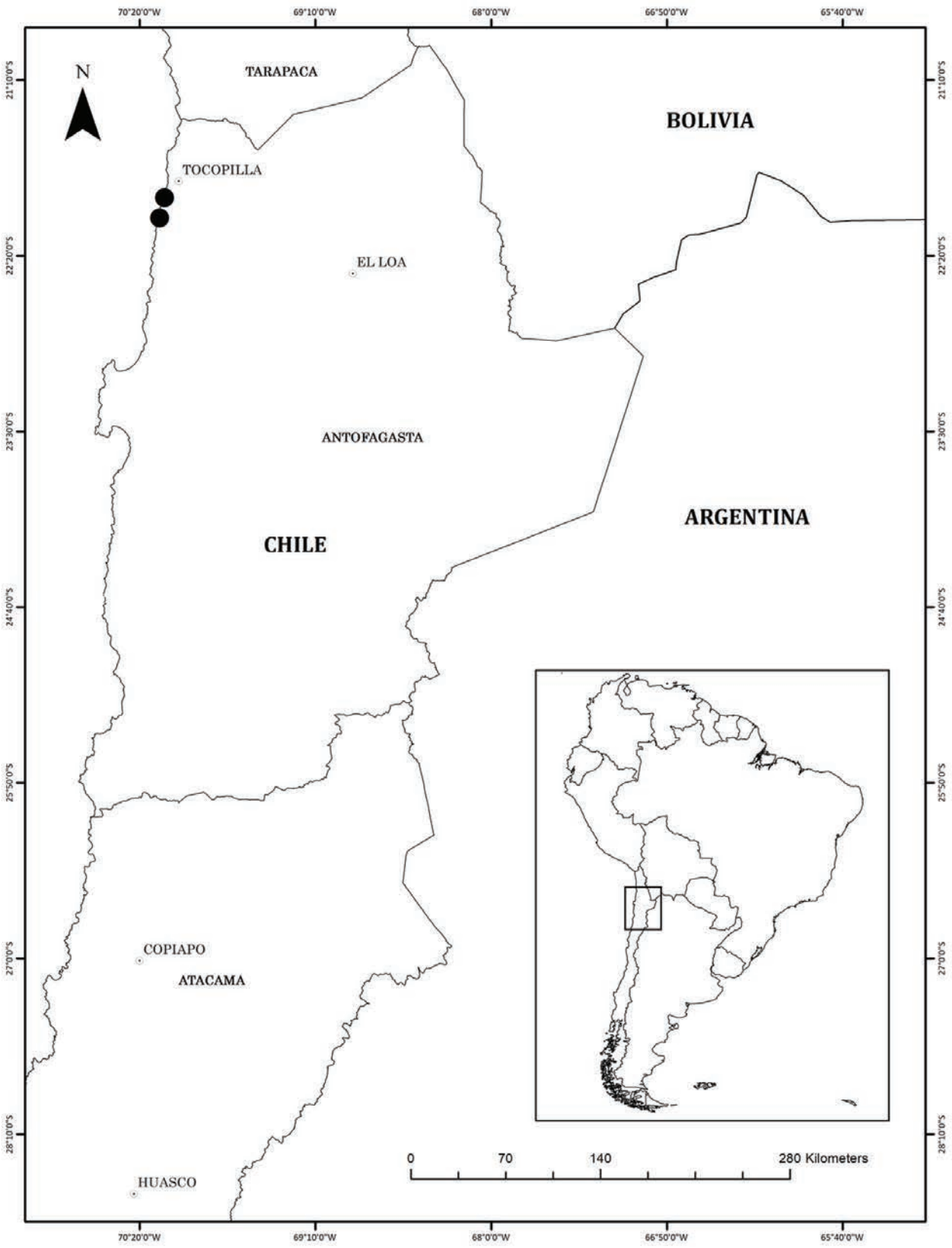


FIGURE 353. Distribution of *Nolana tocopillensis* (I.M. Johnst.) I.M. Johnst.

FIGURE 354. *Nolana tocopillensis*. Small shrubs most closely resembling *N. diffusa* distributed to the south.

Homotypic synonym: *Dolia villosa* Reiche, Anal. Univ. Chile 125. 503. 1910. *Bargemontia villosa* (Phil.) I.M. Johnst., Contrib. Gray Herb. 85: 112. 1929.

Subshrubs to shrubs, 10–30 cm tall, 30–200(–900) cm in diam.; stems branching, decumbent, densely pubescent with dendritic trichomes. *Leaves* alternate to decussate, blades oblong, 5–15 mm long, ca. 1 mm wide, strongly concave adaxially, loosely tomentose to villous with dendritic trichomes, occasionally individuals are nearly glabrous or sparsely pubescent with dendritic trichomes. *Inflorescences* of solitary flowers, terminal and axillary, pedicels 0.8–1.2 cm long. *Flowers* 5-merous; calyces 6–7 mm long, campanulate, 5-lobed, lobes subequal, linear-lanceolate, 4–5 mm long, ca. 2 mm wide, erect, terete; corollas narrowly tubular, weakly infundibular, 9–10 mm long, limb 6–8 mm wide, white to pinkish or pale blue; stamens unequal; filaments pubescent; anther thecae white; nectary disc patelliform; style as long as the shorter filaments, gynobasic; stigma bi-capitate. *Mericarps* 3–5, unequal, globose, smooth, shiny, the larger ca. 2 mm in diam.; seeds 1–3 per mericarp. Chromosome number: unknown.

Etymology: The species epithet is from the Latin, *villosus*, hairy with pubescence, and refers to the dense pubescence on the entire plant giving it a decidedly gray or canescent appearance.

Distribution and Ecology: Chile, Regions of Antofagasta and Atacama; (55–)100–1700 m.a.s.l. (Fig. 355). It is recorded over a large area, common in sandy/rocky soils, and over a wide elevational range; Matorral Desértico Tropical Costero (Luebert and Pliscoff, 2006).

Nolana villosa grows in low perennial mats that can reach very large dimensions (Fig. 356). The corollas are white to pale blue or lavender and are very slightly zygomorphic with different shaped lobes (Fig. 357A). The leaves, calyces, and outer corolla surfaces are covered with dense, dendritic trichomes (Fig. 357B–D).

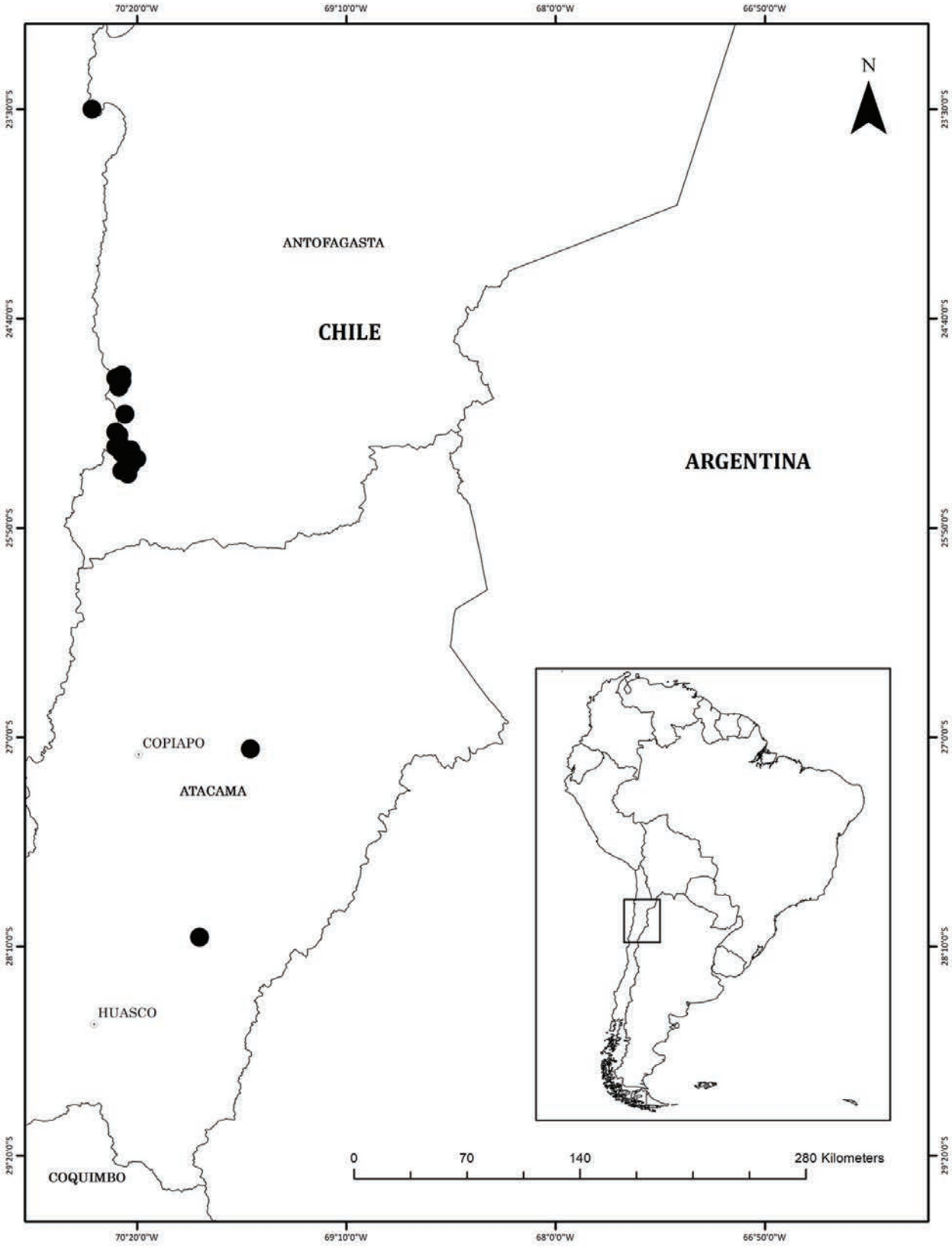


FIGURE 355. Distribution of *Nolana villosa* (Phil.) I.M. Johnst.

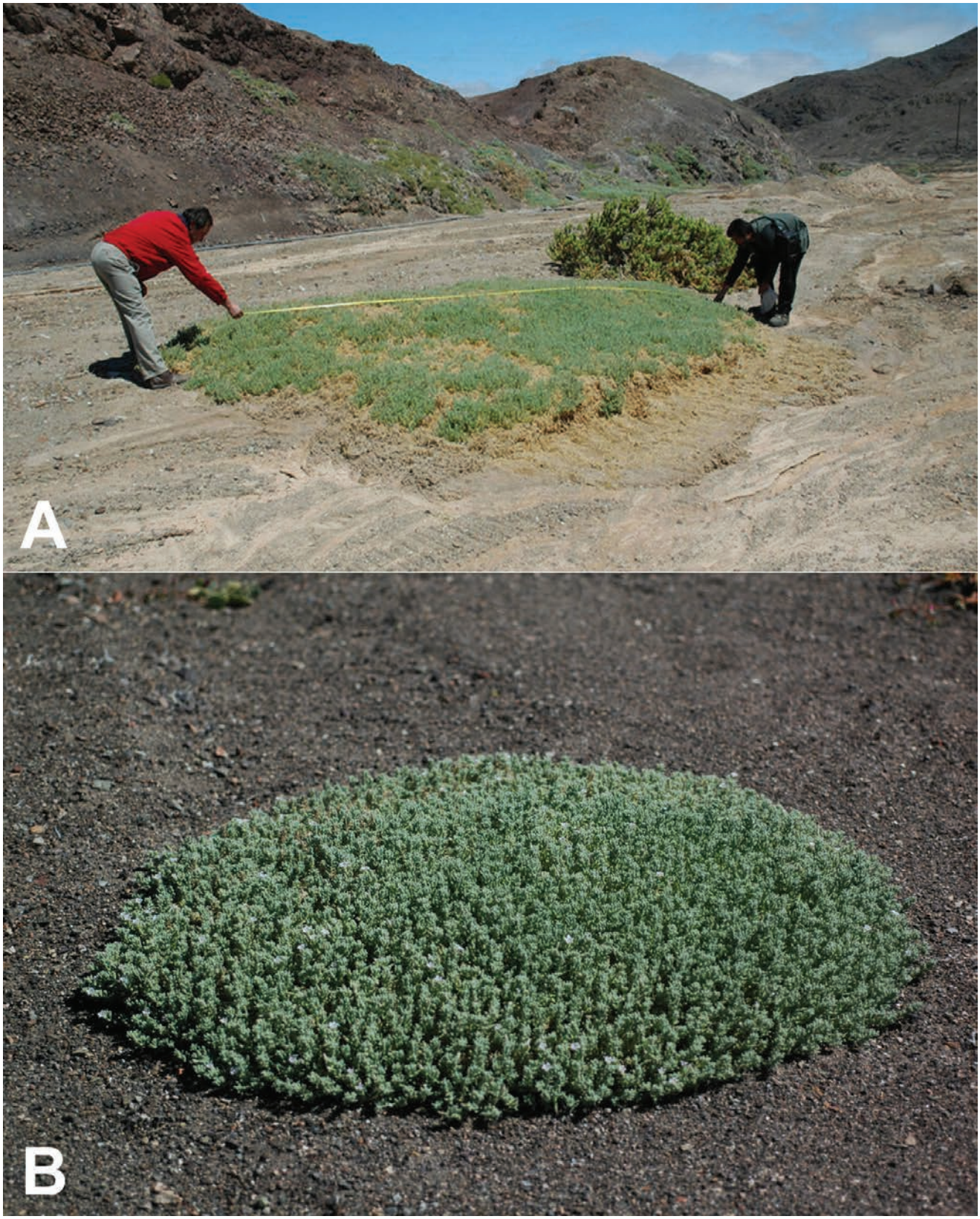


FIGURE 356. *Nolana villosa*. **A**, Low perennial mats reaching over nine meters; **B,** Small individual to less than one meter in diameter.

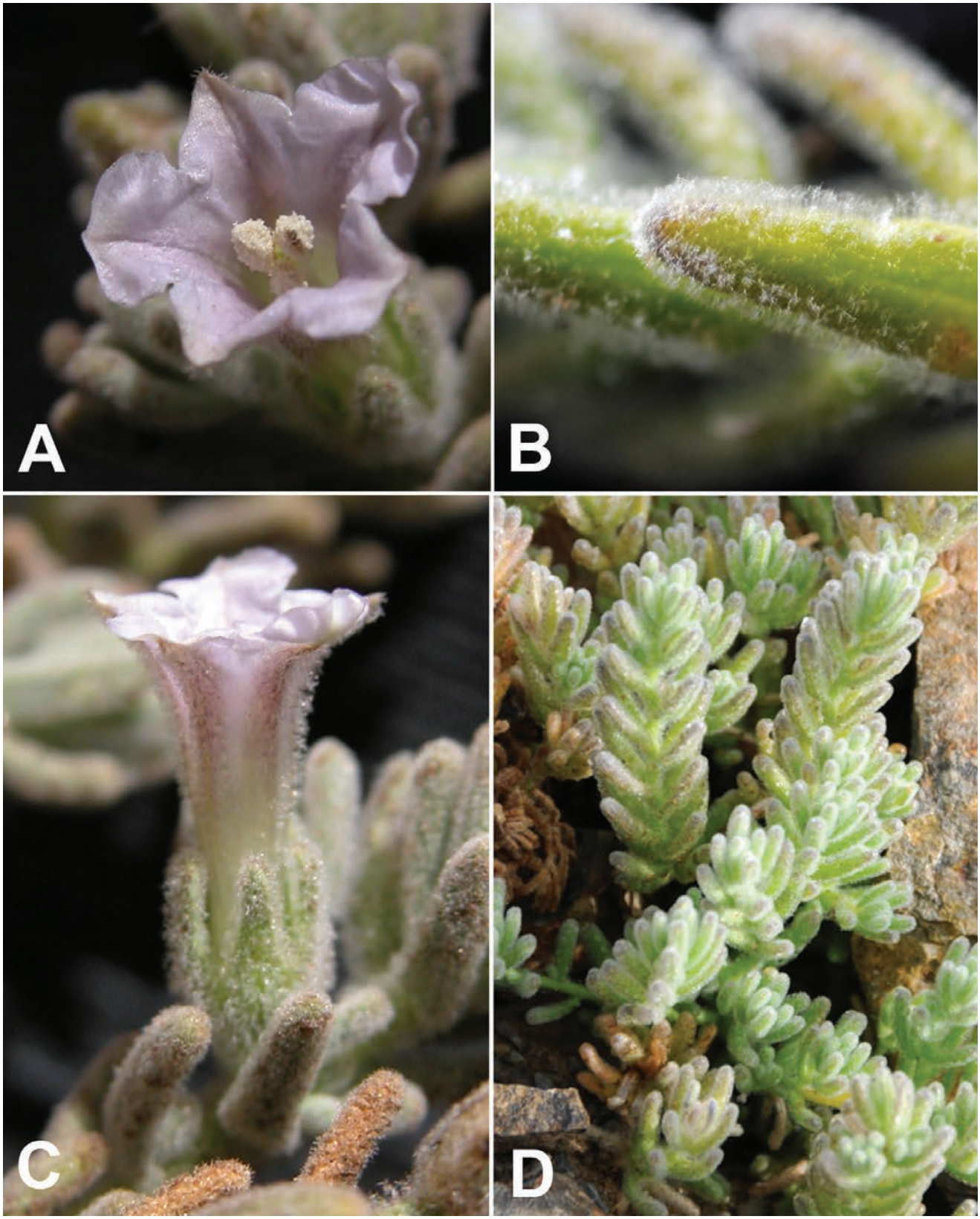


FIGURE 357. *Nolana villosa*. **A**, Frontal view of corollas, anther thecae and white pollen; **B**, Leaves covered with dense, dendritic trichomes; **C**, Calyces and outer corolla surfaces with dendritic trichomes; **D**, Densely set leaves appearing decussate.

Within the population at La Brea, near Taltal in northern Chile, there are two distinct morphs of *Nolana villosa* that are abundant and completely sympatric at the site (Fig. 358A–D). The "typical" morph for the species possesses densely villous stems and leaves and appears whitish or canescent (Fig. 358C). The other morph appears to be much greener, essentially due to the absence of the dense pubescence (Fig. 358D). They both have the same dendritic trichomes; however, the density is so different that they could be interpreted as different species. The underlying leaf morphology is essentially identical, and no differences have been detected in the flowers. A detailed analysis is needed to confirm the taxonomic status of these two morphs.

Nolana villosa is marked by its tendency to "auto-combustion" like that exhibited by *N. mollis*. As the plants end their life cycle, their senescence involves decomposing stems and leaves, which leave a white halo on the ground after they disintegrate (Fig. 22, Fig. 359A–C). This residual ash contains up to 40% dry weight of salts (Rundel et al., 1991).

Johnston (1929: 112) described *Nolana villosa* as, "A pallid plant with decumbent branches forming depressed masses 1.0–2.5 dm tall and 3–20 dm broad. Except near Aguada Panulcito where it was growing on the very arid ridge-crests above the fertile belt, the plant was observed only in the gravel of dry stream-ways. It is not noticeably succulent. The corollas are white or rarely pink and are sparsely villous to quite glabrous within. The indumenta on the stems and leaves consists usually of very abundant soft dendritic or forking hairs. The plant has been collected in our area at Cachinal de la Costa (*Philippi*), Posada Hidalgos (*I. M. Johnston 5663*, *5664*), western end of Llano Colorado (*Johnston 5653*), Breadal (*Philippi*, type), Breas (*Larrañaga*), Valle de la Brea (*L. Darapsky 38*), near Caleta de Hueso Parado (*Johnston 5639*) and near Ag. Panulcito (*Johnston 5462*)."

Only *Nolana leptophylla* shares some characters with *N. villosa*, but their different floral morphology separates the two species. The *Werdermann 454* material collected between Puquios and La Puerta, Cordillera Maricunga, 1800 m.a.s.l., October 1924, is notable for having some forked hairs intermixed with the simple hairs that form the mass of its indumenta. Typically, *N. leptophylla* has entirely simple hairs. Werdermann's specimen, as well as similarities in the shape of the revolute leaves in *N. leptophylla* and *N. villosa*, suggested to Johnston that these two species were related. Other collections possess dendritic or branching trichomes and approach *Nolana leptophylla* in general morphology, as erect shrubs with elongate, blue corollas. Two collections at CONC, *Ricardi & Marticorena 3719* and *3761*, are here reassigned from *N. leptophylla* to *N. villosa*. These come from higher elevations, 1450 m.a.s.l. and 1700 m.a.s.l., respectively, and from more inland localities outside of the influence of coastal fog. Given that the questionable *N. leptophylla* collections come from similar areas, these localities should be resampled to check for possible sources of morphological variation. While cited under *N. villosa*, they clearly approach *N. leptophylla* in possessing shorter leaves and longer corollas. Furthermore, cited here is a collection from the Quebrada de Paipote, *S. Teillier & J. Delaunoy 5551*, that approaches *N. leptophylla* in overall morphology, but has dendritic pubescence. The leaves are short (4–5 mm) and the corollas are 12–13 mm long, with a slightly flared throat like those in *N. leptophylla*.

As with other records by O. Zalensky, his collection of *N. villosa* from extreme northern Chile at 4200 m.a.s.l. is clearly outside of its usual parameters (Arica & Parinacota: Prov. Tarapacá, en pendientes lado sur del Lago Chungará, en suelos arenosos, 4200 m.a.s.l., 27 May 1968, *O. Zalensky XV-862*, SGO 678525). I visited this locality during field studies and found the environmental conditions to be quite unsuitable for *Nolana villosa*. It is possible that the label data is illegitimate, or the plants could have been under cultivation (Sebastián Teillier, pers. comm.).

Initially, several CONC collections were designated as *N. clivicola* or *N. inconspicua*, but these collections possess dendritic trichomes and a floral morphology consistent with *N. villosa*. Due to a superficial resemblance, *Eggli, et al. 2697*, *R. Rodríguez 3079*, and *R. Rodríguez 3093* were all originally incorrectly assigned to *N. clivicola* or *N. inconspicua* but are here treated as *N. villosa*.

Additional specimens examined: CHILE. **Antofagasta**: Prov. Antofagasta, Lomas de Taltal, 25°27'50"S, 70°26'42"W, 360 m.a.s.l., 24 October 2002, *M. Ackermann 464* (CONC 157508, SGO 150948); Quebrada de Bolsico, 23°29'S, 70°36'W, 55 m.a.s.l., *C. Aedo 7024* (CONC 161681, MA); Taltal, cumbre del Cerro Perales, 25°25'10"S, 70°25'33"W, 1032 m.a.s.l., 23 November 2008, *R. Baines, M. Gardner, P. Hechenleitner, C. Morter, & D. Ray 96* (E00230463); hills S of Taltal, 100 m.a.s.l., 25 February 1939, *A. A. Beetle 26171* (GH, K); Mineral Esmeralda, 75 km S de Taltal, 700–800 m.a.s.l., 3 February 1947, *W. Biese 2268* (SGO 74199); Punta Gualaguala, *W. Biese 2776* (SGO 97235); Taltal, Aguada Isla, *W. Biese 3218* (SGO 96821); Caleta Cifuncho, 50–300 m.a.s.l., 14 December 1949, *W. Biese 3361* (SGO 75168); Península Moreno, cerros al lado Oeste de Juan López, *G. Baumann 22* (CONC 122433, SGO 127845); 12 km into canyon road which goes to Taltal from Hwy 5, *O. F. Clarke 17-13* (CONC 158523); upper valley 5 km N of Taltal intersection, *O. F. Clarke 16.5-01* (CONC 158487); Quebrada Paposo, ca. 12 km E of Caleta Paposo, 950 m.a.s.l., 25°01'S, 70°25'W, 910 m.a.s.l., 7 December 1987, *M. O. Dillon & S. Teillier 5119* (F 2010704, GH); Quebrada Paposo, ca. 12 km E of Caleta Paposo, 25°01'S, 70°25'W, 910 m.a.s.l., 7 December 1987, *M. O. Dillon & S. Teillier 5136* (CONC, E, F 2010721, GH, SGO); Hueso Parado, ca. 5 km N of Taltal, 25°24'S, 70°33'W, 60 m.a.s.l., 9 December 1987, *M. O. Dillon & S. Teillier 5193* (CONC, E, F 2010846, GH, SGO); Quebrada del Griton on route to Pta. Tórtolas, ca. 15 km SSW of Taltal, 350 m.a.s.l., 25 December 1987, *M. O. Dillon 5400* (CONC, E, GH, F 2011552, SGO, US 3470026); Quebrada Los Zanjones, 5 km SW on B-900 to Cifuncho, 25°31'S, 70°25'W, 610–620 m.a.s.l., 25 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5500* (CONC, E, F 2011622, GH, SGO, US); Quebrada Los Zanjones, 5 km SW on B-900 to Cifuncho, 25°31'S, 70°25'W, 610–620

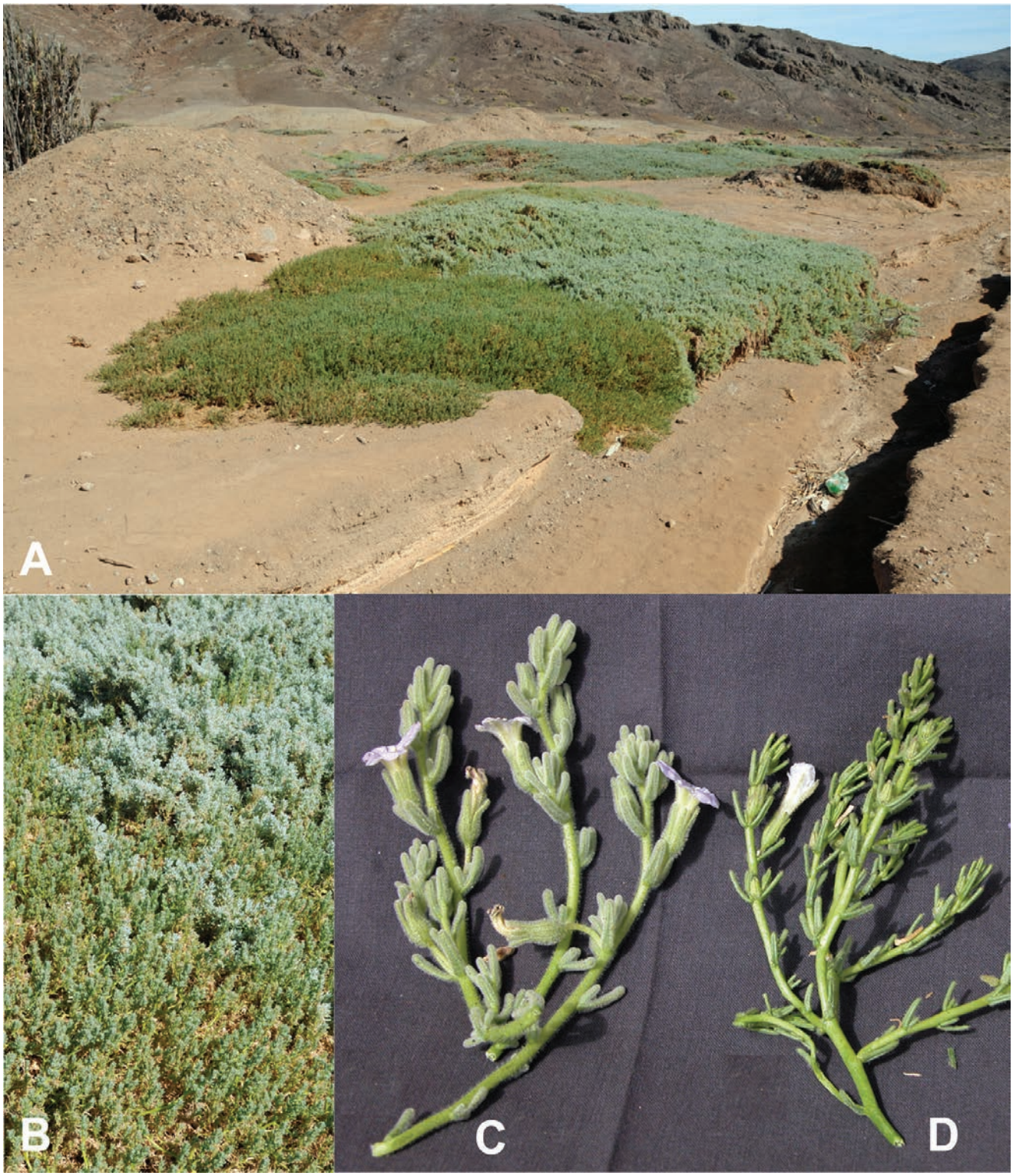


FIGURE 358. *Nolana villosa*. **A–B**, Population at La Brea, Chile with two distinct leaf color morphs sympatric; **C**, Common form with densely villous stems and leaves, whitish or canescent; **D**, Greener form due to less dense pubescence.

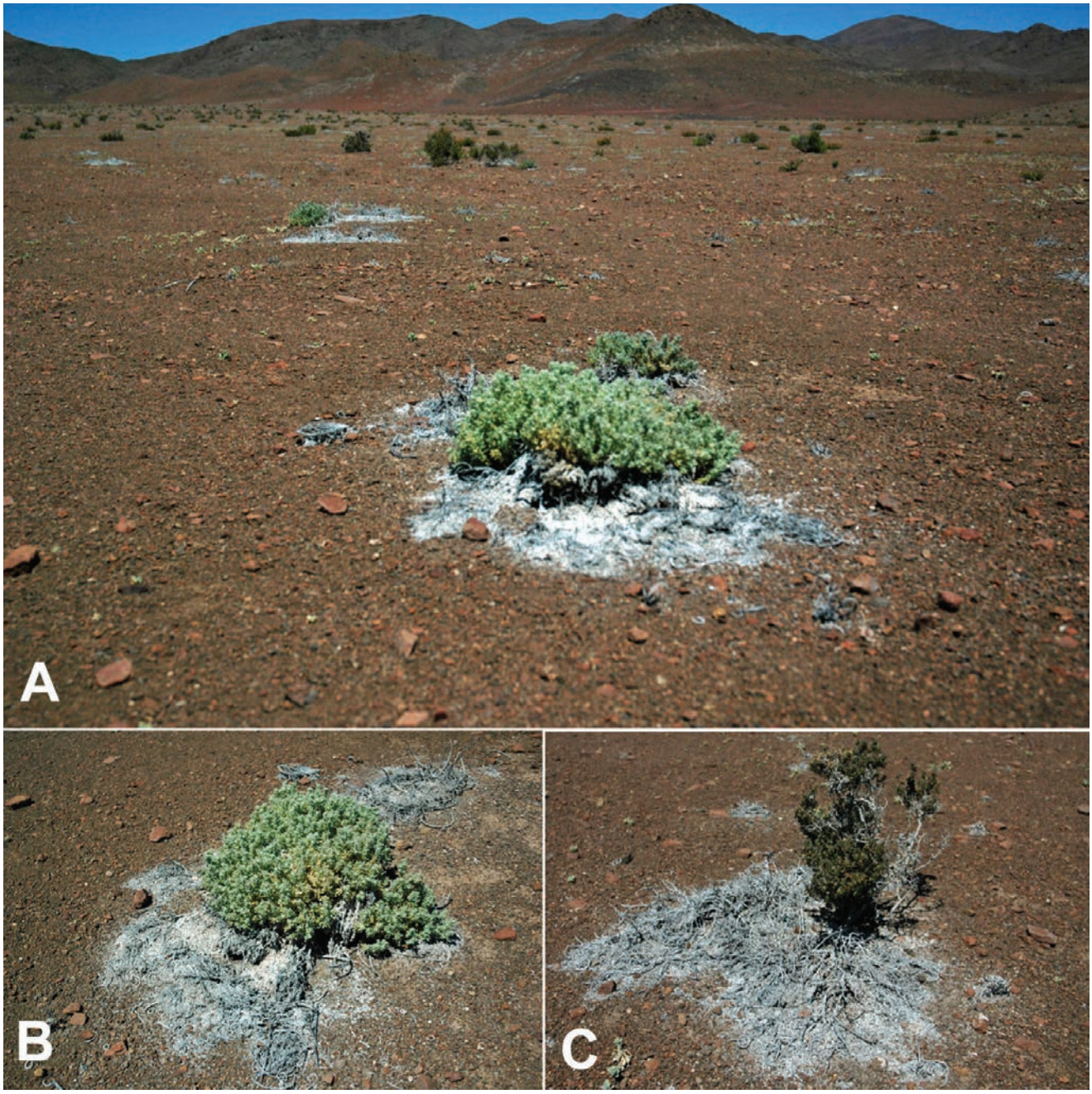


FIGURE 359. *Nolana villosa*. **A–C**. Sequence of auto-combustion as senescence involves decomposing stems and leaves as in *N. mollis*.

m.a.s.l., 25 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5500A* (CONC, F 2011621, E, GH); Quebrada Paposo, 5–12 km E of Caleta Paposo, 25°01'S, 70°25'W, 28 September 1988, *M. O. Dillon, D. Dillon, & V. Poblete 5554* (CONC, E, F 2010216, GH); Hueso Parado, ca.5 km N of Taltal, 25°24'S, 70°33'W, 60–70 m.a.s.l., *M. O. Dillon & D. Dillon 5642* (E, F 2013650, GH, SGO); Hueso Parado, ca.5 km N of Taltal, 25°24'S, 70°33'W, 60–70 m.a.s.l., *M. O. Dillon & D. Dillon 5643* (CONC, E, F 2013649, GH, K, SGO, TEX, US); ca. 13 km E of Taltal, 0.5 km into Quebrada Estación Breas, 25°30'S, 70°25'W, 600 m.a.s.l., 29 October 1988, *M. O. Dillon & D. Dillon 5801* (E, F 230867, GH, SGO, US); 11 km E of Breas, 25°27'S, 70°20'W, 820 m.a.s.l., 29 October 1988, *M. O. Dillon & D. Dillon 5811* (F 2330865); Cerro Perales, 25°25'S, 70°25'W, 550–600 m.a.s.l, 1 November 1988, *M. O. Dillon & D. Dillon 5821* (CONC, E, F 2144380, GH, SGO, TEX, US); Cerro Perales, 25°25'S, 70°25'W, 550–600 m.a.s.l, 1 November 1988, *M. O. Dillon & D. Dillon 5824* (CONC, E, F 2144381, GH, SGO, TEX, US); Cerro Perales, 25°25'S, 70°25'W, 550–600

m.a.s.l, 1 November 1988, *M. O. Dillon & D. Dillon 5825* (CONC, E, F 2144382, GH, TEX, US); Hueso Parado, N of Taltal, 25°23'S, 70°27'W, 40 m.a.s.l., 13 November 1997, *M. O. Dillon & C. Trujillo C. 8024* (CONC 149990, E, F 2183336, GH, K, SGO 143692); Quebrada Paposo, 24°59'S, 70°25'W, 980 m.a.s.l., 15 November 1997, *M. O. Dillon & C. Trujillo C. 8036* (F 2183334); Quebrada Agua de Cascabeles, 25°18'S, 70°27'W, 110 m.a.s.l., 28 November 1997, *M. O. Dillon 8144* (F 2182961); Quebrada de Taltal, near desvío to Cifuncho, 23°30'35"S, 70°24'47"W, 500 m.a.s.l., 14 October 2004, *M. O. Dillon & M. Finger C. 8564* (F 229804, SGO 158706), *8565* (CONC 179086, F 2292803, SGO 158705); road to Cifuncho, 25°31'41"S, 70°25'43"W, ca. 90 m.a.s.l., 7 October 2005, *M. O. Dillon & A. Casareggio M. 8702* (F 2294693, GH, SGO); 14 km E (above) Taltal, Quebrada Taltal, *U. Eggli & B. E. Leuenberger 2865* (B, CONC 138491, SGO 146040); *U. Eggli & B. E. Leuenberger 2684* (CONC 138422, SGO 145878); 2 km s de Taltal, Quebrada de Changos, ca. 2 km S of Taltal, Quebrada de Changos, ca. 0.8 km inland from sea, S slopes of Cerro Barazarte, 25°38'S, 70°30'W, 80–250 m.a.s.l., 16 February 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2686* (B, CONC 138424, SGO 145876); Peninsula Moreno, SW flank of Morro Moreno above Caleta Errázuria, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2697* (B, CONC 138563, SGO 145882); Taltal, La Quinta, 12 October 1983, *M. Elgueta s.n.* (SGO 145521); Cerro Moreno, 18 August 1963, *W. Hermosilla s.n.* (SGO 77387); Paposo, 25 August 1963, *W. Hermosilla s.n.* (SGO 77386); Taltal, *F. Jaffuel 2589* (GH, CONC 92376); al norte de Quebrada de Taltal, *C. Jiles 4950* (CONC 43018); bajada de Taltal, *C. Jiles 5374* (CONC 103466); Aguada Panulcito, 24°49'S, 5 December 1925, *I. M. Johnston 5462* (GH); vicinity of Taltal, 11 December 1925, *I. M. Johnston 5639* (GH, K, US 1473982); Dept. Taltal, western end of Llano Colorado, 13 December 1925, *I. M. Johnston 5653* (GH, K, US 1473983); Posada Hidalgos, 13 December 1925, *I. M. Johnston 5663* (GH, K), Posada Hidalgos, 13 December 1925, *I. M. Johnston 5664* (GH, K); Trayecto Agua Verde–Chañaral, 26 February 2001, *C. Latorre, C. Villagrán, & A. Maldonado 247* (CONC 150766); Cerro Moreno, 23°29'06"S, 70°35'28"W, 570 m.a.s.l., 2 October 2005, *F. Luebert & N. Garcia 2605/999* (F 2329903); Breas, 25°30'S, 70°23'W, 570 m.a.s.l., 10 October 2005, *F. Luebert & N. García 2733/1127* (F 2290718, SGO 159460), *2733A/1127A* (F 2290716, SGO 159461); Sierra Cifuncho, 25°41'S, 70°34'W, 270 m.a.s.l., 12 October 2005, *F. Luebert & N. García 2775/1169* (F 2290699, SGO 159454); valle de Chimba, 200 m.a.s.l., August 1945, *G. Martín s.n.* (CONC 6711); road to Taltal, W of Pan American Hwy 5, 11 September 2001, *M. McMahon & L. Hufford 553* (F 2243061); Quebrada Cascabeles, 10 m.a.s.l., 16 September 1941, *C. Muñoz P. & G. T. Johnson 2843* (SGO 118315); Entrada nueva a Taltal Km 4, 25°32'40"S, 70°22'48"W, 754 m.a.s.l., 29 September 2005, *M. Muñoz S. 4584* (SGO 153611); Cruce entrada a Taltal, *M. Muñoz S. & I. Meza P. 2274* (SGO 137715); Quebrada Portezuelo, *M. Quezada & E. Ruiz 225* (CONC 121078); Mina Abundancia, Quebrada Paposo, *M. Ricardi 2635* (CONC 14428); Camino Antofagasta–Chañaral, quebradas superiores desvío a Taltal, *M. Ricardi 5525* (CONC 36157); cumbres del lado sur del Cerro Moreno, 1000 m.a.s.l., 22 October 1965, *M. Ricardi, C. Marticorena, & O. Matthei 1411* (CONC 43017); Quebrada frente a Juan López, 23°30'S, 70°32'W, 150 m.a.s.l., 10 November 1996, *R. Rodríguez 3079* (CONC 136599, SGO 152965); carretera Antofagasta–Tocopilla, 6 km al N de acceso a Mejillones, 23°08'S, 70°30'W, 11 November 1996, *R. Rodríguez 3093* (CONC 136613, SGO 151595); base of Morro Moreno, 23°30'S, 70°30'W, 50 m.a.s.l., *F. Schlegel 7781* (CONC 99794, SGO 105239); Quebrada Bandurrias, *F. Schlegel 7864* (CONC 99808); road into Taltal, 25°32'19"S, 70°23'14"W, 740 m.a.s.l., 13 April 1994, *C. Taylor & A. Pool 11581* (CONC 143565, SGO 147810), *11583* (CONC 143570, SGO 147808); Quebrada Guanillos, 25°03'S, 70°30'W, 1040 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2750* (F 2114624); Quebrada Guanillos, 25°03'S, 70°30'W, 950 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2758* (F 2114627); Quebrada Guanillos, 25°03'S, 70°30'W, 950 m.a.s.l., 16 September 1992, *S. Teillier, P. Rundel, & P. García 2760a* (SGO 129379); Quebrada Matancilla, 25°26'S, 70°35'W, 185 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2928* (F 2114620); Quebrada Matancilla, 25°26'S, 70°35'W, 185 m.a.s.l., 18 September 1992, *S. Teillier, P. Rundel, & P. García 2931* (SGO 129377); Quebrada La Chimba, 25 October 1959, *A. Torres E. s.n.* (SGO 135489); entre Mejillones y Tocopilla, 23°20'S, 70°34'W, January 2000, *M. A. Trivelli s.n.* (SGO 144328). **Atacama**: Prov. Atacama. Estancia Manflas, 1450 m.a.s.l., *M. Ricardi & C. Marticorena 3719* (CONC 23861); Estancia Manflas, Quebrada de Pauna, 1700 m.a.s.l., *M. Ricardi & C. Marticorena 3761* (CONC 23898). Prov. Copiapó. Quebrada 5 km más allá Canto del Agua hacia Carrizal, 170 m.a.s.l., 23 September 1977, *M. Muñoz S., I. Meza P., & E. Barrera M. 1085* (SGO 108777); Quebrada de Paipote, 540 m.a.s.l., *S. Teillier & J. Delaunoy 5551* (CONC 163832); Tierra Amarilla, 700 m.a.s.l., September 1924, *E. Werdermann 403* (BM000941309, CONC 68829, E00130942, F 565225, GH, K).

G25. ***Nolana werdermannii*** I.M. Johnst., Contrib. Gray Herb. 112: 67. 1936. TYPE: CHILE. Atacama: Prov. Atacama, Vallenar, Alto del Carmen, November 1923, [28°44'57"S, 70°29'27"W], *E. Werdermann 169* (Holotype: GH [00282357]; Isotypes: BM [BM000021203], E [E00130921], F [F 549293, F neg. 566680], G [G00383966], K [K000532250], UC [UC 238288]). Fig. 360–362.

Digital Image: Holotype of *Nolana werdermannii* from Harvard University Herbaria, Cambridge [GH00 282357]. https://s3.amazonaws.com/huhwebimages/D70A7A90D2544BE/type/full/282357.jpg

Homotypic synonym: *Nolana crassulifolia* Poeppig ssp. *crassulifolia* Mesa, Fl. Neotrop. Monogr. 26: 88. 1981.

Erect to spreading *shrubs*, stems 1.0–1.5 m tall, pale green to gray, densely pubescent with dendritic trichomes,

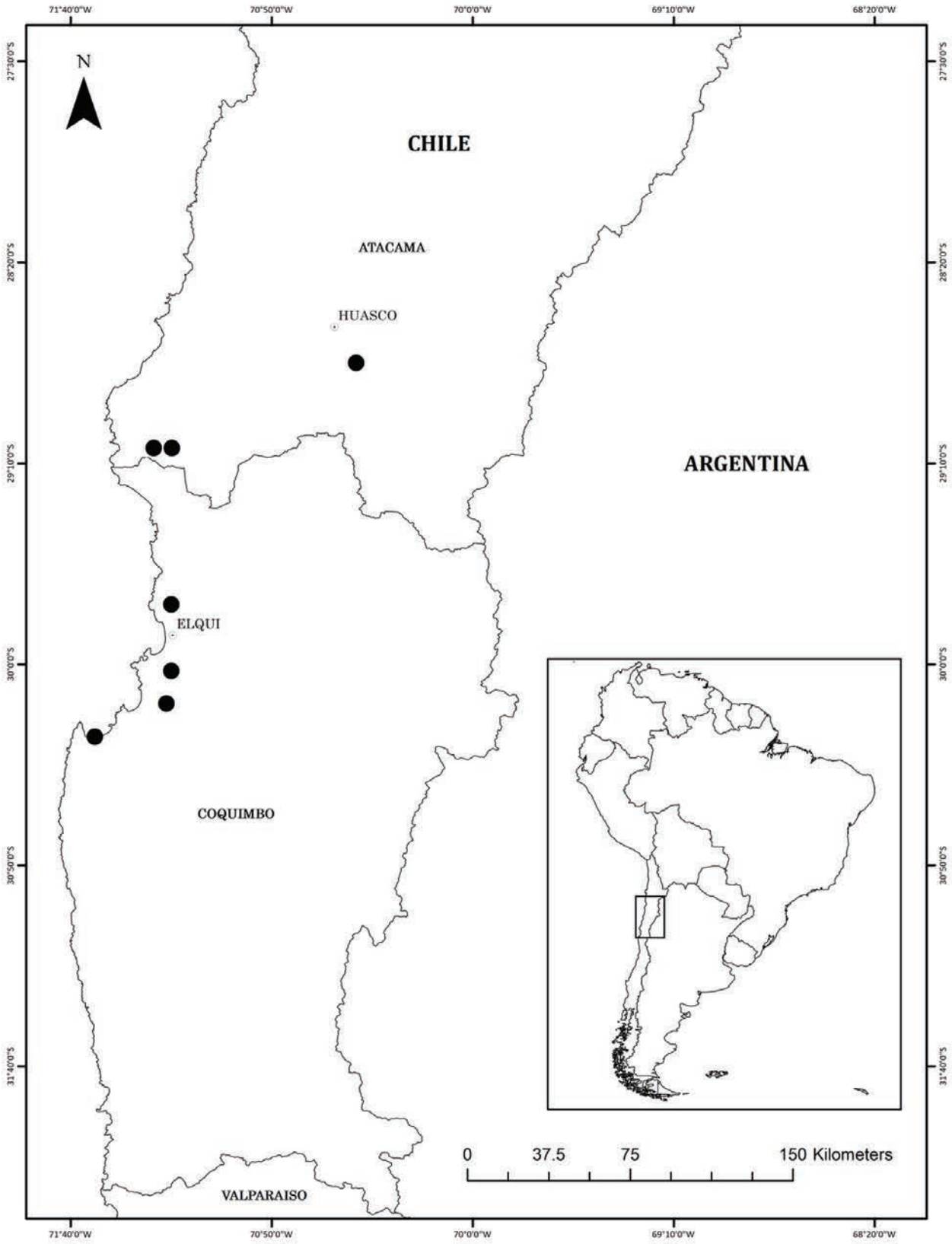


FIGURE 360. Distribution of *Nolana werdermannii* I.M. Johnst.

FIGURE 361. *Nolana werdermannii*. **A**, Intricately branched shrubs to one meter or more in height; **B**, Leaves with dendritic pubescence; **C**, Calyces actinomorphic.

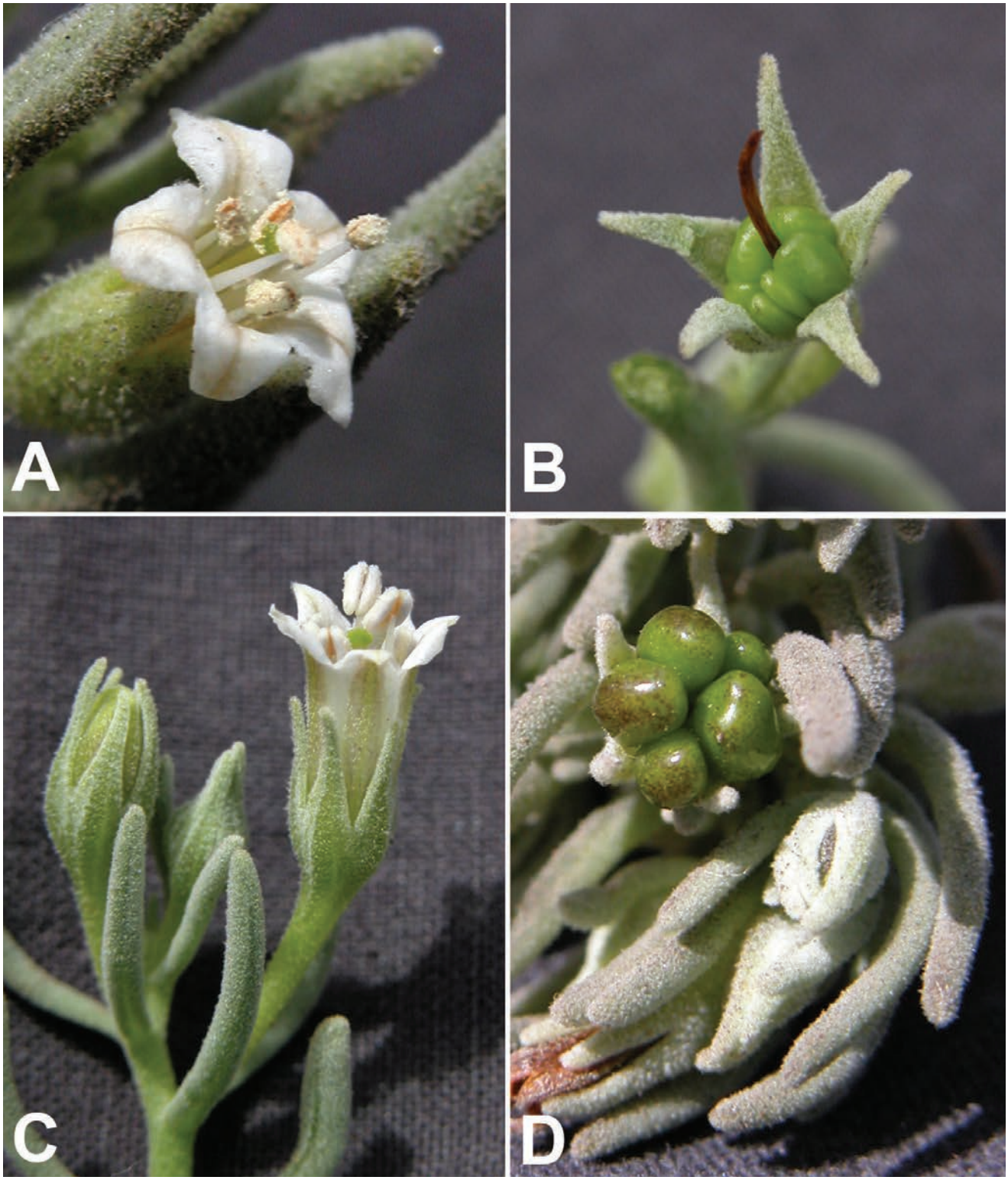


FIGURE 362. *Nolana werdermannii*. **A**, Closeup of flower with white anther thecae and pollen; **B**, Gynoecium with gynobasic style; **C**, Lateral view of flower; **D**, Maturing mericarps.

inconspicuously glandular. *Leaves* linear to linear-spathulate, strongly concave abaxially, 15–25 mm long, 1.0–2.5 mm wide, gray-green, tomentose. *Inflorescences* of solitary flowers in distal leaf axils, pedicels to ca. 10 mm long. *Flowers* 5-merous; calyces narrowly campanulate to cupulate, 6–7 mm long, ca. 5 mm wide at anthesis, tube 2.0–2.5 mm long, lobes narrowly deltoid, ca. 5 mm long, ca. 2 mm wide, gray-green, dendritic pubescence; corollas actinomorphic, tubular, 7–8 mm long, 6–7 mm wide, tube 5–6 mm long, lobes triangular, ca. 1 mm long, white or, rarely, lavender; stamens 5, filaments completely exserted, unequal, 2.5–3.5 mm long, white. *Mericarps* 5, angular-ovoid, 2.5–3.0 mm long, basifixed, seeds 2–4 per mericarp. Chromosome number: unknown.

Etymology: The species epithet commemorates Dr. Erich Werdermann (b. 1892–d. 1959), a German botanist and mycologist who, in 1923, undertook a four-year research trip to Chile and neighboring countries. He was responsible for collecting type material for three new species and over 25 collections of various *Nolana* species between 1923 and 1925 (Braidwood et al., 2014).

Distribution and Ecology: Chile, Regions of Atacama and Coquimbo; 50–510 m.a.s.l. (Fig. 360). It is recorded from near-ocean sites to well away from the ocean, up to 80 km inland; Matorral Desértico Tropical Costero and Matorral Desértico Mediterráneo Costero (Luebert and Pliscoff, 2006).

Nolana werdermannii is a gray, or canescent, intricately branched shrub to one meter or more in height (Fig. 361). The leaves have dense, dendritic pubescence giving them a gray or whitish appearance (Fig. 361B–C). The calyces are actinomorphic, as are the corolla lobes; the anther thecae and pollen are invariably white (Fig. 362A, C). The gynoecium has the typical gynobasic style and five smooth, shiny mericarps (Fig. 362D).

Nolana werdermannii has dendritic pubescence like that in *N. albescens*, *N. crassulifolia*, *N. incana*, and *N. peruviana*, all congeners that are distributed to the north (Dillon et al., 2009, pp. 471–472).

Johnston (1936: 67) believed this taxon belonged to the *Nolana crassulifolia* group, that is characterized by its small corollas, slender leaves, and well-developed pedicels. He suggested that its nearest relative was likely *N. albescens*, which grows to the north of *N. werdermannii* and in habitats more distant from the from the coast. Mesa placed *N. werdermannii* in synonymy with *N. crassulifolia* ssp. *crassulifolia* Mesa, a species concept that reduced several species recognized in this treatment, including *N. albescens*, *N. incana*, and *N. werdermannii*.

Additional specimens examined: CHILE. **Atacama**: Huasco, 26 December 1971, *K. Beckett, M. Cheese, & J. Watson 4706* (SGO 110277); Vallenar, October 1927, *Bro. Claude-Joseph 5027* (US 1804276); W of Ruta 5 toward Carrizal Bajo, 100 m.a.s.l., 29 November 2004, *M. O. Dillon & M. Finger C. 8665* (SGO 158940); 18 km E of Huasco, 28°30'21"S, 71°07'33"W, 200 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8649* (SGO 158920); road to Aguada Tongoy, 5 km SE of Huasco, 28°29'28"S, 71°09'24"W, 100 m.a.s.l., 13 November 2004, *M. O. Dillon & J. Guerra G. 8654* (SGO 158915); Copiapó, Quebrada de Totoral, 160–180 m.a.s.l., 24 November 1941, *E. Pisano V. & R. Bravo F. 804* (CONC 144540, SGO 156613); Huasco, Freirina–Portezuelo Varilla km 27 Ruta C-452, 28°24'27"S , 70°53'53"W, 510 m.a.s.l., 24 February 2012, *M. Rosas 7936 [INIA-1232]* (K). **Coquimbo**: Prov. Choapa, Huentelauquén–Punta Totoral, 31°17'S, 71°37'W, *S. Teillier & J. Delaunoy 6109* (CONC 171069). Prov. Elqui, La Higuera, Tres Cruces, 28°57'04"S, 70°57'27"W, 450 m.a.s.l., 27 January 2010, *M. Acosta & M. Rosas 1033* (K). Prov. Limarí, Estero Pachingo, Tongoy, 30°18'08"S, 71°34'24"W, 40 m.a.s.l., 11 December 2004, *M. O. Dillon & G. Arancio 8687* (ULS); 50 m.a.s.l., *M. O. Dillon & G. Arancio 8691* (ULS); Mun. Ovalle, first hill N of the mouth of the Quebrada San Pedro, W of the culmination of the Panamericana N of Puente Teniente, 30°59'12"S, 71°38'19"W, 80–140 m.a.s.l., 18 October 1997, *U. Eggli & B. E. Leuenberger 2952* (B, SGO 144064). Prov. Elqui, 0.5 km S of Puente Juan Soldado, 29°39'35"S, 71°18'17"W, 200 m.a.s.l., 10 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2879* (B, CONC 138565, SGO 144061); Prov. Elqui, ca. 0.5 km S of Puente Juan Soldado, 32 km N of La Serena, 29°39'35"S, 71°18'17"W, 200 m.a.s.l., 10 March 1997, *U. Eggli, B. E. Leuenberger, & S. Arroyo-Leuenberger 2880* (B, CONC 138503, SGO 144062); Carretera Panamericana, entre Vallenar y La Serena, cerca del extremo inferior de Quebrada Honda, ca. 3 km al N de Caleta Hornos, 125 m.a.s.l., *C. Marticorena, T. Stuessy, & C. M. Baeza P. 9945* (CONC 163311). Prov. Ovalle, Quebrada del Ingenio, *C. Jiles 1481* (CONC 36181); Talinay, 18 October 1951, *C. Jiles 2047* (CONC 36174); Quebrada Honda, *C. Marticorena, O. Matthei, & R. Rodríguez 384* (CONC 43025); Carretera Panamericana, 19 km al N de la Quebrada del Teniente, *C. Marticorena, R. Rodríguez, & E. Weldt 1432* (CONC 43003); 30 km N of La Serena, 10 ft, 2 November 1981, *R. T. Schuh & N. I. Platnick 12* (US 2933411), *14* (US 2933414); Fray Jorge, 10 October 1947, *B. Sparre 2971* (SGO 98470); Cuesta de Buenos Aires, 5 km N of Los Hornos, *E. J. Tepe, A. Marticorena, & P. B. Pelser 1766* (CONC 187869, F 2282501); Fray Jorge, 200 m.a.s.l., November 1925, *E. Werdermann 886* (A, B, BM000941300, CONC 56152, E, F 564331, K, US 1444781, US 3310809); Quebrada las Barrancas, 100 m.a.s.l., 21 November 1935, *J. West 3927* (GH).

Doubtful and Excluded Names and Names Not Validly Published

Alona microphylla Miers = *Phrodus microphyllus* (Miers) Miers

Dolia atacamensis W. Brandt, Bot. Jahrb. Syst. 69(2): 184. 1938. (~ *Nolana crassulifolia* Poepp.)

Fabiana squamuligera Dunal, in DC Prodr 13: 561. 1852.

Nolana bilabiata Gaudich. – Rejected manuscript name for *N. humifusa* from a collection label, never published.

Nolana ventricosa Ruiz & Pav., Fl. Peruv. 2: 7. 1799. – Rejected herbarium name for *N. inflata*, never formally published.

Nolana bipartita Ruiz & Pav., Fl. Peruv. 2: 7, t. 113a. 1799. – Rejected herbarium name for *N. spathulata*, never formally published.

Nolana prostrata (*gallinacea*), Pers., Synop. 1: 168. 1805.

Nolana gallinacea Pers. ex Steudel, [Nom. 556, 1821] Syn. *Nolana humifusa*.

Nolana fruticosa Penny, Hort. Epsom. 34; ex Loud. Gard. Mag. 5: 471. 1829.

Nolana fruticosa Young, Hort. Epsom. 1: 34. 1828, nomen. Johnston (1936: 80) stated that this name appeared without any descriptive matter. Loudon, Gard. Mag. 5: 471 (1829) attributed the name to George Penny who was a gardener at the Young's Epsom Nursery, but whose name is not mentioned in the Hortus Epsomensis. The following data was published regarding the species: "*Nolana* (L.) *fruticosa* Penny in Hort. Eps. p. 34 (*tenella* Lindl. Hort. Trans. vol. vii part ii. p 252). Mr. Lindley erroneously considers this plant an annual. It has remained perfectly shrubby, for several years, in a greenhouse, to which it is no common ornament: hence I have retained the above original and expressive name."

Literature Cited

Addison, M. 1763. Families Naturelles des Plantas, 2: 500.

Adedeji, O., O. Y. Ajuwon, and O. O. Babawale. 2007. Foliar Epidermal Studies, Organographic Distribution and Taxonomic Importance of Trichomes in the family Solanaceae. Int. J. Botany 3(3): 276–282.

Alfaro, M. E., and A. Mesa-M. 1979. El origen morfológico del floema intraxilar en Nolanáceas y la posición sistemática de esta familia. Bol. Soc. Argent. Bot. 18(3–4): 123–126.

Angulo, A. O., and T. S. Olivares. 2005. *Hemieuxoa polymorpha* Forbes 1933 primer registro para Chile: ¿relicto o dispersión? (Lepidoptera, Noctuidae, Noctuinae) / *Hemieuxoa polymorpha* Forbes 1933 first record to Chile: ¿relictual or dispersal? (Lepidoptera, Noctuidae, Noctuinae). Gayana (Concepc.) 69(1): 144–146.

Armstrong, J. E. 1986. Comparative floral anatomy of Solanaceae: a preliminary survey. Pages 101–113 in W. G. D'Arcy, ed., *Solanaceae: Biology and Systematics*. Chapman and Hall, London.

Barboza, G. E., A. T. Hunziker, G. Bernardello, A. A. Cocucci, C. Carrizo García, V. Fuentes, M. O. Dillon, V. Bittrich, M. T. Cosa, R. Subils, A. Romanutti, S. Arroyo, and A. Anton. 2016. Solanaceae. Pages 295–375 in K. Kubitzki and J. W. Jeffrey, eds., *The Families and Genera of Vascular Plants. Asterales. Vol. 8*. Springer Verlag, Berlin.

Bate-Smith, E. C. 1962. The Phenolic Constituents of Plants and their Taxonomic Significance. I. Dicotyledones. Bot. J. Linnean Soc. 58: 95–173.

Bentham, G., and J. D. Hooker. 1873. Genera Plantarum 2: 879–880.

Betancourt, J. L., K. A. Rylander, C. Peñalba, and J. L. McVickar. 2000. A 22,000-yr record of monsoonal precipitation from northern Chile's Atacama Desert. Science 289: 1542–1546.

Braidwood, D. W., V. Morales, and M. F. Gardner. 2014. Werdermann's 'Plantae Chilensis' at the Royal Botanic Garden Edinburgh. Edinb. J. Bot. 71(3): 385–406. doi:10.1017/S0960428614000195.

Bridson, D. R. G. 2004. BPH-2: Periodicals with Botanical Content. Hunt Institute for Botanical Documentation, Pittsburgh. Available and searchable online [http://fmhibd.library.cmu.edu/fmi/iwp/cgi?-db=BPH_Online&-loadframes].

Bondeson, W. E. 1986. Gynoecial morphology and funicular germination plugs in the Nolanaceae. Nord. J. Bot. 6: 183–198.

Bruno, G. B. 1994. Organizacion y vasculatura del gineceo de *Nolana crassulifolia* y *N. rostrata* (Nolanaceae) Bol. Soc. Argent. Bot. (1–2): 51–57.

Bruns, F. 1929. Beitrage zur Keenntnis der Vegetation des peruanischen Kustengebietes. Mitt. Inst. Allg. Bot. Hamburg 8: 1–85.

Cabrera, E., J. Hepp, M. Gómez, and S. Contreras. 2015. Seed dormancy of *Nolana jaffuelii* I.M. Johnst. (Solanaceae) in the coastal Atacama Desert. Flora 214: 17–23.

Campin, M. G. 1924. A cytological study of pollen development in *Nolana*. New Phytol. 24(1): 17–23.

Carlquist, S. 1987. Wood anatomy of Nolanaceae. Aliso 11: 463–471.

Castro, S. A., A. Camousseight, M. Muñoz-Schick, and F. M. Jansic. 2006. Rudolfo Amando Philippi, el naturalista de mayor aporte al conociminto taxonómico de la Diversidad biológica de Chile. Rev. Chil. Hist. Nat. 79: 133–143.

Chamorro, S., R. Heleno, J. M. Olesen, C. K. McMullen, and A. Traveset. 2012. Pollination patterns and plant breeding systems in the Galápagos: a review. Ann. Bot. 110: 1489–1501. doi:10.1093/aob/mcs132, online: www.aob.oxfordjournals.org.

Chamy, M. C., J. A. Garbarino, M. Piovano, J. L. López-Perez, M. Nicoletti, R. Gandolfo, and A. San Feliciano. 1997. 9-epi-Labdane diterpenoids from *Nolana rostrata* var. *rostrata*. Phytochemistry 45: 797–800.

Chamy, M. Piovano, and J. A. Garbarino. 2002. Diterpenoids from *Nolana elegans*. Bol. Soc. Chil. Quím. 47(4): 367–370.

Chiang, F. 1983 [1984]. El numero cromosomico de *Grabowskia geniculata* (Solanaceae). Bol. Soc. Bot. Mex. 45: 141–142.

Chiarini, F. E., N. C. Moreno, G. E. Barboza, and G. Bernardello. 2010. Karyotype characterization of Andean Solanoideae (Solanaceae). Caryologia 63(3): 278–291.

Chiarini, F. E., R. Deanna, and L. Bohs. 2022. Phylogeny, character evolution and biogeography of the genus *Sclerophylax* (Solanaceae). Taxon 71(6): 1251–1267.

Cifuentes, F., J. Palacios, J. Bórquez, A. Paredes, C. Parra, A. Bravo, and M. J. Simirgiotis. 2020. Fast Isolation of Flavonoids from the Endemic Species *Nolana ramosissima* I.M. Johnst. and Its Endothelium-Independent Relaxation Effect in Rat Aorta. Molecules. 25(3): 520. doi:10.3390/molecules25030520.

CONAF. 1993. Decretos Supremos relativos a las áreas Silvestres Protegidas de Chile (1988–1993). Documento de trabajo N°10. Corporación Nacional Forestal, Santiago.

Cronquist, A. 1981. *An integrated system of classification of the Angiosperms*. Columbia Univ. Press, New York. 1262 pages.
Curtis's Botanical Magazine. 1825. *Nolana paradoxa*. 52: 2604.
Curtis's Botanical Magazine. 1862. *Nolana lanceolata*. 88: 5327.
Dahlgren, B. E. 1940. Travels of Ruíz, Pavón, and Dombey in Peru and Chile (1777–1778). By Hipólito Ruíz, with an epilogue and official documents added by Augustín Jesús Barreiro. Translation by B. E. Dahlgren. Fieldiana Bot. 21: 1–372.
Dahlgren, R. M. T. 1980. A revised system of classification of the Angiosperms. Bot. J. Linnean Soc. 80: 91–124.
Dandy, J. E. 1967. Index of generic names of vascular plants, 1753–1774. Regn. Veg. 51: 1–130.
D'Arcy, W. 1979. The classification of the Solanaceae. Pages 3–48 in J. G. Hawkes, R. N. Lester, and A. D. Skelding, eds., *The Biology and Taxonomy of the Solanaceae*. Academic Press, London.
D'Arcy, W. 1991. The Solanaceae since 1976, with a review of its biogeography. Pages 75–137 in J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada, eds., *Solanaceae 3: Taxonomy–Chemistry–Evolution*. Royal Botanic Garden, Richmond, U.K.
Darwin, C. 1877. *The Different Forms of Flowers on Plants of the Same Species*. 352 pages. London: John Murray, Albemarle Street.
Dassanayake, M., and J. C. Larkin. 2017. Making Plants Break a Sweat: The Structure, Function, and Evolution of Plant Salt Glands. Frontiers Plant Science Review. Pages 1–20. doi:10.3389/fpls.2017.00406.
Datta, S. 1933. Embryological and cytological studies in *Nolana atriplicifolia* and *N. prostrata*. J. Indian Bot. Soc. 12: 131–152.
De la Torre-González, A., D. Montesinos-Pereira, B. Blasco, and J. M. Ruiz. 2018. Influence of the proline metabolism and glycine betaine on tolerance to salt stress in tomato (*Solanum lycopersicum* L.) commercial genotypes. J. Plant Physiol. 231: 329–336. doi:10.1016/j.jplph.2018.10.013.
Di Fulvio, T. E. 1969. Embriologa de *Nolana paradoxa* (Nolanaceae). Kurtiziana 5: 39–54.
Di Fulvio, T. E. 1984. Numero cromosomico de *Nolana rostrata*. Kurtiziana 17: 169.
Dillon, M. O. 1997. *Lomas* Formations–Peru. Pages 519–527, in S. D. Davis, V. H. Heywood, O. Herrera-McBryde, J. Villa-Lobos, and A. C. Hamilton, eds., *Centres of Plant Diversity, A Guide and Strategy for their Conservation*. *WWF*, Information Press, Oxford, U.K.
Dillon, M. O. 2005. Solanaceae of the *Lomas* formations of Coastal Peru and Chile. Pages 131–155, in V. Hollowell, T. Keating, W. Lewis, and T. Croat, eds., A Festschrift for William G. D'Arcy: The Legacy of a Taxonomist. Monographs in Systematic Botany from the Missouri Botanical Garden 104.
Dillon, M. O. 2007. *Nolana sphaerophylla* (Phil.) Mesa ex M.O. Dillon. Page 239 in F. O. Zuloaga, O. Morrone, and M. J. Belgrano. Novedades Taxonómicas y Nomenclaturales para la Flora del Cono Sur de Sudamérica/Taxonomical and Nomenclatural Novelties for the Vascular Flora of the Southern Cone of South America. Darwiniana 45(2): 236–241.
Dillon, M. O. 2009. Nomenclatural changes in *Nolana* (Nolaneae, Solanaceae)—Cambios nomenclaturales en *Nolana* (Nolaneae, Solanaceae) Gayana Bot. 66(2): 294–296.
Dillon, M. O. 2017. *Nolana* (Solanaceae). Pages 343–344 in G. E. Barboza, A. T. Hunziker, G. Bernardello, A. A. Cocucci, A. E. Moscone, C. Carrizo Garcia, V. Fuentes, M. O. Dillon, V. Bittrich, M. T. Cosa, R. Subils, A. Romanutti, A. Arroyo, and A. Anton, eds., The Families and Genera of Vascular Plants. Asterales. Vol. 8. Springer-Verlag, Berlin.
Dillon, M. O., G. Arancio, and F. Luebert. 2007a. Five new species of *Nolana* (Solanaceae–Nolaneae) from Chile. Arnaldoa 14: 197–227.
Dillon, M. O., S. Leiva-G., and V. Quipuscoa-S. 2007b. Five new species of *Nolana* (Solanaceae–Nolaneae) from Peru and notes on the classification of additional taxa. Arnaldoa 14: 171–190.
Dillon, M. O., T. Tu, A. Soejima, T. Yi, Z. Nie, A. Tye, and J. Wen. 2007c. Phylogeny of *Nolana* (Nolaneae, Solanoideae, Solanaceae) as inferred from granule-bound starch synthase I (GBSSI) sequences. Taxon 54: 1000–1011. doi: 10.2307/25065900. http://www.jstor.org/stable/25065900
Dillon, M. O., T. Tu, L. Xie, S. Quipuscoa V., and J. Wen. 2009. Biogeographic diversification in *Nolana* (Solanaceae), a ubiquitous member of the Atacama and Peruvian Deserts along the western coast of South America. J. Syst. Evol. 47: 457–476. doi:10.1111/j.1759-6831.2009.00040.x
Dillon, M. O., and A. E. Hoffmann-J. 1997. *Lomas* Formations of the Atacama Desert, Northern Chile. Pages 528–535 in S. D. Davis, V. H. Heywood, O. Herrera-McBryde, J. Villa-Lobos, and A. C. Hamilton, eds., Centres of Plant Diversity, A Guide and Strategy for their Conservation. WWF, Information Press, Oxford, United Kingdom.
Dillon, M. O., M. Nakazawa, and S. Leiva. 2003. The *Lomas* Formations of Coastal Peru: Composition and Biogeographic History. Pages 1–9 in J. Haas and M. O. Dillon, eds., "El Niño in Peru: Biology and Culture Over 10,000 Years." Fieldiana Bot., N.S. 43, publ. 1524.
Dillon, M. O., and V. Quipuscoa-S. 2023. Two New Species of *Nolana* L.f. (Nolaneae–Solanaceae) from Southern Peru. Harvard Pap. Bot. 28(1): 1–13.
Dillon, M. O., and P. W. Rundel. 1990. The botanical response of the Atacama and Peruvian Desert flora to the 1982–83 El Niño event. Pages 487–504 in P. W. Glynn, ed., *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation*. Elsevier, New York.
Douglas, A. C. 2016. Sexual compatibility between eight *Nolana* L.f. (Solanaceae) species from Peru and Chile. Euphytica 208: 33–46. doi:10.1007/s10681-015-1483-3.
Douglas, A. C., and R. Freyre. 2010. Floral development, stigma receptivity and pollen viability in eight *Nolana* (Solanaceae) species. Euphytica 174:105–117. doi:10.1007/s10681-010-0145-8.
Dumesh, S., and L. Packer. 2013. Three new species of *Neofidelia* (Hymenoptera: Apoidea: Megachiliae) from Northern Chile. Zootaxa 3609(5): 471–483.
Dumortier, B. C. 1829. Analyse des familles des plantes. Page 24. Tournay.
Dunal, M. F. 1852. Solanaceae. Pages 8–21 in A. P. de Candolle, ed., Prodromus systematis naturalis regni vegetabilis. 13(1).
Dupin, J., N. J. Matzke, T. Särkinen, S. Knapp, R. G. Olmstead, L. Bohs, and S. D. Smith. 2017. Bayesian estimation of the global biogeographical history of the Solanaceae. J. Biogeogr. 44(4): 887–899. http://wileyonlinelibrary.com/journal/jbi, doi:10.1111/jbi.12898.
Ehert, G. D. 1764. XXVII. An account of a new Peruvian plant lately introduced into the English gardens; the several characters of which differ from all the genera hitherto described. Philos. Trans. 53: 130–132.
Ehleringer, J. R., P. W. Rundel, B. Palma, and H. A. Mooney. 1998. Carbon isotope ratios of Atacama Desert plants reflect hyperaridity of region in northern Chile. Rev. Chil. Hist. Nat. 71: 79–86.
Eliasson, U. H. 1970. Studies in Galápagos Plants IX, New Taxonomic and Distributional Records. Bot. not. 123: 346–357.

Engler, A., and K. A. Prantl. 1895. Die Natürlichen Pflanzenfamilien Teil. 4, Abt. 3b.

Escalante-Magaña, C., L. F. Aguilar-Caamal, I. Echevarría-Machado, F. Medina-Lara, L. Sánchez-Cach, and M. Martínez-Estévez. 2019. Contribution of Glycine Betaine and Proline to Water Deficit Tolerance in Pepper Plants. HortScience 54(6): 1044–1054. doi:10.21273/HORTSCI13955-19.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. 40: 503–537.

Ferreyra, R. 1953. Comunidades des vegetales de algunas lomas costaneras del Perú. Estac. Exp. Agricola "La Molina," Bol. 53: 1–88.

Ferreyra, R. 1955. Nuevas especies de *Nolana* del Perú. Mus. Hist. Nat. "Javier Prado" 10: 1–15.

Ferreyra, R. 1961. Revisión de las especies peruanas del género *Nolana*. Mem. Mus. Hist. Nat. "Javier Prado" 12: 1–53.

Ferreyra, R. 1974. Una nueva especie de *Nolana* para el Perú. Bol. Soc. Peruana Bot. 7(1–2): 3–5.

Feuillée, L.E. 1725. Journal des observations physiques, mathematiques et botaniques. 3., t. 44. Paris: Giffort.

Finot, V. L., C. Marticorena, and A. Marticorena. 2018. Pollen grain morphology of *Nolana* L. (Solanaceae: Nolanoideae: Nolaneae) and related genera of southern South American Solanaceae, Grana, 57: 415–455. doi:10.1080/00173134.2018.1458897.

Freyre, R., A. Douglas, and M. O. Dillon. 2005. Artificial Hybridizations in Five Species of Chilean *Nolana* (Solanaceae). HortScience 40(3): 532–536.

Fuster-Calvo A., M. Nogales, R. Heleno, C. Vera, and P. Vargas. 2021. Sea dispersal potential and colonization of the Galápagos littoral flora. J. Biogeogr. 48: 1904–1916. doi:10.1111/jbi.14120.

Garbarino, J. A., M. C. Chamy, and V. Gambaro. 1986. Labdane diterpenoids from *Nolana rostrata*. Phytochemistry 25: 2833–2833.

Garbarino, J. A., M. C. Chamy, M. Piovano, and V. Gambaro. 1988. Labdane diterpenoids from *Nolana filifolia*. Phytochemistry 27: 1795–1796.

Garbarino, J. A., M. C. Chamy, M. P. Montagna, and V. Gambaro. 1993. Sesquiterpenoids in *Nolana coelestis*. Phytochemistry 32: 987–989.

Gaudichaud, C. 1841–1852. Botanique du voyage autour du monde sur la corvette "La Bonite", 1836–1837. Bot. Atlas, pl. 8, 28, 33, 101–113. Paris.

Gibson, A. C. 1996. *Nolana mollis* and other Atacama Shrubs. Pages 146–147 in *Structure-Function Relations of Warm Desert Plants (Adaptations of Desert Organisms)*, ISBN-13: 978-3642646386, ISBN-10: 3642646387.

Gibson, A. C., and P. W. Rundel. 2012. Chapter 28. Ecophysiology of photosynthesis in desert ecosystems. Pages 440–452 in J. Flexas, F. Loreto, and H. Medrano, eds., *Terrestrial Photosynthesis in a Changing Environment: A Molecular, Physiological, and Ecological Approach*. Cambridge University Press, Cambridge, U.K.

Gouan, A. 1762. Hortus Regius Monspelliensis, 106 (March–June). Lyon.

Guerrero, P. C., M. Rosas, M. T. K. Arroyo, and J. J. Wiens. 2013. Evolutionary lag times and recent origin of the biota of an ancient desert (Atacama-Sechura). Proc. Natl. Acad. Sci. USA 110(28): 11469–11474.

Gupta, B., and B. Huang. 2014. Mechanism of Salinity Tolerance in Plants: Physiological, Biochemical, and Molecular Characterization. Int. J. Genomics; Article ID 701596, 18 pps. doi:10.1155/2014/701596.

Haegi, L. A. R. 1991. Trichomes of Solanaceae Tribe Anthocercideae. Pages 181–195 in J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada, eds., *Solanaceae 3: Taxonomy-Chemistry-Evolution*. Royal Botanic Garden, Richmond, U.K.

Hartley, A. J., G. Chong, J. Houston, and A. E. Mather. 2005. 150 million years of climatic stability: evidence from the Atacama Desert, northern Chile. J. Geol. Soc. 162: 421–424.

Hepp, J., and M. O. Dillon. 2018. A new endemic species of *Nolana* (Solanaceae-Nolaneae) from near Iquique, Chile. Arnaldoa 26: 323–338.

Herrera, C., E. Custodio, and J. Jódar. 2017. Effect of past wetter periods on current conditions in arid zone aquifers. Pages 189–194 in M. L. Calvache, C. Duque, and D. Pulido-Velazquez, eds., *Impacts of Global Change On Western Mediterranean Aquifers Granada, Oral and posters presentations submitted to the International Congress on Groundwater and Global Change in the Western Mediterranean*, 6–9 November, Granada, Spain.

Hoke, G. D., and C. N. Garzione. 2008. Paleoelevation and geomorphic constraints on the Late Miocene Rise of the Andes. Earth Planet. Sci. Lett. 271: 192–201.

Hooker, W. J., and G. Arnott. 1841. The botany of Captain Beechey's voyage; comprising an account of the plants collected by Messrs. Lay and Collie, and other officers of the expedition, during the voyage to the Pacific and Behring's Strait, performed in His Majesty's ship Blossom, under the command of Captain F. W. Beechey... in the years 1825, 1826, 1827, and 1828. H. G. Bohn, London.

Houston, J. 2006a. The great Atacama flood of 2001 and implications for Andean hydrology. Hydrol. Process. 20: 591–610.

Houston, J. 2006b. Variability of precipitation in the Atacama Desert: its causes and hydrological impact. Int. J. Climatol. 26: 2181–2198.

Huber, K.A. 1980. Morphologische und entwicklungsgeschichtliche Unterschungen an Blüten und Blütenständen von Solanaceen und von *Nolana paradox* Lindl. (Nolanaceae). Pages 1–252, fig. 0–696. Dissertationes botanicae FL-9490 Cramer, Vaduz.

Humaña, A. M., A. Jiménez, and C. E. Valdivia. 2019. *Nolana balsamiflua* (Gaudich.) Mesa (Solanaceae), un arbusto vulnerable del desierto de Atacama dependiente de polinizadores para producir semillas / *Nolana balsamiflua* (Gaudich.) Mesa (Solanaceae), a vulnerable shrub of the Atacama Desert dependent on pollinators for seed set. Gayana Bot. 76(1): 123–125.

Huang, J., W. Xu, J. Zhai, Y. Hu, J. Guo, C. Zhang, Y. Zhao, L. Zhang, C. Martine, H. Ma, and C.-H. Huang. 2023. Nuclear phylogeny and insights into whole genome duplications and reproductive development of Solanaceae plants. Plant Communications. doi:10.1016/j.xplc.2023.100595.

Hunziker, A. T. 2001. *Genera Solanacearum: The Genera of Solanaceae Illustrated, Arranged According to a New System*. A. R. G. Gantner Verlag K.G., Ruggell, Liechtenstein. ISBN 3-904144-77-4.

Ibáñez, N., J. M. Montserrat, and I. Sorino. 2006. Collections from the Royal Spanish Expeditions to Latin America in the Institut Botanic de Barcelona (BC), Spain. Willdenowia 36 (Special Issue): 595–599.

Jewell, C., A. D. Papineau, R. Freyre, and L. C. Moyle. 2012. Patterns of reproductive isolation in *Nolana* (Chilean bellflower). Evolution 66(8): 2628–2636. doi:10.1111/j.1558-5646.2012.01607.

Johnson, H. B. 1975. Plant Pubescence: an ecological perspective. The Botanical Review 44(3): 233–258.

Johnston, I. M. 1929. Papers on the flora of northern Chile. Contrib. Gray Herb. 85: 1–180.

———. 1930. Some notes on the flora of northern Chile. Rev. Chilena Hist. Nat. 34: 228–234.

———. 1931. Vascular Flora of the Guano Islands of Peru. Contrib. Gray Herb. 95: 26–35.
———. 1936. A study of the Nolanaceae. Contrib. Gray Herb. 112: 1–83.
———. 1944. Publication dates of Gaudichaud's Botany of the Voyage of the Bonite. J. Arnold Arbor. 25: 481–487.
Knapp, S. 2002. Tobacco to tomatoes: a phylogenetic perspective on fruit diversity in the Solanaceae. J. Exp. Bot. 53: 2001–2022. doi:10.1093/jxb/erf068.
Knapp, S. 2013. A revision of the Dulcamaroid Clade of *Solanum* L. (Solanaceae). PhytoKeys. 2013; (22): 1–432. Published online May 10, 2013. doi:10.3897/phytokeys.22.4041 PMCID: PMC3689140.
Lengyel, S., A. D. Gove, A. M. Latimer, J. D. Majer, and R. R. Dunn. 2010. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: A global survey. Perspect. Plant Ecol. Evol. Syst. 12(1): 43–55.
Lindley, J. 1824. *Nolana paradoxa*. Cluster-fruited *Nolana*. Bot. Reg. 10, tab. 865.
———. 1830. LX. *Nolana tenella*. In XXVII Report upon the new or rare plants which flowered in the garden of the Horticultural Society at Chiswick, between March 1825, and March 1826. Part II. Hardy Plants. Trans. Hort. Soc. London. 7: 252.
———. 1844. *Alona coelestis*. [*Nolana*, division of the genus]. Edwards's Bot. Reg. 30. (ns) 7: pl. 46.
Linnaeus, C. 1762. *Species Plantarum*, ed. 2, Tomus 1. Stockholm.: i–xvi, 1–784.
Linnaeus fl., C. 1762. Decas prima (et secunda) plantarum rariorum horti Upsaliensis 1: 3. Stockholm.
Luebert, F., and P. Pliscoff. 2006. Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago.
Lujea, N. C., and F. E. Chiarini. 2017. Differentiation of *Nolana* and *Sclerophylax* (Solanaceae) by means of heterochromatin and rDNA patterns. N. Z. J. Bot. 55(2): 163–177. doi:10.1080/0028825X.2016.1269812.
Marticorena, C., and M. Quezada. 1974. Dos especies de *Nolana* (Nolanaceae) nuevas para Chile. Bol. Soc. Biol. Concepc. 48: 91–97.
———. 1985. Catálogo de la flora vascular de Chile. Gayana Bot. 42(1–2): 1–157.
Martins, T. R., and T. J. Barkman. 2005. Reconstruction of Solanaceae phylogeny using the nuclear gene SAMT. Syst. Bot. 30: 435–447.
McCue, K. F., and A. D. Hanson. 1990. Drought and salt tolerance: towards understanding and application. Trends Biotechnol. 8: 358–362.
Mesa-M., A. 1976. Consideraciones acerca de la sistemática de la familia nolanaceae. Bol. Soc. Biol. Concepc. 50: 15–26.
———. 1981. Nolanaceae. Flora neotropica, monograph, 26: 1–197. http://www.jstor.org/stable/4393742.
———. 1986. The classification of the Nolanaceae. Pages 86–90 in W. G. D'Arcy, ed., *Solanaceae: Biology and Systematics*. Columbia University Press, New York.
———. 1997. Nolanáceae de Distribución Chileno–Peruana: su status taxonómico. Bol. Mus. Nac. Hist. Nat. Chile. 46: 23–32.
———. 1998. Nolanaceas del Desierto De Atacama: Endemismo y Status Taxonomico. Soc. Biol. Chile, Not. Biol. (abst.) 6(5): 199.
Mesa-M., A., M. Muñoz-Schick, and R. Pinto B. 1998. Presencia de *Nolana adansonii* (Roemer y Schultes) Johnst. y *Nolana intonsa* Johnst. (Nolanaceae) en el desierto costero de Iquique, norte de Chile. Not. Men. Museo Nac. Hist. Nat. 333: 3–7.
Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 pages.
Miers, J. 1845. The Flora of South America. London J. Bot. 4: 321–371, 498–515.
———. 1850. Illustrations of South American Plants I: 1–183, I–IV, pl. 1–34. H. Baillière, London.
———. 1853. Illustrations of South American Plants. II: Appendix 41. H. Baillière, London.
Miklasevskaja, M., and L. Packer. 2015. Fluctuating asymmetry in an extreme morphological adaptation in the Chilean bee *Xeromelissa rozeni* (Hymenoptera: Colletidae). Can. J. Zool. 93: 833–840.
Mir Sharifi, N., L. Graham, and L. Packer. 2019. Fifteen new species of *Liphanthus* Reed (Hymenoptera: Andrenidae) with two submarginal cells. Zootaxa 4645 (1): 1–80. doi:10.11646/zootaxa.4645.1.1.
Mooney, H. A., S. L. Gulmon, J. Ehleringer, and P. W. Rundel. 1980. Atmospheric water uptake by an Atacama Desert shrub. Science 209: 693–694.
Morales, P., and M. J. Montanola. 2018. Development of *Nolana carnosa* micropropagation protocol. Acta Hortic. 1224: 229–234. doi:10.17660/ActaHortic.2018.1224.31.
Muñoz-P., C. 1959. Sinopsis de la flora chilena. Pages 1–840, Universidad de Chile, Santiago de Chile.
———. 1960. Las especies de plantas descritas por R. A. Philippi en el siglo XIX, estudio critico en la identificación de sus tipos nomenclaturales. Pages 1–189, Universidad de Chile, Santiago de Chile.
———. 1966. Flores silvestres de Chile. Pages 1–245, Universidad de Chile. Editorial Universitaria, Santiago de Chile.
Muñoz-S., M. 1973. Complemento de "Las especies de plantas descritas por R. A. Philippi durante el siglo XIX". Anal. Univ. Chile 128(151–156): 5–69.
———. 2000. Novedades en la familia Alstroemeriaceae. Gayana Bot. 57(1): 55–59.
Muñoz-S., M., R. Pinto, A. Mesa-M., and A. Moreira-M. 2001. "Oasis de neblina" en los cerros costeros del sur de Iquique, Región de Tarapacá, Chile, durante el evento El Niño 1997–1998. Rev. Chil. Hist. Nat. 74: 389–405.
Muñoz-S., M., and A. Moreira-M. 2022. Documentos sobre la flora del norte de Chile / Ivan M. Johnston. Pages 1–257, Piedra Molle, Limache, Chile.
Murry, L. E., and W. H. Eshbaugh. 1971. A palynological study of the Solaninae (Solanaceae). Grana 11: 65–78.
Ohga, N. 1991. Distribution Patterns of Buried Seeds in the Herbaceous Lomas Community over the Entire Plateau on Loma Ancon in the Coastal Desert of Central Peru. J. Arid Land 1: 41–51.
———. 1992. Buried seed population in the herbaceous lomas on Loma Ancon in the coastal desert of central Peru. Ecol. Res. 7: 341–353.
Olmstead, R. G., and L. Bohs. 2007. A summary of molecular systematic research in Solanaceae: 1982–2006. Pages 255–268 in D. M. Spooner, L. Bohs, J. Giovannoni, R. G. Olmstead, and D. Shibata, eds., Solanaceae VI: Genomics Meets Biodiversity. Proceedings of the Sixth International Solanaceae Conference. Acta Hortic. 745. International Society for Horticultural Science, Leuven.
Olmstead, R. G., L. Bohs, H. A. Migid, E. Santiago-Valentin, V. F. García, and S. M. Collier. 2008. A molecular phylogeny of the Solanaceae. Taxon 57(4): 1159–1181.
Olmstead, R. G., and J. D. Palmer. 1992. A chloroplast DNA phylogeny of the Solanaceae: Subfamilial relationships and character evolution. Ann. Mo. Bot. Gard. 79: 346–360.

Olmstead, R. G., J. A. Sweere, R. E. Spangler, L. Bohs, and J. D. Palmer. 1999. Phylogeny and provisional classification of the Solanaceae based on chloroplast DNA. Pages 111–137 in M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop, eds., Solanaceae IV: advances in biology and utilization. Royal Botanic Gardens, Kew.

Orchard, C., P. León-Lobos, and R. Ginocchio. 2009. Phytostabilization of massive mine wastes with native phytogenetic resources: potential for sustainable use and conservation of the native flora in north-central Chile. Cien. Inv. Agr. 36(3): 329–352.

Ossa, P. G., F. Pérez, and J. J. Armesto. 2013. Phylogeography of two closely related species of *Nolana* from the coastal Atacama Desert of Chile: post-glacial population expansions in response to climate fluctuations. J. Biogeogr. 40: 2191–2203.

Osses, P., R. Escobar, C. del Rio, R. Garcia, and C. Vargas. 2017. El Clima desértico costero con nublados abundantes del desierto de Atacama y su relación con los recursos naturales energía solar y agua de niebla. Caso de estudio Alto Patache (20,5°S), región de Tarapacá, Chile. Revista de Geogr. Norte Gd. 68: 33–48.

Packer, L. 2012. *Penapis larraini* Packer, a new species of rophitine bee (Hyenoptera: Halictidae) from fog oasis in Northern Chile. Zootaxa 3408: 54–58.

Palchetti, V. M., M. Reginato, A. Llanes, J. Hornbacherd, J. Papenbrock, G. E. Barboza, V. Luna, and J. J. Cantero. 2021. New insights into the salt tolerance of the extreme halophytic species *Lycium humile* (Lycieae, Solanaceae). Plant Physiol. Biochem. 163: 166–177.

Payne, W. 1978. A glossary of plant hair terminology. Brittonia 30(2): 239–255. doi:10.2307/2806659.

Philippi, R. A. 1857–1858. Plantarum novarum Chilensium, centuria quarta. Linnaea 29: 1–47.

———. 1860. Viaje al Desierto de Atacama hecho por el Gobierno de Chile, en el verano de 1853–54. Flórula Atacamensis I–IV: 1–236.

———. 1864–1865. Plantarum novarum Chilensium Centurae, inclusis quibusdam Mendocinis et Patagonicis. Linnaea 33: 1–308.

———. 1884. Bemerkungen über *Alona rostrata* Lindl. Gartenflora 33: 39, 356, tab. 1175.

———. 1895. Plantas nuevas chilenas. Annales Univ. Chile 91: 5–47.

Pinto, R., and F. Luebert. 2009. Datos sobre la flora vascular del desierto costero de Arica y Tarapaca, Chile, y sus relaciones fitogeograficas con el sur de Perú / Data on the vascular flora of the coastal desert of Arica and Tarapaca, Chile, and its phytogeographical relationships with Southern Peru. Gayana Bot. 66: 28–49.

Pliscoff, P., N. Zanetta, J. Hepp, and J. Machuca. 2017. Efectos sobre la flora y vegetación del evento de precipitación extremo de agosto 2015 en Alto Patache, Desierto de Atacama, Chile. Revista de Geogr. Norte Gd. 68: 91–103.

Quipuscoa-S.,V., C. Tejada-P., C. Fernández-A., A. Pauca-T., and M. O. Dillon. 2016. Diversidad de plantas vasculares de las Lomas de Yuta, provincia de Islay, Arequipa Perú / Diversity of vascular plants in Lomas de Yuta, Islay province, Arequipa, Peru. Arnaldoa 23(2): 517–546.

Quipuscoa-S., V., and M. O. Dillon. 2018. Four new endemic species of *Nolana* (Solanaceae-Nolaneae) from Arequipa, Peru. Arnaldoa 25(2): 295–322.

Rafinesque, C. S. 1815. Analyse de Nature, ou Tableau de l'Universe et des Corps Organisés [Palermo]: Jean Barravecchia.

Reiche, K. 1910a. Nolanaceae. Annals Univ. Chile 125: 482–507.

———. 1910b. Flora of Chile, 83. Familia Nolanaceae. 5: 410–435.

Roe, K. E. 1971. Terminology of hairs in the genus *Solanum*. Taxon 20: 501–508.

Roemer, J. J., and J. A. Schultes. 1819. Systema vegetabilium. 4: 355.

Rozen, J. G., Jr. 2003. A new tribe, genus, and species of South American panurgine bee (Andrenidae: Panurginae), oligolectic on *Nolana* (Nolanaceae). Appendix: Evidence for the phylogenetic position of *Nolanomelissa* from nuclear EF-1 sequence data by John S. Ascher. Pages 93–108 in G. A. R. Melo and I. Alves-dos-Santos, eds., Apoidea Neotropica: Homenagem aos 90 Anos de Jesus Santiago Moure, Editora UNESC, Circima, Brazil.

Rozen, J. G., and E. S. Wyman. 2015. The Chilean bees *Xeromelissa nortina* and *X. sielfeldi*, their nesting biologies and immature stages, including biological notes on *X. rozeni* (Colletidae: Xeromelissinae). Am. Mus. Novit. 3838: 1–20.

Ruiz-López, H., and J. Pavón. 1799. Flora Peruviana, et Chilensis, sive descriptiones, et icones Plantarum Peruvianarum, et Chilensium, secundum systema Linnaeanum digestae, cum characteribus plurium generum evulgatorum reformatis. v. 2: 6–8, plates 112–113.

Rundel, P. W., M. O. Dillon, and B. Palma. 1996. The vegetation and flora of Pan de Azúcar National Park in the Atacama Desert of northern Chile. Gayana Bot. 53: 295–315.

Rundel, P. W., J. R. Ehleringer, S. L. Gulmon, and H. A. Mooney. 1980. Patterns of drought response in leaf succulent shrubs of the coastal Atacama Desert in northern Chile. Oecologia 46: 196–200.

Rundel, P. W., M. O. Dillon, B. Palma, H. A. Mooney, S. L. Gulmon, and J. R. Ehleringer. 1991. The phytogeography and ecology of the coastal Atacama and Peruvian Deserts. Aliso, 13: 1–50. doi:10.5642/aliso.19911301.02.

Sagredo, E., H. Larraín, P. Cereceda, A. Ugarte, P. Osses, and M. Farías. 2002. Variación espacio-temporal de la entomofauna de coleópteros en el oasis de niebla de Alto Patache (20°49'S, 70°09'W) y su relación con factores geográficos. Revista de Geogr. Norte Gd. 29: 121–133.

Särkinen, T., L. Bohs, R. G. Olmstead, and S. Knapp. 2013. A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. BMC Evolutionary Biology 13: 214–229. doi:10.1186/1471-2148-13-214.

Saunders, E. R. 1934. The history, origin and characters of certain interspecific hybrids in *Nolana* and their relation to *Nolana paradoxa* (with plates XXXII–XXXVI). Jour. Genetics 29: 387–419.

———. 1936. On certain unique features of the gynoecium in Nolanaceae. New Phytol. 35: 423–431.

Simirgiotis, M. J., J. Benites, C. Areche, and B. Sepúlveda. 2015. Antioxidant Capacities and Analysis of Phenolic Compounds in Three Endemic *Nolana* Species by HPLC-PDA-ESI-MS. Molecules 20: 11490–11507. doi:10.3390/molecules200611490.

Smith, J. A. C., and K. Winter. 1996. Taxonomic distribution of crassulacean acid metabolism. Ecological Studies—Analysis and Synthesis 114: 427–436.

Stavenga, D. G., and C. J. van der Kooi. 2016. Coloration of the Chilean Bellflower, *Nolana paradoxa*, interpreted with a scattering and absorbing layer stack model. Planta 243:171–181. doi:10.1007/s00425-015-2395-0.

Steele, A. 1964. Flowers for the King: The Expedition of Ruiz and Pavón and the Flora of Peru. Duke University Press, Durham.

Tago, M. 1999. The Evolution of *Nolana* L. (Solanaceae) at *lomas* in South America. Ph.D. diss. Tokyo Metropolitan University.

Tago-Nakawaza, M., and M. O. Dillon. 1999. Biogeografía y Evolución en el Clado *Nolana* (Solaneae-Solanaceae). Arnaldoa 6(2): 81–116.

Takhtajan, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

Taylor, C. M., and M. Munoz-S. 1994. The botanical works of Philippi, father and son, in Chile. Ann. Missouri Bot. Gard. 81: 743–748.

Tello, V., R. Vargas, J. Araya, and A. Cardemil. 2009. Biological parameters of *Cydnodromus picanus* and *Phytoseiulus persimilis* raised on the carmine spider mite, *Tetranychus cinnabarinus* (Acari: Phytoseiidae, Tetranychidae). Cienc. Investiga Agrar. 36(2): 277–290.

Tepe, E. J. 2018. A series of unfortunate events: the forgotten botanist and the misattribution of a type collection. PhytoKeys 109: 33–39. doi:10.3897/phytokeys.109.28144.

Thompson, M., M. Holbrook, and B. Palma L. 1998. Relaciones hidricas de *Nolana flaccida* en el Parque Nacional "Pan de Azúcar", Chile. PHAROS 5(2): 5–26.

Thorne, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6: 57–66.

———. 1983. Proposed new realignments in the angiosperms. Nord. J. Bot. 3: 85–117.

Tripp, E. A., Y. E. Tsai, Y. Zhuang, and K. G. Dexter. 2017. RADseq dataset with 90% missing data fully resolves recent radiation of *Petalidium* (Acanthaceae) in the ultra-arid deserts of Namibia. Ecol. Evol. 2017: 1–17.

Tu, T., M. O. Dillon, H. Sun, and J. Wen. 2008. Phylogeny of *Nolana* (Solanaceae) of the Atacama and Peruvian Deserts inferred from sequences of four chloroplast markers and the nuclear *LEAFY* second intron. Mol. Biol. Evol. 49: 561–573. doi:10.1016/j.ympev.2008.07.018.

Tupayachi-H., A. 2003. Especies de la flora lomal en el afloramiento geologico cretácico "Yuncaypata" en Urubamba: Cusco. Cantua (12): 22–26.

Vargas C., C. 1954 [1955]. Especies nuevas o críticas del Perú. Revista Univ. (Cuzco). 43(107): 151–155.

Vargas, P., B. Rumeu, R. H. Heleno, A. Traveset, and M. Nogales. 2015. Historical Isolation of the Galápagos Carpenter Bee (*Xylocopa darwini*) despite Strong Flight Capability and Ecological Amplitude. PLoS ONE 10(3): e0120597. doi:10.1371/journal.pone.0120597.

Vargas, R., D. Stanton, and P. Nelson. 2017. Aportes al conocimiento de la biota liquénica del oasis de neblina de Alto Patache, Desierto de Atacama. Revista de Geogr. Norte Gd. 68: 49–64.

Vio-Michaelis, S., G. Apablaza-Hidalgo, M. Gómez, R. Peña-Vera, and G. Montenegro. 2012. Antifungal activity of three Chilean plant extracts on *Botritis cinerea*. Bot. Sci. 90: 179–183.

Watts, S., and R. Kariyat. 2021. Morphological characterization of trichomes shows enormous variation in shape, density and dimensions across the leaves of 14 *Solanum* species, AoB PLANTS, Vol. 13, Issue 6, December 2021, plab071. doi:10.1093/aobpla/plab071.

Weberbauer, A. 1945. *El mundo vegetal de los andes peruanos*. Lima, Perú: Ministerio de Agricultura, Dirección de Agricultura, Estación Experimental Agrícola de la Molina.

Whaley, O. Q., A. Orellana-G., and J. O. Pecho-Q. 2019. An Annotated Checklist to Vascular Flora of the Ica Region, Peru: With notes on endemic species, habitat, climate and agrobiodiversity. Phytotaxa 389 (1): 1–125. doi:10.11646/phytotaxa.389.1.1.

Wiggins, I. L., and D. M. Porter. 1971. *Flora of the Galápagos Islands*. Pages 1–998. Stanford University Press, Stanford, California.

Appendix I
Index to Numbered Collections (Exsiccate)

Collector names are in alphabetical order; numbers in bold in parentheses refer to the species clade and number in the treatment. Absent collector numbers, herbarium accession numbers or barcodes are provided.

Acevedo s.n. [SGO 73502] (**G1**).

Ackermann 461 (**G11**); *463* (**B1**); *464* (**G24**); *466* (**G20**); *486* (**B1**); *488* (**G2**); *520* (**C5**).

Acosta & Leon 114 (**C4**).

Acosta & Rosas 1033 (**G25**); *1119* (**B5**).

Acosta & al. 029 (**C4**); *057* (**G19**); *062* (**G16**); *085* (**G21**); *418* (**G21**); *423* (**G19**); *434* (**G17**).

Aedo 6865 (**B1**); *7017* (**G17**); *7024* (**G24**); *7052* (**G2**); *7200* (**B5**).

Anabalón s.n. [SGO 126922] (**G17**); *s.n.* [SGO 126924] (**G2**); *s.n.* [SGO 126925] (**G12**); *s.n.* [SGO 126926] (**G12**); *s.n.* [SGO 126927] (**G12**).

Andaur s.n. [CONC 129686] (**B1**).

Anderson & al. 7844 (**F11**); *7867* (**F17**); *7868* (**D14**); *7869* (**F3**); *7871* (**D14**); *7961* (**F18**); *7967* (**D6**); *7974* (**D6**).

Angulo 31 (**F11**); *s.n.* [HUT 2553] (**D14**); *s.n.* [HUT 2570] (**F1**); *s.n.* [HUT 1239] (**F10**); *s.n.* [HUT 1202] (**F11**); *s.n.* [HUT 2566] (**F17**); *s.n.* [HUT 1386] (**F11**); *s.n.* [HUT 1991] (**F11**).

Angulo & López s.n. [HUT 1291] (**F11**).

Arancio 92-623 (**G11**).

Arancio & Squeo 10009 (**G11**); *10016* (**G11**); *10017* (**G11**); *10025* (**G11**); *10028* (**G11**); *10029* (**G11**); *10033* (**G11**); *10041* (**G11**); *10047* (**G11**); *10069* (**G11**); *10158* (**G11**); *10381* (**G11**).

Aravena 7 (**B5**).

Arias & Alvarez s.n. [SGO 135546] (**G21**).

Arriagada, J. s.n. [(SGO 165076] (**B5**).

Arriagada, L. 226 (**G21**).

Asplund 13794 (**F11**).

Ayers & al. 1544 (**C5**).

Baeza & al. 1995 (**B5**).

Bailey s.n. [SGO 132742] (**C3**); *s.n.* [SGO 132732] (**C4**).

Baines & al. 1 (**G12**); *3* (**G17**); *6* (**G11**); *11* (**G19**); *12* (**G19**); *13* (**G12**); *32* (**B9**); *34* (**G2**); *67* (**G21**); *94* (**G20**); *96* (**G24**); *119* (**G13**).

Ball s.n. [K] (**G21**).

Barros, E. s.n. [CONC 14022] (**B1**); *s.n.* [CONC 14026] (**C4**); *5591* (**G21**).

Barros, M. 7091 (**G11**).

Bassano s.n. [SGO 137635] (**C4**); *s.n.* [SGO 137364] (**G3**).

Baumann 1 (**G14**); *2* (**G17**); *8* (**G21**); *22* (**G24**); *59* (**B1**).

Beckett & al. 4024 (**C3**); *4053* (**C4**); *4054* (**B2**); *4108* (**B5**); *4159* (**C5**); *4568* (**G21**); *4694* (**G20**); *4695* (**G20**); *4696* (**B9**); *4706* (**G25**); *4737* (**G11**); *4741* (**G11**).

Beetle 26111 (**C2**); *26114* (**G3**); *26129* (**C2**); *26136* (**B9**); *26142* (**G2**)*; 26153* (**B6**); *26161* (**G22**); *26165* (**B9**); *26167* (**G6**); *26171* (**G24**); *26180* (**G12**); *26184* (**G9**); *26185* (**G17**).

Behn 1 (**B1**); *s.n.* [CONC 8951] (**B2**); *s.n.* [CONC 36253] (**B1**); *s.n.* [CONC 25371] (**B5**); *s.n.* [CONC 8288] (**B9**); *s.n.* [CONC 8987] (**B2**); *s.n.* [CONC 8988] (**B9**); *s.n.* [CONC 28593] (**C4**); *s.n.* [CONC 36140] (**C5**); *s.n.* [CONC 36141] (**C5**); *s.n.* [CONC 30859] (**C5**); *s.n.* [CONC 30860] (**B2**); *s.n.* [CONC 30861] (**G2**); *s.n.* [CONC 30926] (**B2**); *s.n.* [CONC 28569] (**G11**); *s.n.* [CONC 30808] (**G11**); *s.n.* [CONC 36159] (**G17**); *s.n.* [CONC 36162] (**G1**); *s.n.* [CONC 36170] (**B2**); *s.n.* [CONC 30873] (**G20**); *s.n.* [CONC 8594] (**G20**); *s.n.* [CONC 22593] (**G21**); *s.n.* [CONC 22591] (**G21**); *s.n.* [CONC 22592] (**G21**); *s.n.* [F 694345] (**G21**).

Belmonte 20-102 (**E3**); *97-710* (**G21**); *97-713* (**F12**); *97-715* (**B4**); *97-770* (**G15**); *96-346* (**E5**).

Bernardi 16409 (**F11**).

Berninger 441 (**G12**).

Bertero 1181 (**G3**); *1183* (**G3**).

Biese 530 (**G21**); *2243* (**G2**); *2252* (**G16**); *2256* (**G13**); *2268* (**G24**); *2277* (**G20**); *2475* (**B9**); *2480* (**G21**); *2583* (**C4**); *2616* (**B3**); *2634* (**G11**); *2655* (**G11**); *2659* (**G6**); *2659* (**G11**); *2660* (**G11**); *2662* (**B2**); *2674* (**G11**); *2676* (**G21**); *2755* (**G11**); *2774* (**G21**); *2776* (**G24**); *2782* (**G11**); *2799* (**G17**); *2800* (**G21**); *2801* (**G17**); *2803* (**C1**); *2928* (**C5**); *3038* (**C4**); *3072* (**G23**); *3073* (**G11**); *3083* (**B4**); *3084* (**B4**); *3129* (**G12**); *3141* (**G17**); *3143* (**G21**); *3149* (**G17**); *3179* (**B1**); *3180* (**B1**); *3205* (**G19**); *3218* (**G24**); *3219* (**G13**); *3230* (**G8**); *3231* (**G8**); *3243* (**G2**); *3260* (**G6**); *3263* (**G8**); *3265* (**G13**); *3297* (**G2**); *3342* (**G19**); *3345* (**G2**); *3347* (**B9**); *3348* (**G13**); *3361* (**G24**); *3376* (**B2**); *3724* (**G11**).

Borchers s.n. [SGO 55171] (**G13**).

Bridges 1322 [K00053215] (**B1**); *1322* [E00130952] (**B2**); *1323* (**C3**); *1324* (**G6**); *1326* (**C5**); *1327* (**C5**); *1328* (**C2**); *1329* (**C3**); *1331* (**G21**); *1332* (**B2**); *s.n.* [K000532253] (**G3**); *s.n.* [K] (**G21**).

Brinck s.n. [SGO 122819] (**E3**); *s.n.* [SGO 122821] (**G2**); *s.n.* [SGO 122833] (**G12**).

Bro. Claude-Joseph 979 (**G3**); *1201* (**G3**); *1720* (**G3**); *4418* (**C3**); *4427* (**G6**); *4584* (**C3**); *5020* (**G6**); *5021* (**C5**); *5023* (**G6**); *5024* (**C5**); *5027* (**G25**); *5028* (**G21**); *5033* (**C5**); *5440* (**C3**); *5452* (**G6**).

Buchanan s.n. [CONC 36954] (**G17**).

Buchtien s.n. [GH] (**B3**); [US 1134922] (**B5**); *s.n.* [US 1157076] (**G3**).

Bull 671 (**B9**); *672* (**C6**); *673* (**G2**); *674* (**B1**); *675* (**G22**); *676* (**G2**).

Cabrera 11338 (**B1**); *11358* (**G17**); *11360* (**G17**); *11383* (**G21**); *11385* (**G21**); *11387* (**B5**); *11424* (**C4**); *12638* (**C5**); *24176* (**G17**).

Cano & al. 5085 (**F10**); *19388a* (**F17**); *19588* (**D9**); *19856* (**D9**).

Cardenas & al. KPP9 (**D14**); *KPP97* (**F17**).
Castillo L. 177-74 (**E5**).
Cea s.n. [CONC 185214] (**B5**); *21* (**B1**).
Chamy & Piovano 10 (**C5**); *11* (**B9**).
Clarke 4-05 (**B1**); *6-04* (**C5**); *16.5-01* (**G24**); *17-13* (**G24**); *18.5-02* (**G20**).
Collantes s.n. [CONC 129689] (**B1**); *s.n.* [CONC 129554] (**C3**); *s.n.* [CONC 21947] (**G20**).
Collie & Lay s.n. [G 005319-1] (**C4**); *s.n.* [E000369176] (**G21**).
Contreras & Caviedes 109 (**C4**); *197* (**C4**).
Coppinger s.n. [K] (**C3**).
Correa 50 (**C4**); *s.n.* [K] (**G21**).
Correll & Smith P172 (**D18**).
Cruckshanks s.n. (**C4**).
Cruzat s.n. [SGO 133709] (**G2**).
Cuming 481 (**C3**); *627* (**B5**); *627* (**B5**); *856* (**B1**); *887* (**B9**); *857* (**C3**); *862* (**G6**); *863* (**C2**); *887* (**B9**); *893* (**G21**); *956* (**G11**); *1068* (**F10**).
Dalannais 48 (**E5**); *49* (**E5**).
Dandois & De Schrevel s.n. [F 2330856] (**G6**).
D'Arcy 17802 (**B5**).
De Vore 1549 (**B1**).
Dillon 5351 (**C6**); *5352* (**B3**); *5353* (**G2**); *5354* (**G17**); *5355A* (**G19**); *5356* (**G12**); *5367* (**G20**); *5382* (**G6**); *5383* (**B1**); *5385* (**B1**); *5397* (**G8**); *5400* (**G24**); *8094* (**G20**); *8097* (**G8**); *8099* (**G12**); *8100* (**B1**); *8101* (**G16**); *8103* (**G8**); *8137* (**G6**); *8144* (**G24**); *8145* (**G2**); *8146* (**B9**); *8148* (**G16**); *8149* (**G2**); *8150* (**G13**); *8152* (**G21**); *8154* (**G8**); *8156* (**G20**); *8157* (**G7**); *8158* (**G13**); *8159* (**G8**); *8176* (**G20**); *8177* (**G6**); *8504* (**D4**); *8752* (**G20**); *9050* (**G14**)**;** *9112* (**B2**); *9123* (**G17**); *9127* (**B1**); *9132* (**B6**); *9133* (**C5**); *9134* (**C2**); *9136* (**B2**); *9149* (**G1**); *9157* (**G6**); *9163* (**B3**); *9165* (**C5**); *9168* (**C5**); *9170* (**G6**); *9172* (**G3**); *9173* (**C2**); *9202* (**C5**); *9218* (**G2**); *9225* (**G14**).
Dillon & Arancio 8686 (**B5**); *8687* (**G25**); *8688* (**B3**); *8689* (**C4**); *8690* (**B8**); *8691* (**G25**).
Dillon & Casareggio 8700 (**B1**); *8701* (**G20**); *8702* (**G24**); *8703* (**G20**); *8704* (**G8**); *8705* (**G6**); *8706* (**G21**); *8707* (**B3**); *8708* (**G20**); *8709* (**G11**); *8710* (**B3**); *9099* (**B6**); *9104* (**G1**); *9113* (**B3**); *9179* (**G19**).
Dillon & Concha 9085 (**B9**); *9089* (**B1**); *9092* (**B1**); *9092A* (**B1**); *9093* (**B1**); *9094* (**B1**).
Dillon & Dillon 3645 (**D18**); *3656* (**F8**); *3657* (**F8**); *3666* (**D11**); *3673* (**D10**); *3677* (**F8**); *3693* (**F8**); *3695* (**D8**); *3703* (**F20**); *3744* (**F1**); *3757* (**D18**); *3759* (**D14**); *3768* (**F3**); *3767* (**D18**); *3772* (**D2**); *3773* (**F17**); *3778* (**D2**); *3788* (**F17**); *3801* (**D6**); *3836* (**D2**); *3837* (**D18**); *3838* (**F4**); *3844* (**D6**); *3846* (**F17**); *3848* (**F17**); *3849* (**F17**); *3851* (**F3**); *3852* (**F17**); *3853* (**F17**); *3860* (**F17**); *3861* (**F3**); *3862* (**F7**); *3888* (**D11**); *3894* (**D18**); *3899* (**F8**); *3908* (**F18**); *3917* (**F1**); *3918* (**F18**); *3919* (**D18**); *3921* (**F25**); *3955* (**F25**); *5621* (**G11**); *5622* (**G17**); *5624* (**G18**); *5625* (**G18**); *5628* (**G2**); *5630* (**C6**); *5633A* (**G2**); *5634* (**G17**); *5637* (**G2**); *5642* (**G24**); *5643* (**G24**); *5644* (**G5**); *5651* (**G8**); *5660* (**G2**); *5661* (**B3**); *5662* (**C6**); *5663* (**C6**); *5664* (**C6**); *5666* (**G6**); *5670* (**G2**); *5674* (**G21**); *5681* (**G13**); *5695* (**G17**); *5707* (**G4**); *5708* (**G17**); *5709* (**C6**); *5713* (**E1**); *5721* (**E1**); *5722* (**G17**); *5724* (**G14**); *5725* (**G4**); *5726* (**C1**); *5727* (**G12**); *5728* (**G4**); *5729* (**G14**); *5730* (**G11**); *5780* (**G21**); *5795* (**B1**); *5798* (**G8**); *5799* (**G8**); *5800* (**G8**); *5801* (**G24**): *5803* (**G6**); *5810* (**G6**); *5811* (**G24**); *5818* (**G20**); *5819* (**G21**); *5821* (**G24**); *5824* (**G24**); *5825* (**G24**); *5826* (**G8**); *5846* (**G19**); *5879* (**G12**); *5880* (**G17**); *5882* (**G21**); *5890* (**G12**); *5894* (**G2**); *5897* (**G19**); *5899* (**G19**); *5901* (**G17**); *5909* (**C6**); *5933* (**B3**); *5955* (**G19**); *6039* (**B9**); *6040* (**G8**); *6043* (**G13**); *6046* (**G6**); *6047* (**C2**); *6048* (**G8**); *6049* (**G6**).
Dillon & Finger 8563 (**G8**); *8564* (**G24**); *8565* (**G24**); *8566* (**G6**); *8572* (**G19**); *8591* (**G10**); *8592* (**G12**); *8593* (**G17**); *8603* (**G16**); *8606* (**B9**, 2 sheets); *8607* (**G22**); *8608* (**G7**); *8609* (**G6**); *8610* (**C2**); *8611* (**C5**); *8612* (**B2**); *8613* (**G1**); *8615* (**C5**); *8616A* (**G20**); *8616B* (**G20**); *8617* (**G3**); *8618* (**G20**); *8619* (**G1**); *8622* (**C6**); *8623* (**G19**); *8629* (**G12**); *8636* (**G19**); *8637* (**C6**); *8638* (**G17**); *8639* (**G2**); *8640* (**G8**); *8641* (**G22**); *8641B* (**G22**); *8642* (**G11**); *8642B* (**G22**); *8644* (**A1**); *8644A* (**G11**); *8644B* (**G11,** 2 sheets); *8657* (**G6**); *8658* (**G3**); *8659* (**G3**); *8661* (**G1**); *8862* (**G20**); *8663* (**C5**); *8664* (**G6**); *8665* (**G25**); *8666* (**G1**); *8667* (**B3**); *8668* (**G19**); *8669* (**G19**); *8675* (**B9**); *8676* (**G5**); *8677* (**G2**); *8678* (**B3**); *8679* (**G19**); *8680* (**C6**); *8681* (**G17**); *8682* (**G21**); *8683* (**G5**); *9052* (**A1**); *9062* (**B9**); *9063* (**G21**); *9064* (**C6**); *9065* (**G2**); *9066* (**G19**); *9068* (**G19**); *9069* (**G11**); *9219* (**G14**); *9220* (**G14**); *9221* (**G14**); *9222* (**G14**); *9223* (**G14**), *9224* (**G14**); *9225* (**G14**).
Dillon & Guerra 8649 (**G25**); *8650* (**G6**); *8651* (**G21**); *8652B* (**C5**); *8653* (**G1**); *8654* (**G25**); *8655* (**C4**); *8656* (**C2**); *9203* (**B2**); *9205* (**B2**); *9210* (**C3**).
Dillon & Moreira 9213 (**B5**).
Dillon & Santisteban 4714 (**F11**).
Dillon & Schulz 9055 (**G6**); *9057* (**G22**); *9058* (**G16**); *9059* (**G7**); *9060* (**G8**).
Dillon & Teillier 4973 (**C4**); *5006* (**C5**); *5025* (**C5**); *5040* (**B7**); *5051* (**C2**); *5055* (**G2**); *5056* (**B1**); *5057* (**G16**); *5065* (**G13**); *5084* (**G20**); *5085* (**B9**); *5086* (**G7**); *5117* (**C6**); *5119* (**G24**); *5135* (**G21**); *5136* (**G24**); *5193* (**G24**); *5218* (**G11**); *5290* (**B3**); *5295* (**C6**); *5303* (**G17**); *5305* (**G2**); *5310* (**B3**); *5312* (**G5**); *5339* (**G6**); *5340* (**G12**); *5345* (**G21**); *5346* (**G17**).
Dillon & Trujillo 8005 (**B9**); *8007* (**G21**); *8010* (**G8**); *8012* (**G20**); *8014* (**B3**); *8015* (**G13**); *8016* (**G2**); *8017* (**G6**); *8018* (**G16**); *8019* (**G7**); *8022* (**B1**); *8024* (**G24**); *8035* (**G12**); *8036* (**G24**); *8037* (**G17**); *8038* (**G19**); *8039* (**B3**); *8045* (**G11**); *8046* (**G8**); *8047* (**G20**); *8048* (**G6**); *8053* (**B1**); *8071* (**B3**); *8093* (**C2**).
Dillon & Turner 1491 (**F10**).
Dillon & Villarroel 8115 (**G19**); *8136* (**G21**).
Dillon & al. 2714 (**F11**); *3058* (**F11**); *3219* (**D18**); *3225* (**D14**); *3237* (**F10**); *3240* (**F3**); *3242* (**F10**); *3245* (**F17**); *3262* (**D2**); *3263* (**F1**); *3284* (**D18**); *3286* (**D18**); *3287* (**F25**); *3315* (**D18**); *3318* (**F13**); *3383* (**F8**); *3388* (**D11**); *3621* (**F11**); *4654* (**F11**); *4676* (**F10**); *4694* (**F11**); *4739* (**F10**); *4740* (**F10**); *4759* (**D11**); *4773* (**E3**); 4778 (**F8**); *4784* (**D18**); *4819* (**F18**); *4835* (**F25**); *5420* (**B8**); *5434*

(**G21**); *5435* (**G3**); *5436* (**C3**); *5454* (**C5**); *5464* (**C5**); *5472* (**G2**); *5483* (**B3**); *5484* (**G1**); *5485* (**G20**); *5496* (**B9**); *5497* (**B1**); *5500* (**G24**); *5501* (**G6**); *5545* (**G17**); *5547* (**G21**); *5552* (**G12**); *5554* (**G24**); *5563* (**G2**); *5592* (**G7**); *5603* (**G12**); *5604* (**G13**); *5605* (**G2**); *5606* (**B3**); *5607* (**G11**); *5608* (**G16**); *5743* (**C6**); *8055* (**G19**); *8056* (**B3**); *8076* (**G5**); *8078* (**G19**); *8085* (**G19**); *8091* (**G17**); *8196* (**F3**); *8197* (**D14**); *8199* (**F1**); *8200* (**D2**); *8201* (**F3**); *8202* (**F4**); *8203* (**D6**); *8204* (**D18**); *8205* (**F17**); *8206* (**F3**); *8207* (**D17**); *8208* (**D18**); *8209* (**D17**); 8209 (**D17**); *8210* (**F7**); *8211* (**D18**); *8212* (**F7**); *8215* (**F7**); *8217* (**F7**); *8218* (**D18**); *8219* (**D8**); *8220* (**F18**); *8221* (**F13**); *8222* (**D18**); *8224* (**D11**); *8225* (**F13**); *8226* (**D11**); *8227* (**D10**); *8233* (**D18**); *8234* (**D11**); *8236*, (**F8,** 2 sheets); *8238* (**D11**); *8239* (**D18**); *8242* (**F25**); *8243* (**F25**); *8246* (**D6**); *8711* (**G20**); *8715* (**G20**); *8747* (**B8**); *8760* (**D2**); *8761* (**D18**); *8762* (**D18**); *8763* (**D18**); *8766* (**D2**); *8772* (**D18**); *8780* (**D18**); *8782* (**D14**); *8784* (**F17**); *8789* (**D2**); *8790* (**F3**); *8791* (**F17**); *8793* (**F3**); *8802* (**F17**); *8805* (**D6**); *8806* (**F4**); *8811* (**F4**); *8813* (**F9**); *8816* (**F4**); *8832* (**D6**); *8834* (**F9**); *8871* (**D2**); *8873* (**F4**); *8874* (**D6**); *8875* (**D18**); *8876* (**F4**); *8877* (**D18**); *8879* (**F10**); *8880* (**D6**); *8898* (**D18**); *8907* (**D18**); *8912* (**D2**); *8913* (**F1**); *8914* (**D2**); *8916a* (**D6**); *8916b* (**D6**); *8918* (**F1**); *8919* (**D2**); *8928* (**F4**); *8938* (**F17**); *8940* (**D17**); *8943* (**D17**); *8948* (**D18**); *8949* (**F7**); *8957* (**F4**); *8961* (**F7**); *8969* (**D10**); *8973* (**D8**); *8974* (**F1**); *8977* (**F18**); *8979* (**F18**); *8982* (**F20**); *8983* (**F18**); *8984* (**F1**); *8985* (**D8**); *8988* (**F20**); *8989* (**F5**); *8990* (**F18**); *8991* (**F20**); *8992* (**F20**); *8993* (**F1**); *8994* (**F18**); *8995* (**F5**); *8996* (**F18**); *8997* (**F20**); *8998* (**F18**); *8999* (**F18**); *9002a* (**F18**); *9002b* (**F18**); *9002c* (**F18**); *9002d* (**F18**); *9002e* (**F18**); *9003* (**F18**); *9004* (**F18**); *9005* (**F18**); *9006* (**F18**); *9007* (**F18**); *9008* (**F18**); *9009* (**F18**); *9011* (**F13**); *9014* (**D18**); *9018a* (**F1**); *9019* (**D3**); *9171* (**G2**).

d'Orbigny s.n. [*1805*] (**F1**).

Eggli 2895 (**G21**).

Eggli & Leuenberger 1175 (**G21**); *1659* (**G3**); *1660* (**G21**); *1744* (**C5**); *1778* (**G16**); *1783* (**B9**); *2594* (**C5**); *2595* (**G6**); *2607* (**G11**); *2632* (**G22**); *2692* (**G9**); *2865* (**G24**); *2930* (**B5**); *2952* (**G25**); *2961* (**B1**); *2962* (**B6**); *3007* (**G6**); *3020* (**C4**); *3030a* (**C3**); *3031* (**C5**).

Eggli & al. 2682 (**G16**); *2682a* (**G22**); *2683* (**G1**); *2684* (**G24**); *2685* (**G8**); *2686* (**G24**); *2690* (**G12**); *2696* (**G21**); *2697* (**G24**); *2698* (**G17**); *2699* (**G21**); *2760* (**E3**); *2792* (**E3**); *2834* (**D15**); *2838* (**G21**); *2840* (**G12**); *2841* (**G17**); *2842* (**G17**); *2844* (**G11**); *2845* (**G17**); *2846* (**G9**); *2849* (**G17**); *2853* (**G12**); *2857* (**G17**); *2858* (**G21**); *2859* (**G21**); *2860* (**G19**); *2861* (**G21**); *2864* (**G24**); *2867* (**G6**); *2871* (**G1**); *2872* (**G20**); *2875* (**G6**); *2876* (**B5**); *2879* (**G25**); *2880* (**G25**); *3034a* (**G3**); *3089b* (**G21**); *3089c* (**G3**); *3106* (**G3**); *3122A* (**B5**).

Elgueta 22 (**B1**); *30* (**C6**); *38* (**G5**); *49* (**B3**); *s.n.* [SGO 145521] (**G24**).

Eliasson & Eliasson 266 (**D4**); *1623* (**D4**).

Ellenberg 2712 (**F1**).

Elliot 4 (**B1**); *5* (**C4**); *91* (**C3**); *94* (**C4**); *513* (**C4**); *522* (**G21**); *525* (**B9**); *541* (**G6**); *s.n.* (**G3**).

Espasto s.n. [MOL00004729] (**D8**).

Espinosa s.n. [SGO 139536] (**E1**); *s.n.* [SGO 139539] (**G2**); *s.n.* [SGO 139544] (**E1**); *s.n.* [SGO 139550] (**G17**); *s.n.* [SGO 139551] (**G17**); *s.n.* [SGO 143257] (**B4**); *s.n.* [SGO 143258] (**G12**); *s.n.* [SGO 143262] (**E1**); *s.n.* [SGO 143263] (**G23**); *s.n.* [SGO 143274] (**G12**); *s.n.* [SGO 143275] (**G12**); *s.n.* [SGO 143276] (**E1**); *s.n.* [SGO 143278] (**E1**).

Eyerdam 25153 (**D18**); *25154* (**D18**); *25156* (**F1**); *25171* (**F20**); *25174* (**D10**).

Eyzaguirre s.n. [SGO 152456] (**B5**); *7* (**C5**); *45* (**C5**).

Faúndez s.n. [SGO 154419] (**C1**); *s.n.* [SGO 154420] (**C1**).

Fernández & Espinoza 5 (**F20**).

Fernández & Fernández 55 (**F10**); *58* (**D6**).

Fernández & Pauca 49 (**F9**).

Fernández & al. 7 (**E4**); *42* (**F9**).

Fernández & Niemeyer 91-118 (**C4**); *91-130* (**G21**); *91-140* (**G19**); *91-153* (**B2**).

Ferreyra s.n. [USM 13385] (**F3**); *1386* (**D18**); *1391* (**D14**); *1418* (**D18**); *1457* (**D20**); *1488* (**D6**); *1509* (**D14**); *2057* (**F10**); *2452* (**F11**); *2457* (**F10**); *2512* (**D14**); *2524* (**F4**); *2535* (**F16**); *2538* (**D17**); *2558* (**F7**); *2560* (**D18**); *3846* (**F10**); *3909* (**F11**); *4050* (**F11**); *4065* (**B1**); *4097* (**F11**); *6112* (**D9**); *6387* (**F1**); *6388* (**F20**); *6390* (**F18**); *6439* (**F7**); *6452* (**F17**); *6454* (**F3**); *6460* (**D18**); *6472* (**D6**); *6474* (**F4**); *7232* (**D18**); *8027* (**F11**); *8381* (**F11**); *8595* (**D18**); *8604* (**F8**); *8725A* (**F11**); *8756* (**F10**); *8799* (**D14**); *8805* (**D18**); *8806* (**F21**); *8811* (**D6**); *8823* (**D18**); *8826* (**F7**); *8857* (**F7**); *8861* (**F22**); *8865* (**F22**); *8872* (**F3**); *8876* (**D11**); *8876* (**F17**); *8880* (**F17**); *8883* (**F22**); *8903* (**F4**); *8989* (**F10**); *9148* (**F11**); *9532* (**F11**); *11072* (**D9**); *11431* (**D14**); *11458* (**D18**); *11483* (**F4**); *11487* (**D14**); *11493* (**F3**); *11496* (**F3**); *11560* (**F18**); *11564* (**D8**); *11584* (**F1**); *11588* (**F18**); *11600* (**F13**); *11646* (**D10**); *11648* (**D11**); *11650* (**D1**); *11652* (**D10**); *11652a* (**F8**); *11654* (**F8**); *11663* (**D1**); *11694* (**F3**); *11699* (**D17**); *11711* (**F3**); *11719* (**D18**); *11727* (**D2**); *11743* (**F3**); *11745* (**D2**); *11747* (**F1**); *11749* (**D3**); *11751* (**F1**); *11755* (**D18**); *11758* (**D14**); *11931* (**D18**); *11937* (**D18**); *11943* (**F4**); *11959* (**D18**); *11999* (**F3**); *12003* (**F4**); *12016* (**D18**); *12115* (**D6**); *12486* (**D18**); *12490a* (**F15**); *12492* (**F15**); *12499* (**F8**); *12501* (**D10**); *12506* (**F8**); *12514* (**D10**); *12518* (**D1**); *12523* (**D11**); *12524* (**D1**); *12527* (**D1**); *12530* (**F8**); *12535* (**F1**); *12541* (**D10**); *12546* (**D18**); *12548* (**D10**); *12570a* (**D18**); *12572* (**F13**); *12583* (**F13**); *12589* (**F1**); *12591* (**D8**); *12593* (**F18**); *12600* (**D8**); *12622* (**D18**); *12628* (**D17**); *12635* (**F7**); *12640* (**D10**); *12643* (**D1**); *12644* (**F8**); *12648* (**F13**); *13375* (**D14**); *13378* (**D18**); *13387* (**D14**); *13391* (**D14**); *13409* (**D14**); *13448* (**D14**); *13488* (**F4**); *13902* (**F15**); *13915* (**F15**); *13932* (**F1**); *13951* (**F1**); *13952* (**D6**); *14018* (**F3**); *14021* (**D18**); *14275* (**E3**); *17086* (**F1**); *17149* (**D6**); *17720* (**F13**); *17806* (**F1**); *17962* (**D9**); *18638* (**D18**); *18647* (**D18**); *18651* (**F1**); *18668* (**D18**); *18684* (**D14**); *19830* (**D2**); *19833* (**D6**); *20720* (**D14**).

Ferreyra & Ono 20312 (**D14**); *20323* (**D20**).

Ferreyra & al. 8634 (**D18**); *8638* (**D18**); *8652* (**D18**); *8663* (**D14**); *19774* (**D18**); *19779* (**D14**); *19781* (**D18**); *19807* (**D1**); *19811* (**D1**); *19828* (**D18**); *19852* (**D14**); *19862* (**F3**).
Feuillée s.n. [illustration] (**F1**).
Fonck s.n. [SGO 55199] (**C4**).
Fosberg et al. 28237 (**F11**).
Fournier 184 (**D4**).
Fröden 233 (**C4**).
Gálvez & al. 11 (**G2**); *13* (**G2**); *14* (**B9**); *17* (**G2**).
Garaventa 4290 (**C4**); *4297* (**C3**); *4395* (**B2**); *4753* (**C4**); *5560* (**C4**); *7081* (**B2**); *7082* (**G2**); *7083* (**G2**).
Gardner & Knees 4155 (**B5**); *5881* (**A1**).
Gaudichaud s.n. (**F10**); *s.n.* [P00605851] (**F11**); *s.n.* [F 1000362] (**F11**); *s.n.* [GH] (**G23**); (**G2**); *4* (**E1**); *6* (**G11**); *7* (**C1**); *8* (**G17**); *66* (**C3**); *67* (**B9**); *120* (**G3**).
Gay s.n. [G00137949] (**G21**); *2* (**C4**); *1205* (**C3**); *1207* (**B1**).
Geisse 39 (**G20**); *56* (**G21**); *60* (**C5**); *125* (**C5**); *7997* (**G21**); *s.n.* [SGO 72457] (**B1**); *s.n.* [SGO 072447] (**B1**); *s.n.* [SGO 55136] (**B2**); *s.n.* [SGO 72451] (**B2**); *s.n.* [SGO 71693] (**B2**); *s.n.* [SGO 55103] (**B2**); *s.n.* [SGO 42669] (**B6**); *s.n.* [Herb. Gunckel 7995; CONC 129679] (**G1**); *s.n.* [Herb. Gunckel 7996; CONC 129683] (**B6**); *s.n.* [SGO 72453] (**C2**); *s.n.* [SGO 55202] (**C2**); *s.n.* [SGO 72448] (**C2**); *s.n.* [SGO 72449] (**C3**); *s.n.* [SGO 55190] (**C3**); *s.n.* [CONC 129564] (**C5**); *s.n.* [SGO 55165] (**G1**); *s.n.* [SGO 55130] (**G6**); *s.n.* [SGO 150003] (**G6**); *s.n.* [SGO 55129] (**G20**).
Gengler 63 (**D15**); *84* (**G17**); *85* (**G12**).
Germain s.n. [BM000941317] (**B5**).
Gigoux s.n. [GH00282367] (**G1**); *s.n.* [GH] (**B2**); *s.n.* [GH] (**G6**); *s.n.* [GH] (**C2**); *s.n.* [GH] (**G21**); *30* (**B3**); *39* (**G20**); *41* (**G21**); *56* (**G20**).
Gleisner 39 (**G20**); *56* (**G21**); *60* (**C5**); *66* (**B2**); *67* (**B2**); *125* (**C5**).
Gonzáles, P. 1629 (**D19**); *1710* (**D9**); *4024* (**D14**).
Gonzáles, P. & Castañada 1578 (**D6**).
Gonzáles, P. & al. 2968 (**D10**).
Gonzáles, J. & al. s.n. [CONC 185307] (**D15**); *s.n.* [CONC 185312] (**D15**).
Goodspeed 23314 (**B5**).
Gourlay 131 (**D18**); *122* (**D10**); *123* (**F1**); *124* (**F20**).
Grandjot 250 (**C4**); *987* (**G21**); *993* (**B9**).
Grau 2213 (**G2**).
Gülland s.n. [CONC 129668] (**G17**).
Gunckel 15156 (**B5**); *21390* (**G21**); *21941* (**B5**); *23427* (**B5**); *35712* (**B5**); *36615* (**B5**); *39510* (**B5**); *43251* (**B5**); *43252* (**G21**); *43402* (**B5**).
Günther s.n. [US 1134917] (**F1**).
Günther & Buchtien 109 (**F1**); *110* (**D18**); *113* (**D18**); *115* (**D18**); *117* (**F18**); *123* (**D18**).
Haenke s.n. [F 1532704] (**C4**).
Harding s.n.[GH] (**G21**); *2* (**G12**); *3* (**G16**).
Hartmann s.n. [CONC 32322] (**G17**); *s.n.* [CONC 31174] (**G21**); *s.n.* [CONC 36263] (**G8**).
Harvey s.n. [K] (**C4**); *s.n.* [K](**G3**).
Hastings 586 (**C3**).
Hempel s.n. [CONC 13254] (**B1**); *s.n.* [CONC 13252] (**C4**).
Herb. John Miers 343 (**B5**).
Herb. R. Monton Middleton s.n. [BM000941318] (**B5**).
Heredia & Huallpa 29 (**F25**).
Hermosilla s.n. [SGO 77387] (**G24**); *s.n.* [SGO 77386] (**G24**).
Herzog 2319 (**G12**); *2457* (**B1**).
Hill 341(**G21**); *342* (**F1**).
Hjerting 1135 (**F4**).
Hoffmann 8934 (**E5**).
Hoffmann & Rodríguez 3 (**B1**); *4* (**G2**); *12* (**G21**); *15* (**G17**); *51* (**B1**).
Holt 164 (**D6**).
Howell 10002 (**D4**).
Hutchison 1018 (**D6**); *1287* (**D18**); *1288* (**D2**); *1289* (**F17**); *1314* (**F1**); *1316* (**D18**); *1323* (**F3**); *1354* (**F11**); *1845* (**F8**); *1847* (**D1**); *1848* (**D11**); *6303* (**F11**).
Hutchison & Wright 1846 (**D10**); *7150* (**F8**); *7156* (**D1**); *7255* (**F1**).
Ibáñez & Kuschel s.n. [SGO 130626] (**B8**); *s.n.* [SGO 130627] (**C4**); *s.n.* [SGO 130625] (**G3**); *s.n.* [SGO 130624] (**G21**).
Ibáñez & al. 9183 (**G8**).
Iltis & Iltis 1525 (**F3**).
Iltis et al. 1540 (**F17**); *1542* (**D18**); *1555* (**F1**).
Isern 2502 (**F25**).
Jaffuel 261 (**G21**); *960* (**G4**); *1004* (**B4**); *1016* (**E1**); *1022* (**G23**); *1023* (**E1**); *1031* (**E1**); *1040* (**G23**); *1043* (**G17**); *1046* (**G2**); *1118* (**G17**); *1128* (**G12**); *1152* (**G21**); *1170* (**G21**); *1173* (**C3**); *1182* (**B9**); *1190* (**C3**); *2502* (**G12**); *2503* (**E1**); *2513* (**E1**); *2517* (**G17**); *2526* (**G23**); *2589* (**G24**); *2590* (**G2**); *2594* (**G17**); *2595* (**G13**); *2596* (**E1**); *2598* (**G21**); *2620* (**G17**); 2624 (**E1**); *2625a* (**G12**); *2626* (**G12**); *2643* (**E1**).
Jaffuel & Pirion 3613 (**B5**); *3949* (**B5**).
Jiles 322 (**C4**); *323* (**C4**); *672* (**B8**); *673* (**C4**); *1339* (**B1**); *1419* (**G21**); *1421* (**B1**); *1481* (**G25**); *2047* (**G25**); *2050* (**G21**); *2079* (**C5**); *2080* (**G21**); *2083* (**G1**); *2177* (**B2**); *2186* (**C5**); *2187* (**C5**); *2188* (**C5**); *2199* (**B2**); *2223* (**C5**); *3167* (**C4**); *4003* (**G21**); *4024* (**C4**); *4283* (**C4**); *4283* (**C4**); *4365* (**G21**); *4480* (**C4**); *4511* (**C4**); *4920* (**G21**); *4938* (**B9**); *4941-A* (**G2**); *4943* (**C5**); *4944-A* (**G16**); *4945* (**C5**); *4950* (**G24**); *4964* (**C6**); *4975* (**C19**); *5268* (**G21**); *5270* (**B2**); *5278* (**C5**); *5295* (**G20**); *5308* (**G8**); *5314* (**B1**); *5325* (**G2**); *5347* (**E1**); *5358* (**E1**); *5374* (**G24**); *5477* (**B1**); *5483* (**B2**); *5504* (**G1**); *5833* (**B1**); *6358* (**B1**).
Jimenez & Rosas 1228 [*Rosas 7932*] (**G16**); *1298* [*Rosas 8337*] (**G16**).
Johnston 3603 (**G23**); *3604* (**B4**); *3637* (**G12**); *3638* (**B1**); *3639* (**G2**); *3663* (**G11**); *4767* (**G21**); *4768* (**B9**); *4769* (**B1**); *4770* (**G7**); *4814* (**G2**); *5014* (**G1**); *5047* (**C2**); *5128* (**G8**); *5167* (**G19**); *5243* (**G2**); *5272* (**C6**); *5383* (**B3**); *5384* (**G5**); *5435* (**G21**); *5461* (**G12**); *5462* (**G24**); *5511* (**B3**); *5551* (**G21**); *5570* (**G5**); *5590* (**G19**); *5639* (**G24**); *5653* (**G24**); *5662* (**G8**); *5663* (**G24**); *5664*

(**G24**); *5675* (**G20**); *5694* (**G6**); *5695* (**G13**); *5770* (**B9**); *5834* (**G16**); *5835* (**G13**); *6307* (**E1**).
Junge s.n. [CONC 4802] (**B5**).
Kausel 4308 (**B5**); *4433* (**B5**); *4440* (**B5**); *4576* (**C3**); *4962* (**B1**); *5063* (**G13**); *5067* (**G2**); *5084* (**C2**); *5088* (**C5**); *5089* (**C5**); *5090* (**C5**); *5098* (**C5**); *5134* (**B1**); *5136* (**G6**); *5175* (**B5**); *5178* (**C4**); *5261* (**C4**); *5326* (**C4**); *5447* (**C4**); *5468* (**B2**); *5472* (**C5**); *5477* (**C5**); *5478* (**C5**); *5492* (**G20**).
King s.n. [E0013095] (**B2**), *s.n.* [SGO 75657] (**C5**); *s.n.* [SGO 55142] (**B1**).
Klitgaard & al. KPP6 (**F3**).
Knapp & al. 10643 (**F14**).
Knapton 81 (**E3**); *83* (**D15**); *88* (**D15**); *90* (**E3**); *91* (**E2**).
Kohler 74 (**C2**); *103* (**G8**); *114* (**C2**); *115* (**B9**); *116* (**C2**); *128* (**B2**, 2 sheets); *129* (**B2**, 2 sheets); *139* (**B2**); *159* [CONC 33084] (**C2**); *159* [CONC 129562] (**C5**); *181* (**C4**); *183* (**B1**); *541* (**B2**); *H33084* (**C2**).
Köie s.n. [USM 242147] (**D21**).
Krause s.n. [SGO 55148] (**B5**).
Kummerow s.n. [CONC 42633] (**G20**); *s.n.* [CONC 42634] (**B8**); *s.n.* [CONC 42636] (**B2**); *s.n.* [CONC 42637] (**G21**).
Kuntze s.n. [F 297512] (**B9**).
Lammers & al. 7504 (**B5**); *7615* (**C5**); *7622* (**G6**); *7624* (**G11**); *7634* (**G21**); *7635* (**B9**); *7717* (**G21**); *7743* (**B5**).
Landbeck s.n. [SGO 55127] (**G21**).
Landero 495 (**C4**)*; 507* (**G21**).
Landrum 3437 (**G3**).
Landrum & Landrum 9823 (**C3**); *11517* (**B3**).
Landrum & al. 7479 (**G2**), *7484* (**G19**); *7496* (**C6**).
Larraín s.n. [SGO 169085] (**F1**); *97661* (**E3**); *97668* (**G11**).
Larrañaga s.n. [SGO 55163] (**G8**); *s.n.* [SGO 55167] (**G20**).
Latorre & al. 182 (**A1**); *241* (**B1**); *242* (**G11**); *245* (**G8**); *247* (**G24**); *248* (**G11**); *249* (**A1**); *243a* (**G11**)
Leiva & al. 842 (**F14**); *2144* (**F11**); *2147* (**F11**); *2158* (**F11**); *2165* (**F2**); *2212* (**F14**); *2241* (**F14**); *2250* (**F14**); *2601* (**F11**); *2603* (**F10**).
Leon & Narria 061 (**C5**); *068* (**C4**); *1147* (**C5**).
Levi-Heins 760 (**C4**).
Llatas 3876 (**F11**).
Lobb 433 (**C5**).
Looser 3664 (**C3**); *4304* (**C4**); *5527* (**G21**).
A. López 145 (**F10**); *880* (**F11**); *s.n.* [HUT 7378] (**F1**); *s.n.* [HUT 4817] (**F11**).
R. López s.n. [CONC 129572] (**G8**); *s.n.* [CONC 129585] (**B1**); *s.n.* [CONC 129682] (**G8**).
Lourteig 2565 (**G19**).
Loyola 19 [CONC] (**G19**).
LUDEÑA [USM 12565] (**D8**).
Luebert & Becker 2840 (**G22**); *2840* (**G7**); *2842* (**G6**); *2846* (**C2**); *2847* (**B1**); *2848* (**G21**) *2849* (**G20**); *2869* (**C2**); *2887* (**G1**); *2895* (**B6**); *2900* (**C5**); *2913* (**B8**); *2914* (**G3**).
Luebert & García 2493/887 (**G1**); *2500/894* (**G20**); *2502/896* (**G11**); *2544/938* (**G21**); *2559/953* (**G17**); *2576/970* (**G21**); *2605/999* (**G24**); *2611/1005* (**G11**); *2612/1006* (**G9**); *2613/1007* (**G17**); *2615/1009* (**G19**); *2616/1010* (**G12**); *2617/1011* (**B3**); *2619/1013* (**G2**); *2630/1024* (**G19**); *2632/1026* (**G5**); *2674/1068* (**G21**); *2678/1072* (**B3**); *2679/1073* (**C6**); *2680/1074* (**G2**); *2683/1077* (**G8**); *2711/1115* (**G19**); *2720/1114* (**G12**); *2733/1127* (**G24**); *2733A/1127A* (**G24**); *2735/1129* (**B3**); *2736/1130* (**G6**); *2737/1131* (**G8**); *2738/1132* (**G21**); *2744/1138* (**G11**); *2751/1146* (**B3**); *2758/1152* (**G8**); *2765/1159* (**B3**); *2775/1169* (**G24**); *2776/1170* (**G16**); *2778/1142* (**G16**); *2798/1192* (**G19**); *2591/985* (**G10**); *2748/1142* (**G16**); *2757* (**G13**); *2777/1171* (**G6**); *2784/1178* (**B9**); *2812/1206* (**G16**); *2816/1210* (**G6**); *2817/1211* (**G20**); *2818/1212* (**G8**); *2820/1214* (**B3**).
Luebert & Kritzner 1882 (**G3**).
Luebert & Moreira 2986 (**G17**); *2988* (**G12**); *2990* (**E1**); *3002* (**G11**); *3011* (**G19**).
Luebert & al. 2562/956 (**G12**); *2563/957* (**G17**); *2567/961* (**G21**); *2576A/961A* (**C1**); *2606/1000* (**G17**).
Maekawa & al. s.n. [MAK 141145] (**F11**); *s.n.* [MAK 141144] (**F11**); *s.n.* [MAK 197077] (**F1**).
Macbride 5858 (**F11**); *5859* (**F11**); *5883* (**F11**); *5937* (**F10**); *5941* (**F10**).
McLean s.n. [K] (**F10**).
Macrae s.n. [K] (**B5**). *s.n.* [as *McRae,* CGE05014] (**C4**); *16* [as *Macray*] (**G20**).
Mahu 9261 (**G6**).
Martens s.n. [GH00282340] (**F12**).
Marticorena, A. & al. 704 (**C6**).
Marticorena, C, & Matthei 201 (**B1**).
Marticorena, C. & al. 294 (**B5**); *361* (**C4**); *381* (**G21**); *384* (**G25**); *492* (**G11**); *592* (**C5**); *1321* (**G21**); *1406* (**C4**); 1443 (**C4**); *1432* (**G25**); *1536* (**C5**); *1619* (**C4**); *1647* (**B2**); *1667* (**B2**); *1740* (**C4**); *1793* (**B2**); *1796* (**G21**); *1854* (**C2**); *1855* (**C5**); *1868* (**B2**); *1871* (**C2**); *1877* (**G20**); *1878* (**B9**); *1888* (**G1**); *1897* (**G22**); *9806* (**C5**); *9816* (**G11**); *9881* (**G11**); *9893* (**G22**); *9903* (**G2**); *9914* (**B1**); *9924* (**C5**); *9945* (**G25**); *9961* (**C4**).
Martín s.n. [CONC 6711] (**G24**).
Martinet 287 (**F10**).
Mathews s.n. [GH] (**B5**); *310* (**G3**); *836* (**F10**); *837* (**F10**).
Matthei 469 (**G17**); *471* (**G12**); *472* (**G17**); *476* (**G17**); *478* (**G12**); *485* (**G17**); *489* (**C1**); *490* (**E1**); *491* (**G12**); *492* (**C1**); *494* (**G14**); *503* (**G14**); *527* (**G14**); *522* (**G12**).
McMahon & Hufford 546 (**F1**); *553* (**G24**); *576* (**F18**).
McMahon & al. 582 (**F11**).
Medina 929 (**C4**); *3077* (**G1**); *3121* (**G1**); *3125* (**B2**); *3129* (**G6**); *3130* (**G6**); *3131* (**G6**); *3134* (**B2**); *3138* (**G6**); *3139* (**B2**); *3285* (**C3**).
Medina & Gamboa 358 (**C3**); *467* (**C3**).
Medina & Romero s.n. [SGO 159007] (**G5**); *s.n.* [SGO 159008] (**G8**).
Mendivil & al. 8 (**D19**); *10* (**D19**).
Mexia 4027 (**F11**); *4182* (**F1**); *7773* (**F1**).
Meza s.n. [SGO 152449] (**G3**).

Mieres s.n. [CONC 179993] (**B2**); *s.n.* [CONC 179836] (**G1**); *s.n.* [CONC 179840] (**G1**).
Miers 295 (**G3**).
Mohamedov s.n. [SGO 116981] (**G22**).
Monsalve s.n. [SGO 132146] (**C4**); *s.n.* [SGO 132151] (**B5**).
G. Montero 216 (**B5**); *1824* (**B9**); *1843* (**B1**); *2445* (**B5**); *2827* (**G3**); *2868* (**G6**); *2883* (**G5**); *2902* (**G5**); *2906* (**G6**); *2955* (**G13**); *2996* (**G21**); *3002* (**B6**); *6317* (**B1**); *7228* (**B1**); *7568* (**C4**); *7573* (**C4**).
R. Montero 2902 (**G21**); *7687* (**G21**); *10821* (**G21**).
Montesinos 3233 (**F18**).
Mora s.n. [SGO 131747] (**B5**); *s.n.* [SGO 131743] (**G21**).
Moreira 699 (**G6**); *704* (**B3**); *709* (**G21**).
Morong s.n. [K] (**G1**); *1186* (**G21**); *1227* (**B9**); *1247* (**G20**); *1279* (**G1**); *1274* (**C2**); *1373* (**B2**).
Mostacero & Mejía 1471 (**F11**); *260* (**F11**); *1473* (**F11**).
Mostacero & al. 703 (**F11**); *811* (**F11**); *1064* (**F11**); *1433* (**F11**); *3300* (**F11**).
Muller & Chávez 3591 (**D5**).
Muller & al. 12236 (**D5**).
Muñoz-P., C. & Johnson 1869 (**G21**); *1888* (**C2**); *1895* (**B6**); *1898* (**C5**); *1902* (**C5**); *1934* (**B6**); *1977* (**B1**); *1978* (**B2**); *2057* (**G20**); *2772* (**B9**); *2783* (**G21**); *2843* (**G24**); *2846* (**G2**); *2848* (**G11**); *2849* (**G21**); *2880* (**G19**); *2932* (**B9**).
Muñoz-P., C. & Pisano 3254 (**C3**).
Muñoz-P., C. 3268 (**G21**); *3275* (**C4**); *3323* (**B5**); *3433* (**B8**); *3640* (**G21**); *3643* (**G17**); *3645* (**G10**); *3944* (**G11**); *4010* (**C5**); *4154* (**C4**); *4294* (**C4**); *19634* (**G21**); *B-61* (**G21**); *B-62* (**G21**); *B-63* (**G3**); *B-80* [SGO 57766] (**G6**); *B-306* (**G1**).
Muñoz-S., C. s.n. (**E5**); *3* (**C4**); *34* (**B2**); *76* (**E3**); *77* (**E5**).
Muñoz-S., C. & al. 1002 (**B2**); *1003* (**B2**); *1004* (**B2**); *1008* (**B2**); *1034* (**B2**).
Muñoz-S., M. 1649 (**B5**); *1890* (**B3**); *1903* (**B3**); *1929* (**C3**); *1930* (**C3**); *1935* (**C4**); *2014* (**C5**); *2018* (**B1**); *2416* (**B1**); *2473* (**C4**); *3042* (**B1**); *3061* (**C2**); *4061* (**C4**); *4071* (**C4**); *4077* (**B9**); *4230* (**C2**); *4477* (**C4**); *4487* (**C4**); *4488* (**C4**); *4573* (**G20**); *4576* (**B6**); *4579* (**G22**); *4580* (**B1**); *4582* (**G12**); *4584* (**G24**); *4585* (**G6**); *4673* (**C6**); *4873* (**B5**); *4873* (**B5**); *3082A* (**B3**).
Muñoz-S., M. & Meza 2192 (**G21**); *2219* (**C4**); *2246* (**G16**); *2255* (**G22**); *2262* (**G8**); *2265* (**G16**); *2270* (**B1**); *2274* (**G24**); *2279* (**G2**); *2301* (**B1**); *2306* (**G13**); *2319* (**G11**); *2347* (**C5**); *2357* (**B9**).
Muñoz-S., M. & Moreira 4912 (**E5**); *4916* (**E5**).
Muñoz-S., M. & al. 1001 (**C5**); *1014* (**G6**); *1035* (**B6**); *1071* (**C2**); *1075* (**G6**); *1085* (**G24**); *1101* (**G3**); *1104* (**B9**); *1105* (**G6**); *2228* (**C5**); *2633* (**C3**); *2681* (**C5**); *2701* (**G1**); *2719* (**G11**); *2720* (**C5**); *2732* (**A1**); *2747* (**G11**); *2762* (**A1**); *2776* (**G11**); *2785* (**G6**); *2787* (**G22**); *2800* (**B3**); *2815* (**G2**); *2847* (**G13**); *2864* (**C2**); *2885* (**C5**); *2915* (**B7**); *2917* (**B7**); *2940* (**C5**).
Murphy 3472 (**D7**).
Navarro s.n. [SGO 055143] (**B1**).
Niemeyer & Fernández 9594 (**G3**); *9597* (**B5**); *H2* (**G11**).
Niemeyer s.n. [F 2065893] (**G17**); *s.n.* [SGO 128296] (**G11**).
Nuñez s.n. [CONC 129676] (**G2**).
Ochoa, C. 2708 (**B5**); *11258* (**F25**, 2 sheets).
Ochoa, R. s.n. (**C4**).
Ohga s.n. [MAK 225311] (**F3**).
Oka s.n. [MAK 229699] (**F3**).
Ono s.n. [MAK 274948] (**C3**); *s.n.* [MAK 225310] (**G16**); *s.n.* [MAK 274946] (**G2**); *s.n.* [MAK 274965] (**G6**).
Ono & Masuy s.n. [USM 35847] (**D18**).
Ono & Masuzawa s.n. [MAK 274964] (**B2**); *s.n.* [MAK 274963] (**G1**); *s.n.* [MAK 274961] (**G12**); *s.n.* [MAK 274952] (**G12**); *s.n.* [MAK 274956] (**G12**); *s.n.* [MAK 274955] (**G17**); *s.n.* [MAK 229697] (**D14**); *s.n.* [MAK 229691] (**F11**); *s.n.* [MAK 274958] (**G14**); *s.n.* [MAK 274959] (**G14**); *s.n.* [MAK 274960] (**G14**); *s.n.* [MAK 274950] (**G14**); *s.n.* [MAK 274953] (**G14**).
Ono & Oka s.n. [MAK 274962] (**B2**).
Ono & Suzuki s.n. [MAK 274056] (**B9**); *s.n.* [MAK 274055] (**B9**); *s.n.* [MAK 274036] (**C2**); *s.n.* [MAK 274037] (**C2**) *s.n.* [MAK 274057] (**C5**); *s.n.* [MAK 274059] (**G1**); *s.n.* [MAK 274034] (**G1**); *s.n.* [MAK 274035] (**G2**); *s.n.* [MAK 274067] (**G6**); *s.n.* [MAK 274070] (**G6**); *s.n.* [MAK 274044] (**G7**); *s.n.* [MAK 274045] (G7); *s.n.* [MAK 27406] (**G7**); *s.n.* [MAK 274050] (**G16**); *s.n.* [MAK 274043] (**G16**); *s.n.* [MAK 274061] (**G21**); *s.n.* [MAK 274063] (**G21**); *s.n.* [MAK 274062] (**G21**); *s.n.* [MAK 274039] (**G20**); *s.n.* [MAK 274041] (**G20**); *s.n.* [MAK 274042] (**G20**); *s.n.* [MAK 274038] (**G20**).
Ono & al. s.n. [MAK 274957] (**B4**); *s.n.* [MAK 274947] (**C5**); *s.n.* [MAK 229690] (**D18**); *s.n.* [MAK 197081] (**F11**); *s.n.* [MAK 197080] (**F11**); *s.n.* [MAK 197082] (**F11**); *s.n.* [MAK 229693] (**F16**); *s.n.* [MAK 229686] (**F4**); *s.n.* [MAK 197078] (**G10**); *s.n.* [MAK 197079] (**F10**).
Ortega s.n. [SGO 42646] (**B2**); *s.n.* [SGO 55105] (**B2**); *s.n.* [SGO 55191] (**C5**); *s.n.* [SGO 30844] (**D1**); *s.n.* [SGO 55135] (**F11**).
Páez s.n. [SGO 141775] **(B1);** *s.n.* [CONC 143324] (**B3**).
Parra & Torres 172 (**B5**).
Pauca 352 (**F9**); *396* (**F7**).
Pauca & Chavez 482 (**F25**).
Pauca & al. 311 (**F25**); *497* (**D18**).
Pearce 657 (**F8**); *659* (**F8**); *s.n.* [BM000941326] (**B4**); *s.n.* [K000532260] (**C2**); *s.n.* [BM000941265] (**D1**); *s.n.* [BM000941311] (**D11**); *s.n.* [K000532278] (**D12**); *s.n.* [BM000941266] (**F1**); *s.n.* [BM000941352] (**F8**); *s.n.* [K] (**G17**); *s.n.* [BM000941269] (**E3**).
Peña s.n. [CONC 129561] (**C5**).
Pennell 13017 (**G17**); *13019* (**B1**); *13021* (**G12**); *13027* (**G12**); *13035* (**G21**); *14280* (**F20**); *14789* (**F10**); *14808* (**F11**).

Perry 4328 (**G17**); *6076* (**G17**); *6974* (**G17**); *6981* (**G17**); *s.n.* [CONC 4387] (**E1**).
Petersen s.n. [CONC 42600] (**C4**); *s.n.* [CONC 42600] (**C4**); *s.n.* [CONC 42599] (**G21**); *s.n.* [CONC 42573] (**G21**).
Pfister 9520 (**G17**); *s.n.* [CONC 9540] (**G19**); *s.n.* [CONC 9513; CONC 117896] (**G21**); *s.n.* [CONC 9525] (**G21**).
F. Philippi s.n. [SGO 55089] (**B2**); *s.n.* [SGO 55145] (**B7**); *s.n.* [BM000941324] (**B2**); *s.n.* [BM000941284] (**B2**); *s.n.* [BM000021200] (**B5**); *s.n.* [BM000941331] (**B6**); *s.n.* [BM000941327] (**B9**); *s.n.* [SGO 55128] (**C2**); *s.n.* [BM000941288] (**C2**); *s.n.* [SGO 55204] (**C2**); *s.n.* [SGO] (**C4**); *s.n.* [SGO 055128] (**C5**); *s.n.* [SGO 55164] (**E2**); *s.n.* [SGO 055176] (**E5**); *s.n.* [SGO 55160] (**G1**); *s.n.* [SGO 55152] (**G3**); *s.n.* [SGO 55166] (**G20**); *s.n.* [SGO 42683] (**G20**); *s.n.* [BM000992195] (**C3**); *s.n.* [BM000941342] (**C5**); *s.n.* [BM000941348] (**C5**); *s.n.* [BM000941345] (**C5**); *s.n.* [BM000941363] (**G21**); *s.n.* [BM000941301] (**B7**); *s.n.* [BM000941307] (**B1**).
Philippi. & Borchers s.n. [BM000941316] (**B5**); *s.n.* [SGO 55123] (**B7**); *s.n.* [SGO 42674] (**B7**); *s.n.* [BM000941328] (**B9**); *s.n.* [BM000941285] (**C2**); *s.n.* [BM000941290] (**G1**); *s.n.* [BM000941337] (**G6**).
Philippi. R. A. s.d. [SGO] (**C2**); *s.n.* [SGO 55149] (**B9**); *s.n.* [K000532193] (**B2**); *s.n.* [SGO 42670] (**B2**); *s.n.* [SGO 55086] (**B2**); *s.n.* [SGO 55147] (**B3**); *s.n.* [SGO 55140] (**B5**); *s.n.* [SGO 55131] (**B5**); *s.n.* [SGO 55116] (**B5**); *s.n.* [SGO 55133] (**B5**); *s.n.* [SGO 55113] (**B6**); *s.n.* [SGO 42670] (**B6**); *s.n.* [SGO 55146] (**B9**); *s.n.* [SGO 55203] (**C2**); *s.n.* [SGO 42638] (**C2**); *s.n.* [SGO 42655] (**C3**); *s.n.* [SGO 55188] (**C5**); *s.n.* [SGO 42638] (**C5**); *s.n.* [SGO 55193] (**C5**); *s.n.* [SGO 42694] (**E2**); *s.n.* [K000532196] (**E2**); *s.n.* [K000532196] (**E5**); *s.n.* [SGO 55198] (**G2**); *s.n.* [SGO 55126] (**G8**); *s.n.* [SGO 55077] (**G11**); *s.n.* [SGO 55184] (**G13**); *s.n.* [SGO 55170] (**G19**); *s.n.* [SGO 55169] (**G20**); *s.n.* [SGO 55196] (**G20**); *s.n.* [SGO 55082] (**G22**); *s.n.* [SGO 55125] (**G24**).
Pinto 138 (**G21**); *181* (**G21**); *182* (**G17**); *705* (**G11**); *s.n.* [SGO 142972] (**B4**); *s.n.* [SGO 142973] (**B4**); *s.n.* [SGO 142974] (**D10**); s.n. [SGO 142966] (**F1**); *s.n.* [SGO 142965] (**F1**); *s.n.* [SGO 142969] (**F12**); *s.n.* [SGO 142968] (**F12**); *s.n.* [SGO 142977] (**F12**); *s.n.* [SGO 142978] (**F12**); *s.n.* [SGO 142975] (**F15**); s.n. [SGO 142976] (**F15**); *s.n.* [SGO 142981] (**G17**); *s.n.* [SGO 142970] (**G17**); *s.n.* [SGO 142971] (**G17**); *s.n.* [SGO 142979] (**G21**); *s.n.* [SGO 142980] (**G21**); *s.n.* [SGO 142967] (**G21**).
Pirion s.n. [CONC 129608] (**G3**); *265* (**G3**).
Pisano & Bravo 223 (**G2**); *251* (**G2**); *505* (**B6**); *512* (**G7**); *515* (**G22**); *516* (**G16**); *531* (**B9**); *559* (**G2**); *580* (**B1**); *722* (**G11**); *796* (**C5**); *804* (**G25**); *822* (**C5**); *823* (**C2**); *961* (**C5**); *1671* (**G12**); *1677* (**G10**).
Plowman s.n. [AMES 30446] (**B5**); *11054* (**F11**); *14482* (**F11**); *14512* (**B5**).
Poeppig 67 (**G3**); *68* (**G21**); *144* (**G21**); *313* (**G3**).
Quezada & López 13 (**B5**).
Quezada & Ruiz 10 (**G2**); *11* (**G17**); *13* (**G2**); *16* (**E1**); *17* (**E3**); *19* (**G12**); *60* (**G21**); *65* (**G14**); *86* (**G21**); *98* (**B1**); *101* (**G2**); *132* (**G18**); *135* (**G11**); *191* (**G21**); *225* (**G24**); *310* (**G2**).
Quispe 193 (**F18**); *195* (**D18**); *196* (**D8**).
Quipuscoa 2879 (**F7**); *2881* (**F7**); *2883* (**F7**); *2886* (**F7**); *2890* (**F7**); *2893* (**F4**); *2895* (**D17**); *3646* (**E3**); *3693* (**E3**).
Quipuscoa & Balvin 6860 (**F6**); *6861* (**F5**); *6862* (**D8**); *6863* (**F5**).
Quipuscoa & Cáceres 2495 (**D3**).
Quipuscoa & Dillon 2835 (**F1**); *2837* (**F18**); *2837* (**F20**); *2839* (**F18**); *2841* (**D10**); *2843* (**F1**); *2845* (**F18**); *2847* (**F18**); *2849* (**D8**).
Quipuscoa & Durand 3644 (**E4**).
Quipuscoa & Tejada 5220 (**F25**); *5247* (**F18**); *5253* (**E4**).
Quipuscoa & al. 2785 (**D3**); *2803* (**F20**); *2805* (**F18**); *2808* (**D10**); *2823* (**D8**); *2826* (**F18**); *2829* (**F1**); *2850* (**D3**); *2913* (**D10**); *2914* (**F1**); *2915* (**D10**); *2918* (**F20**); *2919* (**F13**); *2921* (**F13**); *2924* (**F18**); *2925* (**D11**); *2930* (**F6**); *2931* (**F18**); *2932* (**F18**); *2933* (**F6**); *3375* (**F9**); *3378* (**F10**); *3379* (**D2**); *3380* (**F4**); *3391* (**F9**); *3411* (**F25**); *3413* (**D11**); *3414* (**F8**); *3415* (**D18**); *3427* (**D18**); *3428* (**D14**); *3429* (**D11**); *3430* (**D18**); *3431* (**F13**); *3432* (**F13**); *3434* (**D18**); *3437* (**F13**); *3455* (**D18**); *3467* (**F25**); *3483* (**F7**); *3488* (**F7**); *3493* (**D21**); *3499* (**D21**); *3505* (**D11**); *3517* (**F17**); *3520* (**F17**); *3525* (**F10**); *3527* (**D14**); *3529* (**F3**); *3532* (**D14**); *3533* (**F17**); *3535* (**F3**); *3545* (**D6**); *3557* (**D2**); *3559* (**F4**); *3580* (**F10**); *3587* (**F4**); *3591* (**D20**); *3597* (**F17**); *5115* (**F25**); *5119* (**D18**); *5418* (**D3**); *5421* (**D3**); *5841* (**E4**); *6008* (**E4**); *6226* (**F5**); *6229* (**F5**); *6231* (**D18**); *6242* (**F1**); *6244* (**D8**); *6245* (**F18**); *6255* (**F6**); *6264* (**F13**); *6306* (**D18**); *6309* (**F6**); *6335* (**F5**); *6338* (**F5**); *6350* (**F25**); *6352* (**D18**); *6374* (**F18**); *6391* (**D18**); *6403* (**F25**); *6421* (**F18**); *6433* (**F23**); *6456* (**F25**); *6464* (**D8**); *6467* (**F18**); *6479* (**F25**); *6527* (**F7**); *6542* (**F7**); *6545* (**F3**); *6550* (**F17**); *6589* (**F3**); *6590* (**F17**); *6595* (**F3**); *6603* (**D14**); *6604* (**F3**); *6621* (**D2**); *6629* (**D6**); *6633* (**F4**); *6636* (**F4**); *6638* (**F9**); *6639* (**D6**); *6662* (**F9**); *6688* (**D6**); *6698* (**F17**); *6702* (**F9**); *6707* (**D6**); *6717* (**D20**); *6725* (**D20**); *6728* (**E4**); *6735* (**E4**); *6763* (**F19**); *6802* (**F4**); *6845* (**D6**); *6847* (**F17**); *6851* (**F3**); *6852* (**D6**); *6854* (**F4**); *6857* (**F6**); *6858* (**D18**); *6859* (**F6**); *7573* (**D2**); *7575* (**F1**); *7585* (**D2**); *7614* (**F19**); *7617* (**D19**); *7633* (**F1**); *7636* (**F19**); *7642* (**F19**); *7644* (**D20**); *7647* (**D14**); *7649* (**F3**); *7651* (**D6**); *7657* (**D6**); *7658* (**F4**); *7663* (**F9**); *7694* (**E4**); *7710* (**E4**); *7716* (**E4**); *7780* (**D1**); *7781* (**D1**); *7782* (**E4**); *7823* (**F4**); *7865* (**F7**); *8027* (**D5**); *8029* (**D16**); *8033* (**F8**).
Rahmer s.n. [SGO 55205] (**C2**).
Rahn 63 (**D2**).
Ràfols s.n. [SGO 75657] (**C4**).
Raimondi s.n. [USM 10856] (**D2**); *9086* (**F17**); *10971* (**F17**).
Ramos & Fernández 1837 (**D18**); *1839* (**D10**).
Rauh 558 (**E4**).

Rauh & Hirsch P468 (**D18**); *P469* (**D3**); *P1957* (**F11**); *P2015* (**D6**).
Rechinger & Rechinger 63498 (**B16**); *63510* (**G6**); *63624* (**C5**); *63625* (**C5**).
Reed s.n. [BM000941289] (**C3**); *s.n.* [K000532262] (**C5**); *s.n.* [K] (**B5**).
Reiche s.n. [SGO 61464] (**G22**); *s.n.* [SGO 61463] (**G22**).
Reyes & Letelier 1330 (**G11**).
Ricardi 1075 (**G12**); *1093* (**B1**); *2049* (**G21**); *2071* (**C4**); *2099* (**B8**); *2223* (**C5**); *2486* (**G8**); *2493* (**G20**); *2515* (**G2**); *2536* (**G8**); *2569* (**G20**); *2635* (**G24**); *2647* (**G2**); *2685* (**C6**); *2720* (**B3**); *3025* (**G17**); *3032* (**G9**); *3033* (**G23**); *3055* (**G21**); *3056* (**G10**); *3065* (**B1**); *3077* (**G13**); *3078* (**B1**); *3084* (**G20**); *3360* (**E3**); *3555* (**G21**); *3675* (**G11**); *5249* (**G21**); *5267* (**C4**); *5485* (**G2**); *5490* (**B2**); *5496* (**G16**); *5505* (**G12**); *5508* (**G2**); *5517* (**G12**); *5518* (**E3**); *5525* (**G24**); *5539* (**G12**); *5540* (**G16**); *5549* (**C5**); *9059* (**B5**); *10917* (**B5**).
Ricardi & Marticorena 3676 (**G1**); *3719* (**G24**); *3761* (**G24**); 3798 (**C5**); *3807* (**G1**); *3820* (**C5**); *3903* (**C5**); *3937* (**G1**); *3938* (**B9**); *3947* (**C4**); *4389/744* (**C5**); *4418/803* (**B2**); *4602/987* (**G1**); *4604/989* (**G1**); *4611/996* (**G11**); *4613/998* (**G22**); *4631/1016* (**G5**).
4848/1233 (**C5**); *4850/1235* (**G21**); *4924/1309* (**B1**); *4926/1311* (**C5**).
Ricardi & Parra 89 (**G2**); *93* (**C5**).
Ricardi & al. 17 (**G16**); *19* (**E5**); *37* (**D15**); *50* (**D15**); *355* (**E5**); *415* (**G11**); *506* (**C5**); *513* (**G11**); *1051* (**G21**); *1066* (**G17**); *1075* (**G6**); *1080* (**G9**); *1111* (**G11**); *1235* (**C4**); *1280* (**G20**); *1401* (**G21**); *1411* (**G24**); *1412* (**G10**); *1450* (**B3**); *1452* (**G2**); *1509* (**B7**); *1565* (**G11**).
Richardson 2104 (**F3**); *2131* (**F8**); *2177* (**G20**).
Ridoutt s.n. [USM 14661] (**D17**).
Rojas s.n. [CONC 129584] (**B2**); *s.n.* [SGO 160917] (**E3**).
Rivero s.n. [SGO 55137] (**B2**).
Robinson s.n. [K] (**G3**).
Rodríguez, E & Aguilar 2072 (**F11**).
Rodríguez, E. & Alvítez 2257 (**F11**).
Rodríguez, R. 2639 (**B9**); *2678* (**G2**); *2777* (**C5**); *3079* (**G24**); *3081* (**G14**); *3088* (**G17**); *3089* (**G12**); *3093* (**G24**); *3113* (**G8**); *3115* (**G19**).
Rodríguez, R. & Marticorena 1611 (**G1**).
Rodríguez, R. & Rivera 35 (**G16**); *56* (**G11**); *58* (**C5**).
Rodríguez, R. & Ruiz 3547 (**A1**).
Rodríguez, R. & al. 4033 (**B5**).
Roque 265, (**D18,** 2 sheets).
Rorud 15 (**D4**).
Rosas 3163 (**C5**); *7189* (**G19**); *7191* (**G11**); *7936* (**G25**); *9144* (**B2**).
Rose & Rose 18578 (**F11**); *19264* (**C4**); *19282* (**B1**); *19416* (**G9**); *19420* (**G17**); *19448 (***B4**).
Ruiz & Pavón s.n. [K000532276] (**D9**).
Saá s.n. [CONC 129677] (**G20**); *s.n.* [CONC 129613] (**G21**); *s.n.* [CONC 129575] (**G1**); *s.n.* [CONC 129578] (**G1**); *s.n.* [CONC 129692] (**B2**).
Sagástegui 10944 (**F11**).
Sagástegui & Cabanillas 8754 (**F11**).
Sagástegui & López 10998 (**F11**).
Sagástegui & Mostacero 10436 (**F11**); *11031* (**F10**); *11369* (**F11**).
Sagástegui & al. 9140 (**F10**); *9141* (**F10**); *10427* (**F11**); *11010* (**F11**); *12940* (**F11**); *17443* (**F14**).
Sandeman s.n. [BM000076943] (**B5**).
San Román s.n. [SGO 55132] (**A1**); *s.n.* [SGO 55122] (**B3**); *s.n.* [SGO 055139] (**G12**); *s.n.* [SGO 42657] (**G16**); *s.n.* [SGO 55197] (**G20**); *s.n.* [SGO 042659] (**G22**).
Santesson 794 (**C3**).
Särkinen & al. 4093 (**D13**); *4094* (**E3**); *4688* (**F14**).
Schilling s.n. [CONC 129546] (**C5**).
Schlegel 2806 (**C4**); *2962* (**B5**); *3169* (**C4**); *3171* (**B5**); *3885* (**B2**); *3891* (**B2**); *3915* (**B1**); *4296* (**C4**); *4380* (**C4**); *5235* (**C4**); *7693* (**E3**); *7709* (**G17**); *7715* (**G17**); *7730* (**B4**); *7736* (**E1**); *7742* (**G21**); *7781* (**G24**); *7782* (**G14**); *7850* (**G20**); *7852* (**G19**); *7864* (**G24**); *7871* (**G2**); *7904* (**G21**); *7973* (**B3**); *7999* (**C5**); *8093* (**C2**); *3902-1* (**C3**); *7877-1* (**G11**).
Schuh & Platnick 4 (**C4**); *12* (**G25**); *14* (**G25**).
Schulz 2 (**B1**); *6* (**G19**); *16* (**G5**); *17* (**G1**); *33* (**G5**); *35* (**C6**).
Selander 1-83 (**G6**).
Sielfeld 8 (**G17**); *9* (**G21**); *15* (**G12**); *32* (**G15**); *38* (**G21**); *42* (**B4**); *46* (**F12**); *67* (**C2**); *s.n.* [SGO 144338] (**F12**).
Sielfeld & Pinto s.n. [SGO 144332] (**F12**).
Silva s.n. [CONC 44041] (**C3**).
Simpson s.n. [CONC 160018] (**C5**).
Skottsberg & Skottsberg 718 (**G21**); *844* (**B8**); *850* (**C3**); *907* (**B8**); *1044* (**G3**); *1049* (**B1**); *1449* (**C4**).
Soa s.n. [CONC 129548] (**C5**).
Solomon 2800 (**F3**).
Soukup 1284 (**F11**); *2158* (**F10**); *3139* (**F11**); *3942* (**F10**).
Sparre 2503 (**B3**); *2583* (**B1**); *2737* (**C4**); *2801* (**G3**); *2809* (**B5**); *2917* (**B8**); *2971* (**G25**); *2985* (**G6**); *2990* (**G21**); *9964* (**B5**).
Squeo 87-061 (**B5**); *88-193* (**B1**); *88-201* (**G1**).
Squeo & Letelier 1236 (**G11**).
Stafford 29 (F1); *51* (**D9**); *55* (**F20**); *56* (**D8**); *65* (F18); *282* (**F18**); *288* (**F18**); *294* (**F20**); *840* (**D18**); *880* (**D10**); *881* (**F25**); *893* (**F18**); *904* (**F18**); *912* (**F8**); *921* (**F1**); *1020* (**F18**); *1024* (**D18**); *1025* (**F18**).
Stebbins 8585 (**G21**).
Stebbins & Weisser 8571 (**C3**).
Stork & Vargas 9352 (**F11**).
Stork & al. 9158 (**F11**); *9187* (**F10**); *9236* (**F11**); *9581* (**F11**).
Suzuki s.n. [MAK 274058] (**G1**); *s.n.* [MAK 274040] (**G6**).
Tafalla s.n. [MA815130] (**D6**); *s.n.* [MA815133] (**D18**); *s.n.* [MA815123] (**F9**).
Taylor, C. & Pool 11525 (**G20**); *11526* (**C5**); *11581* (**G24**); *11583* (**G24**); *11629* (**C3**).

Taylor, C. & al. 10641 (**C4**); *10692* (**B9**); *10693* (**G20**); *10733* (**G2**); *10748* (**B3**).
Taylor, T. W. J. 97 (**D4**).
Teillier s.n. [F 2324241] (**E5**); *438* (**G11**); *452* (**B1**); *457* (**G10**); *459* (**G21**); *481* (**B1**); *483* (**G18**); *565* (**G19**); *585* (**G19**); *620* (**B1**); *660* (**G16**); *828* (**B2**); *860* (**C5**); *920* (**C4**); *1025* (**C5**); *3410* (**G14**); *3411* (**G12**); *3413* (**G14**); *4132* (**G11**); *4790* (**G17**); *4791* (**G12**); *4798* (**E5**); *4803* (**E5**); *5535* (**G1**); *5972* (**G2**); *6005* (**G20**).
Teillier & Cofré 96-4240 (**G1**).
Teillier & Buben 6587 (**D15**).
Teillier & Delaunoy 5551 (**G24**); *5561* (**C5**); *6341* (**C2**).
Teillier & Dillon 4924 (**G22**); *4926* (**B2**); *4928* (**C2**).
Teillier & Escobar 8133 (**G1**).
Teillier & Lund 7920 (**G1**).
Teillier & Márquez 4849 (**C4**).
Teillier & al. 2637 (**G11**); *2666* (**G20**); *2667* (**G20**); *2669* (**G11**); *2670* (**G6**); *2672* (**G21**); *2684* (**G6**); *2698* (**G8**); *2711* (**G16**); *2728* (**G13**); *2739* (**G2**); *2740* (**B9**); *2746* (**G11**); *2748* (**G12**); *2750* (**G24**); *2751* (**G11**); *2758* (**G24**); *2760a* (**G24**); *2763a* (**G8**); *2787* (**G19**); *2824* (**B1**); *2836* (**G20**); *2839* (**G11**); *2847* (**G12**); *2867* (**G11**); *2878* (**G2**); *2879* (**G13**); *2886* (**G12**); *2888* (**C6**); *2902* (**G21**); *2905* (**G21**); *2916* (**C6**); *2919* (**G2**); *2921* (**G21**); *2928* (**G24**); *2930* (**G11**); *2931* (**G24**); *8401* (**B1**).
Tejada & al. 788 (**E4**).
Tepe & al. 1695 (**G3**); *1766* (**G25**); *1772* (**G21**); *1798* (**C5**); *1887* (**B5**).
Tillett 6610-8 (**F10**).
Toro s.n. [SGO 135191] (**G3**).
Toro & Fernández 81 (**A1**).
Torres s.n. [SGO 128746] (**B3**); *s.n.* [SGO 128781] (**B3**); *s.n.* [SGO 135488] (**G2**); *s.n.* [SGO 128749] (**G2**); *s.n.* [SGO 133969] (**G11**); *s.n.* [CONC 25159] (**G21**); *s.n.* [SGO 135489] (**G24**).
Torro s.n. [SGO 135191] (**G3**).
Tovar 2700 (**D6**); *2707* (**D6**); *2735* (**D14**); *3471* (**F7**).
Trivelli s.n. [SGO 144327] (**G12**); *s.n.* [SGO] (**G24**).
Troll 3300 (**E3**).
Tryon & Tryon 6574 (**F11**).
Tupayachi 3858 (**F24**).
van der Werff & al. 14456 (**F10**).
Vargas 2000 (**F7**); *7864* (**F24**); *8463* (**F1**); *8468* (**F20**); *8470* (**D8**); *8570* (**F13**); *8613* (**D10**); *10943* (**F1**); *12644* (**E3**); *12656* (**D18**); *13045* (**F8**); *13052* (**D1**); *13079* (**D10**); *13084* (**E3**); *13085* (**D18**); *17982* (**F8**); *17984* (**F13**); *18002* (**F13**); *18046* (**F8**); *18063* (**F8**); *18064* (**D1**); *18093* (**F25**); *18100* (**F25**); *18151* (**F7**); *18175* (**D17**); *18208* (**F1**); *18211* (**F1**); *18212* (**D6**); *18219* (**F15**); *18220* (**F15**); *18224* (**D6**); *18228* (**F3**); *18233* (**F1**); *18239* (**F1**); *18240* (**D6**); *18252* (**F1**); *18260* (**D6**); *18299* (**F1**); *19559* (**E3**); *19932* (**F1**); *22886* (**F8**).
Velarde 523 (**D2**).
Vilcapoma 2414 (**D9,** 2 sheets).
Villagrán 119 (**C2**); *3437* (**B5**).
Villagrán & Kalin-Arroyo 4501 (**G11**).
Villagrán & al. 9040 (**E5**); *s.n.* [SGO 123683] (**C5**).
von Bohlen V. s.n. [SGO 163967] (**C5**); *269* (**G13**); *296* (**C4**); *443* (**B2**); *472* (**B1**); *674* (**B1**); *1074* (**B5**); *1075* (**B5**); *1218* (**B1**); *1297* (**G5**); *1298* (**B1**); *1332* (**C5**); *1389* (**B2**).
Wagenknecht 304 (**C3**).
Weberbauer 1498 (**D8**); *1517* (**D10**); *1606* (**F10**); *5385* (**D19**); *5701* (**F11**); *7183* (**F17**); *7190* (**D14**); *7382* (**F8**); *7455* (**D13**); *7457* (**E3**).
Weigend & Förther 97/537 (**F11**); *97/639* (**E4**); *97/692* (**D2**); 97/693 (**D2**); *97/694* (**D2**); *97/719* (**F17**); *97/754* (**D6**); *97/755* (**D18**); *97/766* (**E4**); *97/806* (**F13**); *97/811* (**D18**); *97/823* (**D11**); *97/829* (**D10**); *97/837* (**F13**); *97/839* (**D18**); *97/840* (**D18**); *97/862* (**F20**); *97/866* (**F1**); *97/881* (**F25**); *97/923* (**F4**).
Weigend & Schwarzer 8043 (**F14**).
Weigend & al. 7359 (**F11**); *7362* (**F11**); *8396* (**E3**); *2000/645* (**F11**); *97/469* (**F10**).
Weldt 228 (**B5**); *454* (**G17**).
Werdermann 112 (**B9**); *150* (**C5**); *169* (**G25**); *370* (**G6**); *379* (**G1**); *383* (**C2**); *387* (**G21**); *398* (**G1**); *402* (**G24**); *403* (**G24**); *412* (**C5**); *440* (**G21**); *444* (**B2**); *454* (**G11**); *460* (**B6**); *461* (**G6**); *720* (**F8**); *723* (**D18**); *728* (**D11**); *730* (**D1**); *741* (**E5**); *757* (**B4**); *769* (**B1**, 2 sheets); *774* (**G2**); *834* (**G6**); *886* (**G25**); *893* (**B8**); *928* (**C4**); *974* (**G2**).
West 3860 (**G12**); *3861* (**G17**); *3867* (**B9**); *3871* (**G2**); *3927* (**G25**); *3958* (**G3**).
Wiggins 18699 (**D4**).
Wiggins & Porter 563 (**D4**).
Wilkes Explor. Exped. s.n. [US 44325] (**G3**); *s.n.* [US 57458] (**F11**), *s.n.* [US 57460] (**B5**).
Worth & Morrison 9113 (**F11**); *15637* (**D6**); *15640* (**F17**); *15706* (**F17**); *15709* (**D8**); *15725* (**F1**); *15726* (**F20**); *15734* (**F18**); *15735* (**D18**); *15736* (**D8**); *15772* (**B1**); *15787* (**G20**); *16124* (**G13**); *16126* (**G2**); *16141* (**B3**); *16155* (**G20**); *16186* (**G6**); *16218* (**C5**); *16219* (**G1**); *16221* (**B9**); *16321* (**C4**); *16407* (**B1**); *16411* (**B1**); *16425* (**B8**).
Zalensky XV-836 (**C5**); *XV-841a* (**C5**); *XV-849* (**C5**); *XV-857* (**G6**); *XV-862* (**G24**).
Zimny s.n. [K] (**F3**).
Zöllner 890 (**G11**); *1705* (**C5**); *1709* (**G8**); *1850* (**G21**); *1851* (**B1**); *2474* (**B1**); *2807* (**G20**); *2812* (**C2**); *3528* (**G21**); *3610* (**C1**); *4353* (**C4**); *6908* (**C4**); *6927* (**C3**); *8862* (**G21**); *9300* (**C5**); *9803* (**C5**); *10104* (**G11**).
Zuleta s.n. [CONC 129566] (**C5**).

Appendix II
Index to Scientific Names

Alibrexia brevifolia Phil. = **Nolana sedifolia** Poepp.
Alibrexia gayana Gaudich. = **Nolana gayana** (Gaudich.) Koch
Alibrexia incana Phil. = **Nolana incana** (Phil.) I.M. Johnst.
Alibrexia philippii A. Braun ex W. Brandt = **Nolana crassulifolia** Poepp.
Alibrexia revoluta Miers = **Nolana pallida** I.M. Johnst.
Alibrexia rupicola Miers = **Nolana crassulifolia** Poepp.
Alibrexia tomentosa Miers = **Nolana crassulifolia** Poepp.
Alibrexia villosa Phil. = **Nolana villosa** (Phil.) I.M. Johnst.
Alona baccata Lindl. = **Nolana baccata** (Lindl.) Dunal
Alona balsamiflua Gaudich. = **Nolana balsamiflua** (Gaudich.) Mesa
Alona carnosa Lindl. = **Nolana carnosa** (Lindl.) Miers ex Dunal
Alona chastenayana (Gaudich.) Gaudich. ex Wettst. = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Alona coelestis Lindl. = **Nolana coelestis** (Lindl.) Miers ex Dunal
Alona coelestis Lindl. var. *ericifolia* (Miers) W. Brandt = **Nolana coelestis** (Lindl.) Miers ex Dunal
Alona deserticola Phil. = **Nolana leptophylla** (Miers) I.M. Johnst.
Alona dubia Phil. = **Nolana leptophylla** (Miers) I.M. Johnst.
Alona ericifolia Miers = **Nolana coelestis** (Lindl.) Miers ex Dunal
Alona filifolia (Hook. & Arn.) I.M. Johnst. = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Alona flaccida Phil. = *Nolana flaccida* (Phil.) I.M. Johnst. = **Nolana patula** (Phil.) Mesa ex M.O. Dillon
Alona floribunda Phil. = **Nolana coelestis** (Lindl.) Miers ex Dunal
Alona fonckii Phil. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Alona glandulosa Lindl. = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Alona lepidophylla (Phil.) Reiche = **Nolana carnosa** (Lindl.) Miers ex Dunal
Alona longifolia Lindl. = **Nolana rupicola** Gaudich.
Alona micrantha Phil. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Alona miersii Phil. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Alona mollis Phil. = **Nolana mollis** (Phil.) I.M. Johnst.
Alona obtusa Lindl. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Alona patula Phil. = **Nolana patula** (Phil.) Mesa ex M.O. Dillon
Alona phylicifolia Phil. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Alona rigida Phil. = **Nolana divaricata** (Lindl.) I.M. Johnst.
Alona rostrata Lindl. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Alona sedifolia Phil. = **Nolana carnosa** (Lindl.) Miers ex Dunal
Alona sphaerophylla Phil. = **Nolana sphaerophylla** (Phil.) Mesa ex M.O. Dillon
Alona stenophylla (I.M. Johnst.) I.M. Johnst. = **Nolana stenophylla** I.M. Johnst.
Alona tomentosa Lindl. = **Nolana crassulifolia** Poepp.
Alona vernicosa Phil. = **Nolana carnosa** (Lindl.) Miers ex Dunal
Alona xerophila Phil. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Aplocarya divaricata Lindl. = **Nolana divaricata** (Lindl.) I.M. Johnst.
Bargemontia albescens (Phil.) I.M. Johnst. = **Nolana albescens** (Phil. ex Wettst.) I.M. Johnst.
Bargemontia alibrexioides (Gaudich.) I.M.Johnst. = **Nolana leptophylla** (Miers) I.M. Johnst.
Bargemontia aplocaryoides (Gaudich.) I.M. Johnst. = **Nolana aplocaryoides** (Gaudich.) I.M. Johnst.
Bargemontia clavata (Miers) I.M. Johnst. = **Nolana divaricata** (Lindl.) I.M. Johnst.
Bargemontia clivicola I.M. Johnst. = **Nolana clivicola** (I.M. Johnst.) I.M. Johnst.
Bargemontia confinis I.M.Johnst. = **Nolana confinis** (I.M. Johnst.) I.M. Johnst.
Bargemontia crassulifolia (Poepp.) I.M. Johnst. = **Nolana crassulifolia** Poepp.
Bargemontia deflexa I.M. Johnst. = **Nolana linearifolia** Phil.
Bargemontia deserticola (Phil.) I.M. Johnst. = **Nolana leptophylla** (Miers) I.M. Johnst.
Bargemontia divaricata (Lindl.) I.M. Johnst. = **Nolana divaricata** (Lindl.) I.M. Johnst.
Bargemontia eremobia (Phil.) I.M. Johnst. = **Nolana incana** (Phil.) I.M. Johnst.
Bargemontia flaccida (Phil.) I.M. Johnst. = **Nolana patula** (Phil.) Mesa ex M.O. Dillon
Bargemontia foliosa (Phil.) I.M. Johnst. = **Nolana foliosa** (Phil.) I.M. Johnst.
Bargemontia glauca I.M. Johnst. = **Nolana glauca** (I.M. Johnst.) I.M. Johnst.
Bargemontia gracillima I.M. Johnst. = **Nolana gracillima** (I.M. Johnst.) I.M. Johnst.
Bargemontia inconspicua I.M. Johnst. = **Nolana inconspicua** (I.M. Johnst.) I.M. Johnst.
Bargemontia leptophylla (Miers) I.M. Johnst. = **Nolana leptophylla** (Miers) I.M. Johnst.
Bargemontia linearifolia (Phil.) I.M. Johnst. = **Nolana linearifolia** Phil.
Bargemontia micrantha (Phil.) I.M. Johnst. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Bargemontia mollis (Phil.) I.M. Johnst. = **Nolana mollis** (Phil.) I.M. Johnst.
Bargemontia patula (Phil.) I.M. Johnst. = **Nolana patula** (Phil.) Mesa ex M.O. Dillon

Bargemontia peruviana Gaudich. = **Nolana peruviana** (Gaudich.) I.M. Johnst.
Bargemontia platyphylla I.M.Johnst. = **Nolana platyphylla** (I.M. Johnst.) I.M. Johnst.
Bargemontia salsoloides I.M.Johnst. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Bargemontia sedifolia (Poepp.) I.M. Johnst. = **Nolana sedifolia** Poepp.
Bargemontia sphaerophylla (Phil.) I.M. Johnst. = **Nolana sphaerophylla** (Phil.) Mesa ex M.O. Dillon
Bargemontia tarapacana I.M.Johnst. = **Nolana tarapacana** (Phil.) I.M. Johnst.
Bargemontia tocopillensis I.M. Johnst. = **Nolana tocopillensis** (I.M. Johnst.) I.M. Johnst.
Convolvulus filifolius Hook. & Arn. = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Dolia albescens Phil. ex Wettst. = **Nolana albescens** (Phil. ex Wettst.) I.M. Johnst.
Dolia atacamensis W. Brandt = **Nolana crassulifolia** Poepp.
Dolia brevifolia (Phil.) Phil. ex Wettst. = **Nolana sedifolia** Poepp.
Dolia canescens Phil. = **Nolana albescens** (Phil.) I.M. Johnst.
Dolia clavata auct. *non* Miers = **Nolana crassulifolia** Poepp.
Dolia clavata Miers = **Nolana divaricata** (Lindl.) I.M. Johnst.
Dolia clavata Miers var. *puberula* (Phil.) Reiche = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Dolia crassifolia Poepp. ex Kuntze = **Nolana crassulifolia** Poepp.
Dolia deserticola (Phil.) W. Brandt = **Nolana leptophylla** (Miers) I.M. Johnst.
Dolia divaricata (Lindl.) Hook. & Arn. ex W. Brandt = **Nolana divaricata** (Lindl.) I.M. Johnst.
Dolia dubia (Phil.) W. Brandt = **Nolana leptophylla** (Miers) I.M. Johnst.
Dolia eremobia Phil. = **Nolana incana** (Phil.) I.M. Johnst.
Dolia foliosa Phil. = **Nolana foliosa** (Phil.) I.M. Johnst.
Dolia grandiflora Phil. = **Nolana crassulifolia** Poepp.
Dolia hirsutula Phil. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Dolia incana (Phil.) Benth. & Hook. ex W. Brandt = **Nolana incana** (Phil.) I.M. Johnst.
Dolia incana (Phil.) Wettst. = **Nolana incana** (Phil.) I.M. Johnst.
Dolia laxa Miers = **Nolana laxa** (Miers) I.M. Johnst.
Dolia leptophylla Miers = **Nolana leptophylla** (Miers) I.M. Johnst.
Dolia macrocalyx Phil. = **Nolana mollis** (Phil.) I.M. Johnst.
Dolia macrocalyx Phil. ex Herzog = **Nolana peruviana** (Gaudich.) I.M. Johnst.
Dolia micrantha (Phil.) Reiche = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Dolia philippi (Braun) W. Brandt = **Nolana crassulifolia** Poepp.
Dolia puberula Phil. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Dolia revoluta (Ruiz & Pav.) Benth. & Hook.f. = **Nolana pallida** I.M. Johnst.
Dolia rupicola (Miers) Benth. & Hook. ex Wettst. = **Nolana crassulifolia** Poepp.
Dolia salsoloides auct. *non* Lindl. = **Nolana ramosissima** I.M. Johnst.
Dolia salsoloides Lindl. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Dolia tarapacana Phil. = **Nolana tarapacana** (Phil.) I.M. Johnst.
Dolia tomentosa (Lindl.) Benth. = **Nolana crassulifolia** Poepp.
Dolia vermiculata Lindl. = **Nolana sedifolia** Poepp.
Dolia verticillata Walp. = **Nolana sedifolia** Poepp.
Dolia villosa (Phil.) Reiche = **Nolana villosa** (Phil.) I.M. Johnst.
Fabiana grandiflora Dunal = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Fabiana lanuginosa Hook. & Arn. = **Nolana sedifolia** Poepp.
Gubleria baccata Gaudich. = **Nolana baccata** (Lindl.) Dunal
Ipomoea cruckshanksii Choisy = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Leloutrea aplocaryoides Gaudich. = **Nolana aplocaryoides** (Gaudich.) I.M. Johnst.
Nolana acuminata (Miers) Miers ex Dunal = *Nolana angustifolia* Phil., *Nolana lanceolata* (Miers) Miers ex Dunal, *Sorema acuminata* Miers, *Sorema lanceolata* Miers, *Sorema longifolia* auct. *non* (Lindl.) Miers
Nolana adansonii (Roem. & Schult.) I.M. Johnst. = *Tula adansonii* Roem. & Schult.
Nolana aenigma M.O. Dillon, S. Leiva, & Quip.
Nolana albescens (Phil.) I.M. Johnst. = *Bargemontia albescens* (Phil.) I.M. Johnst., *Dolia albescens* Phil. ex Wettst., *Dolia canescens* Phil.
Nolana angustifolia Phil. = **Nolana acuminata** (Miers) Miers ex Dunal
Nolana aplocaryoides (Gaudich.) I.M. Johnst. = *Bargemontia aplocaryoides* (Gaudich.) I.M. Johnst., *Leloutrea aplocaryoides* Gaudich., *Nolana sedifolia* Poepp. var. *aplocaryoides* (Gaudich.) Mesa
Nolana arenicola I.M. Johnst.
Nolana arequipensis M.O. Dillon & Quip.
Nolana aticoana Ferreyra
Nolana atriplicifolia D. Don = **Nolana paradoxa** Lindl.
Nolana atriplicifolia D. Don var. *cuneifolia* Dunal = **Nolana paradoxa** Lindl.
Nolana baccata (Lindl.) Dunal = *Alona baccata* Lindl., *Gubleria baccata* Gaudich., *Nolana carrera* Phil., *Nolana carrera* Phil. var. *leucantha* (Phil.) Reiche, *Nolana debilis* Phil., *Nolana leucantha* Phil., *Nolana linearis* (Miers) Miers ex Dunal, *Nolana stans* Phil., *Periloba stans* (Phil.) I.M. Johnst., *Sorema linearis* Miers, *Nolana pulchella* Reiche.

Nolana balsamiflua (Gaudich.) Mesa = *Alona balsamiflua* Gaudich.

Nolana bipartita Ruiz & Pav. = **Nolana spathulata** Ruiz & Pav.

Nolana bombonensis Quip. & M.O. Dillon

Nolana bracteosa (Phil.) Reiche = **Nolana rupicola** Gaudich.

Nolana carnosa (Lindl.) Miers ex Dunal = *Alona carnosa* Lindl., *Alona lepidophylla* (Phil.) Reiche, *Alona sedifolia* Phil., *Alona vernicosa* Phil., *Nolana rostrata* (Lindl.) Miers ex Dunal var. *carnosa* (Lindl.) Mesa, *Osteocarpus lepidophyllus* Phil.

Nolana carrera Phil. = **Nolana baccata** (Lindl.) Dunal

Nolana carrera Phil. var. *leucantha* (Phil.) Reiche = **Nolana baccata** (Lindl.) Dunal

Nolana cerrateana Ferreyra

Nolana chancoana M.O. Dillon & Quip.

Nolana chapiensis M.O. Dillon & Quip.

Nolana chastenayana Gaudich. = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.

Nolana clivicola (I.M. Johnst.) I.M. Johnst. = *Bargemontia clivicola* I.M. Johnst.

Nolana coelestis (Lindl.) Miers ex Dunal = *Alona coelestis* Lindl., *Alona coelestis* Lindl. var. *ericifolia* (Miers) W. Brandt, *Alona ericifolia* Miers, *Alona floribunda* Phil., *Nolana ericifolia* (Miers) Miers ex Dunal

Nolana confinis (I.M. Johnst.) I.M. Johnst. = *Bargemontia confinis* I.M. Johnst.

Nolana coronata Ruiz & Pav.

Nolana crassulifolia Poepp. = *Alibrexia philippii* A. Braun ex W. Brandt, *Alibrexia rupicola* Miers, *Alibrexia tomentosa* Miers, *Alona tomentosa* Lindl., *Bargemontia crassulifolia* (Poepp.) I.M. Johnst., *Dolia clavata* auct. *non* Miers, *Dolia crassifolia* Poepp. ex Kuntze, *Dolia grandiflora* Phil., *Dolia philippi* (Braun) W. Brandt, *Dolia rupicola* (Miers) Benth. & Hook. ex Wettst., *Dolia tomentosa* (Lindl.) Benth., *Nolana grossulifolia* Kunze ex Gay.

Nolana debilis Phil. = **Nolana baccata** (Lindl.) Dunal

Nolana decemloba Herzog = **Nolana linearifolia** Phil.

Nolana deflexa (I.M. Johnst.) I.M. Johnst. = **Nolana linearifolia** Phil.

Nolana dianae M.O. Dillon

Nolana diffusa I.M. Johnst.

Nolana divaricata (Lindl.) I.M. Johnst. = *Alona rigida* Phil., *Aplocarya divaricata* Lindl., *Bargemontia clavata* (Miers) I.M. Johnst., *Bargemontia divaricata* (Lindl.) I.M. Johnst., *Dolia clavata* Miers, *Dolia divaricata* (Lindl.) Hook. & Arn. ex W. Brandt, *Nolana peruviana* (Gaudich.) I.M. Johnst. subsp. *divaricata* (Lindl.) Mesa, *Osteocarpus clavatus* Phil.

Nolana elegans (Phil.) Reiche = *Sorema elegans* Phil.

Nolana ericifolia (Miers) Miers ex Dunal = **Nolana coelestis** (Lindl.) Miers ex Dunal

Nolana filifolia (Hook. & Arn.) I.M. Johnst. = *Alona chastenayana* (Gaudich.) Gaudich. ex Wettst., *Alona filifolia* (Hook. & Arn.) I.M. Johnst., *Alona glandulosa* Lindl., *Convolvulus filifolius* Hook. & Arn., *Fabiana grandiflora* Dunal, *Ipomoea cruckshanksii* Choisy, *Nolana chastenayana* Gaudich., *Nolana glandulosa* (Lindl.) Miers ex Dunal, *Osteocarpus foliolosus* Phil.

Nolana flaccida (Phil.) I.M. Johnst. = **Nolana patula** (Phil.) Mesa ex M.O. Dillon

Nolana foliosa (Phil.) I.M. Johnst. = *Bargemontia foliosa* (Phil.) I.M. Johnst., *Dolia foliosa* Phil.

Nolana galapagensis (Christoph.) I.M. Johnst. **=** *Periloba galapagensis* Christoph.

Nolana gayana (Gaudich.) Koch = *Alibrexia gayana* Gaudich.

Nolana geminiflora Phil. = **Nolana paradoxa** Lindl.

Nolana glandulosa (Lindl.) Miers ex Dunal = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.

Nolana glauca (I.M. Johnst.) I.M. Johnst. = *Bargemontia glauca* I.M. Johnst., *Nolana peruviana* (Gaudich.) I.M. Johnst. var. *glauca* (I.M. Johnst.) Mesa

Nolana glutinosa (Phil.) Reiche = **Nolana rupicola** Gaudich.

Nolana gracillima (I.M. Johnst.) I.M. Johnst. = *Bargemontia gracillima* I.M. Johnst., *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa, p.p.

Nolana grandiflora Herzog = **N. acuminata (**Miers) Miers ex Dunal

Nolana grandiflora Lehm. ex G.Don = **Nolana paradoxa** Lindl.

Nolana grossulifolia Kunze ex Gay = **Nolana crassulifolia** Poepp.

Nolana guentheri I.M. Johnst. = **N. spathulata** Ruiz & Pav.

Nolana hoxeyi M.O. Dillon & Quip.

Nolana humifusa (Gouan) I.M. Johnst.

Nolana humifusa (Gouan) I.M. Johnst. subsp. *spathulata* (Ruiz & Pav.) Mesa = **Nolana spathulata** Ruiz & Pav.

Nolana incana (Phil.) I.M. Johnst. = *Alibrexia incana* Phil., *Dolia incana* (Phil.) Benth. & Hook. ex W. Brandt, *Dolia incana* (Phil.) Wettst.

Nolana inconspicua (I.M. Johnst.) I.M. Johnst. = *Bargemontia inconspicua* I.M. Johnst.

Nolana inflata Ruiz & Pav.

Nolana insularis (I.M. Johnst.) I.M. Johnst. = *Periloba insularis* I.M. Johnst.

Nolana intonsa I.M. Johnst.

Nolana ivaniana Ferreyra = **Nolana latipes** I.M. Johnst.

Nolana jaffuelii I.M. Johnst.

Nolana johnstonii Vargas

Nolana lachimbensis M.O. Dillon & Luebert

Nolana lanceolata (Miers) Miers ex Dunal = **Nolana acuminata** (Miers) Miers ex Dunal

Nolana lanceolata auct. *non* (Miers) Miers ex Dunal = **Nolana rupicola** Gaudich.

Nolana latipes I.M. Johnst.

Nolana laxa (Miers) I.M. Johnst. = *Dolia laxa* Miers

Nolana lepidophylla (Phil.) I.M. Johnst. = **Nolana rostrata** (Lindl.) Miers ex Dunal

Nolana leptophylla (Miers) I.M. Johnst. = *Alona deserticola* Phil., *Alona dubia* Phil., *Bargemontia alibrexioides* (Gaudich.) I.M.Johnst., *Bargemontia deserticola* (Phil.) I.M. Johnst., *Bargemontia leptophylla* (Miers) I.M. Johnst., *Dolia deserticola* (Phil.) W. Brandt, *Dolia dubia* (Phil.) W. Brandt, *Dolia leptophylla* Miers, *Velpeaulia alibrexioides* Gaudich.

Nolana leptophylla (Miers) I.M. Johnst. subsp. *mollis* (Phil.) Mesa = **Nolana mollis** (Phil.) I.M. Johnst.

Nolana leucantha Phil. = **Nolana baccata** (Lindl.) Dunal

Nolana lezamae M.O. Dillon, S. Leiva, & Quip.

Nolana linearifolia Phil. = *Bargemontia deflexa* I.M. Johnst., *Bargemontia linearifolia* (Phil.) I.M. Johnst., *Nolana decemloba* Herzog, *N. deflexa* (I.M. Johnst.) I.M. Johnst.

Nolana linearis (Miers) Miers ex Dunal = **Nolana baccata** (Lindl.) Dunal

Nolana litoralis (Miers) Dunal = **Nolana paradoxa** Lindl.

Nolana longifolia (Lindl.) Miers ex Dunal = **Nolana rupicola** Gaudich.

Nolana lycioides I.M. Johnst. = *Nolana sedifolia* Poepp. subsp. *confinis* (I.M. Johnst.) Mesa, p.p.

Nolana mariarosae Ferreyra

Nolana minor Ferreyra

Nolana mollis (Phil.) I.M. Johnst. = *Alona mollis* Phil., *Bargemontia mollis* (Phil.) I.M. Johnst., *Dolia macrocalyx* Phil., *Nolana leptophylla* (Miers) I.M. Johnst. subsp. *mollis* (Phil.) Mesa

Nolana obtusa (Lindl.) Miers ex Dunal = **Nolana rostrata** (Lindl.) Miers ex Dunal

Nolana ochrocarpa Phil. ex Wettst. = **Nolana paradoxa** Lindl.

Nolana onoana M.O. Dillon & M. Nakaz.

Nolana pallida I.M. Johnst. = *Alibrexia revoluta* Miers, *Dolia revoluta* (Ruiz & Pav.) Benth. & Hook.f.

Nolana pallidula I.M. Johnst.

Nolana paradoxa Lindl. = *Nolana atriplicifolia* D. Don, *Nolana atriplicifolia* D. Don var. *cuneifolia* Dunal, *Nolana geminiflora* Phil., *Nolana grandiflora* Lehm. ex G. Don, *Nolana litoralis* (Miers) Dunal, *Nolana ochrocarpa* Phil. ex Wettst., *Nolana paradoxa* Lindl. subsp. *atriplicifolia* (D. Don) Mesa, *Nolana paradoxa* Lindl. var. *glaberrima* Dunal, *Nolana paradoxa* Lindl. var. *violacea* Van Houtte, *Nolana petiolata* (Phil.) Reiche, *Periloba paradoxa* (Lindl.) Raf., *Sorema atriplicifolia* (D. Don) Lindl., *Sorema litoralis* Miers, *Sorema paradoxa* (Lindl.) Lindl., *Sorema paradoxa* (Lindl.) Lindl. var. *atriplicifolia* (D. Don) Miers, *Sorema petiolata* Phil.

Nolana paradoxa Lindl. var. *glaberrima* Dunal = **Nolana paradoxa** Lindl.

Nolana paradoxa Lindl. var. *violacea* Van Houtte = **Nolana paradoxa** Lindl.

Nolana paradoxa Lindl. subsp. *atriplicifolia* (D. Don) Mesa = **Nolana paradoxa** Lindl.

Nolana parviflora (Phil.) Phil. = *Periloba parviflora* (Phil.) I.M. Johnst., *Sorema parviflora* Phil.

Nolana patula (Phil.) Mesa ex M.O. Dillon

Nolana pearcei I.M. Johnst.

Nolana peruviana (Gaudich.) I.M. Johnst. = *Bargemontia peruviana* Gaudich., *Dolia macrocalyx* Phil. ex Herzog

Nolana peruviana (Gaudich.) I.M. Johnst. var. *glauca* (I.M. Johnst.) Mesa = **Nolana glauca** (I.M. Johnst.) I.M. Johnst.

Nolana peruviana (Gaudich.) I.M. Johnst. subsp. *divaricata* (Lindl.) Mesa = **Nolana divaricata** (Lindl.) I.M. Johnst.

Nolana petiolata (Phil.) Reiche = **Nolana paradoxa** Lindl.

Nolana philippiana M.O. Dillon & Luebert

Nolana pilosa I.M. Johnst.

Nolana platyphylla (I.M. Johnst.) I.M. Johnst. = *Bargemontia platyphylla* I.M. Johnst.

Nolana plicata I.M. Johnst.

Nolana polymorpha Gaudich. = **Nolana humifusa** (Gouan) I.M. Johnst.

Nolana pterocarpa Phil. ex Wettst. = *Nolana pterosperma* Phil., *Periloba pterosperma* (Phil.) I.M. Johnst.

Nolana pterosperma Phil. = **Nolana pterocarpa** Phil. ex Wettst.

Nolana pulchella Reiche = **Nolana baccata** (Lindl.) Dunal

Nolana ramosissima I.M. Johnst. = *Dolia salsoloides* auct. *non* Lindl.

Nolana reichei M.O. Dillon & Arancio

Nolana rhombifolia Martic. & Quez.

Nolana rostrata (Lindl.) Miers ex Dunal = *Alona fonckii* Phil., *Alona miersii* Phil., *Alona obtusa* Lindl., *Alona phylicifolia* Phil., *Alona rostrata* Lindl., *Nolana lepidophylla* (Phil.) I.M. Johnst., *Nolana obtusa* (Lindl.) Miers ex Dunal, *Osteocarpus brevifolius* Phil., *Osteocarpus rostratus* (Lindl.) Phil., *Rayera teretifolia* Gaudich.

Nolana rostrata (Lindl.) Miers ex Dunal var. *carnosa* (Lindl.) Mesa = **Nolana carnosa** (Lindl.) Miers ex Dunal

Nolana rupestris Phil. ex Wettst. = ***Nolana rupicola*** Gaudich.

Nolana rupicola Gaudich. = *Alona longifolia* Lindl., *Nolana bracteosa* (Phil.) Reiche, *Nolana glutinosa* (Phil.) Reiche, *Nolana lanceolata* auct. *non* (Miers) Miers ex Dunal, *Nolana longifolia* (Lindl.) Miers ex Dunal, *Nolana triquetra* Koch & Bouché, *Periloba longifolia* (Lindl.) I.M. Johnst., *Sorema bracteosa* Phil., *Sorema glutinosa* Phil., *Sorema longifolia* (Lindl.) Miers

Nolana salsoloides (Lindl.) I.M. Johnst. = *Bargemontia micrantha* (Phil.) I.M. Johnst., *Dolia clavata* Miers var. *puberula* (Phil.) Reiche, *Dolia hirsutula* Phil., *Dolia micrantha* (Phil.) Reiche, *Dolia salsoloides* Lindl., *Osteocarpus spathulatus* Phil.
Nolana samaensis M.O. Dillon & Quip.
Nolana scaposa Ferreyra
Nolana sedifolia Poepp. = *Alibrexia brevifolia* Phil., *Bargemontia sedifolia* (Poepp.) I.M. Johnst., *Dolia brevifolia* (Phil.) Phil. ex Wettst., *Dolia vermiculata* Lindl., *Fabiana lanuginosa* Hook. & Arn., *Salsola glomerulata* Meyen.
Nolana sedifolia Poepp. var. *aplocaryoides* (Gaudich.) Mesa = **Nolana aplocaryoides** (Gaudich.) I.M. Johnst.
Nolana sedifolia Poepp. subsp. *confinis* (I.M. Johnst.) Mesa, p.p. = **Nolana gracillima** (I.M. Johnst.) I.M. Johnst.
Nolana sedifolia Poepp. subsp. *confinis* (I.M. Johnst.) Mesa, p.p. = **Nolana lycioides** I.M. Johnst.
Nolana sessiliflora Phil. = *Nolana sessilifolia* Phil. ex I.M. Johnst., *Periloba sessiliflora* (Phil.) I.M. Johnst.
Nolana sessilifolia Phil. ex I.M. Johnst. = **Nolana sessiliflora** Phil.
Nolana spathulata Ruiz & Pav.
Nolana spergularioides Ferreyra
Nolana sphaerophylla (Phil.) Mesa ex M.O. Dillon
Nolana stans Phil. = **Nolana baccata** (Lindl.) Dunal
Nolana stenophylla I.M. Johnst.
Nolana tarapacana (Phil.) I.M. Johnst.
Nolana thinophila I.M. Johnst.
Nolana tocopillensis (I.M. Johnst.) I.M. Johnst.
Nolana tomentella Ferreyra
Nolana tovariana Ferreyra
Nolana triquetra Koch & Bouché = **Nolana rupicola** Gaudich.
Nolana urubambae Vargas
Nolana villosa (Phil.) I.M. Johnst.
Nolana volcanica Ferreyra
Nolana weberbaueri I.M. Johnst.
Nolana weissiana Ferreyra
Nolana werdermannii I.M. Johnst.
Nolana willeana Ferreyra
Osteocarpus brevifolius Phil. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Osteocarpus clavatus Phil. = **Nolana divaricata** (Lindl.) I.M. Johnst.
Osteocarpus foliolosus Phil. = **Nolana filifolia** (Hook. & Arn.) I.M. Johnst.
Osteocarpus lepidophyllus Phil. = **Nolana carnosa** (Lindl.) Miers ex Dunal
Osteocarpus rostratus (Lindl.) Phil. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Osteocarpus spathulatus Phil. = **Nolana salsoloides** (Lindl.) I.M. Johnst.
Periloba galapagensis Christoph. **= Nolana galapagensis** (Christoph.) I.M. Johnst.
Periloba longifolia (Lindl.) I.M. Johnst. = **Nolana rupicola** Gaudich.
Periloba paradoxa (Lindl.) Raf. = **Nolana paradoxa** Lindl.
Periloba parviflora (Phil.) I.M. Johnst. = **Nolana parviflora** (Phil.) Phil.
Periloba pterosperma (Phil.) I.M. Johnst. = **Nolana pterocarpa** Phil. ex Wettst.
Periloba sessiliflora (Phil.) I.M. Johnst. = **Nolana sessiliflora** Phil.
Periloba stans (Phil.) I.M. Johnst. = **Nolana baccata** (Lindl.) Dunal
Rayera teretifolia Gaudich. = **Nolana rostrata** (Lindl.) Miers ex Dunal
Salsola glomerulata Meyen = **Nolana sedifolia** Poepp.
Sorema acuminata Miers = **Nolana acuminata** (Miers) Miers ex Dunal
Sorema atriplicifolia (D. Don) Lindl. = **Nolana paradoxa** Lindl.
Sorema bracteosa Phil. = **Nolana rupicola** Gaudich.
Sorema elegans Phil. = **Nolana elegans** (Phil.) Reiche
Sorema glutinosa Phil. = **Nolana rupicola** Gaudich.
Sorema lanceolata Miers = **Nolana acuminata** (Miers) Miers ex Dunal
Sorema linearis Miers = **Nolana baccata** (Lindl.) Dunal
Sorema litoralis Miers = **Nolana paradoxa** Lindl.
Sorema longifolia (Lindl.) Miers = **Nolana rupicola** Gaudich.
Sorema longifolia auct. *non* (Lindl.) Miers = **Nolana acuminata** (Miers) Miers ex Dunal
Sorema paradoxa (Lindl.) Lindl. = **Nolana paradoxa** Lindl.
Sorema paradoxa (Lindl.) Lindl. var. *atriplicifolia* (D. Don) Miers = **Nolana paradoxa** Lindl.
Sorema parviflora Phil. = **Nolana parviflora** (Phil.) Phil.
Sorema petiolata Phil. = **Nolana paradoxa** Lindl.
Tula adansonii Roem. & Schult. = **Nolana adansonii** (Roem. & Schult.) I.M. Johnst.
Velpeaulia alibrexioides Gaudich. = **Nolana leptophylla** (Miers) I.M. Johnst.

GUSTAVIA MONTANA (LECYTHIDACEAE): A NEW SPECIES FROM THE ANDES IN COLOMBIA

Xavier Cornejo,[1,2] David Gutiérrez-Duque,[3,4] Juan Sebastián Arango-González,[5] Julio Andrés Sierra-Giraldo,[4,6] and Diana Medellin-Zabala[7]

Abstract. *Gustavia montana*, a new species of Lecythidaceae from the montane rain forests along the western slopes of Central Cordillera and the northeastern Western Cordillera in Colombia is formally described and illustrated, and its relationship to morphologically closely related species is discussed.

Keywords: Andes, central cordillera, Colombia, Endemics, montane forest, western cordillera

Resumen. *Gustavia montana*, una nueva especie de Lecythidaceae de los bosques lluviosos montanos de las estribaciones occidentales de la cordillera Central y del noreste de la cordillera occidental de Colombia es formalmente descrita e ilustrada, se discute sus relaciones con las especies morfológicamente cercanas.

Palabras claves: Andes, bosque montano, Colombia, cordillera central, cordillera occidental, endémica

Gustavia L. is a genus of Neotropical Lecythidaceae characterized by the presence of showy actinomorphic flowers; androecium of a thin-walled staminal cup that bears numerous incurved filaments along the rim of the margin, oblong-elongate poricidal anthers; and indehiscent fruits. The genus forms a clade clearly defined by both molecular and morphological characters (Mori 1979, Mori et al. 2007, Huang et al. 2015). *Gustavia* was first studied by Mori (1979), and four additional Ecuadorian species have been described since then (Mori and Cornejo, 2013; Cornejo & Mori, 2019). With this new taxon, the genus now includes 47 species (Mori et al. 2017). Because of the beautiful, sweetly scented flowers, the members of *Gustavia* have ornamental potential and are sometimes planted as green elements in urban environments (e.g., Macas city, Ecuador). The abundant poricidal anthers suggest bee pollination, providing food resources for native bees and also for introduced honey bees, such as *Apis mellifera* (Mori and Boom, 1987; pers. obs.). Because of the edible mesocarp, the fruit of some species, such as *Gustavia macarenensis* Philipson, known as Paso, are sold in local markets. Rodents, such as squirrels and agouties, also feed on these fruits (Sork, 1987; Mori et al. 2017; Cornejo, pers. obs.). The taxonomic study of *Gustavia* requires field work and observation of several flowering and fruiting key stages to produce useful information for recognizing species. Recent field work by the coauthors in the montane rain forests of the western cordillera in Colombia, as well as herbarium study, yielded a distinctive new species that is formally presented here.

Materials and Methods

All relevant specimens at COL, CUVC, FAUC, HUA, HUQ, JAUM, NY, and UDBC were studied (herbarium abbreviations follow Thiers, 2022). Measurements are from herbarium specimens, rehydrated flowers, and fresh specimens. The botanical terms used in the species descriptions follow Jackson (1991) and Mori et al. (2015). Images of pollen grains were captured with a FEI-QUANTA 250 microscope-SEM in the Scanning Electron Microscopy Laboratory at the Instituto de Investigaciones en Estratigrafía–IIES, Universidad de Caldas. Terminology presented in Punt et al. (2007), Halbritter et al. (2018), Jain (2020) and Pardo-Trujillo et al. (2021) was utilized for the description of the palynomorphs. Measurements of the morphological structures were performed using ImageJ 1.51n software

We would like to express our deepest appreciation to the indigenous reservations "Territorio Ancestral Indígena San Lorenzo" and "Resguardo Indígena Nuestra Señora Candelaria de La Montaña" and their indigenous authorities and their people, for allowing us to enter to their territory and study the sacred mountains that they so zealously protect. The studies in the reservations were carried out in the framework of the court ruling 025/2018. We would like to thank Sori Morales, Carlos Betancur, Sergio Melchor, Lubian Melchor, Faiber Alarcón and Jaime Alarcón for granting us the permits, showing us more populations of the species throughout their indigenous community, hosting us for the days we were there, monitoring the phenology of the population and sharing with us the common name of this species. We are also thankful to Andrés Miguel Betancourth for his commentaries about *Gustavia romeroi* ecology. We are grateful to the staff of COL, FAUC, HUA, HUQ, JAUM and UDBC for letting us know their respective collections, and especially to the staff of FAUC for letting us prepare the specimens and for their support and advice throughout this study. We express our gratitude to Gustavo Adolfo Bolaños from the Instituto de Investigaciones en Estratigrafía-IIES, Universidad de Caldas, for granting us access to the palynology laboratory and the optical equipment, including the SEM.

[1] Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo (campus Mapasingue), Guayaquil, Ecuador. https://orcid.org/0000-0002-4081-4047

[2] Corresponding author: xcornejoguay@gmail.com

[3] Grupo de Investigación BIONAT, Biodiversidad y Recursos Naturales, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Colombia; davidgd2015@gmail.com

[4] Herbario FAUC, Universidad de Caldas, Manizales, Colombia; andresierra25@gmail.com

[5] Territorio Ancestral Indígena San Lorenzo, Riosucio, Caldas; sebastian.arango@utp.edu.co

[6] Fundación Conservación de la Selva Colombiana, Manizales, Colombia.

[7] Department of Ecology and Evolutionary Biology, University of Michigan, U.S.A. https://orcid.org/0000-0003-2775-8922.

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 647–653.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n2, Published online: 31 December 2023

(Schindelin et al., 2012). The mean and standard deviation of the equatorial diameter in equatorial view, polar diameter in equatorial view, diameter in polar view were calculated. Specific characteristics of pollen grains, such as colpi, pores, apertures, ornamentation were described (Prance and Mori, 1979; Roubik and Moreno 1991). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were estimated using rCAT (Moat, 2020) in the statistical software R (R Core Team, 2020) based on the geographical data from the specimens. The IUCN Red List category for the species was assessed following the guidelines of the International Union for Conservation of Nature (IUCN, 2022).

Taxonomy

Gustavia montana Cornejo, D. Gut. & J.S. Arango-G., *sp. nov.*

TYPE: COLOMBIA. Caldas: Cordillera occidental, Mun. Ríosucio, Territorio Ancestral Indígena San Lorenzo, Comunidad Honduras, cassava and plantain crop, 1635 m, 5°28'29.9"N, 75°41'46.2"W, 8 July 2023 (fl), *D. Gutiérrez-Duque & J. S. Arango-González 645* (Holotype: FAUC; Isotypes: COL, HUA, HUQ, JAUM). Fig. 1–4.

Gustavia montana is similar to *G. sessilis* S.A. Mori by the sessile narrow leaves, ecostate hypanthium and large floral bracts, but differs from the latter species by the many branched (vs. unbranched to few-branched) growth form, leaves with 20 to 27 (vs. 40) pairs of lateral veins, a rather multiflorous inflorescence (usually 12 to 20 vs. 4- or 5-flowered), and calyces with 6 to 8 (vs. 4) sepals.

Several to many-branched *trees*, to 6 m tall × 15 cm DBH. Trunk covered with lichens; *bark* slightly roughened, lenticellate, peeling in long strips, inner bark orangish-red. *Leaves* clustered at the ends of branches, subsessile, the midvein at base usually crescent-moon shaped in cross section, flattened adaxially and convex, but not carinate, abaxially; blades oblanceolate, 35–80 × 12–20 cm, somewhat glossy adaxially, glandular-punctate, and short hyaline-pilose on veins abaxially, lower part of blade tapered to base, base cuneate to broadly obtuse, margins often inconspicuously crenulate, barely undulate, apex short-acuminate; venation brochidodromous, midrib salient adaxially and abaxially, secondary veins in 20 to 27 pairs, plain or prominulous adaxially, salient abaxially, intersecondary veins sometimes present, tertiaries more or less scalariform, higher order veins reticulate. *Inflorescences* terminal, racemose, bearing 12–25 flowers but one at anthesis at a time, rachis ca. 150 × 5–7 mm, occasionally shorter, few flowered and axillary at subterminal branches; *floral bract* lanceolate, ca. 4 × 1.5 cm, red to purplish-red, carinate and short pilose abaxially, soon deciduous; pedicels 80–150 mm long, short hyaline-tomentose to tomentulose, at distal half bearing 2 *bracteoles*, lanceolate, ca. 11–15 × 7–8 mm, red to purplish-red, carinate and short pilose abaxially, soon deciduous. *Flowers* ca. 10 cm diam.; hypanthium tomentose, without costae; calyx lobes 6 to 8, broadly triangular to ovate, ca. 3–5 × 8–11 mm, purplish towards apex, tomentose; petals 7 to 9, obovate to obovate-elliptic, ca. 50–60 × 25–35 mm, salmon to pink and short pilose in bud, at anthesis white on both sides, salmon tinged at base abaxially; connate androecial tube ca. 5–7 mm high, outermost filaments ca. 12–17 mm long, white; anthers ca. 3 mm, light yellow; ovary 6- to 8-locular, style ca. 2 mm long, obconical; stigma with 6 to 8 stigmatic lines. *Fruit* subglobose, nearly smooth, broadly obtuse to almost rounded at apex, ca. 4 × 5 cm, yellowish-brown at maturity; calycine rim persisting, inserted at summit of fruit, infracalycine zone rounded to base, supracalycine zone prominent; pulp creamy; exocarp leathery, 3–7 mm thick. *Seeds* subglobose, ca. 38 × 25 mm, seed coat thin, smooth; caruncle broadly conical, funicular aril contorted, well-developed, ca. 20 mm long, with irregular bumps, yellow, adpressed to seed.

Because the leaves are arranged in tightly congested clusters at the end of branches, and the suprafoliar terminal inflorescences with relatively large basal floral bracts and presence of pedicellary bracteoles, *Gustavia montana* resembles *G. sessilis* S.A. Mori, *G. grandibracteata* Croat & S.A. Mori, and *G. pubescens* Tafalla ex O. Berg. However, *G. montana* differs from all of those by the many-branched form (vs. unbranched or/to few-branched), more rounded seeds with distinctive developed funicular arils, and distinctive pattern of distribution, over 1600 m (versus sea level to 1000 m). Additional differences between *G. montana* and *G. sessilis* are described in the diagnosis. *Gustavia montana* differs from *G. grandibracteata* by the subsessile leaves (versus petiolate), bearing blades with fewer secondary veins (20–27 versus 45–54), and the calyx with 6 to 8 lobes (versus 4 calyx lobes). *Gustavia montana* also differs from *G. pubescens* by the smaller flowers at anthesis (ca. 10 cm in diam. versus 12 to 17 cm), bearing 7 to 9 petals (versus 6), smooth hypanthium (versus costate hypanthium), more inconspicuous pubescence and a different pattern of distribution, that is endemic to the central and western cordillera of Colombia (versus restricted to western Ecuador). By the leaves arrangement, size and shape of leaf blades, and similar number of lateral veins *Gustavia montana* may resemble *G. occidentalis* Cuatrec., but the former species differ from the later by the subsessile leaves (versus 1 to 5 cm petiolate), pedicels tomentose to tomentulose (versus glabrous), seeds with a well developed funicular aril (versus seeds without developed funicular aril), and the distinctive mentioned montane pattern of distribution over 1600 m (versus sea level to 1500 m in the Pacific slopes of southwestern Colombia and northwestern Ecuador).

Palynology: Monad; prolate; amb circular; isopolar; symmetry radial; tricolporate; pore lolongate; colpi with apex acute; reticulate; heterobrochate; lumina smaller than 1 μm; equatorial view length (polar axis) 21.1 μm (19.3–23.8, n = 10); equatorial view width (equatorial diameter) 15.8 μm (13.4–17.5, n = 10); polar view length 17.4 μm (15.8–19.3, n = 10); colpi length 15 μm (12.9–18.3, n = 10); colpi width 1.4 μm (0.5–2.2, n = 10); pore length 2.6 μm (2.4–2.8, n = 2); pore width 1.8 μm (1.7–1.9, n = 2).

In some pollen grains the pore was not observed, apparently presenting a tricolpate aperture. The possible fusion of two colpi at the pole of the pollen grain was also

FIGURE 1. *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. Based on the holotype (FAUC). Photograph by Santiago Guzmán.

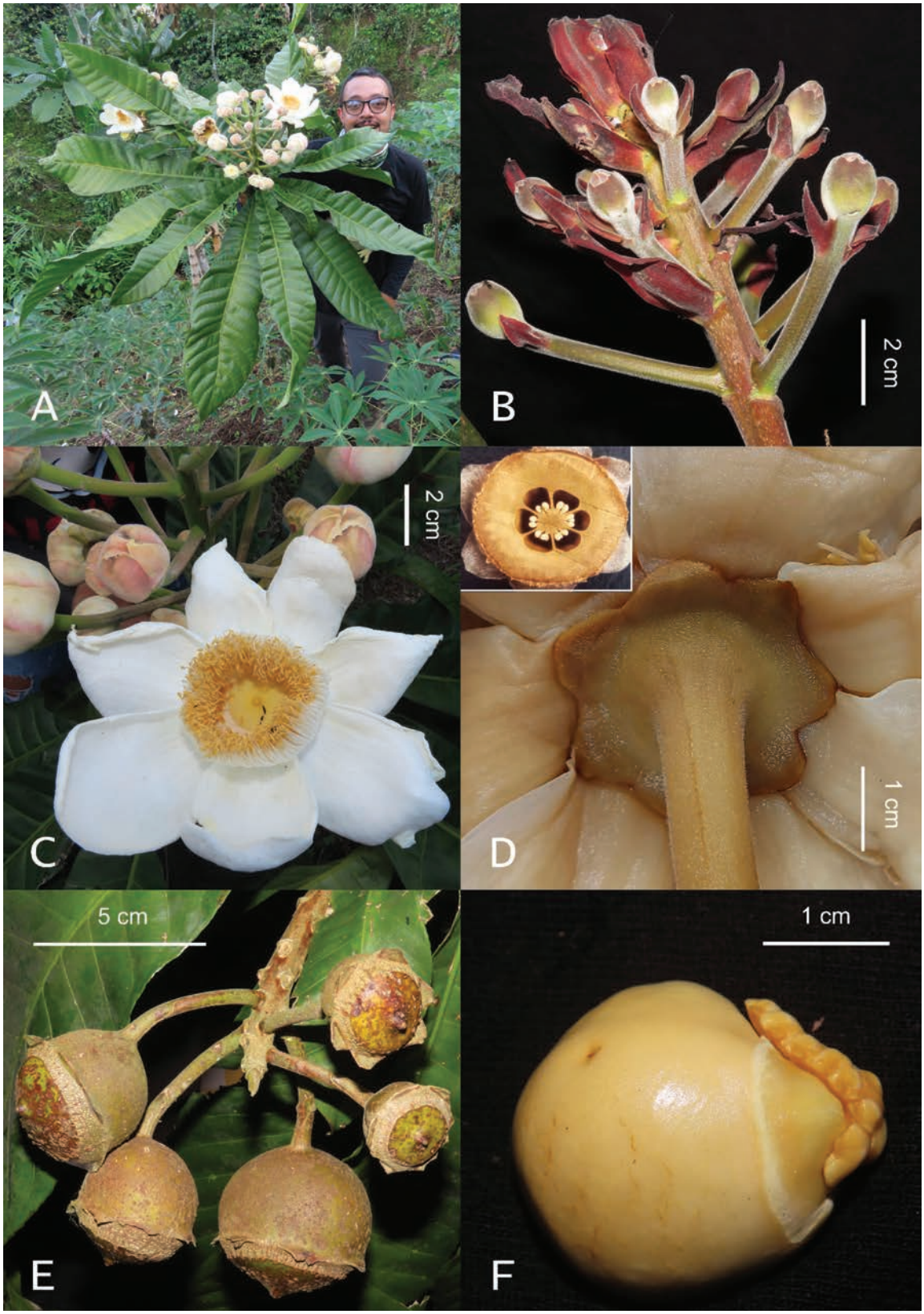


FIGURE 2. *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. **A**, terminal leafy branch and inflorescence held by Juan Sebastián Arango, adaxial view; **B**, bracteate young inflorescence, lateral view; **C**, flower at anthesis; **D**, close-up of calyx and base of petals, with a cross-section of ovary displaying 6 locules at upper left; **E**, infructescence; **F**, seed crowned by caruncle and funicular aril. A, C, D, are based on the holotype *Gutiérrez-Duque & Arango-González 645* (FAUC); B, E, F are based on the paratype *Arango 003* (FAUC). Photographs A, B, C, E, F by Juan Sebastián Arango, D by David Gutiérrez-Duque.

observed (Fig. 3D); therefore, it is necessary to continue analyzing the pollen morphology in *G. montana* in order to determine if these characteristics occur in other populations and how it is related to other species in the genus.

Etymology: The epithet refers to the highly distinctive pattern of distribution of *Gustavia montana*, which is restricted to montane Andean forests, 1635–2176 m elevation on the slopes of the western and central cordilleras of Colombia. This montane pattern of distribution is unusual in a predominantly tropical genus.

Common names: Known as "cocolleto," which means coconut pot in "Resguardo Indígena Nuestra Señora Candelaria de La Montaña" (Riosucio, Caldas).

Habitat and distribution: Currently known only from the Andes mountains of Colombia and distributed in the northeastern area of the Western Cordillera in the departments of Caldas and Risaralda, and throughout the Central Cordillera in the departments of Antioquia, Quindío and Risaralda. From its biogeographic affinities (see González-Orozco, 2021), it is possible that it is also found in the Western Cordillera in the department of Antioquia, and in the Central Cordillera in the department of Caldas. It grows at (1635–) 1949–2176 m of elevation, being not only the species of *Gustavia* that is distributed at the highest altitude in Colombia, but also in the entire genus. *Gustavia montana* usually inhabits secondary sub-Andean forests (Rudas et al., 2007); however, it has been found growing in the midst of cassava and plantain crops (*Gutiérrez-Duque 645*), and planted in farm gardens (*Arango-González et al. 003*, *Vélez and L. C. Serna 7097*).

Phenology: Flowers were recorded in herbarium material and observed in the field during 2022 and 2023, from July to August and November to February, and fruits from July to October and December to February. The flowering periods can be more frequent during the dry season (Jaramillo, 2005), which is also the case in several species of the family (Prance and Mori, 1979).

Uses: Two individuals (*Arango-González et al. 003*, *C. Vélez and L. C. Serna 7097*) were found planted in farm gardens. Because of its large flowers, and the relatively short size of the trees, this species could be cultivated as an ornamental.

Conservation status: *Gustavia montana* is endemic to Colombia, currently known from 10 locations along the Central Cordillera and the northeastern sector of the Western Cordillera. Despite its restricted distribution, it was found widely distributed in a forest in Riosucio (*D. Gutiérrez-Duque and J. F. Alarcón 647*), with more than 100 individuals in less than 300 square meters. More than an ecological characteristic of the species, it could be an ecological strategy within a restricted distribution. This phenomenon, where a species with a restricted distribution has very dense populations, has been seen in other species of the genus, such as *G. parviflora* S.A. Mori (Lárez-Rivas,

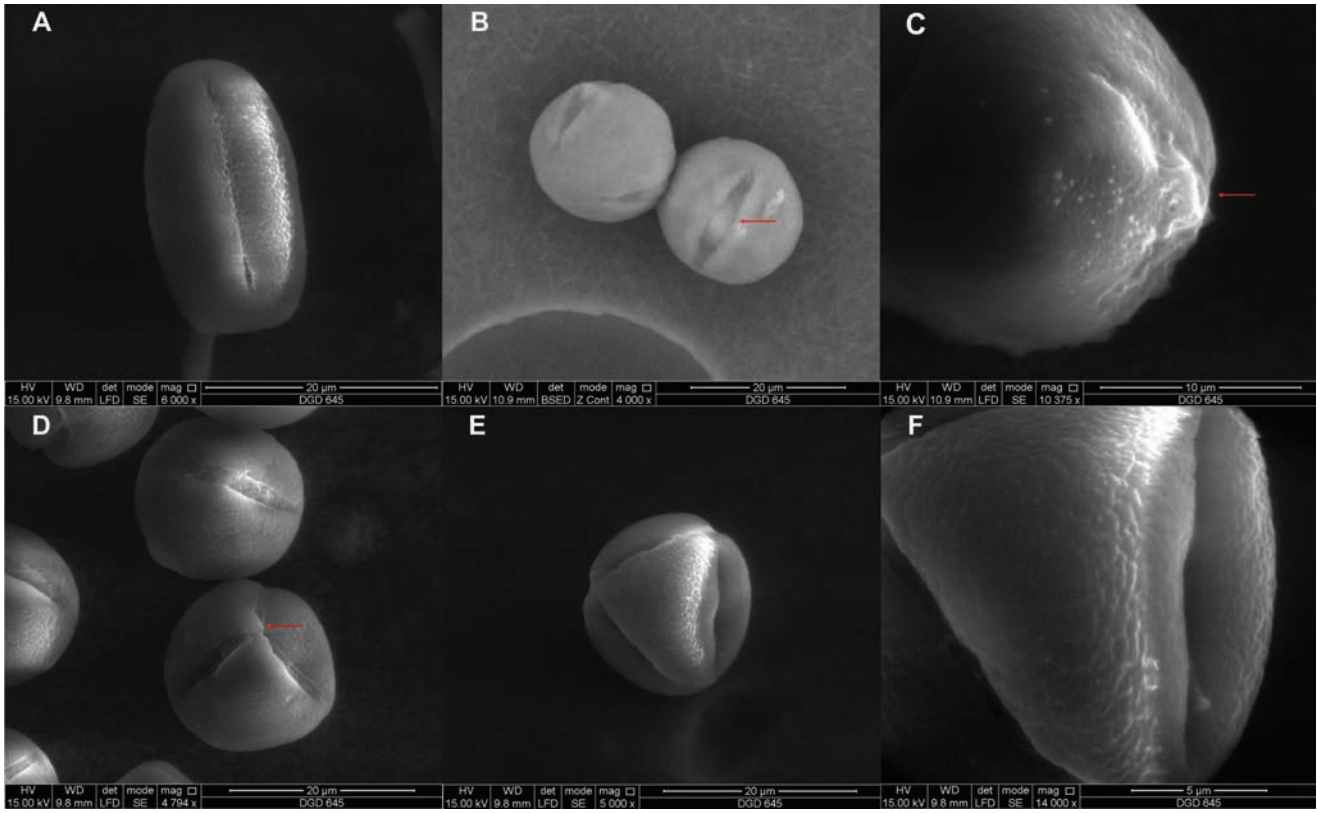


FIGURE 3. Pollen morphology in *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. **A**, equatorial view; **B**, polar view (left) and general view (right); the red arrow indicates the colporate aperture; **C**, pore detail; **D**, possible fusion of two colpi at the pole of the pollen grain; **E**, general view; **F**, ornamentation detail. Photographs by Gustavo Bolaños.

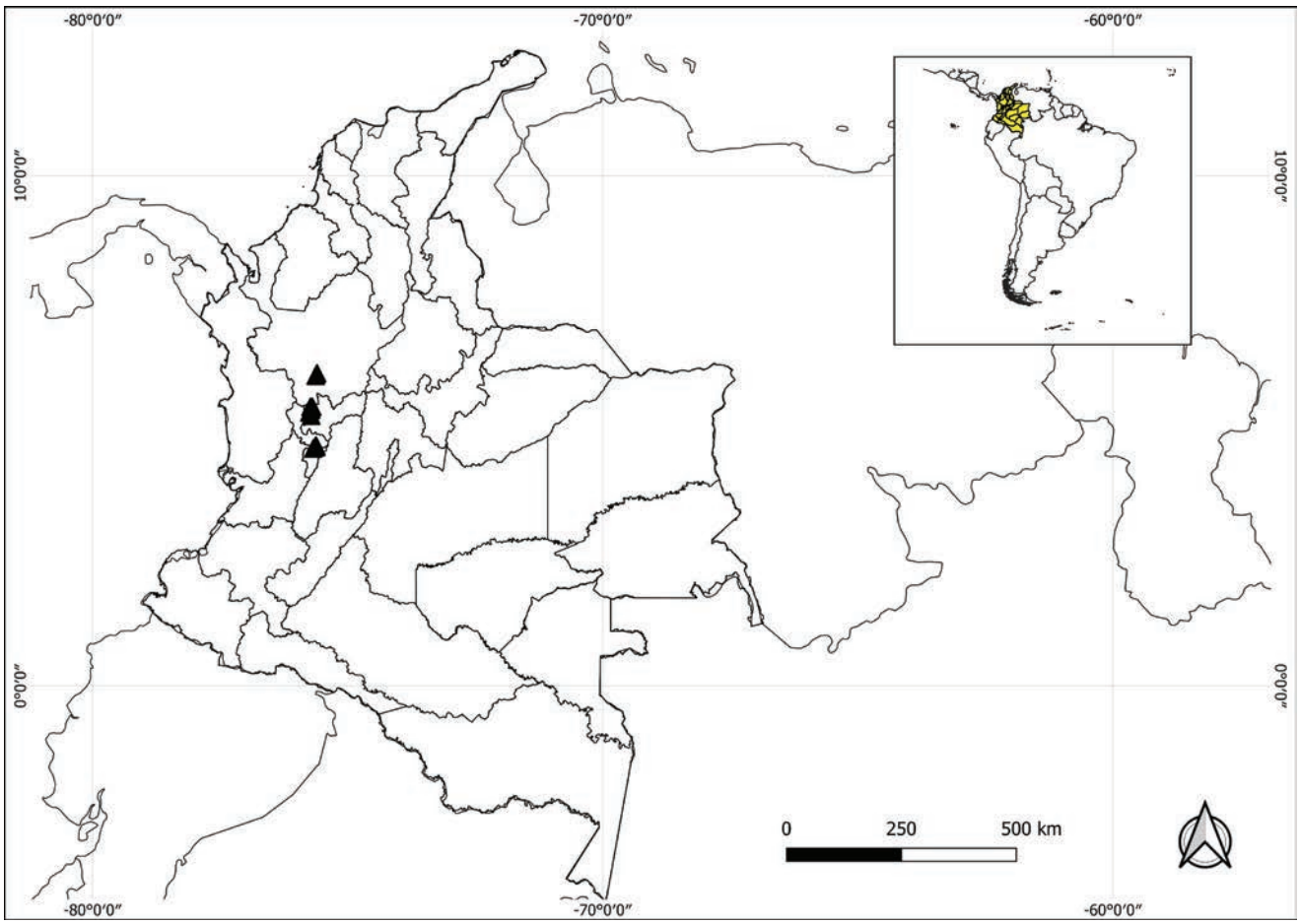


FIGURE 4. *Gustavia montana* Cornejo, D. Gut. & J.S. Arango-G. Distribution map. Prepared by Juan Sebastián Arango.

2000) and *G. romeroi* S.A. Mori & García-Barr. (A. M. Betancourth, pers. comm.). This phenomenon constitutes the risk of rapidly losing populations of the species in the few forests where it has been found. Additionally, it should also be taken into account in conservation and restoration processes.

The new species inhabits one of the most disturbed regions in Colombia, where deforestation, urban expansion, livestock and coffee plantations predominate (Rudas et al., 2007; Myster, 2020). For that reason, its populations are highly threatened by habitat loss and fragmentation. Its extent of occurrence (EOO) was estimated to be 1579.59 km2, with an area of occupancy (AOO) of 44 km^2. The species is listed as Endangered (EN) under criteria B1ab(iii)+2ab(ii, iii, iv). Future studies on ecology, floral biology, population size and genetic diversity are needed in order to promote its long-term conservation.

Additional Specimens Examined: Antioquia: Cordillera central, Mun. Caldas, Vereda La Corrala, finca La Zarza, antes del alto de la Cruz, relicto de bosque, 1950 m, 6°4'51.9"N, 75°37'37.1"W, 27 Dec 2013 (fr), *J. Betancur and Álvaro Idárraga 18508* (COL, HUA, JAUM); Cordillera central, Mun. Sabaneta, Vía a la Romera, antes de ingresar por la portada de la reserva, 1919 m, 6°07'38.7"N, 75°36'02.7"W, 02 February 2020 (fr), *J. Mesa 10* (HUA). Caldas: Cordillera occidental, Mun. Riosucio, Resguardo Indígena Nuestra Señora Candelaria de La Montaña, Comunidad La Cabaña, Sector La Ermita, árbol sembrado en jardín de la finca La Unión, 1949 m, 5°27'45.5"N, 75°43'08.7"W, 23 July 2023 (y. fl, fr), *S. Arango-González et al. 003* (FAUC, COL); Ibid., bosque Monte viejo, interior de bosque, 2083 m, 5°28'18.4"N, 75°43'39.4"W, 24 Jul 2023 (st), *D. Gutiérrez-Duque, J. F. Alarcón 647* (FAUC); Ibid., Cerro Ingrumá, 2176 m, 5°25'07.0"N 75°42'52.0"W, 19 Aug 2023 (fl), J. *S. Arango-González, D. Gutiérrez-Duque 004* (FAUC). Quindío: Cordillera central, Mun. Filandia, bosque aledaño a la granja Bengala, 2033 m, 4°41'06.7"N, 75°37'02.2"W, 12 Aug 2009 (fr), *C. A. Maya 69* (HUQ); vda. La Cauchera, 1900 m, 4°39'18.2"N, 75°40'29.1"W, 7 Jul 2003 (fr), *F. Viveros, C, Vélez, S. Muñoz 477* (HUQ). Risaralda: Cordillera central, Mun. Pereira, Corregimiento Arabia, Vereda El Cedral, jardín casa, 2000 m, 4°42'59.8"N, 75°37'22.9"W, 23 Sep 2000 (fr), *C. Vélez, L. C. Serna 7097* (HUQ, 2 sheets); cordillera occidental, Mun. Guática, Vereda Barroblanco, 1964 m, 5°21'40.4"N, 75°44'57.8"W, 20 February 2020 (fl), *M. A. Serna-Sánchez and S. Peláez-Vélez 325* (UDBC); Cordillera occidental, Mun. Quinchía, Vereda Matecaña, Predios de Minería Quinchía, 2020 m, 5°17'49"N, 75°42'56"W, 11 December 2021 (fr), *C. Paz 473* (UDBC).

Literature cited

Cornejo, X. and S. A. Mori. 2019. *Gustavia esmeraldana* and *G. graciae*: New species of Lecythidaceae from northwestern Ecuador and a key to the species of *Gustavia* in Ecuador. Phytotaxa 418: 89–96.

Gonzalez-Orozco, C. E. 2021. Biogeographical regionalization of Colombia: a revised area taxonomy. *Phytotaxa* 484: 247–260. DOI: 10.11646/phytotaxa.484.3.1

Halbritter, A. H., H. Halbritter, S. Ulrich, Grimsson, M. Weber, and R. Zetter. 2018. *Illustrated pollen terminology*. Springer, Berlin.

IUCN Standards and Petitions Committee. 2022. Guidelines for Using the IUCN Red List Categories and Criteria. Version 15. Prepared by the Standards and Petitions Committee. Downloadable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed July 1, 2022).

Jackson, B. D. 1991. A Glossary of Botanic terms with their derivation and accent 4th ed. Duckworth, London.

Jain, S. 2020. Pollen and Spores. Pages 43–65 in Fundamentals of Invertebrate Palaeontology. Springer Geology. Springer, New Delhi.

Jaramillo, B. D. 2005. Clima andino y café en Colombia. Cenicafé, Manizales.

Láres-Rivas, A. 2000. Observaciones preliminares sobre la densidad y estructura poblacional de *Gustavia parviflora* Mori (Lecythidaceae) en la Serranía de Turimiquire, estado Monagas, Venezuela. Acta Botanica Venezuelica 23: 157–161.

Moat, J. 2020. rCAT: Conservation Assessment Tools. R package version 0.1.6. https://CRAN.R-project.org/package=rCAT

Myster, R. W. 2020. Disturbance and Response in the Andean Cloud Forest: a Conceptual Review. The Botanical Review 86: 119–135. DOI: https://doi.org/10.1007/s12229-020-09219-x

Huang, y.-y., S. A. Mori, and L. M. Kelly. 2015. Toward a phylogenetic-based Generic Classification of Neotropical Lecythidaceae—I. Status of *Bertholletia, Corythophora, Eschweilera* and *Lecythis*. Phytotaxa 203 (2): 85–121. https://doi.org/10.11646/phytotaxa.203.2.1

Mori, S. A. 1979. Lecythidaceae. in G. T. Prance and S. A. Mori. 1979. Lecythidaceae—Part I. The actinomorphic-flowered New World Lecythidaceae. Flora Neotropica Monographs 21: 128–197.

Mori, S. A., C.-H. Tsou, C. C. Wu, B. Cronholm, and A. A. Anderberg. 2007. Evolution of Lecythidaceae: information from combined ndhF and trnL-F sequence data. American Journal of Botany 94(3): 289–301.

Mori, S. A. and B. Boom. 1987. The forest. in S. A. Mori and Collaborators. The Lecythidaceae of a Lowland Forest: La Fumée Mouintain, French Guiana. Memoirs of The New York Botanical Garden 44: 9–29.

Mori, S. A. and X. Cornejo. 2013. Two new species (*Gustavia johnclarkii* and *G. hubbardiorum*) and other contributions to the systematics of *Gustavia* (Lecythidaceae). Brittonia 65: 330–341. https://doi.org/10.1007/s12228-012-9282-9

Mori, S. A., N. P. Smith, X. Cornejo, and G. T. Prance. Cornejo, X. & Prance. 2015 onward. The Lecythidaceae Pages. The New York Botanical Garden, Bronx, New York. Available from: http://sweetgum.nybg.org/lp/index.php (accessed August 23, 2023).

Mori, S. A., E. A. Kiernan, N. P. Smith, L. M. Kelly, Y.-Y. Huang, G. T. Prance, and B. Thiers. 2017. Observations on the phytogeography of the Lecythidaceae clade (Brazil nut family). 2017 (not 2016). Phytoneuron 30: 1–85.

Pardo-Trujillo, A., A. Plata, and C. Gómez. 2021. Palinología Colombiana: Métodos, aplicaciones y estado del conocimiento. Universidad de Caldas. Colombia.

Prance, G. T. and S. A. Mori. 1979. Lecythidaceae—Part I. The actinomorphic-flowered New World Lecythidaceae. Flora Neotropica Monographs 21: 1–270.

Punt, W., P. P. Hoen, S. Blackmore, S. Nilsson, and A. Le Thomas. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143(1–2): 1–81.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Roubik, D. and J. Moreno. 1991. Pollen and Spores of Barro Colorado Island. Missouri Botanical Garden, St. Louis.

Rudas, G. D. Marcelo, D. Armenteras, N. Rodríguez, M. Morales, L. C. Delgado, and A. Sarmiento. 2007. Biodiversidad y actividad humana: Relaciones en ecosistemas de bosque subandino en Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá D. C.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longhair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid, J. Y. Tinevez, D. J. White, V. Hartenstein, K. Eliceiri, P. Tomancak, and A. Cardona. 2012. Fiji: an open-source platform for biological-image analysis. Nature methods, 9(7): 676–682.

Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. Ecology 68 (5): 1341–1350. https://doi.org/10.2307/1939218.

Thiers, B. 2022. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available at http://sweetgum.nybg.org/ih/ (accessed August 1, 2023).

Page 654 intentionally left blank.

STENOSTEPHANUS PURPUREUS (ACANTHACEAE: JUSTICIEAE: ISOGLOSSINAE), A NEW SPECIES FROM COSTA RICA AND PANAMA—OVERLOOKED FOR MORE THAN 150 YEARS

THOMAS F. DANIEL[1,2] AND RICARDO KRIEBEL[1]

Abstract. Comparative studies of macromorphological and palynological characters of plants representing *Stenostephanus silvaticus* from southern Mexico and southern Central America reveal that those from the two geographically isolated regions represent different taxa. *Stenostephanus purpureus* is described as a new species from Costa Rica and Panama. It differs from *S. silvaticus* of Chiapas, Oaxaca, Tabasco, and Veracruz, Mexico by numerous characters, including: pyramidal inflorescences with rachises, dichasial peduncles, and floral pedicels glabrous; corollas blue-purple to purple with both lips recoiled; and pollen subspheroidal with a fossulate interapertural band of exine bearing a medial row of gemmae and baculae. We provide a description of *S. purpureus* and a key to, images of, and map showing the distributions of both species.

Keywords: *Stenostephanus silvaticus*, pollen, nototriby/sternotriby/pleurotriby

Resumen. Los estudios comparativos de caracteres macromorfológicos y palinológicos de plantas que representan a *Stenostephanus silvaticus* del sur de México y el sur de Centroamérica revelan que las de las dos regiones geográficamente aisladas representan taxones diferentes. *Stenostephanus purpureus* se describe como una especie nueva de Costa Rica y Panamá. Se diferencia de *S. silvaticus* de Chiapas, Oaxaca, Tabasco y Veracruz, México por numerosos caracteres, entre ellos: inflorescencias piramidales con raquis, pedúnculos bicaisales y pedicelos florales glabros; corolas azul-púrpura a púrpura con ambos labios retraídos; y polen subesferoidal con una banda interapertural fosulada de exina que lleva una fila medial de yemas y báculas. Proporcionamos una descripción de *S. purpureus* y una clave, imágenes y un mapa que muestra las distribuciones de ambas especies.

Palabras claves: *Stenostephanus silvaticus*, pollen, nototriby/sternotriby/pleurotriby

Stenostephanus Nees is a tropical American genus with some 90 currently accepted species (POWO, 2023) of perennial herbs and shrubs occurring from east-central Mexico (San Luis Potosí, ca. 21°31'N) to southeastern Brazil (São Paulo, ca. 23°47'S). Most species occur in moist to wet montane forests at relatively high elevations (usually above 1000 meters; e.g., cloud forests), with the highest concentration of species in the Andes Mountains of South America (Venezuela to Bolivia). Fifteen species occur in Mexico (Daniel, 1999) and 18 species are currently known from Central America (Daniel, 2005, 2010; Durkee, 1978; Hammel, 2020), three of which also occur in Mexico. These include taxa previously treated under several generic names, including: *Habracanthus* Nees, *Hansteinia* Oerst., *Kalbreyerella* Lindau, and *Razisea* Oerst. (Manzitto-Tripp et al., 2022). Costa Rican and Panamanian plants resembling *S. silvaticus* (Nees) T.F. Daniel of southern Mexico have been treated as pertaining to that species since 1855 (Oersted, 1855). Our studies comparing plants treated as *S. silvaticus* from these two regions reveal significant macro- and micromorphological differences indicating that they should be recognized as distinct species.

Much of the taxonomic history of *Stenostephanus* and related Neotropical genera was discussed by Wood (1988) and Daniel (1999). Based on morphology and preliminary molecular phylogenetic analyses (Kiel et al., 2006), all Isoglossinae in the New World are now treated in *Stenostephanus* (except for the poorly known unispecific Brazilian *Sebastiano-Schaueria* Nees). Its closest relative appears to be the African/Malagasy genus *Brachystephanus* Nees (22 species, including *Oreacanthus* Benth.; Champluvier and Darbyshire, 2009). The combination of the following morphological characteristics distinguishes *Stenostephanus* from other Acanthaceae in the New World: corollas with ascending-cochlear aestivation, an androecium of two stamens and no staminodes, monothecous anthers, and biporate pollen with the ectoapertures greatly enlarged. Species of the genus exhibit corollas with diverse colors and shapes.

Nees (1847) described *Habracanthus silvaticus* based on two collections from southern Mexico in Hooker's herbarium at K: *Linden 181* from Chiapas and *Jurgensen 902* from Oaxaca. Oersted (1855) cited these collections in his account of *H. silvaticus* (as "sylvaticus"), and also indicated that he found the species in the dense forests at Turrialba on the eastern slope of Costa Rica with flowers in May. Subsequent floristic accounts have treated plants from Costa Rica (and Panama) as conspecific with those in Mexico (e.g., Lindau, 1900; Leonard, 1938; Gibson, 1974; Durkee, 1978, 1986; Daniel, 1995; Hammel, 2020). No collections of the species have been located between southern Mexico and Costa Rica, providing a gap of ca.

We are most grateful to Mauricio Bonifacino, Sven Buerki, and Sharon Christoph for providing photographs of living plants and for permission to use them here; Alexander Rodriguez for providing images of selected specimens at CR; Ricardo Pacifico for assistance with photography; the Scanning Electron Microscopy Lab at CAS; John Wood for helpful comments on the manuscript; and the following herbaria for permitting access to their collections via visits and/or loans: A, CAS, CR, DS, F, GH, LSU, MEXU, MO, NY, US.

[1] Department of Botany, Institute of Biodiversity Science and Sustainability, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA, 94118-4599, U.S.A.

[2] Corresponding author: tdaniel@calacademy.org

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 655–662.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n3, Published online: 31 December 2023

1045 km between the nearest known locales for plants from the two regions (i.e., *Martínez S. 18041* in northeastern Chiapas and *Bello 2058* in west-central Alajuela). Plants from both regions share several taxonomically significant characteristics, such as: inflorescences consisting of open thyrses; corollas externally glabrous, with ± cylindric tubes up to 11 (to 16) mm long and one to two mm in diameter, and with the upper lip recurved to recoiled; stamens that do not dehisce toward the lower lip (i.e., flowers not nototribic); and glabrous capsules.

The advent of online color images of plants (e.g., iNaturalist, naturalista) often provides opportunities to observe characteristics of living plants that are not readily apparent on herbarium specimens (e.g., colors and shapes). Indeed, images of plants identified as *S. silvaticus* from the two isolated regions revealed differences in colors of the inflorescence axes and corollas and in shapes of the corolla limb that were not always apparent on herbarium specimens studied. Reexamination of herbarium specimens of plants from both regions revealed additional differences. Altogether, the numerous distinctions coupled with the geographic distributions of plants previously treated as *S. silvaticus* strongly suggest that they do not represent the same taxon.

Materials and Methods

Specimens were studied from the following herbaria: A, C, CAS, CR, DS, F, GH, LSU, MEXU, MO, NY, US. Specimens indicated as "image" were studied only via digital images from herbarium websites or data portals (e.g., SEINet, 2023). Pollen was studied as described by Daniel (1998), and imaged in the Scanning Electron Microscopy Laboratory at the California Academy of Sciences. Palynological terminology follows Walker and Doyle (1975) with some adjustments (e.g., pollen shapes) from Hesse et al. (2009). Pollen was sampled from two collections of *S. purpureus* (*Solomon 19167*, CAS; *Burger & Visconti 10218*, CAS) and three collections of *S. silvaticus* (*Breedlove & Bartholomew 66948*, CAS; *Mexia 9273*, CAS; *Zuill 772*, DS). A provisional conservation assessment for *S. purpureus* is proposed based on IUCN (2022) guidelines, using herbarium specimen data and historical imagery (Google Earth Pro, 2023); extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCat (2023).

Taxonomy

Stenostephanus purpureus T.F. Daniel & Kriebel, *sp. nov.* TYPE: COSTA RICA. Limón: Reserva Biol. Hitoy Cerere, cuenca superior del Río Hitoy, subiendo a Cerro Bitarkara, 09°38'25"N, 083°07'20"W, 27 February 1989 (fl, fr), *G. Herrera & M. Solís 2476* (Holotype: US [3213915]; Isotypes: CR, image [fl], CR, image [fr], F, MEXU, MO). Fig. 1.

Perennial herbs or shrubs to 2 m tall, erect to diffuse (or creeping), young stems subquadrate to quadrate-sulcate, bifariously pubescent (sometimes ± inconspicuously so or only partially along distal portion of internodes, and sometimes only on one side; i.e., unifarious) with mostly retrorse to retrorsely appressed eglandular trichomes 0.05–0.30 mm long, internodes often soon glabrate. *Leaves* petiolate, petioles to 48 mm long, adaxially ± u-shaped, pubescent (at least along margins) with antrorse to antrorsely appressed eglandular trichomes to 0.5 mm long, abaxially glabrous, blades ovate-elliptic to elliptic, 40–162 mm long, 14–68 mm wide, 2.0–3.7 × longer than wide (the pair at a node sometimes anisophyllous), acuminate to caudate at apex, (rounded to) acute at base, adaxially glabrous except for retrorsely appressed eglandular trichomes along midvein, abaxially glabrous, margin ± inconspicuously ciliolate with antrorse to antrorsely appressed eglandular trichomes to 0.1 mm long. *Inflorescences* of terminal, pedunculate, open, ± pyramidally shaped (triangular when pressed), panicle-like thyrses 50–150 mm long (including peduncle and excluding flowers/fruits) and 30–70 mm wide (excluding flowers/fruits), peduncles to 28 mm long, pubescent like young stems, rachis often whitish or bluish, glabrous; dichasia opposite, pedunculate, (3–) 5–15 (or more)-flowered, dichasial peduncles 5–18 mm long, glabrous. *Bracts* subtending dichasia at base of inflorescence sometimes subfoliose, lance-ovate to lanceolate, 5–8 mm long, 0.7–1.5 mm wide, pubescent like leaves, bracts distal to base of inflorescence subulate to lanceolate-linear, 1.5–3.5 mm long, 0.2–0.4 mm wide, abaxially and marginally glabrous. *Bracteoles* subulate to lanceolate-linear, 0.8–2.0 mm long, 0.2–0.4 mm wide, abaxially and marginally glabrous, secondary bracteoles similar to bracteoles or smaller. *Flowers* pedicellate, pedicels 1.5–2.5 mm long, glabrous. *Calyces* deeply 5-lobed, 3.5–6.5 (–8.0) mm long, lobes subequal, subulate to lanceolate-linear, 3.0–5.8 (–7.0) mm long, 0.4–0.8 mm wide, abaxially and marginally glabrous. *Corollas* pale blue-purple to purple (at least internally), (11–) 14–25 (–35) mm long, externally glabrous, tube cylindric to subcylindric, (5–) 7–11 (–16) mm long, 0.7–1.5 mm in diameter, limb (5–) 7–8 (–19) mm long, lips recoiled with lower lip usually more tightly so than upper lip, upper lip slender, 1.0–1.7 mm wide at base, tapered distally, lower lip ± strap-shaped, 2.0–3.5 mm wide. *Stamens* (5.0–) 8.5–20 (–30) mm long, exserted beyond recoiled lips of corolla, filaments glabrous, sometimes spreading laterally away from central floral axis, anthers dehiscing toward upper lip (i.e., flowers sternotribic), thecae blue-purple, (1.3–) 1.9–2.5 mm long. Pollen 2-pororate, subspheroidal (longer equatorial diameter [E]:shorter E = 1.02–1.08), apertural face circular in outline, 35–40 μm in diameter, interapertural face circular in outline, 34–36 μm in diameter, peripheral band continuous, 8 μm wide, fossulate (with foveolae also present) and with a medial row of gemmae and baculae 1.6–3.2 μm high, ectoaperture 31–34 μm in diameter, with gemmae and baculae 0.7–1.9 mm high. *Styles* (9–) 15–20 (–39) mm long, glabrous; stigma subcapitate to minutely bilobed, 0.1 mm long. *Capsules* 12–17 mm long, externally glabrous, stipe 5–9 mm long, head ellipsoid with medial constriction (hourglass-shaped), 6.5–9.0 mm long. *Seeds* up to 4, 2.3–3.0 mm long, 1.7–2.1 mm wide, immature surfaces

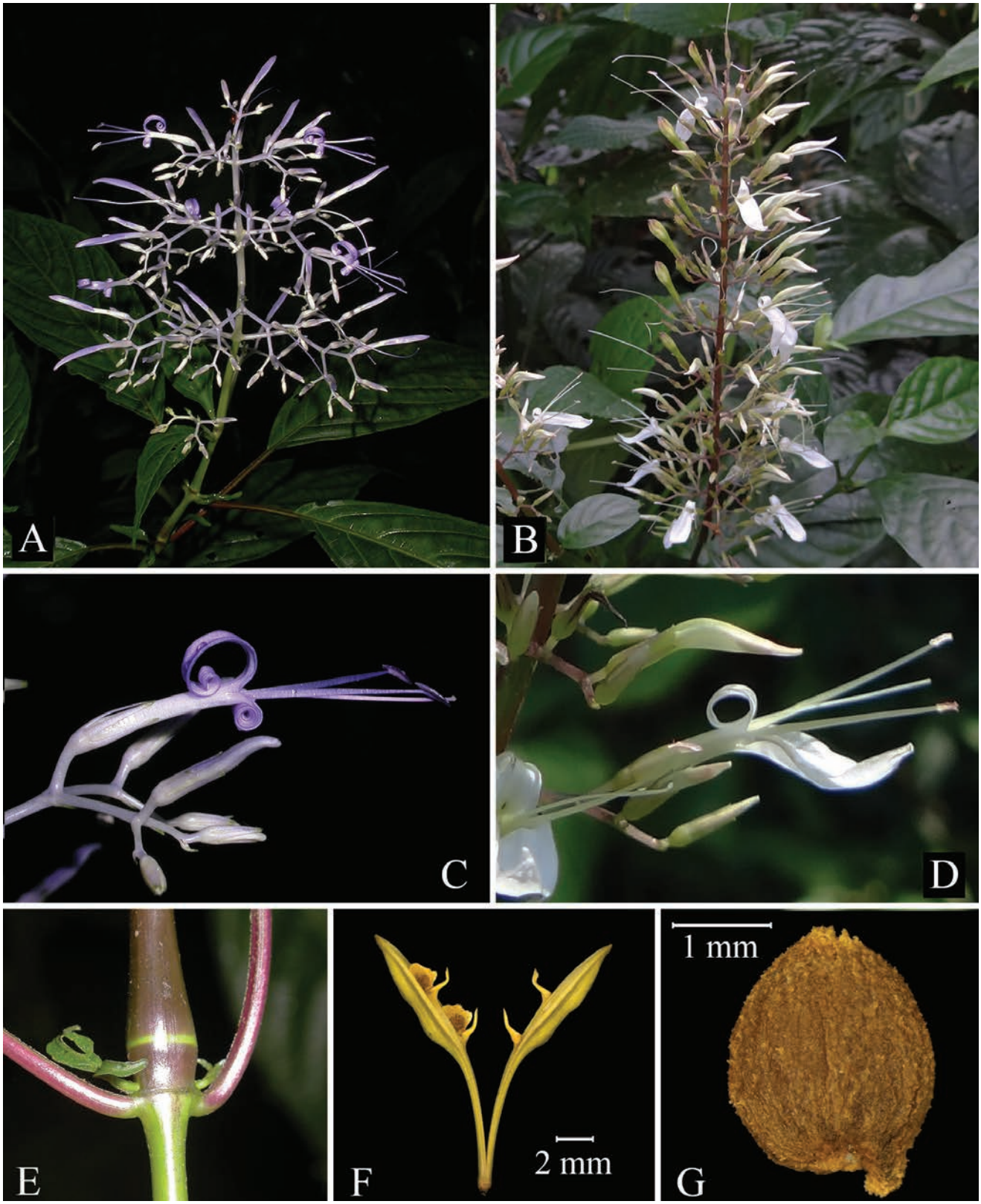


FIGURE 1. *Stenostephanus purpureus* (**A**, **C**, **E–G**) and *S. silvaticus* (**B**, **D**). **A**, inflorescence; **B**, cylindric inflorescence; **C**, flower and bud; **D**, flower and bud; **E**, vegetative node; **F**, capsule; **G**, seed. A, C, and E photos by M. Bonifacino from Costa Rica, used with permission; B and D photos by C. Davidson (Flora of the World website) of *Martínez-Meléndez 3022* from Chiapas, used with permission; F from *Taylor & Skotak 4841* (MO); G from *Burger & Visconti 10218* (MO).

covered with ± barbed and conical tubercles, mature surfaces smooth to slightly rugose with tubercles (if present) few and mostly restricted to margin.

Phenology: Flowering and fruiting throughout the year.

Distribution and habitats: Costa Rica (five provinces) and Panama (one province), primarily (or exclusively?) on the Caribbean escarpments of the Cordillera de Tilarán, Cordillera Central, and Cordillera de Talamanca (Fig. 2). Plants occur in low, damp sites; on slopes; and along watercourses, trails, and roads in tropical moist forests, semi-evergreen forests, evergreen premontane forests, wet montane forests, and cloud forests at elevations from (280–) 400–1800 (–2200) meters.

Illustrations: Ann. Missouri Bot. Gard. 65: 202, fig. 12. 1978; Fieldiana, Bot. (n.s.) 18: 8, fig. 6. 1986.

Local name: "Pavoncillo azul" (*Brenes 4938*).

Conservation: *Stenostephanus purpureus* has an extent of occurrence (EOO) of 7568 km^2 and an area of occupancy (AOO; cell width of 2 km) of 152 km^2. The geographic range of the species from northwest to southeast covers a distance of ca. 260 kilometers. At least 21 of the localities from which collections were made lie within an international park, two national parks, and/or seven biological or forest reserves. Most of the numerous collections of this species are from undisturbed montane regions or reserves that show little or no change in vegetation cover during the past 50 years based on historical imagery (Google Earth Pro, 2023). Where plants occur they are sometimes noted to be locally common or abundant. While threats or potential threats to some populations of the species undoubtedly occur, none have been identified. Thus, despite both the EOO and AOO each suggesting a possible threatened category dependent on other criteria, we provisionally propose a conservation status of least concern (LC) for *S. purpureus*.

Discussion: *Stenostephanus purpureus* can be distinguished from other species of the genus in Costa Rica and Panama by its inflorescences of terminal, ± pyramidal, and panicle-like thyrses bearing blue-purple to purple corollas with recoiled lips at maturity. Significant macromorphological and palynological differences between *Stenostephanus purpureus* and *S. silvaticus* are summarized in the following key:

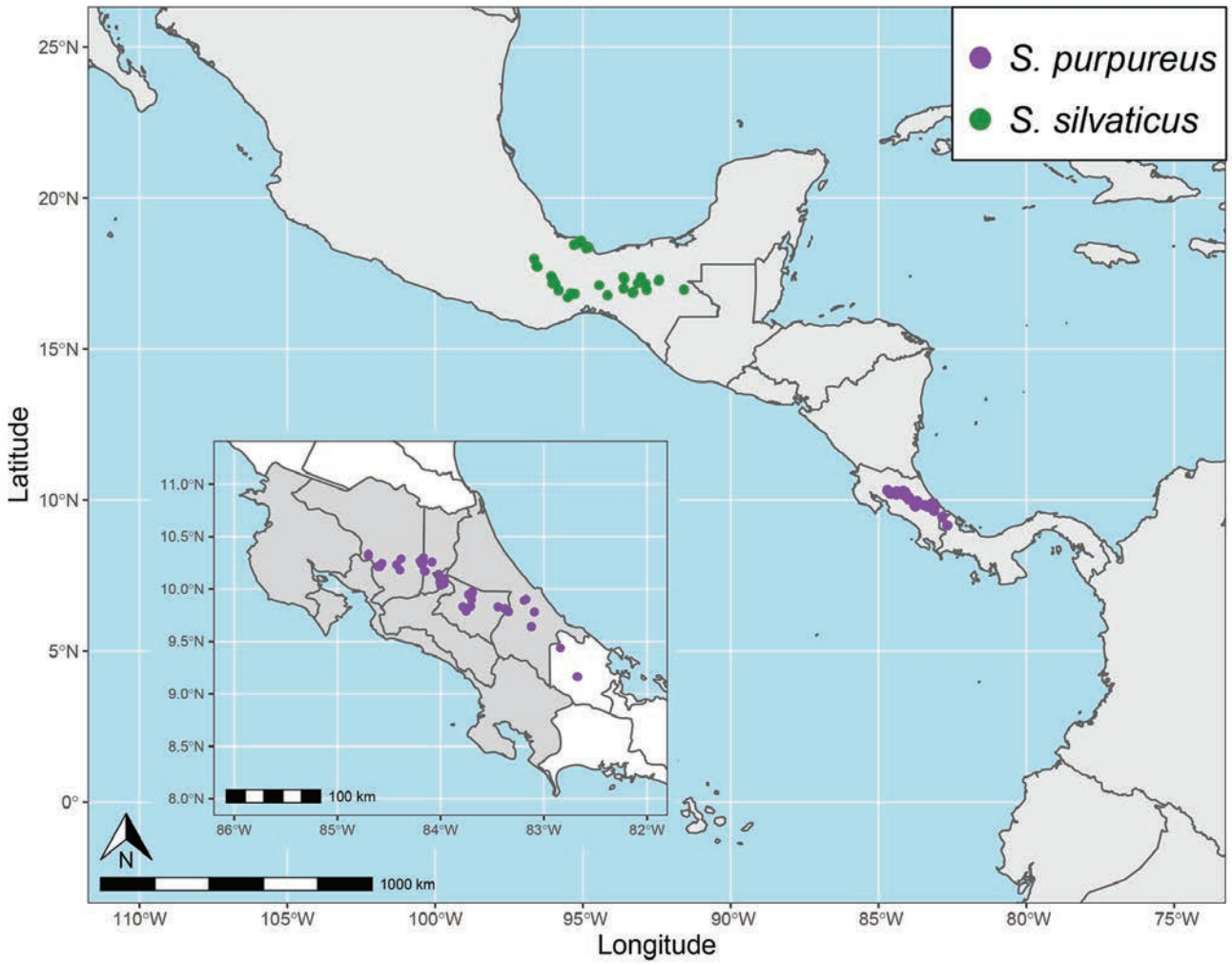


FIGURE 2. Map of Middle America showing distributions of *Stenostephanus purpureus* and *S. silvaticus*. Inset shows detailed distribution of *S. purpureus* in Costa Rica and adjacent western Panama.

1a. Cauline trichomes mostly retrorse to retrorsely appressed; abaxial surface of petioles glabrous; inflorescence usually ± pyramidal (broadly triangular when flattened), 30–70 mm wide (excluding flowers and fruits), rachis, peduncles of dichasia, and pedicels of flowers glabrous and often white or purplish; corolla (at least internally) pale blue-purple to purple, upper and lower lips recoiled at maturity (lower lip more tightly so), lower lip 2–3 mm wide; anther thecae pale blue-purple to purple; pollen subspheroidal, interapertural face circular in outline, 34–36 μm across at equator, peripheral band of exine fossulate (with foveolae also present) and with a medial row of gemmae and baculae 1.6–3.2 μm high, ectoaperture 31–34 mm in diameter, covered with gemmae and baculae 0.7–1.9 μm high; Costa Rica and Panama . . . . . *S. purpureus*

1b. Cauline trichomes mostly antrorse to antrorsely appressed; abaxial surface of petioles pubescent; inflorescence ± cylindric (oblong to lanceolate when flattened), 20–45 mm wide (excluding flowers and fruits), rachis, peduncles of dichasia, and pedicels of flowers pubescent, neither white nor purplish; corolla white (sometimes with pinkish markings or discoloration) internally, only upper lip recoiled at maturity, lower lip 3.0–5.5 mm wide; anther thecae pink; pollen discoid, interapertural face elliptic in outline, 10–17 μm across at equator, peripheral band of exine psilate to foveolate (with gemmae 0.4–0.6 μm high only at junction with ectoaperture on each apertural face), ectoaperture 14–22 μm in diameter, covered with gemmae 0.2–0.7 μm high; Mexico . . . . . *S. silvaticus*

Flowers of *Stenostephanus purpureus* show a considerable range in size (by collection rather than on inflorescences). Corollas are usually 14 to 25 mm in length. Larger corollas, up to 35 mm long, were observed on several collections from both Costa Rica (e.g., *Hammel et al. 17680*, MO) and Panama (*Monro et al. 6140*, MO). These and other collections (including the type) also show atypically long stamens (to 30 mm) and styles (to 39 mm). At the other extreme, corollas 11 mm long, accompanied by atypically shorter stamens and styles were noted among other collections (e.g., *Brenes 3706*, NY). Collector's notes for *S. purpureus* indicate some variation in corolla color; in addition to purple, they include: "pale blue," "blue," "lavender-blue," "pastel violet," "pale violet," "violet-blue," "celeste," "celeste, parte central azul," "violeta," "pale purple," "morada," "lila," "white with lilac lobes," and "white." Buds, including the calyx, have been described as "green" or "white." White flowers were generally noted on specimens with only flower buds present. Thus, the internal surface of corollas is presumed always to be some shade of purple. Other parts of the inflorescence (e.g., rachis, bracts, dichasial peduncles, bracteoles, pedicels, calyces, and staminal filaments) are also sometimes noted to be white, blue-purple, or purple (Fig. 1A). By contrast, portions of the inflorescence in *S. silvaticus* were sometimes noted or observed to be greenish or pinkish to pink-red (Fig. 1C).

The differences in pollen shape and ornamentation between *S. purpureus* and *S. silvaticus* are substantial (Fig. 3). Pollen resembling each occurs elsewhere among Mexican and Central American species of the genus. Pollen of *S. azureus* (D.N. Gibson) T.F. Daniel, *S. gracilis* (Oerst.) T.F. Daniel, *S. latilabris* (D.N. Gibson) T.F. Daniel, *S. leiorhachis* (Lindau) Hammel, *S. madrensis* T.F. Daniel, and *S. purpusii* (Brandegee) T.F. Daniel (e.g., Daniel, 1999: fig. 1e, 2a, i; Daniel, 2010: fig. 9q, r) greatly resembles that of *S. purpureus*, whereas pollen of *S. monolophus* (Donn. Sm.) T.F. Daniel and *S. oaxacanus* T.F. Daniel (Daniel, 1999: fig. 2b–e) is nearly identical to that of *S. silvaticus*. Pollen of *S. chiapensis* T.F. Daniel and *S. guerrerensis* T.F. Daniel (Daniel, 1999: fig. 1c, f, g) appears to differ from that of *S. silvaticus* only by the sculpturing of the peripheral band of exine (verrucate in the former and shallowly fossulate in the latter vs. psilate to foveolate in *S. silvaticus*).

A flowering collection from Veraguas, Panama (vicinity of Santa Fé, slopes of Cerro Tute, [08.482220, -81.0981], *P. Allen 4345*, MO, US), was identified by E. C. Leonard, treated by Durkee (1978), and annotated by T. F. Daniel as *S. silvaticus*. It has the blue-purple corollas, subspheroidal pollen, and other characteristics of *S. purpureus*, but differs from that species in several features, including cauline pubescence antrorse to antrorsely appressed; abaxial surface of the petioles sparsely pubescent; inflorescence rachis, peduncles, and pedicels pubescent; and anther thecae 2.5–3.0 mm long. This collection was made ca. 190 km southeast of the nearest locale for *S. purpureus* in Bocas del Toro. Whether it represents an outlier population of *S. purpureus* with at least atypical pubescence, a possible hybrid, or a different taxon awaits additional collections (including fruit) to assess its taxonomic status. It is not included in the information for *S. purpureus* presented above.

Daniel (1999) alluded to potential differences in the direction of anther dehiscence among species of *Stenostephanus* in Mexico, but noted the difficulty in interpreting this in several species, especially from herbarium specimens. Since then, from our observations of plants in the field and images on websites that show anther dehiscence, directionality often can be ascertained. Based on these observations we have determined the direction of dehiscence for several species of Mexican and Central American *Stenostephanus*. Species with nototribic flowers (i.e., anthers dehiscing toward the lower lip) include: *S. blepharorhachis* (Lindau) Hammel, *S. chiapensis*, *S. leiorhachis*, *S. monolophus*, *S. oaxacanus*, *S. reflexiflorus* (Leonard) J.R.I. Wood, *S. rostellatus* (Lindau) T.F. Daniel et al., *S. sessilifolius* (Oerst.) T.F. Daniel, *S. tacanensis* (Acosta & R. Fernández) T.F. Daniel, *S. ventricosus* (Donn. Sm.) Hammel & McDade and *S. villosus* (Gómez-Laur. & Hammel) McDade. Species with sternotribic flowers (i.e., anther dehiscing toward the upper lip) include *S. haematodes* (Schltdl.) T.F. Daniel, *S. latilabris*, and *S. purpureus*. *Stenostephanus silvaticus* appears to have pleurotribic flowers (i.e., anthers dehiscing toward each other). In this species, before either the corollas have fully expanded or the anthers have dehisced, the stamens are oriented so that the flowers would appear to be nototribic, but when mature, the stamens are spread apart laterally and the anthers open toward each other (or possibly in some instances, toward the upper lip?). Two other Mexican/Central American species, *S. azureus* and *S. harleyi* (Wassh.) T.F. Daniel, also appear to be pleurotribic (and/or possibly sternotribic in some instances). All three orientations of anther dehiscence appear to occur among South American species, as follows:

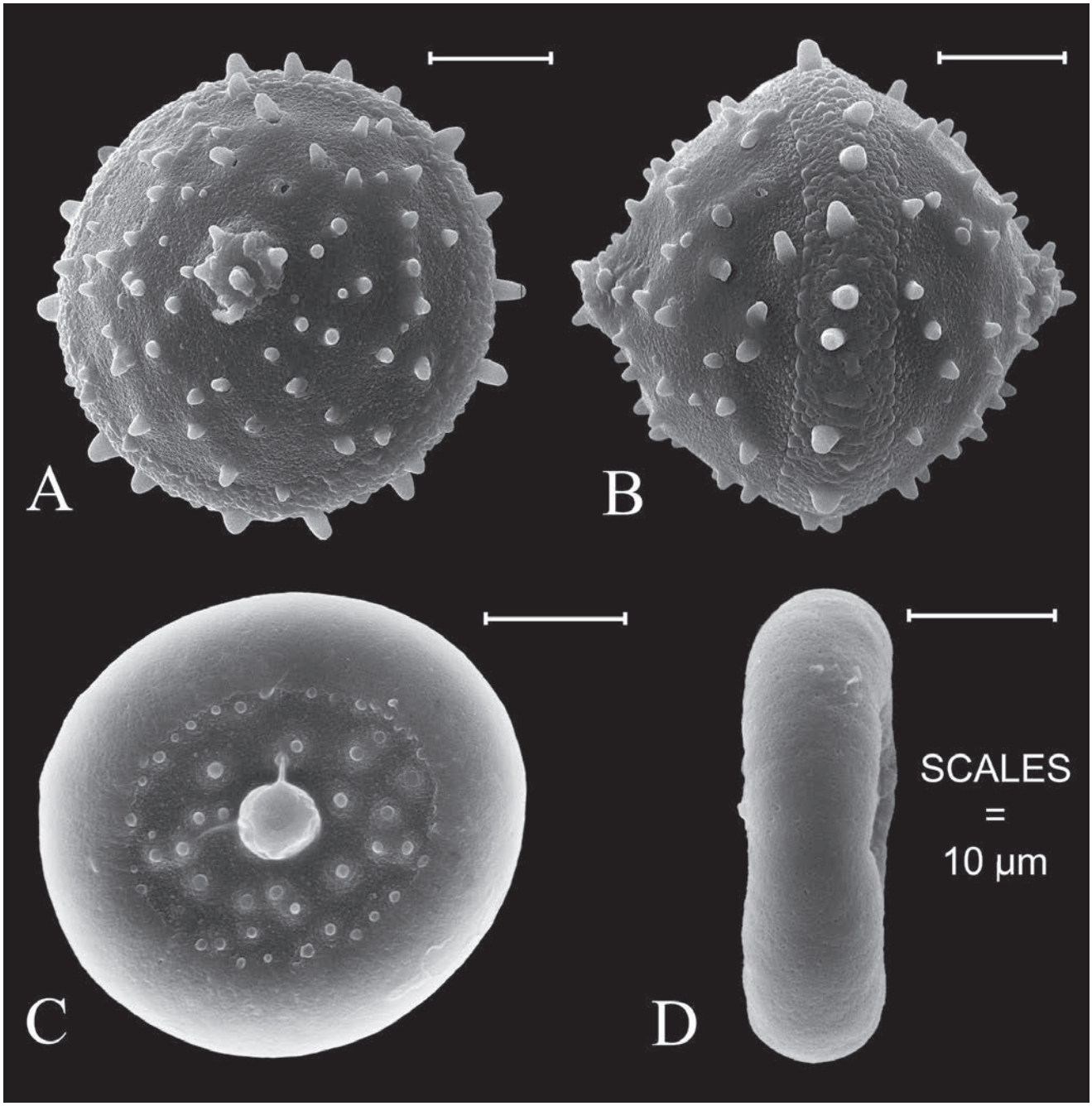


FIGURE 3. Pollen of *Stenostephanus*. **A–B**. *S. purpureus*. **A**, apertural view; **B**, interapertural view**. C–D**. *S. silvaticus*. **C**, apertural view; **D**, interapertural view. A–B from *Solomon 19167* (CAS); C from *Breedlove & Bartholomew 66948* (CAS); D from *Mexia 9273* (CAS).

nototribic (e.g., *S. ampelinus* (Leonard) J.R.I. Wood, *S. ericae* (Wassh.) J.R.I. Wood & R. Villanueva, *S. puberulus* Lindau, *S. sanguineus* (Nees) Wassh., and *S. tenellus* Wassh. & J.R.I. Wood), sternotribic (*S. lyman-smithii* Wassh.), and apparently pleurotribic (*S. spicatus* Wassh. & J.R.I. Wood). The direction of anther dehiscence plays an important role in pollination via the location of pollen deposition on floral visitors and/or pollinators. Pleurotribic flowers appear to be rare among Acanthaceae. Among them, the Mexican endemic *Mexacanthus mcvaughii* T.F. Daniel (Justicieae: Tetrameriinae) has laterally spreading stamens with anthers opening toward each other, an androecial orientation similar to that of *S. silvaticus*. Field observations on *M. mcvaughii* (Holmqvist et al., 2005) reveal visitation by and pollen deposition upon hummingbirds and carpenter bees, and strongly suggest wing pollination by the latter. Floral visitors to and pollinators of *S. purpureus* and *S. silvaticus* remain undocumented; however, the difference in directionality of anther dehiscence between them suggests dissimilar pollen placement on floral visitors and/or pollinators. Another

difference in floral morphology between these two species also suggests pollination by different vectors. The presence of a large "landing pad" formed by the lower corolla lip in *S. silvaticus* (Fig. 1D) suggests pollination by insects. Conversely, the lack of a landing pad in *S. purpureus* suggests possible pollination by hummingbirds. Indeed, *S. purpureus* (as *Habracanthus silvaticus*) was grouped with hummingbird-pollinated species in an annotated checklist of the plants of Monteverde, Costa Rica (Haber, 2000).

Paratypes: COSTA RICA. Alajuela: Reserva Río San Lorenzo de UCR, headwaters of Río San Lorenzo below Finca Volcán Muerte, [ca. 10.229049°, -84.570844°], *K. Barringer & B. Perez 3855* (F); El Silencio de San Ramón, *Hb. Brenes 3685* (F); La Palma de San Ramón, *Hb. A. Brenes 3706* (F, NY), *23028* (NY); La Balsa de San Ramón, *Hb. A. Brenes 4938* (F); Cataratas de San Ramón, *Hb. A. Brenes 13462* (F, NY); Piedades Sur (La Palma) de San Ramón, *Hb. A. Brenes 17164* (F); Reserva Biológica Monteverde, Río Peñas Blancas, 10°20'N, 084°42'W, *E. Bello 2058* (MO); along upper Río Sarapiquí, near Cariblanco and along rd. to Colonia Virgen del Socorro, 10°18'N, 084°10'W, *W. Burger & T. Antonio 11144* (CAS, F, NY); valley of Río Sarapiquí, near bridge to La Virgen del Socorro, 10°18'N, 084°10'W, *W. Burger & T. Antonio 12055* (F); upper Río Sarapiquí, near Cariblanco and along road to Colonia Virgen del Socorro, 10°18'N, 084°10'W, *W. Burger et al. 11853* (F); canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, 10°16'N, 084°12'W, *M. Grayum et al. 6178* (MO); Reserva Forestal de S. Ramón, San Ramón, *J. Gómez-Laurito 9629* (F); Reserva Forestal de S. Ramón, ca. Colonia Palmareña, S. Ramón, [10.2444497, -84.569309], *J. Gómez-Laurito 10507* (F), *10607* (F); Virgen del Socorro, Cañón Río Sarapiqui, *L. Gómez et al. 20952* (MO); Reserva Biológica Monteverde, Río Peñas Blancas, 10°19'N, 084°42'W, *W. Haber & E. Bello 8377* (CAS), *8382* (CAS, MO); Reserva Forestal San Ramón, sender Miramar, 10°12'53"N, 084°36'28"W, *G. Herrera Ch. et al. 150* (CAS, MO); Cantón San Ramón, Los Angeles, Colonia Palmareña, Cuenca media de Río San Lorenzo, 10°12'50"N, 084°35'15"W, *G. Herrera et al. 4923* (MO); NW of Zarcero, ca. 2 km W of Zapote on road to Santa Elena, [10.2312286, -84.4254719], *D. Lellinger & J. White 1360* (F, US); bosques de Juan Viñas, *J. León 142* (F); San Ramón, Cuenca del San Carlos, Colonia Palmareña, R.B. Manuel Brenes, Estación San Lorenzo, 10°12'55"N, 084°35'20"W, *A. Rodríguez 1146* (MO); Cantón San Carlos, Cuenca del San Carlos, San Vicente, camino ruta al Parque Nacional Juan Castro Blanco, 10°17'17"N, 084°22'58"W, *A. Rodríguez et al. 3883* (MO); vicinity of Zarcero, [10.1814498, -84.3934938], *A. Smith H253* (F); Cantón Alfaro Ruiz, Zapote, *A. Smith P2252* (A, US); Cantón Alfaro Ruiz, La Peña de Zarcera, *A. Smith NY1008* (F, NY); near Cariblanco, 2.5–3.0 km from main road on road to Colonia Virgen de Socorro, [10.2383691, -84.18164], *C. Taylor & C. Skotak 4841* (MO); Naranjo, *Wendland 596* (F). Cartago**:** Río Jesus María near Santa Cruz on S slope of Volcán Turrialba, [9.947271, -83.7293089], *W. Burger & M. Burger 8160* (F, image); Cantón Turrialba, Valle del Reventazón, Moravia del Chirripó, 09°49'50"N, 083°26'40"W, *P. Campos & M. Chavarría 11* (MO); Turrialba, Tayutic, 2 km W de Grano de Oro, camino a Llanos del Quetzal, 09°48'50"N, 083°22'40"W, *A. Cascante 656* (MO); stream valley E of Sta. Cruz, S slopes of Volcán Turrialba, *G. DeWolf 412* (LSU, image); Cantón Turrialba, Monumento Nacional Guayabo, 9.9721603, -83.6921981, *R. Kriebel 2955* (CR); Cantón Jiménez, Reserva El Copal, 9.9721603, -83.6921981, *R. Kriebel & D. Solano 2462* (CR); "taette Skove ved Turrialva paa den östlige Skraaning af Costa-Rica," *A. Oersted 10656* (C); Sector Río Guayabo, El Ceibo, 09°57'50"N, 083°41'30"W, *G. Rivera & Y. Hoomans 1762* (F); Cantón Turrialba, Quebrada Barahona, 2 km W of Turrialba on CR 10, 09°54'N, 083°42'W, *J. Solomon 19196* (CAS, MO); Las Vueltas, Tucurrique, [9.8355261, -83.7081359], *A. Tonduz 13015* (US); ca. 2 km E of Cachí along rd. paralleling Río Naranjo towards Cerro Duán, [9.8311125, -83.7853432], *K. Utley 5883* (CAS); Cantón Turrialba, M.N. Guayabo, Cuenca del Reventazón, 09°58'30"N, 083°41'40"W, *L. Diego Vargas & V. Ramírez 232* (MO). Heredia: NW of Vara Blanca, N slope of Central Cordillera, [10°10'23.20"N, 084°09'27.85"W], *M. Chrysler 5103* (F); barranca del Río Sarapiquí, Colonia Virgen del Socorro, *J. Gómez-Laurito 9844* (F); Parque Nac. Braulio Carrillo, Atlantic slope of Volcán Barva, between Río Peje and headwaters of Río Sardinal, 10°15.5'N, 084°05'W, *M. Grayum & G. Herera 7826* (MO); Vara Blanca de Sarapiqui, N slope of Central Cordillera, [10.1689659, -84.1479663], *A. Skutch 3160* (A, MO, NY, US); Yerba Buena, NE of San Isidro, *P. Standley & J. Valerio 50069* (US); Sto. Domingo de Vara Blanca, *M. Valerio 286* (F). Limón: Cantón Limón, Faja Costeña de Limón, Asunción, 09°54'10"N, 083°10'20"W, *A. Estrada 376* (MO); Cantón Limón, Cordillera de Talamanca, headwaters of Quebrada Kakébeta, below divide between ríos Xikiari and Boyei, 09°47'00"N, 083°20'30"W, *M. Grayum 10950* (MO); Reserva Hitoy-Cerere, Río Hitoy y hasta la cima del Cerro Bitárkara, 09°38'30"N, 083°07'09"W, *B. Hammel et al. 17680* (MO); Cantón Limón, Cordillera de Talamanca, Cerro Muchilla, Fila Matama, 09°46'50"N, 83°05'30"W, *R. Robles & A. Chacón 2659* (MO); Cantón Talamanca, Fila de Matama, 09°53'30"N, 083°11'30"W, *A. Rodríguez 593* (MO). San José: Cantón Moravia, P.N. Braulio Barrillo, Cuenca del Sarapiquí, 10°03'40"N, 083°59'10"W, *L. Acosta & V. Ramírez 373* (MO); Río Claro Valley, below La Palma, NE of Jan Jeronimo, 10°03'N, 083°58'W, *W. Burger & M. Burger 7643* (CR, image, F, MO, NY); Río Clara Valley (Bajo La Hondura) below La Palma, NE of San Jerónimo, 10°03'N, 083°58'W, *W. Burger & R. Liesner 6276* (F, NY), *W. Burger et al. 9385* (F, NY); La Palma area, NE of San Jeronimo, above La Hondura Valley, 10°02'N, 084°00'W, *W. Burger & G. Visconti 10218* (CAS, CR, image, F, MO); vicinity of Bajo La Hondura, along road between Paracito and the Río Claro, [10.0625251, -83.9833999], *T. Croat 44505* (MO); Virgen del Socorro, Cañón Río Sarapiquí, [10.2546613, -84.1676727], *L. Gómez et al. 20952* (CAS); old cart road to Limón, 5.6 km N of San Jerónimo, near La Palma, 10°10'N, 084°00'W, *S. Hill et al. 17769* (NY); bajos de La Hondura, *A. Jiménez s.n.* (F); Bajo La Hondura, 10°04'N, 083°59'W, *H. Kennedy & P. DeVries 3814* (F); Cantón Vázquez de Coronado, P.N. Braulio Carrillo, cerca

del tunél, 10.0680556, -84.0069444, *R. Kriebel 4903* (CR); beside Río Hondura, *R. Lent 2040* (F); Parque Nac. Braulio Carrillo, 500 m before Zurquí tunnel, 10°08'35"N, 084°01'00"W, *P. Maas et al. 7800* (MO); Cantón Moravia, P.N. Braulio Barrillo, Cuenca del Sarapiquí, 10°03'35"N, 083°59'15"W, vicinity of La Palma on road to La Hondura, *W. Maxon & A. Harvey 8059* (US); *S. Salas et al. 188* (MO); Alto La Palma, [10.048574, -83.9889233], *C. Schnell 1087* (MO); Cantón Vázquez de Coronado, Parque Nac. Braulio Carrillo, trail from hwy. at La Ventana to Bajo La Hondura, 10°04'N, 083°59'W, *J. Solomon 19167* (CAS, CR, image, F, MO); Parque Braulio Carrillo, Río Bajo de Hondura, 25 km N de San José, *M. Sousa et al. 12666* (MEXU); La Hondura, *P. Standley 36540* (US), *37651* (US), *37859* (US); La Palma, *P. Standley 38237* (US); Peralta, *H. Stork 515* (US); below Bajo La Hondura, where Río Zurqui flows into Río Hondura, 10°04'N, 083°59'W, *J. Taylor & C. Taylor 11928* (MO, NY); just above Río Hondura at Baja La Hondura, *J. Taylor 17887* (NY, US); La Palma, *A. Tonduz 7405* (GH, NY, US); La Hondura de San José, *M. Valerio 697* (F); La Palma, *M. Valerio 1404* (F); Moravia, San Gerónimo, Bajo de la Hondura, Parque Nacional Braulio Carrillo, 10°05'50"N, 083°58'00"W, *O. Valverde 949* (MEXU, image). Province undetermined: au dessus de Sta. Elena, *H. Pittier 13*236 (US); Talamanca, *H. Pittier 9379* (US). PANAMA. Bocas del Toro: Caribbean slopes of Cerro Fábrega at foot of "Falso Fábrega" in Palo Seco Reserve, 09°09'54"N, 082°40'45"W, *A. Monro & S. Cafferty 4735* (MO); Changuinola, PILA, Punto 10, Falso Fábrega, 09°09'48.4"N, 082°40'17"W, *A. Monro et al. 6140* (MO); Changuinola, Parque Internacional La Amistad, Punto 3, 9.4376556, -82.8403107, *D. Solano et al. 5876* (MO).

Literature Cited

Champluvier, D. and I. Darbyshire. 2009. A revision of *Brachystephanus* and *Oreacanthus* (Acanthaceae) in tropical Africa. Syst. & Geogr. Pl. 79: 115–192.

Daniel, T. F. 1995. Acanthaceae. Pages 1–158 in D. E. Breedlove, ed., Flora of Chiapas, No. 4. California Academy of Sciences, San Francisco.

———. 1998. Pollen morphology of Mexican Acanthaceae: Diversity and systematic significance. Proc. Calif. Acad. Sci. 50: 217–256.

———. 1999. Revision of *Stenostephanus* (Acanthaceae) in Mexico. Contr. Univ. Michigan Herb. 22: 47–93.

———. 2005. Catalog of Honduran Acanthaceae with taxonomic and phytogeographic notes. Contr. Univ. Michigan Herb. 24: 51–108.

———. 2010. Catalog of Guatemalan Acanthaceae: Taxonomy, ecology, and conservation. Proc. Calif. Acad. Sci. 61: 291–379.

Durkee, L. H. 1978. Family 177. Acanthaceae. Pages 155–284 in R. E. Woodson, Jr., R. W. Schery, and collaborators, eds., Flora of Panama, Part IX. Ann. Missouri Bot. Gard. 65.

———. 1986. Acanthaceae. Pages 1–87 in W. Burger, ed., Flora Costaricensis. Fieldiana: Bot., new series, no. 18.

Gibson, D. N. 1974. Acanthaceae. Acanthus family. Pages 328–461 in P. C. Standley, L. O. Williams and D. N. Gibson, eds., Flora of Guatemala, Fieldiana: Bot. 24, pt. 10, nos. 3, 4.

GEOCAT. 2023. Geospatial Conservation Assessment Tool. Royal Botanic Gardens Kew (accessed May 2023). https://www.kew.org/science/our-science/projects/geocatgeospatial-conservation-assessment-toolGeoCat.

GOOGLE EARTH PRO. 2023. Google Earth Pro, version 7.3.4.8248. Maps (accessed May 2023). https://sites.google.com/earthoutreach.org/imw-australia/agenda/google-earth-pro.

Haber, W. 2000. Appendix 1–Vascular plants of Monteverde. Pages 457–518 in N. M. Nadkarni and N. Whellwright, eds., Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, New York.

Hammel, B. E. 2020. *Stenostephanus*. Pages 162–173 in B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, eds., Manual de Plantas de Costa Rica, Volume IV, Parte 1 (Acanthaceae; Asteraceae). Missouri Botanical Garden, St. Louis.

Hesse, M., H. Halbritter, R. Zetter, M. Weber, R. Buchner, A. Frosch-Radivo, and S. Ulrich. 2009. *Pollen Terminology, an Illustrated Handbook*. Sprenger-Verlag, Wien.

Holmqvist, J. P., M. Manktelow, and T. F. Daniel. 2005. Wing pollination by bees in *Mexacanthus* (Acanthaceae)? Acta Bot. Mex. 71: 11–17.

IUCN. 2022. Guidelines for Using the IUCN Red List Categories and Criteria. Version 15.1. Standards and Petitions Committee (accessed May 2023). http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Kiel, C. A., L. A. McDade, T. F. Daniel, and D. Champluvier. 2006. Phylogenetic delimitation of Isoglossinae (Acanthaceae: Justicieae) and relationships among constituent genera. Taxon 55: 683–694.

Leonard, E. C. 1938. Acanthaceae. Acanthus Family. Pages 1188–1263 in P. C. Standley, ed., Flora of Costa Rica, Publ. Field Mus. Nat. Hist., Bot. Ser. 18, pt. 4.

Lindau, G. 1900. Acanthaceae. Pages 299–317 in H. Pittier, ed., Primitiae Florae Costaricensis 2. San José, Costa Rica.

Manzitto-Tripp, E. A., I. Darbyshire, T. F. Daniel, C. A. Kiel, and L. A. McDade. 2022. Revised classification of Acanthaceae and worldwide dichotomous keys. Taxon 71: 103–155.

Nees von Esenbeck, C. G. 1847. Acanthaceae. Pages 46–519 in Alph. de Candolle, ed., *Prodromus Systematis Naturalis Regni Vegetabilis 11*. Victoris Masson, Paris.

Oersted, A. S. 1855. Mexico og Centralamerikas Acanthaceer. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 113–181.

POWO. 2023. Plants of the World Online. Royal Botanic Gardens, Kew (accessed May 2023). http://www.plantsoftheworldonline.org/.SEINet. 2023. SEINet Portal Network. http//:swbiodiversity.org/seinet/index.php (accessed April–May 2023).

Walker, J. W. and J. A. Doyle, 1975. The bases of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Gard. 62: 664–723.

Wood, J. R. I. 1988. Colombian Acanthaceae—some new discoveries and some reconsiderations. Kew Bull. 43: 1–51

BLOSSOMING LEGACIES: EIGHT NEW *LEPANTHES* (ORCHIDACEAE: PLEUROTHALLIDINAE) SPECIES FROM LOS FARALLONES DE CALI NATIONAL PARK NAMED IN HONOR OF COLOMBIAN WOMEN

Juan Sebastián Moreno,[1,2,4,5] Robinson Galindo-tarazona,[1] Melisa alegria-Valencia,[2] Mario Alexei Sierra-Ariza,[3] Danny Leandro Mora-A.,[1] and Alejandro Zuluaga Tróchez[2,4]

Abstract. Eight new species of *Lepanthes* from the Farallones National Natural Park in Colombia are described and illustrated. These species are morphologically compared with the most similar species to corroborate their identity. Additionally, each of the eight new species is dedicated to a Colombian woman who has made history in several fields in the country, especially in areas traditionally dominated by men. These women serve as a source of inspiration for future generations and highlight the importance of diversity and inclusion in science and conservation. The article aims not only to contribute to the taxonomic knowledge of Colombian flora, but also to emphasize the crucial role that women have played and continue to play in Colombian society and the world.

Keywords: Andes, Colombia, conservation, systematics, taxonomy, western Andes

Resumen. Se describen e ilustran ocho nuevas especies de *Lepanthes* del Parque Nacional Natural Farallones en Colombia. Estas especies se comparan morfológicamente con las especies más similares para corroborar su nueva identidad. Además, cada una de las ocho nuevas especies se dedica a una mujer colombiana que ha hecho historia en varios campos en el país, especialmente en áreas tradicionalmente dominadas por hombres. Estas mujeres sirven como fuente de inspiración para futuras generaciones y destacan la importancia de la diversidad y la inclusión en la ciencia y la conservación. El artículo tiene como objetivo no solo contribuir al conocimiento taxonómico de la flora colombiana, sino también enfatizar el papel crucial que las mujeres han desempeñado y continúan desempeñando en la sociedad colombiana y en el mundo.

Palabras claves: Andes, Colombia, conservación, cordillera occidental, sistemática, taxonomía

Colombia, a nation renowned for its biodiversity and cultural vibrancy, is facing several challenges in all aspects of society. Taxonomists are racing to describe this amazing biodiversity at the same time that many threats are extinguishing species and destroying their habitats. Plants like orchids are among the most endangered species in this context. One of the genera of orchids in Colombia is *Lepanthes* Sw., which was established by Swartz in 1799 (Swartz, 1799). The genus represents the second most species-rich orchid genus in tropical regions after *Stelis* Sw., boasting now more than 1196 species (Karremans et al., 2023) distributed from Mexico to Bolivia. Yet, when zooming into the species level, there's a noticeable geographical and elevational confinement that makes *Lepanthes* a highly restricted and endemic genus (Luer, 1996; Luer and Thoerle, 2012; Parra-S*á*nchez et al., 2023). Colombia harbors the highest diversity of *Lepanthes* in the neotropics, with 377 species accounting for 20% of the species within the Pleurothallidinae subtribe in Colombia, and it is the second most species-rich genus in the country after *Stelis* (Karremans et al., 2023).

Los Farallones de Cali National Natural Park is situated in the Western Mountain Range of the Andes, covering the southwestern region of the Valle del Cauca department. It falls under the governance of the municipalities of Cali, Jamundí, Dagua, and Buenaventura in Colombia (Fig. 1). Established as a protected region on 15 July 1968, its name is inspired by the mountain range's young rock structures. Spanning 196,364.9 hectares, it stands as the department's most extensive protected land area. The Park primarily aims to safeguard biodiversity, emphasizing its role in supplying goods and services essential for Valle del Cauca's growth (UAESPNN, 2023). Despite being located between two of the world's most diverse regions, the Andes and the Chocó biogeographic region, Los Farallones is one of the least explored parks in the country. Regarding orchid diversity, 819 species were previously recorded in all natural parks, with only 110 species in PNN Farallones. In 2020, a new study recorded 430 orchid species for Los Farallones National Park, representing 10% of the country's species (Galindo-Tarazona et al., 2020). Given its vast expanse, making it one of the largest parks in Colombia, and with much of its forests yet to be explored, new orchid species are uncovered annually (Galindo-Tarazona et al., 2021; Baquero et al., 2021; Wilson et al., 2022; Parra-Sánchez et al., 2023; Moreno et al., 2023).

We would like express our sincere thanks to Álvaro Ortiz, Alvaro Fierro, Alexis Saa Tórrez, Juan José Mamian, and Luis Carlos Mamian from Farallones National Natural Park, who significantly contributed to the description and discovery of the eight new *Lepanthes* species. We also thank Francisco Tobar from Ecuador, who kindly gave us permission to use his photograph of *Lepanthes microprosartima*, and Sebastián Vieira-Uribe for letting us use the pictures of *Lepanthes dianatrujilloana* and *L. volvox*. Finally, We thank the National Natural Park Farallones de Cali for granting the collection permit for the project "Una isla en las nubes: establecimiento de línea base para monitoreo de un páramo aislado frente a cambio climático," funded by the Ministry of Sciences (860-2019, code 75985). We also thank Universidad Javeriana for leading the project mentioned above, which that allow us to collect some of the new species described here.

[1] Parques Nacionales Naturales de Colombia, Dirección Territorial Pacífico, Carrera 117 # 16B-00, Cali, Colombia.
[2] Departamento de Biología, Universidad del Valle, Calle 13 # 100-00, Cali, Colombia.
[3] Grupo de Investigación Schultes, Fundación Ecotonos, Cali, Colombia.
[4] Grupo de Investigación Ecología y Diversidad Vegetal, Universidad del Valle, Calle 13 # 100-00, Cali, Colombia.
[5] Corresponding author: semoreno113@gmail.com

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 663–693.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n4, Published online: 31 December 2023

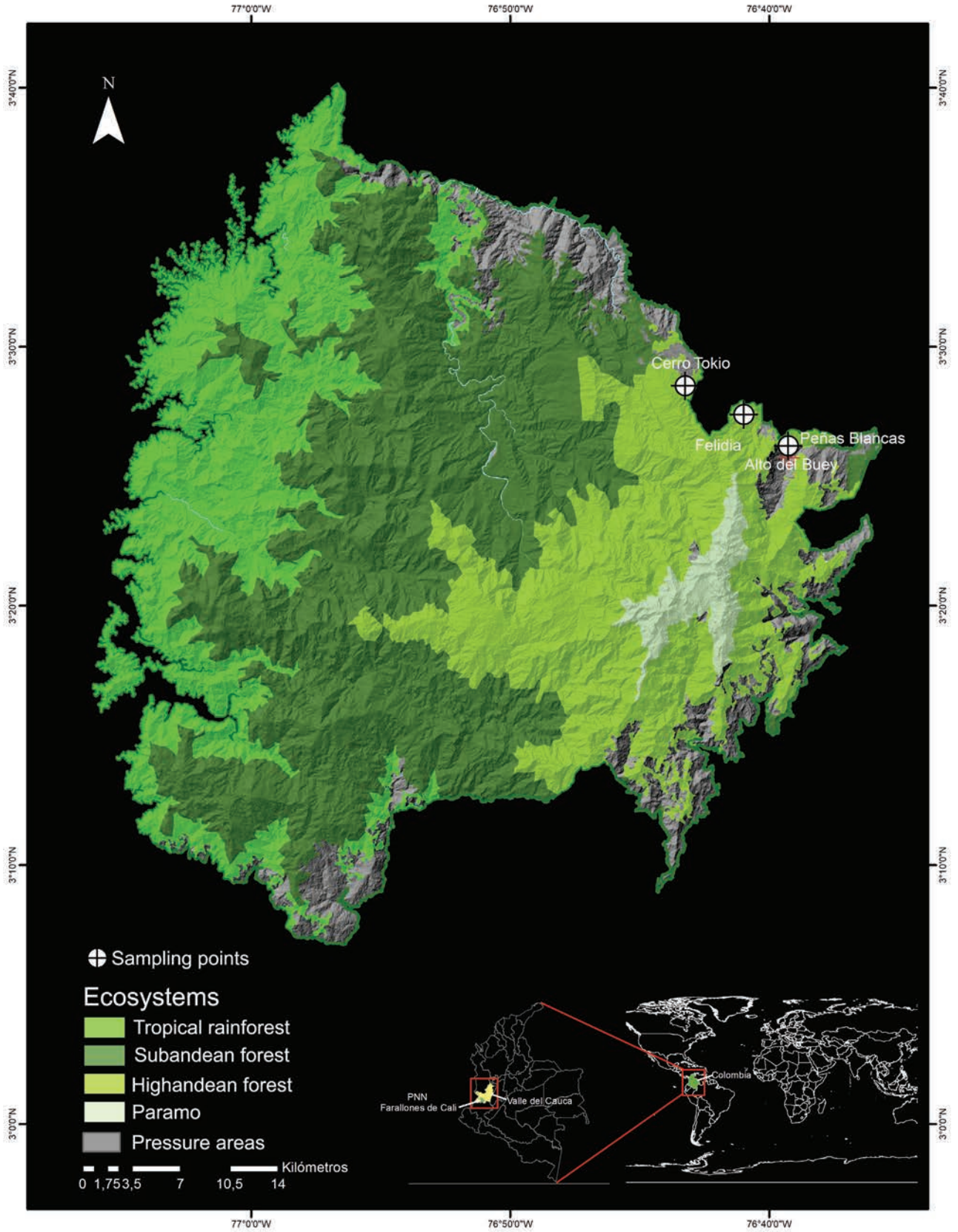


FIGURE 1. Sampling, type locations, and ecosystems of the eight new species of *Lepanthes*, National Natural Park Los Farallones de Cali.

Colombia, in particular, has seen its women rise, consistently breaking barriers and shaping the nation's destiny. Over the past decade, the spotlight on women's rights has been pivotal, reflecting a global trend toward acknowledging and rectifying gender disparities. This decade has borne witness to a paradigm shift, where Colombian women have not only asserted their rights, but have also wielded significant influence in social, political, economic, and scientific spheres. However, the journey toward equality and recognition is far from complete. As we delve into the stories of these remarkable women, it is essential to acknowledge their struggles, celebrate their achievements, and support their ongoing pursuits. Just as our biodiversity thrives amid adversity and flourishes in diverse habitats, Colombian women have exhibited an unyielding spirit in the face of challenges. By intertwining the realms of botany and social advocacy, we hope to offer a unique perspective on the intertwined destinies of nature and humanity and the enduring bloom of Colombian women in a changing world.

This paper introduces eight newly discovered *Lepanthes* species from the Farallones de Cali National Park, each named in honor of a Colombian woman who has left an indelible mark on the nation's fabric. We aim to illuminate their stories, emphasizing the significance of women's rights and contributions in Colombia. In recent years, extensive debates have unfolded regarding the use of eponyms by taxonomists; some have even gone so far as to suggest that taxonomists should abstain from using eponyms altogether, arguing that they constitute a political act that contradicts principles of equality and representation (Guedes et al., 2023). However, we believe, as many other authors do, that eponyms hold particular significance in regions like the Global South, where their elimination could have adverse effects on scientific endeavors in the very region intended to benefit the most from such proposals (Jost et al., 2023; Pethiyagoda, 2023; Slabin, 2023).

Materials and Methods

The descriptions and drawings were prepared from living specimens, and flowers were preserved in 70% alcohol. Flowers were dissected, measured, and photographed using Celestron Handheld Digital Microscope Pro. Vegetative structures were measured from dried material and reproductive structures from spirit material. Digital images were taken with a Nikon D850, D750 and a Nikon 105mm f/2.8 macro lens. Sketches from living and preserved specimens were digitized, and the images were used for diagramming a draft composite template in Adobe Photoshop® CS6. A digital composite line drawing was then made (lines and stippling) in Procreate illustration application for iPad 6th generation tablet computer (Bogarín et al., 2019). The new species were described following the botanical terminology by Beentje (2012) and Stearn (1992). All original descriptions of related species were consulted for detailed comparisons (Luer, 1996; Luer and Thoerle, 2012; Karremans et al., 2023). Specimens from the following herbaria, AMES, COL, CUVC, HUA, JAUM, JBB, VALLE, CAUP and MO (online), were consulted, and no additional material of the new species was found.

Taxonomic Treatment

1. Lepanthes dianatrujilloana J.S. Moreno, Gal.-Tar., Sierra-Ariza, & Zuluaga, *sp. nov.*

TYPE: COLOMBIA, Valle del Cauca, municipality of Dagua, corregimiento del Queremal, Cerro Tokio, Parque Nacional Natural Farallones, 1800 m, 23 January 2021, *R. Galindo-Tarazona, L. Clavijo, & A. Zuluaga 1552* (Holotype: CUVC). Fig. 2–4A.

Lepanthes dianatrujilloana is most similar to *Lepanthes volvox* Luer & R. Escobar, but it can be distinguished mainly by its setiform and thick lip, with a bilaminate, narrowly elliptic and flat blades, with narrowly obtuse apices and bases (vs. lip subcircular, glabrous, with abruptly acuminate apices and rounded bases), the very short and cuneate connectives with adnation to the column near the apex, forming a notably thick body (vs. broadly oblong connectives forming a broad, rounded body connected to the column base), the acute sinus with a triangular, slightly bifid pubescent appendix at the apex, (vs. a rounded sinus with a small, sigmoid, and pubescent oscillating bilobed appendix).

Plant epiphytic, caespitose, 6.1–11.9 cm tall. *Roots* slender, flexuous 0.4–0.7 mm in diameter. *Ramicauls* slender, 2.5–5.7 cm long, erect to suberect, enclosed by 5–10 lepanthiform sheaths, reducing in size towards the base, furrowed, with a dilated and ciliated ostia, acute. *Leaves* green to red adaxially to abaxially suberect, 2.8–4.1 × 0.8–1.4 cm, coriaceous, multiveined, elliptic-lanceolate, acute, apex emarginate with an abaxial central apiculum, base cuneate contracted into a petiole 2.6–4.2 mm long. *Inflorescence* a congested, successively flowered raceme, 1.9–2.2 cm long, including the peduncle, borne on the abaxial side of the leaf by a filiform peduncle, 1.1–1.4 mm long; *floral bract* acuminate, 0.6–1.2 mm long; *pedicel* 0.6–0.7 mm long, terete. *Ovary* costate, 1.3–2.7 mm long. *Flowers* with sepals maroon and midveins maroon-red; petals with the upper and lower lobe red and middle lobe orange; lip red-magenta and column purple. *Dorsal sepal* ovate, glabrous, acute, strongly reflexed, 2.7–4.0 × 1.9–3.0 mm long, 3-veined, connate to the lateral sepals for 0.6–1.1 mm. *Lateral sepals* ovate, glabrous, oblique, acute, short acuminate, longitudinally concave centrally 2.3–3.3 × 1.2–1.9 mm, 2-veined, connate for 0.9–1.5 mm. *Petals* transversely trilobed, setiform, 1-veined, 1.1–1.6 × 1.7–2.4 mm, upper lobe linear, falcate; midlobe triangular, lower lobe short, narrowly triangular. *Lip* setiform, thick, bilaminate, blades narrowly elliptic, flat, with apices and bases narrowly obtuse 1.0–1.2 × 0.3–0.4 mm, connectives very short, cuneate, body very thick, adnate to the column near the apex, sinus acute and appendix triangular, slightly bifid at the apex, pubescent. *Column* terete, up to 1 mm long, anther dorsal and stigma ventral, bilobed with elongated lobes that project beyond the anther. *Anther cap* not seen. *Pollinia* two, white, pyriform, 0.3 mm long.

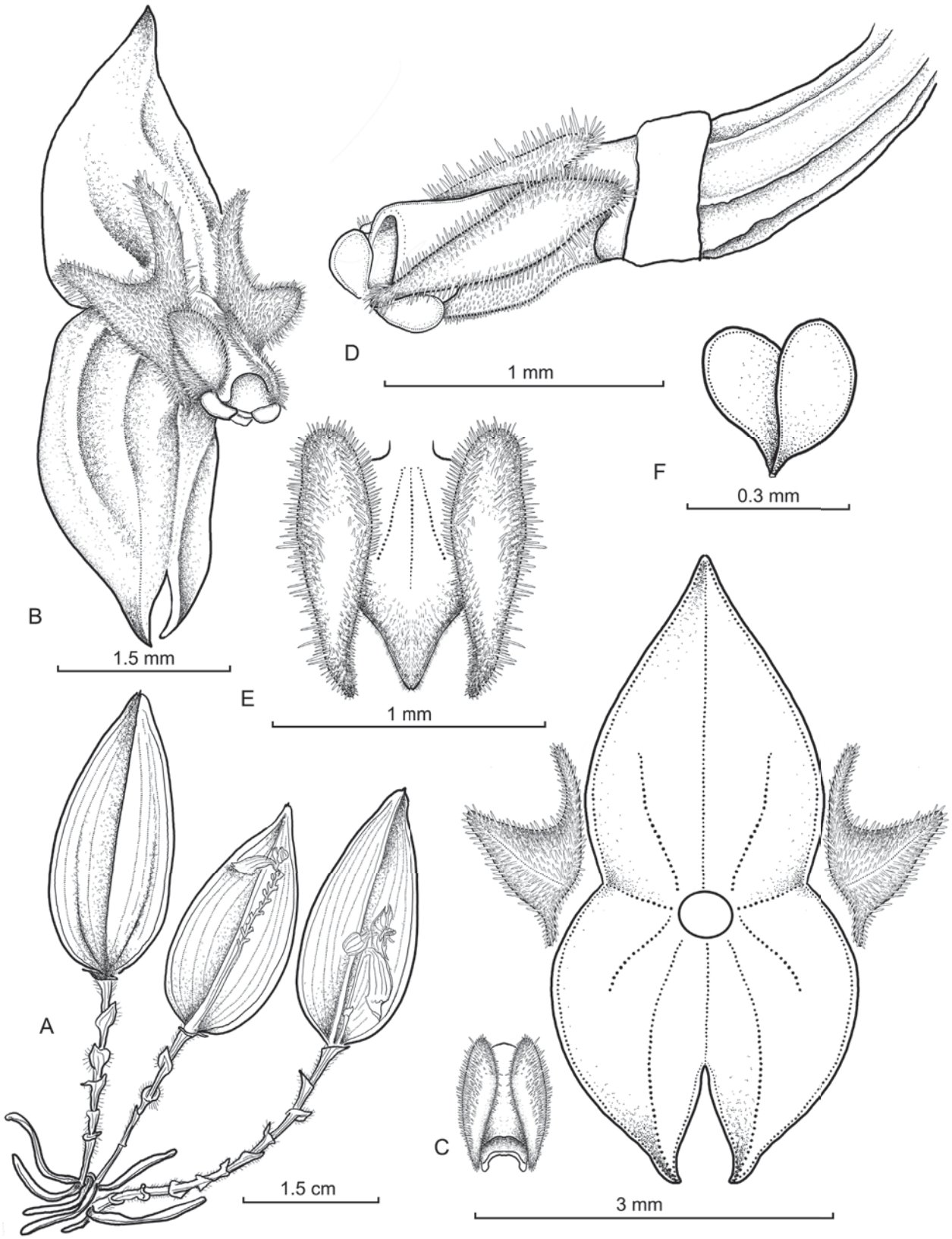


FIGURE 2. *Lepanthes dianatrujilloana* J.S. Moreno, Gal.-Tar., Sierra-Ariza, & Zuluaga. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded; **F**, pollinia. Drawing by J. S. Moreno based on the holotype.

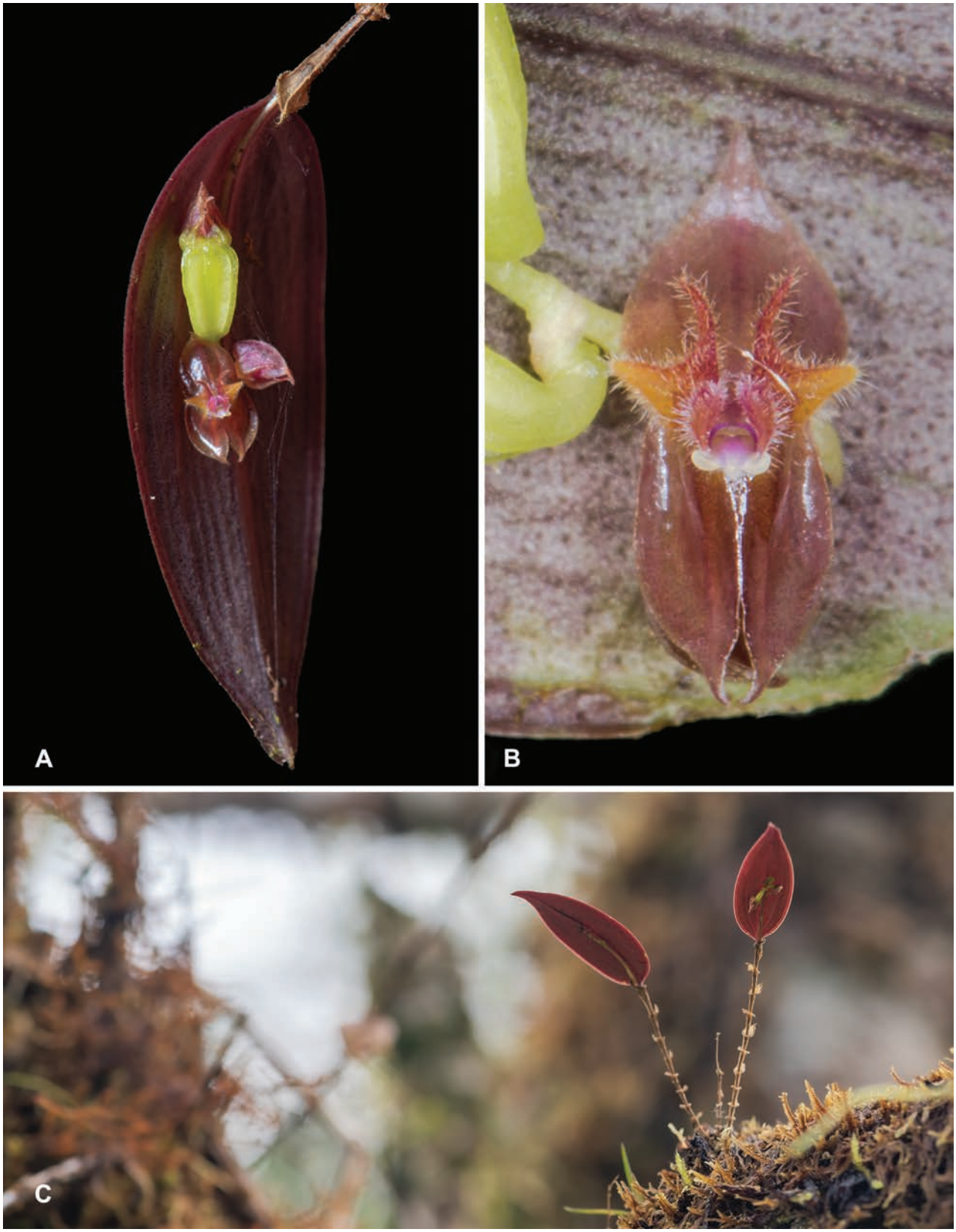


FIGURE 3. In-situ photographs of *Lepanthes dianatrujilloana* J.S. Moreno, Gal.-Tar., Sierra-Ariza, & Zuluaga. **A**, inflorescence and leaf; **B**, flower, front view; **C**, habit and plant. In-situ photographs by J. S. Moreno.

Additional specimens examined: COLOMBIA. Valle del Cauca: municipality of Cali, km 16, new road to Buenaventura, Bosque de niebla de San Antonio, buffer zone Parque Nacional Natural Farallones de Cali, June 2018, *J. S. Moreno & A. L Erazo 355* (Paratype: CAUP). Municipality of Dagua, Corregimiento de San Jose´ del Salado, Altos de San José del Salado, Finca Totogol, 1860 m, 20 Nov 2021, *J. S. Moreno and A. L. Erazo 528* (CAUP).

Eponymy: The name of the new species honors Diana Trujillo Pomerantz, a distinguished Colombian aerospace engineer, who has notably contributed to numerous NASA missions. She garnered significant recognition for her pivotal role in the Mars Curiosity Rover mission, where she initially served as a flight engineer before later taking a leadership position overseeing a team of engineers. Furthermore, Ms. Trujillo played a critical role in the Mars 2020 mission, specifically with the Perseverance rover, which successfully landed on Martian soil in February 2021. As the flight director overseeing the rover's robotic arm operations, she spearheaded a series of groundbreaking initiatives. Notably, she facilitated NASA's inaugural Spanish-language broadcast for a Martian landing, a strategic endeavor aimed at fostering broader engagement within the Spanish-speaking scientific community and promoting inclusivity in space exploration. Finally, she stands as a beacon of inspiration, particularly for young women aspiring to forge careers in the STEM fields (Science, Technology, Engineering, and Mathematics).

Lepanthes dianatrujilloana is a small to medium-sized species characterized by its red, suberect, coriaceous, and multiveined elliptic-lanceolate leaves. The distinguishing feature of this species is its intricate lip structure, with setiform and thick, narrowly elliptic blades that are flat and exhibit narrowly obtuse apices and bases; the connectives are very short, cuneate, forming a significantly thick body with an acute sinus, and a triangular, slightly bifid, pubescent appendix. The most similar species is *Lepanthes volvox* (Fig. 4B), as mentioned above in the diagnosis. The new species also has shorter ramicauls, from 2.5 to 5.7 cm long, enclosed by 5 to 10 lepanthiform sheaths (vs. ramicauls spanning 12–17 cm, enclosed by 13–14 lepanthiform sheaths). It also has smaller leaves that are suberect, coriaceous, multiveined, 2.8–4.1 cm long and 0.8–1.4 cm wide, with elliptic-lanceolate shape (vs. erect, thinly coriaceous, ciliate, multiveined leaves measuring 7–9 cm long and 2.5–2.8 cm wide with an ovate, acute, and acuminate shape). In terms of floral structure, *Lepanthes dianatrujilloana* is distinguished from other species primarily by the unique characteristics of its very small flowers, the majority of which are cleistogamous (Fig. 3A). The sepals are ovate and glabrous, similar in size; the dorsal sepal is acute and strongly reflexed, measuring between 2.7 and 4.0 mm long and 1.9-3.0 mm wide, and the lateral sepals are 2.3–3.3 mm long and 1.2–1.9 mm wide (vs. translucent light rose sepals, and the dorsal sepal is triangular, acute, measuring 8 mm long and 4 mm wide, and the lateral sepals are 7.5 mm long and 6 mm wide). The petals of the new species are orange with red highlights, transversely trilobed, and setiform, measuring 1.1–1.6 mm long and 1.7–2.4 mm wide; the upper lobe is linear and falcate, the midlobe is triangular, and the lower lobe is short and narrowly triangular (vs. yellow, transversely bilobed, pubescent petals measuring 1.5 mm long and 6.5 mm wide, with the lobes being subequal, obliquely ovate basally with slender, attenuated apices). Finally, the pollinia are consistently positioned on either side of the stigmatic cavity, situated beneath the column lobes, establishing a distinctive floral morphology that sets it apart in the genus (Fig. 2D).

2. Lepanthes dianauribeana Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza, *sp. nov.*

TYPE: COLOMBIA, Valle del Cauca, municipality of Dagua, corregimiento del Queremal, Cerro Tokio, predio sr. Alvaro, Parque Nacional Natural Farallones, 1800 m, 12 August 2020, *R. Galindo-Tarazona, L. Mamian & Vanessa Varón, & D. L. Mora 1595* (Holotype: CUVC). Fig. 5–7A.

Lepanthes dianauribeana is most similar to *Lepanthes vestigialis* Bogarín & Pupulin. It can be recognized by its completely reduced and vestigial petals, almost imperceptible (vs. ovate to suborbicular, extremely reduced), and, mainly, by having a triangular lip with a slightly concave base (vs. completely reduced and trichomatous).

Plant epiphytic, caespitose, 2.1–4.2 cm tall; *roots* slender, flexuous, filiform, 0.6 mm in diameter. *Ramicauls* slender, erect to suberect, 1.0–2.8 cm long, enclosed by 5–8 acuminate, furrowed lepanthiform sheaths, with a dilated and microscopically ciliate ostia. *Leaves* suffused with purple abaxially, horizontal, coriaceous, slightly conduplicate at the base, ovate-elliptic, acute, 1.1–1.7 × 0.6–0.8 cm, apex emarginate with an abaxial apiculum in the middle, base cuneate contracted into a petiole 1.2–2.9 mm long. *Inflorescence* up to 2 congested, distichous racemes, 3–19[–many], successively flowered, longer than the leaf, up to 1.9 cm long including the peduncle, distichous, flexuous, born on the adaxial surface of the leaf by a filiform, terete peduncle 6.5–8.6 mm long; *floral bracts* conical, acuminate, 0.83–1.00 mm long; *pedicels* terete, 0.75–1.06 mm long. *Ovary* terete, costate, 0.76 mm long. *Flowers* with sepals yellow-tawny; lip and column white to cream. *Dorsal sepal* repand along the margin, triangular-lanceolate, convex, acute, 3-veined, 2.0–2.9 × 1.0–1.2 mm, connate to the lateral sepals for 0.44 mm. *Lateral sepals* repand along the margins, triangular-lanceolate, oblique, acute, 2-veined, 2.0–2.9 × 0.9–1.2 mm, connate for 0.5 mm. *Petals* extremely reduced, vestigial. *Lip* triangular, slightly concave at the base, 0.6 mm long, adnate to the base of the column. *Column* elongate, terete, 1.5–1.7 mm long, anther dorsal and stigma apical. *Anther cap* cordate, cucullate, 0.3 mm wide. *Pollinia* 2, yellow, pyriform, narrowly obovoid, 0.28 mm long.

Eponymy: The new species is named in honor of Diana Uribe Forero, a Colombian historian and philosopher, who has contributed immensely to the enrichment of historical and philosophical discourse through her insightful radio broadcasts and podcasts. Her dedication to weaving intricate narratives that bridge historical events with contemporary issues has fostered a deeper understanding and appreciation for the diverse cultural and historical landscapes that shape our world today. Moreover, this dedication serves as a

FIGURE 4. Comparison with the most similar species. **A**, *Lepanthes dianatrujilloana* J.S. Moreno, Gal.-Tar., Sierra-Ariza, & Zuluaga; **B**, *Lepanthes volvox* Luer & R. Escobar. Photographs by S.Vieira-Uribe.

beacon, illuminating the pivotal role that women play in the spheres of education, communication, and intellectual discourse. Through her work, Diana Uribe exemplifies the profound impact that women can have in shaping societal narratives and fostering a culture of knowledge and empathy. Her efforts resonate as a testament to the transformative power of women in roles traditionally dominated by men, showcasing the depth, nuance, and richness that a female perspective can bring to the table.

Lepanthes dianauribeana is a small-sized species, and might belong to a group of species, with triangular sepals with a long, conspicuous, and protruding column (Pupulin, et al., 2011; Moreno et al., 2017). Within this virtual group, there are several species that have either somewhat reduced or strongly reduced corollas, as can be observed in the comparison of nearly all of the species in the group (Moreno et al., 2017, Fig. 6 therein). In this case, *Lepanthes equus-frisiae* Pupulin & H. Medina (Fig. 7B) from Ecuador, which has broadly-ovate to suborbicular leaves (vs. narrowly ovate-elliptic), 1-veined lateral sepals (vs. 2-veined lateral sepals), transversely reniform-suborbicular, rounded, concave petals (vs. completely reduced and vestigial petals), and a subspherical, broadly obtuse lip (vs. triangular lip). Finally, as mentioned in the diagnosis, *Lepanthes vestigialis* (Fig 7C) from Costa Rica is probably the most similar species, which has broadly-ovate to suborbicular leaves, 8–11 × 10–13 mm (vs. ovate-elliptic and horizontal, 1.1–1.7 × 0.6–0.8 cm), The petals of *Lepanthes dianauribeana* are extremely reduced and vestigial (vs. ovate to orbicular, less than 0.5 mm long, and trichomatous). Lastly, the lip in *Lepanthes vestigialis* is a vestigial, completely reduced lip forming an appendix, less than 0.5 mm long and trichomatous (vs. triangular and slightly concave at the base, with a length of 0.6 mm).

3. Lepanthes gloriagaleanoana J.S. Moreno, E. Restrepo, & Zuluaga., *sp. nov.*

TYPE: COLOMBIA, Valle del Cauca, Cali, corregimiento Félidia, vereda El Diamante, Parque Nacional Natural Farallones de Cali, 2100 m, 22 June 2020, *R. Galindo-Tarazona, D. Haelterman, & J. C. Ruiz 1462* (Holotype: CUVC). Fig. 8–10A.

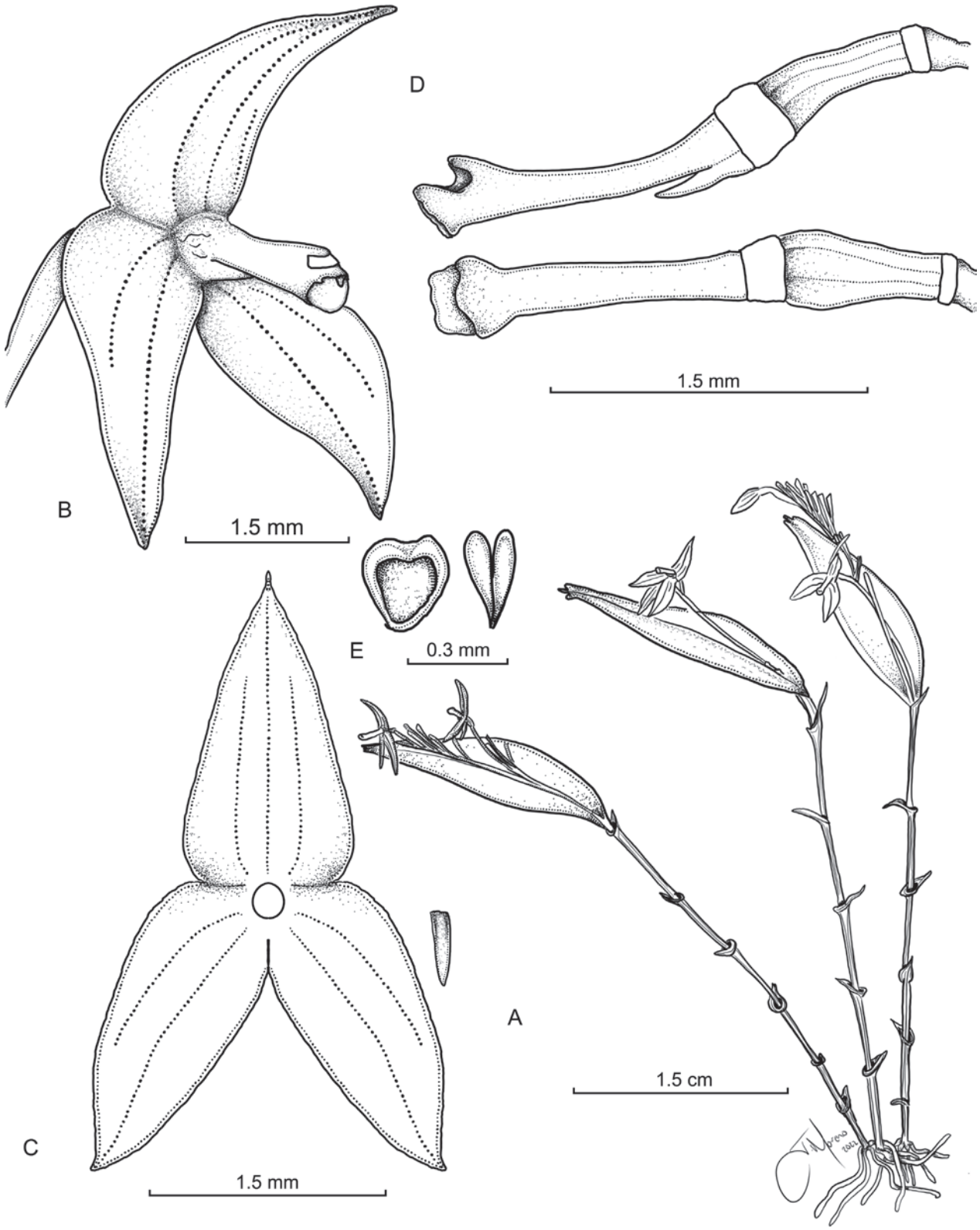


FIGURE 5. *Lepanthes dianauribeana* Gal.-Tar., J.S. Moreno, & Sierra-Ariza. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; E, anther cap and pollinia. Drawing by J. S. Moreno based on the holotype.

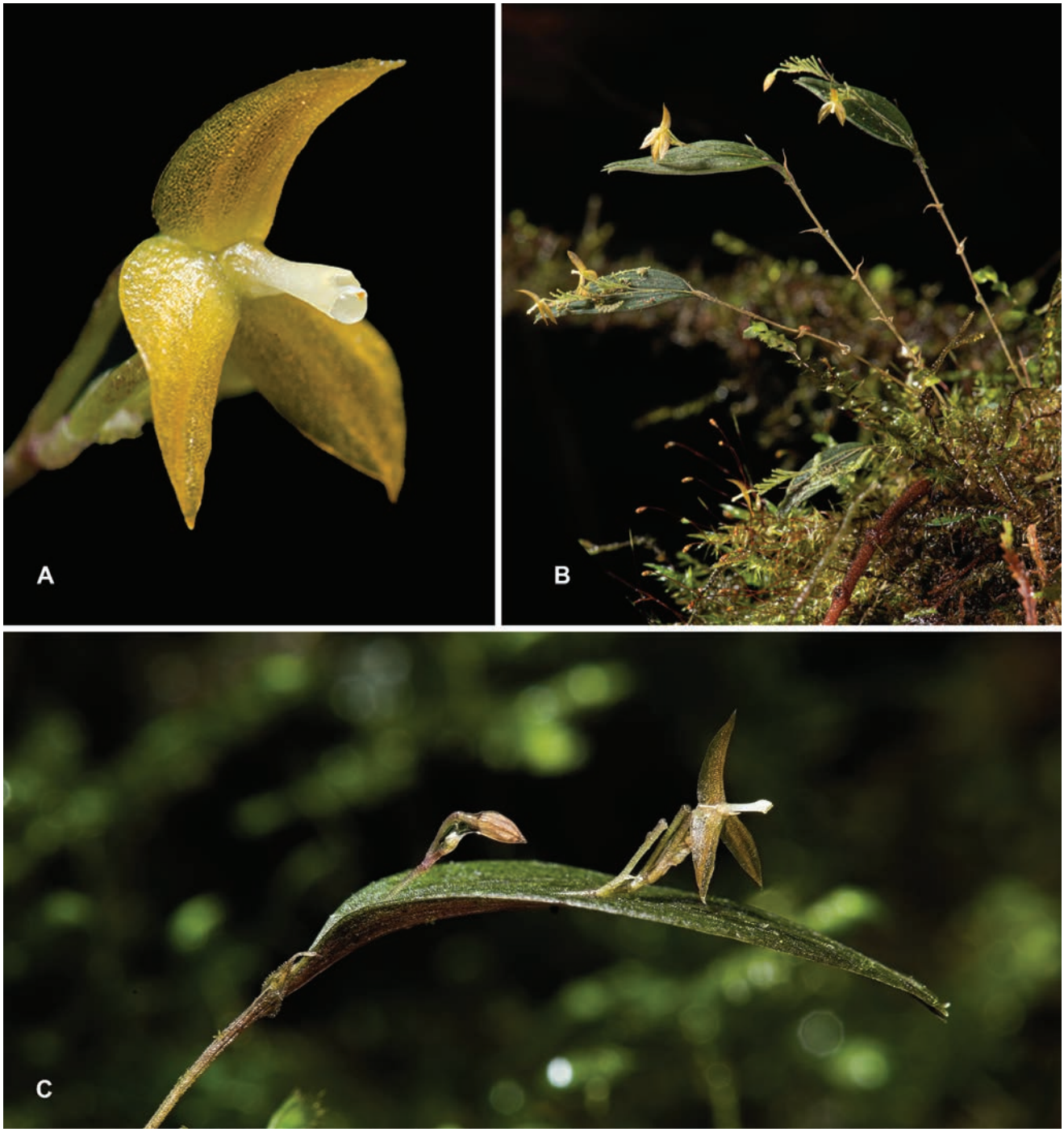


FIGURE 6. In-situ photographs of *Lepanthes dianauribeana* Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza. **A**, flower, lateral view; **B**, habit and plant; **C**, leaves and inflorescence. In-situ photographs by R. Galindo-Tarazona and J. S. Moreno.

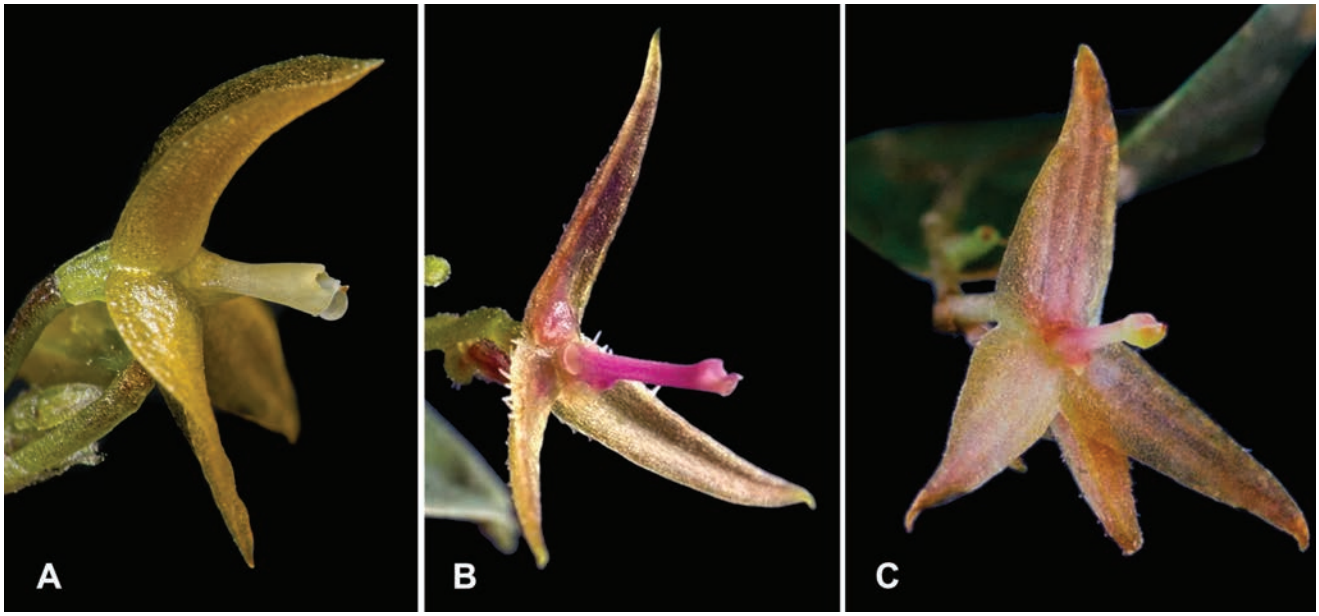


FIGURE 7. Comparison with the most similar species. **A**, *Lepanthes dianauribeana* Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza; **B**, *Lepanthes equus-frisiae* Pupulin & H. Medina; **C**, *Lepanthes vestigialis* Bogarín & Pupulin. Photographs by J. S. Moreno (A) and F. Pupulin (B, C).

Lepanthes gloriagaleanoana is most similar to *Lepanthes ortiziana* O. Perez, E. Parra, & Kolan., but it differs from the latter by its purple sepals, suffused with yellow-green from the second vein to the inner margin in the lateral sepals, 4.8–4.9 × 5.5–5.6 mm dorsal sepal and 5.5–6.6 × 3.2–3.9 mm lateral sepals (vs. yellow-green, 5.0 × ca. 4.0 mm dorsal sepal and lateral sepals 5.0 × 2.8 mm), and by the lip with linear oblong blades, with the upper and lower ends obtuse, 2.5 × 0.9–1.1 mm, with a short triangular, subacuminate appendix with pubescent vertices (vs. narrowly oblong blades with upper and lower ends narrowly rounded, obliquely, ca. 2.3 mm × ca. 0.5 mm, with a small, triapiculate appendix with the central lobe microscopically pubescent).

Plant epiphytic, caespitose, 9.2–11.8 cm tall; *roots* slender, flexuous, filiform, 0.68 mm in diameter. *Ramicauls* slender, suberect to pendent 7.1–8.8 cm long, enclosed by 8–10 acuminate, furrowed, minutely pubescent lepanthiform sheaths, with a wide markedly dilated and ciliate ostia. Immature *leaves* light green, mature leaves purplish-red, iridiscent adaxially, light green abaxially, microscopically pubescent adaxially, coriaceous abaxially, elliptical-ovate, concave, and sulcate, reticulate-veined, acute, 5.5–6.5 × 1.7–2.6 cm, apex emarginate with an abaxial apiculum in the middle, base broadly cuneate contracted into a petiole 1.1–1.7 mm long. *Inflorescence* a congested distichous raceme, up to 2, 6–17[–many] successively flowered, up to 2.5–3.5 cm long including the peduncle, loose, distichous, flexuous, held appressed to the adaxial concave surface of the leaf by a filiform, terete peduncle, 1.1–1.4 cm long; *floral bracts* conical, acuminate, minutely scabrous, 0.9–1.3 mm long; *pedicels* terete, 2.1–2.5 mm long. *Ovary* terete, costate, 3.48 mm long. *Flowers* dorsal sepal purplish red with margins green, lateral sepals purplish red from the second vein to the outer margin and yellow-green from the second vein to the inner margin; petals bicolorous longitudinally, with the inner half dark red and the outer half yellow-green; lip magenta with margins dark red and apices green. *Dorsal sepal* short papillose along margin, broadly ovate, wider than long, acuminate, flat, 3-veined, 4.8–4.9 × 5.5–5.6 mm, connate to the lateral sepals for 1.49 mm. *Lateral sepals* short papillose along the margins, broadly ovate, oblique, acuminate, flat, 2-veined, 5.5–6.6 × 3.2–3.9 mm each, connate for 2.6 mm long. *Petals* transversally bilobed, microscopically pubescent, 1.6–1.7 × 3.7 mm, 1-veined; upper lobe oblong, obtuse; lower lobe narrowly triangular, oblique, obtuse. *Lip* bilaminate, blades linear-oblong, upper ends obtuse and longer than the lower ends, slightly depressed in the middle toward the inner margins, apices uncinate, short ciliate, 2.5 × 0.9–1.1 mm, supported by short cuneate connectives, body broad, adnate to the base of the column, sinus rounded with a short triangular, subacuminate appendix with pubescent vertices. *Column* terete, bilobed, 2.09 mm long, anther dorsal and stigma ventral. *Anther cap* cordate, cucullate, 0.62 mm wide. *Pollinia* 2, yellow, pyriform, narrowly obovoid, 0.3 mm long.

Additional specimen examined: COLOMBIA. Valle del Cauca: municipality of Cali, km 16, new road to Buenaventura, Bosque de niebla de San Antonio, buffer zone Parque Nacional Natural Farallones de Cali, 22October 2023, *J. S.Moreno & A. L Erazo 358* (Paratype: CAUP).

Eponymy: The new species is named in honor of Gloria Galeano Garcés, a prolific Colombian botanist who dedicated her life to the study and conservation of the flora of Colombia, with a special focus on palms. She was a professor at Universidad Nacional de Colombia and also director of the Instituto de Ciencias Naturales. Her tireless dedication and significant contributions to the field have served as a source of inspiration, paving the way for

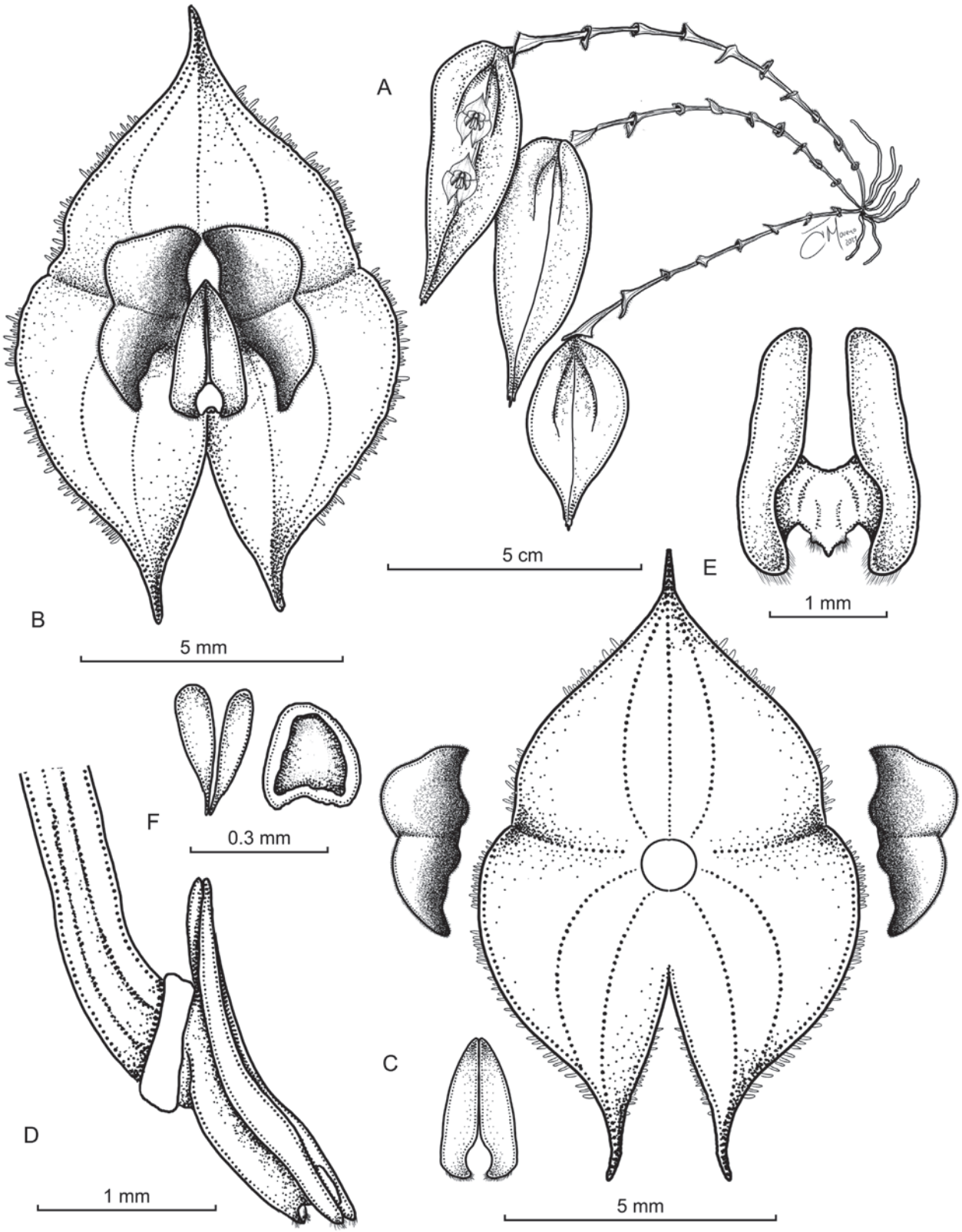


FIGURE 8. *Lepanthes gloriagaleanoana* J.S. Moreno, E. Restrepo, & Zuluaga. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded; **F**, anther cap and pollinia. Drawing by J. S. Moreno based on the holotype.

FIGURE 9. In-situ photographs of *Lepanthes gloriagaleanoana* J.S. Moreno, E. Restrepo, & Zuluaga. **A**, flower, front view; **B**, inflorescence; **C**, habit and plant. In-situ photographs by J. S. Moreno.

FIGURE 10. Comparison with the most similar species. **A**, *Lepanthes gloriagaleanoana* J.S. Moreno, E. Restrepo, & Zuluaga; **B**, *Lepanthes cincinnata* Luer & R. Escobar; **C**, *Lepanthes ortiziana* O. Perez, E. Parra, & Kolan. Photographs by J. S. Moreno.

future generations of botanists, and especially, for young women in science. Gloria is celebrated not only for her scientific excellence, but also for her role as a mentor and leader in the scientific community. Throughout her career, she demonstrated that passion and dedication are the true determinants of success in science, breaking barriers, and overcoming gender stereotypes.

Lepanthes gloriagaleanoana might belong to an informal group of species distributed across all three Andean Ranges in Colombia and Ecuador. This group, referred to as "*manabina*" and proposed by Baquero et al. (2021), includes species that exhibit shared morphological traits, such as deeply concave leaves with margins that recurve from slightly to strongly, and an adaxial surface ranging from microscopically to conspicuously pubescent. The group is also characterized by congested inflorescences with flowers located on the adaxial side of the leaves, accompanied by a synsepal varying from short- to long-caudate and a notably small, inconspicuous triangular appendix. From the "*manabina*" group, there are two species that are very similar: *Lepanthes cincinnata* Luer & R. Escobar (Fig. 10B) from Colombia, which has ovate sepals 8 × 5 mm, with slender acuminate caudas (vs. broadly ovate sepals up to 5.5 × 5.6 mm with no caudas); the lip is 2.5 mm long, with the upper and lower ends of the blades equal in size (vs. the lip 4.6 mm long, with the upper ends longer than the lower ends of the blades); and a tridentate appendix (vs. triangular with two pubescent vertices laterally). Finally, *Lepanthes ortiziana* (Fig. 10C) could be the most similar species to *L. gloriagaleanoana* as mentioned in the diagnosis, but also it can be distinguished and separate from the latter by its larger leaves, 5.5–6.5 × 1.7–2.6 cm (vs. 2.8–ca. 3.8 × 1.5–ca. 2.0 cm), petals with an oblong-obtuse upper lobe and a narrowly triangular, oblique-obtuse lower lobe (vs. uncinate upper lobe with overlapping apices, and a triangular, slightly curved, acute lower lobe).

4. Lepanthes laurarestrepoana J.S. Moreno, Gal.-Tar., & Sierra-Ariza., *sp. nov.*

TYPE: COLOMBIA, Valle del Cauca, Cali, Minas del Socorro, Parque Nacional Natural Farallones de Cali, 3200 m, 29 June 2020, *R. Galindo-Tarazona, A. Fierro, G. Rodriguez, M. Espitia, & G. Marín 1470* (Holotype: CUVC). Fig. 11, 12, 14A.

Lepanthes laurarestrepoana is most similar to *Lepanthes contingens* Luer, but it can be distinguished from the latter by its transversally bilobed petals, with the upper lobe oblong-ovate, oblique, and rounded, noticeably broader than the lower lobe, which is slender, ovate-lanceolate, oblique, and acute (vs. transversely oblong petals, the upper lobe oblong and truncate, and the lower lobe smaller, triangular, and acute) and the lip with blades similar, but with a pubescent, short, and triangular appendix (vs. oblong and slender).

Plant epiphytic, caespitose, up to 9–10 cm tall; *roots* slender, flexuous, filiform, 0.5 mm in diameter. *Ramicauls* slender, suberect to pendent 1.8–6.5 cm long, enclosed by 5–12 acuminate, furrowed, and ciliate lepanthiform sheaths, with a wide markedly dilated and ciliate ostia. Immature *leaves* light green, mature leaves dark green iridescent adaxially, light green abaxially, microscopically pubescent

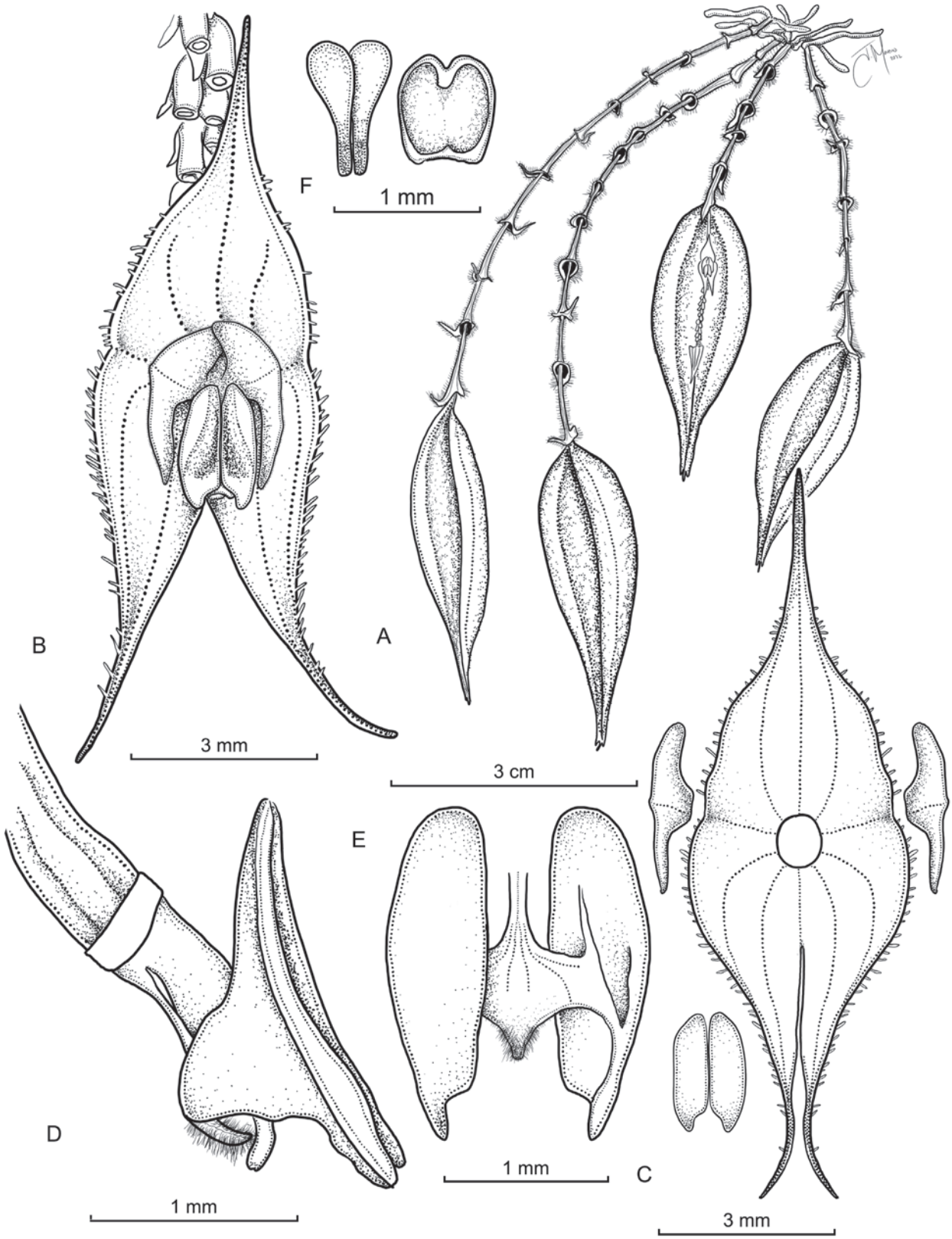


FIGURE 11. *Lepanthes laurarestrepoana*, J.S. Moreno, Gal.-Tar., & Sierra-Ariza. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded; **F**, anther cap and pollinia. Drawing by J. S. Moreno based on the holotype.

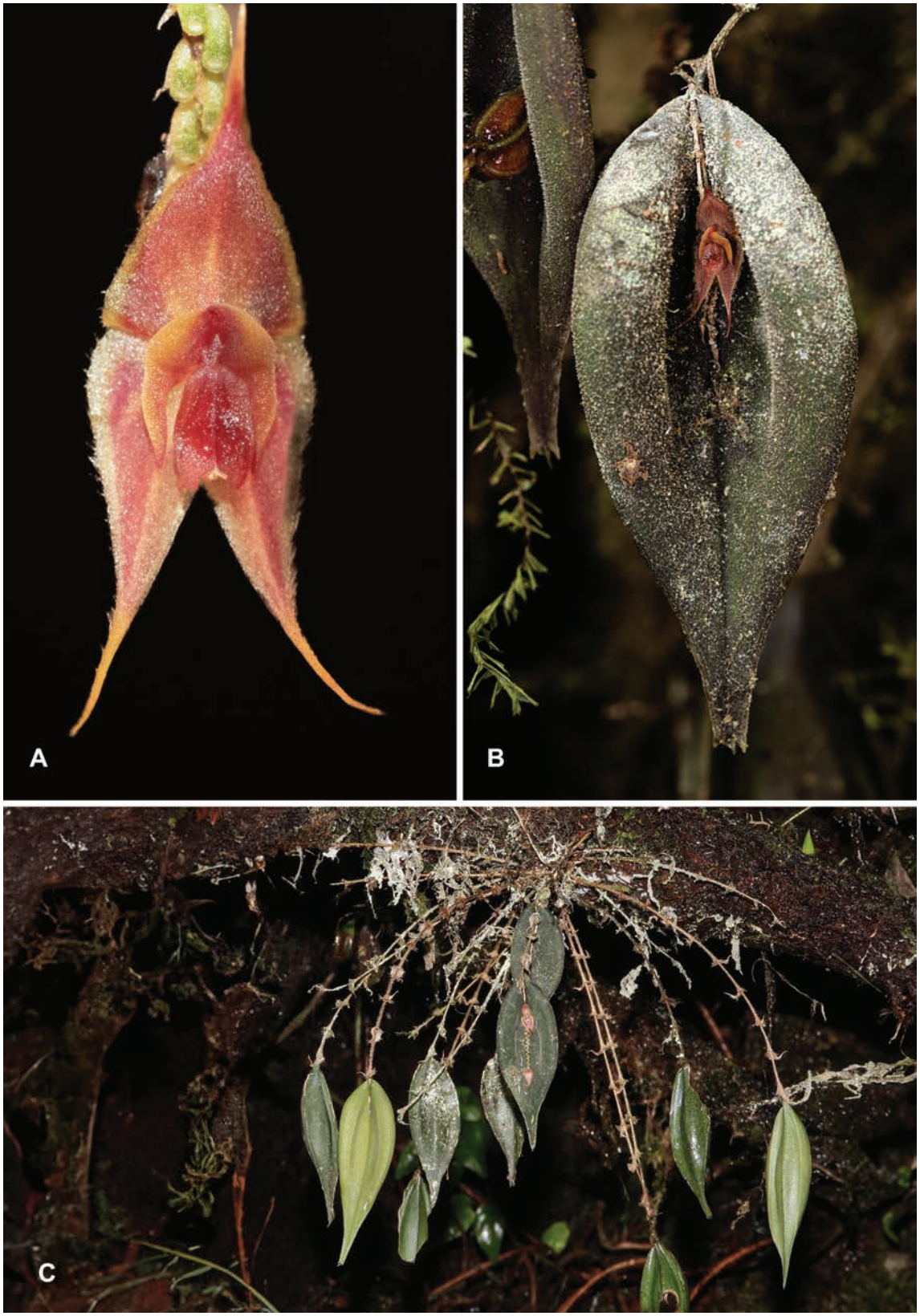


FIGURE 12. In-situ photographs of *Lepanthes laurarestrepoana*, J.S. Moreno, Gal.-Tar., & Sierra-Ariza. **A**, flower, 3/4 view; **B**, leaf and inflorescence; **C**, habit and plant. In-situ photographs by D. L. Mora (A, C) and R. Galindo-Tarazona (B).

FIGURE 13. Close up and lateral view of the appendage within the species of the informal group "*manabina*." Photograph of *Lepanthes* aff. *Troxis* by J. S. Moreno. The white arrow points to the appendage and the blue arrow points to the appendix.

FIGURE 14. Comparison with the most similar species. **A**, *Lepanthes laurarestrepoana* J.S. Moreno, Gal.-Tar., & Sierra-Ariza; **B**, *Lepanthes contingens* Luer; **C**, *Lepanthes troxis* Luer & R. Escobar. Photographs by R. Galindo-Tarazona (A) and J. S. Moreno (B, C).

adaxially, coriaceous abaxially, elliptical-ovate, concave, and sulcate, reticulate-veined, acute, 4.32 × 1.88 cm, apex emarginate with an abaxial apiculum in the middle, base broadly cuneate contracted into a petiole up to 6.14 mm long. *Inflorescence* a distichous raceme of 18–26[–many] successively flowering, up to 2.55 cm long including the peduncle, distichous, flexuous, born at the adaxial surface of the leaf by a filiform, terete peduncle 1.19 mm long; *floral bracts* ovate-lanceolate, acuminate, minutely verrucose, 0.83–1.00 mm long; *pedicels* terete, 0.75–1.06 mm long. *Ovary* terete, costate, 1.71–2.14 mm long. *Flowers* with dorsal sepal red with the mid-vein and cauda orange, lateral sepals with the center red, margins cream and cauda orange; petals bicolorous longitudinally, the inner side red and the outer orange and lip red. *Sepals* caudate, papillose, carinate, margins with filiform papillae. *Dorsal sepal* ovate-lanceolate, 4.20–6.25 × 2.04–3.09 mm, connate to the lateral sepals for 0.94–1.15 mm, 3-veined. *Lateral sepals* ovate-lanceolate, oblique, 4.22–7.01 × 1.24–1.96 mm, connate for 0.86–2.45 mm, 2-veined. *Petals* transversally bilobed, 0.79–0.80 × 3.10–3.14 mm, upper lobe oblong-ovate, oblique, rounded, broader than the lower lobe; lower lobe slender ovate-lanceolate, oblique, acute. *Lip* exhibited liquid droplets, possibly nectar, glabrous, bilaminate, 1.82–2.01 × 0.58–0.61 mm; blades narrowly oblong, upper ends rounded, lower ends with a depression on the outer margin, forming an acute apiculum, connectives short, cuneate; body broad, connate to the base of the column by a long, slender claw; appendix short, strongly pilose, fleshy, triangular, rounded, curved upward when viewed from the side, in contact with a vermiform appendage from the stigma. *Column* slender, clavate, terete, 1.41–1.69 mm long; anther dorsal and stigma ventral. *Anther cap* cordate, cucullate, 0.7 mm wide. *Pollinia* 2, yellow, pyriform, narrowly obovoid, 0.9 mm long.

Eponymy: The new species honors Laura Restrepo Durán, a renowned Colombian writer and journalist. As a prominent female figure in the literary world, she has not only carved a successful career, but has also been a potent voice in advocating for political activism. Her work often transcends the realm of literature, reflecting her profound commitment to addressing various political and social conflicts that have occurred in Colombia and throughout Latin America. In addition to her literary endeavors, Laura has stood as a fervent defender of human rights, collaborating with several non-governmental organizations and groups dedicated to the promotion of human rights. Her steadfast commitment to the social and political issues of Colombia and Latin America is a notable constant in her body of work, marking her a significant female powerhouse in the literary and activist spheres.

Lepanthes laurarestrepoana might also belong to the group mentioned above in *L. gloriagaleanoana*, with its deeply concave leaves and slender ramicauls, but it has a feature that distinguishes it from the flowers of this group and could possibly be a subgroup within the "*manabin*a" group. Additionally, it has a basal slender claw connate to the base of the column with an appendix, in contact with a vermiform appendage (Fig. 13) (a feature also found in the "*manabina*" group and not described by Baquero et al., 2021). Two species share the same traits in the lip structure: *Lepanthes contingens* (Fig. 14B), a species distributed in Colombia and Ecuador, which was compared in the diagnosis, and *Lepanthes troxis* Luer & R. Escobar (Fig. 14C), characterized by its leaves with revolute and undulate margins (vs. margin entire), transversely bilobed petals with the upper lobe oblong, oblique, and the apex truncate and coarsely erose, the lower lobe triangular, acute (vs. the upper lobe oblong-ovate, oblique, rounded, broader than the lower lobe; the lower lobe slender ovate-lanceolate, oblique, acute) and the lip with similar shape but with a vermiform and ciliate appendix (vs. pubescent, short and triangular appendix).

5. Lepanthes margaritamarinoana Gal.-Tar., Zuluaga, J.S. Moreno, & Sierra-Ariza, *sp. nov.*

TYPE: COLOMBIA, Valle del Cauca, municipality of Dagua, corregimiento del Queremal, Cerro Tokio, predio sr. Alvaro, Parque Nacional Natural Farallones, 1852 m, 17 August 2020, *R. Galindo-Tarazona, L. Mamian & V. Varón, & D. L. Mora 1624* (Holotype: CUVC). Fig. 15–17A.

Lepanthes margaritamarinoana is most similar to *Lepanthes gargantua* Rchb.f., (Fig. 17B), but it can be recognized and separated from the latter by its medium size, up to 20 cm tall, including the ramicauls and leaves (vs. large size plants, up to 75 cm tall, including the ramicauls and leaves) and the glabrous, oblong, and slight tridentate appendix of the lip (vs. minutely ciliate and triangular).

Plant up to 37 cm tall, epiphytic, sympodial, caespitose; roots slender, 1.5 mm in diameter. *Ramicauls* erect, stout, up to 15 cm long, enclosed by 11–12 furrowed and scabrous lepanthiform sheaths, with a dilated ostia. *Leaves* erect, coriaceous, oblong-ovate, subacute, acuminate, 4.5–8.5 × 3.5 × 6.5 cm, rounded base contracted into a petiole 1.5 cm long. *Inflorescence* a distichous raceme of 34–49[–many] successively flowered, up to 4.59 cm including peduncle, born at the abaxial surface of the leaf by a filiform peduncle, 1.59–2.49 cm, 1 or 2 inflorescences per ramicaul; *floral bracts* ovate-lanceolate, acuminate, papyraceous, 0.7–0.8 mm long; *pedicels* terete 1.08–1.24 mm long. *Ovary* costate, 3.19–3.24 mm long. *Flowers* with sepals yellow-brown; petals bicolorous, with the apex of the upper lobe and the inner part remainder yellow; lip yellow with the margins red and the column purple. *Sepals* acute, papillose, carinate. *Dorsal sepal* broadly ovate, 4.53 × 5.05 mm, connate to the lateral sepals by 1.98–2.87 mm, 3-veined. *Lateral sepals* ovate to subtriangular, oblique, 3.59–4.09 × 2.81–3.17 mm, each 2-veined, connate for 1.78–1.97 mm, into a widely ovate synsepal. *Petals* microscopically pubescent, transversally bilobed, 1.40–1.71 × 3.82–3.99 mm; upper lobe subelliptic, oblique, rounded, broader than the lower lobe; lower lobe slender, oblong-ovate to subtriangular, acute. *Lip* sub-horizontal, bilaminate; blades microscopically pubescent, slightly oblique in relation to the column axis, oblong-elliptic, upper end rounded, lower end thin, sharp, curved downward, 1.10–1.97 × 0.42–0.74 mm, supported by wide, subquadrate and cuneate connectives; body broad, concave, adnate close to the base of the column,

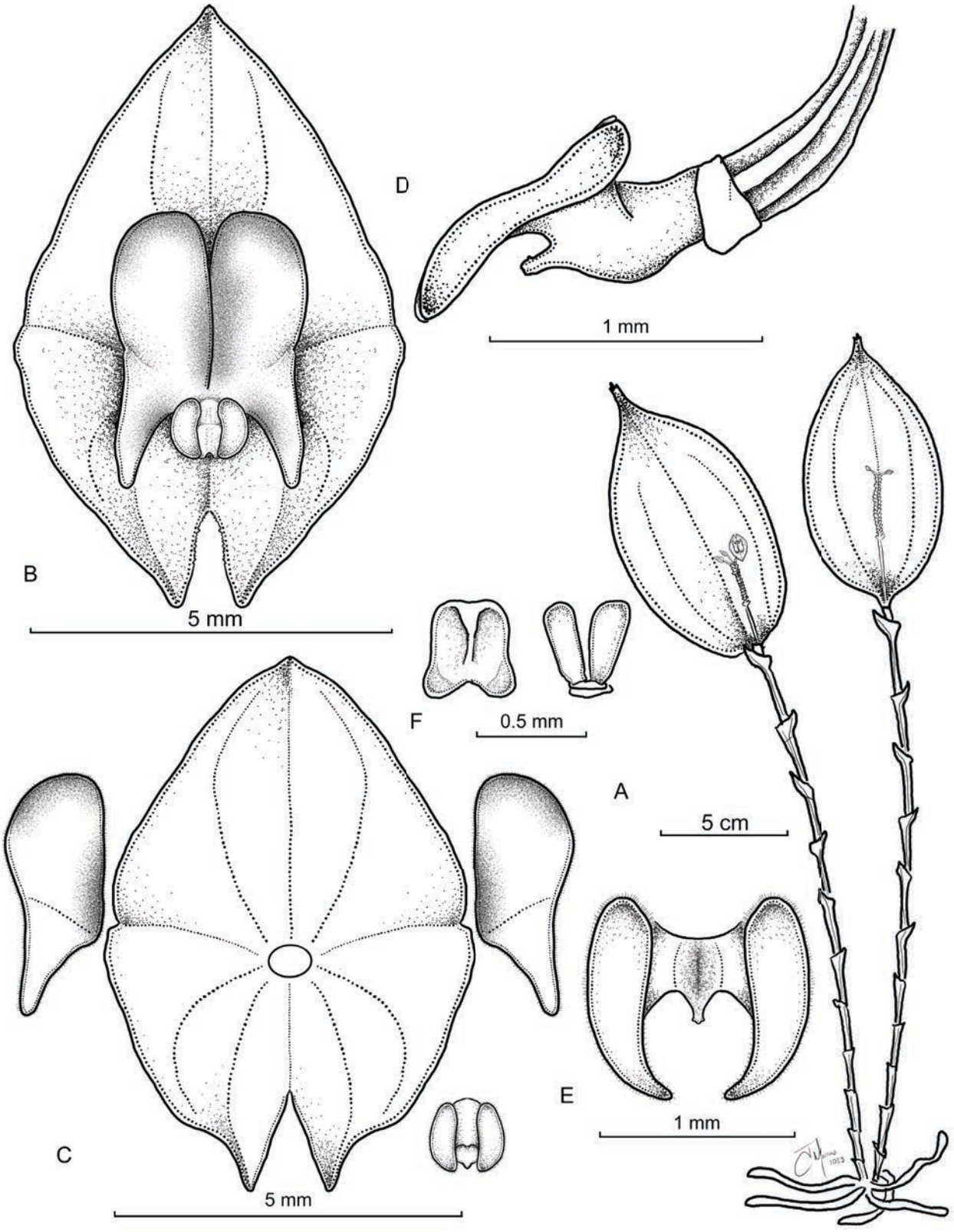


FIGURE 15. *Lepanthes margaritamarinoana,* Gal.-Tar., Zuluaga, J.S. Moreno, & Sierra-Ariza. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded; **F**, anther cap and pollinia. Drawing by J. S. Moreno based on the holotype.

sinus obtuse with the appendix oblong, slightly tridentate, obtuse. *Column* terete, up to 1.95 mm long, anther dorsal and stigma ventral. *Anther cap* elliptic, 0.43 mm wide, with two rounded corners at the base. *Pollinia* 2, yellow, pyriform, oblanceolate, 0.4 mm long.

Eponymy: The new species honors Margarita Marino de Botero, a prominent environmentalist and a pioneer in the defense of the environment in Colombia. As one of the first women in this field, her trajectory serves as a source of inspiration, demonstrating that women can lead and make significant contributions in areas traditionally dominated by men. Margarita has been a central figure in important commissions and international organizations, including the World Commission for the Environment and Development (Brundtland Commission) and the Commission for Education of the 21st Century of UNESCO. Her contributions on the Brundtland Commission were particularly notable, including ideas that helped define the concept of "sustainable development" globally. Throughout her career, she has maintained a humble but passionate perspective, dedicating herself to building an environmental utopia and working towards a more sustainable future, emphasizing the urgency of a social movement that allows for a transition toward an economy that honors the Earth's natural boundaries. Her commitment and fervor for ecological causes highlight her belief in the relevance of learning to coexist with nature, fostering a more balanced and lasting connection with our habitat, especially inspiring other women to take on leadership roles in the protection and conservation of the environment.

Lepanthes margaritamarinoana resembles some species with large size plants with its erect ramicauls up to 60 cm long, with gray to white scabrous lepanthiform sheats, oblong to elliptical ovate leaves, large inflorescences up to 6 cm long, and yellow flowers. Among these species are *Lepanthes caudatisepala* C. Schweinf., *Lepanthes profusa*

FIGURE 16. In-situ photographs of *Lepanthes margaritamarinoana,* Gal.-Tar., Zuluaga, J.S. Moreno, & Sierra-Ariza. **A**, flower, front view; **B**, inflorescence. In-situ photographs by J. S. Moreno.

Luer & Hirtz, *Lepanthes pseudoprofusa* Damian & B.T. Larsen (Damian and Larsen, 2017. These three species can be easily distinguished from the new species by their appendices: whereas *L. caudatisepala*, *L. profusa*, and *L. pseudoprofusa* have biglandular appendices, the new species features a glabrous and oblong slightly tridentate appendix.

6. Lepanthes nidiagongorana Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza, *sp. nov.*
TYPE: COLOMBIA, Valle del Cauca, municipality of Dagua, corregimiento del Queremal, Cerro Tokio, predio sr. Álvaro, Parque Nacional Natural Farallones, 1852 m, 17 August 2020, *R. Galindo-Tarazona, L. Mamian & V. Varón, & D. L. Mora 1497*. Fig. 18–20A.

Lepanthes nidiagongorana is most similar to *Lepanthes filamentosa* Luer & Hirtz, but it differs from the latter mainly by its lip, which has narrowly oblong blades with the upper ends rounded, the lower ends acutely angled on the inner margin with a narrowly obtuse apex, and a short microscopically pubescent, semicircular, concave appendix (vs. the lobes auricular with the upper end above the column thickened to form an ill-defined lamina, the middle of the lower lobe falcate with broadly-rounded, incurved, overlapping apices, without an appendix).

Plant epiphytic, caespitose, 3.6–4.1 cm tall; *roots* slender, flexuous, filiform, 0.55 mm in diameter. *Ramicauls* erect, slender, 1.6–2.1 cm long, enclosed by 3–4 acuminate, minutely pubescent lepanthiform sheaths, with a dilated and ciliate ostia. *Leaves* dark-purple abaxially, horizontal, coriaceous, narrowly ovate, acute, 1.73–1.97 × 3.60–4.16 cm, apex emarginate with an abaxial apiculum in the middle, base cuneate contracted into a petiole, 2.6–3.18 mm long. *Inflorescence* congested distichous racemes, up to 2, 7–21[–many] successively flowered, up to 1.51–2.16 cm long including the peduncle, loose, slender, held appressed to the adaxial surface of the leaf by a filiform, terete peduncle, 7.02–8.95 cm long; *floral bracts* conical, acuminate, minutely scabrous, 0.38–0.48 mm long; *pedicels* terete, 0.86–1.21 mm long. *Ovary* terete, costate, 0.69 mm long. *Flowers* with the dorsal sepal pale yellow, the center purplish-red, lateral sepals cream; petals light-yellow; lip cream and column yellow. *Dorsal sepal* narrowly ovate, long-acuminate, acute, 3-veined, 4.26–4.42 × 0.97 mm, connate to the lateral

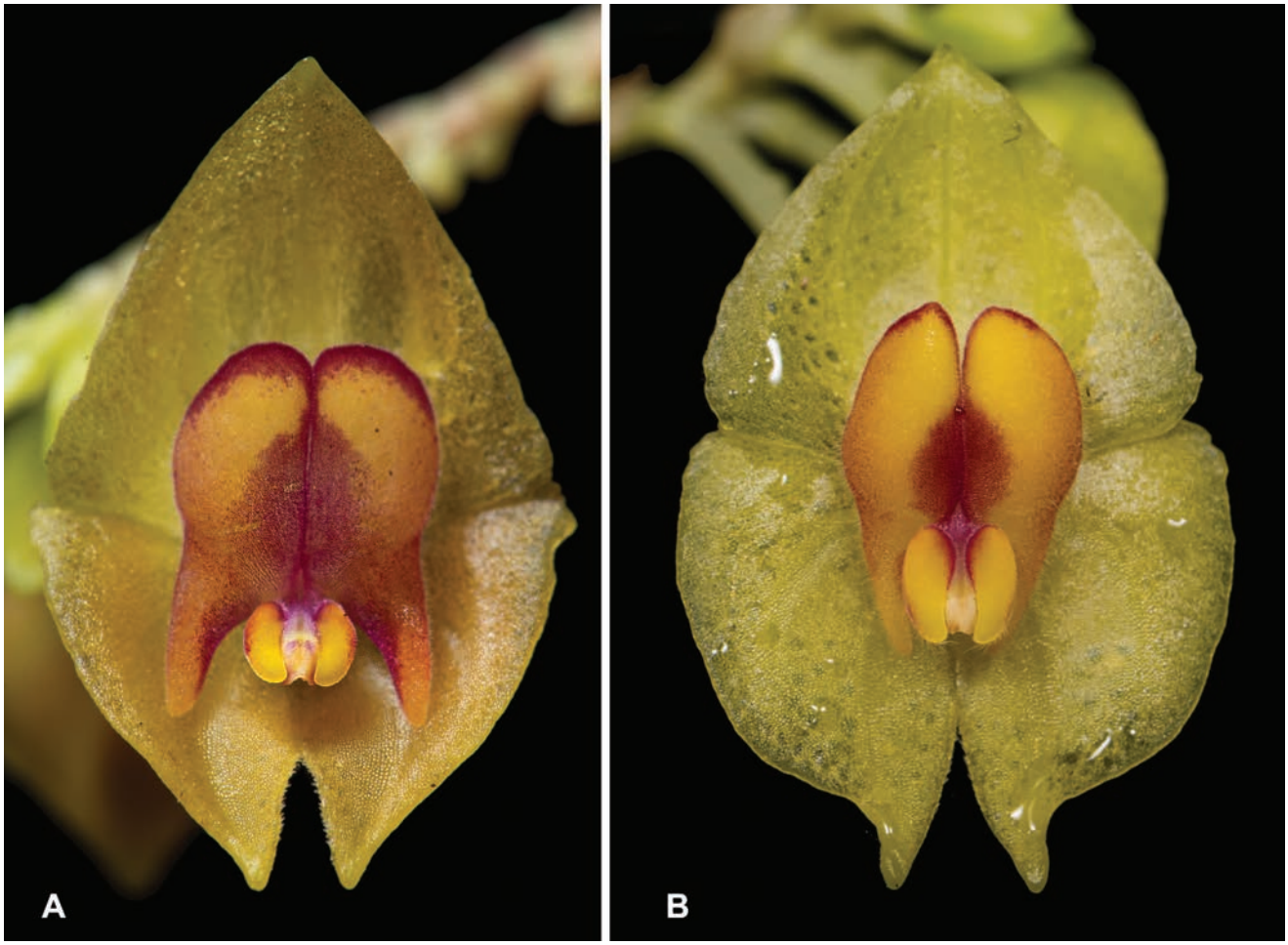


FIGURE 17. Comparison with the most similar species. **A**, *Lepanthes margaritamarinoana,* Gal.-Tar., Zuluaga, J.S. Moreno, & Sierra-Ariza; **B**, *Lepanthes gargantua* Rchb.f. Photographs by J. S. Moreno.

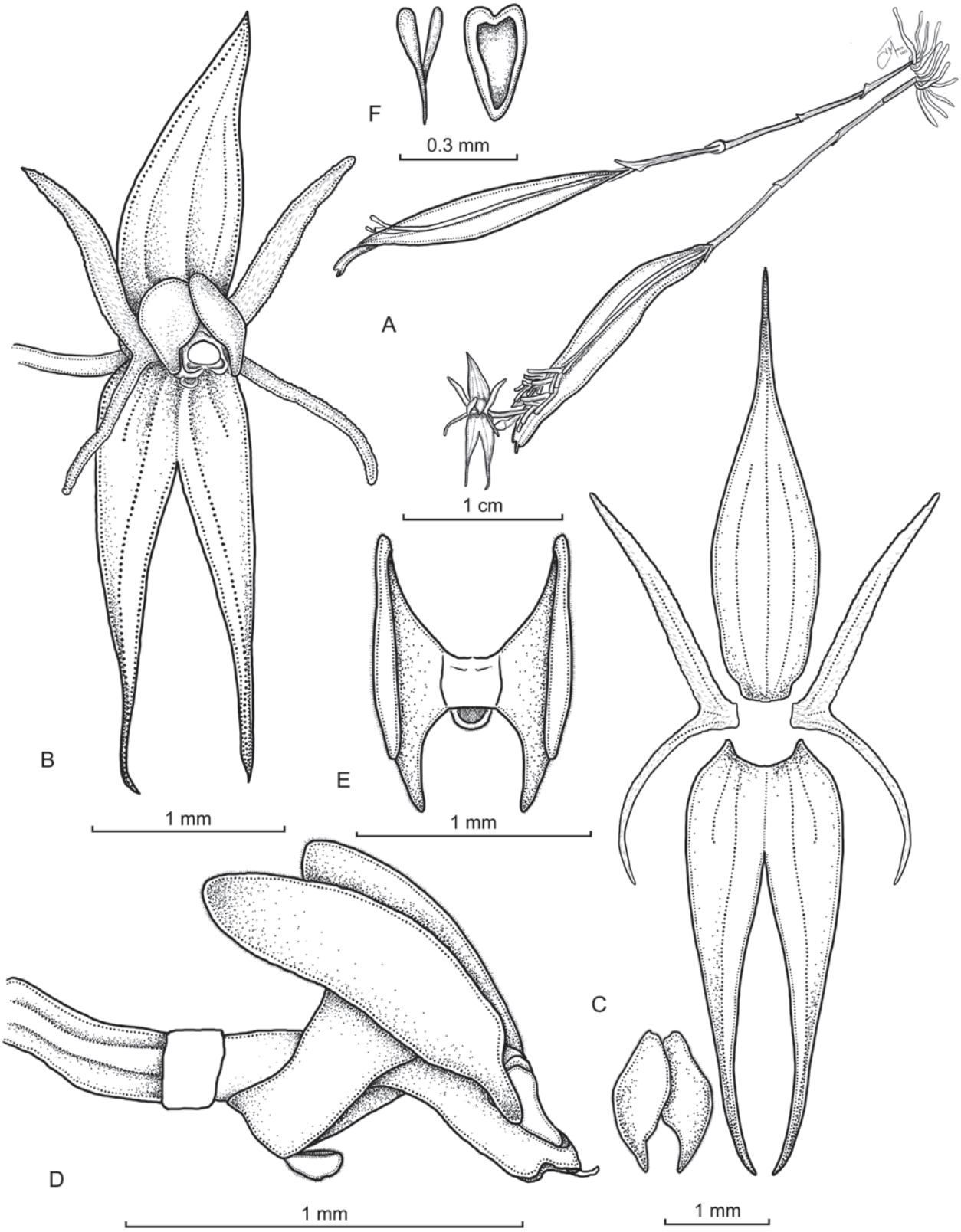


FIGURE 18. *Lepanthes nidiagongorana* Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded; **F**, anther cap and pollinia. Drawing by J. S. Moreno based on the holotype.

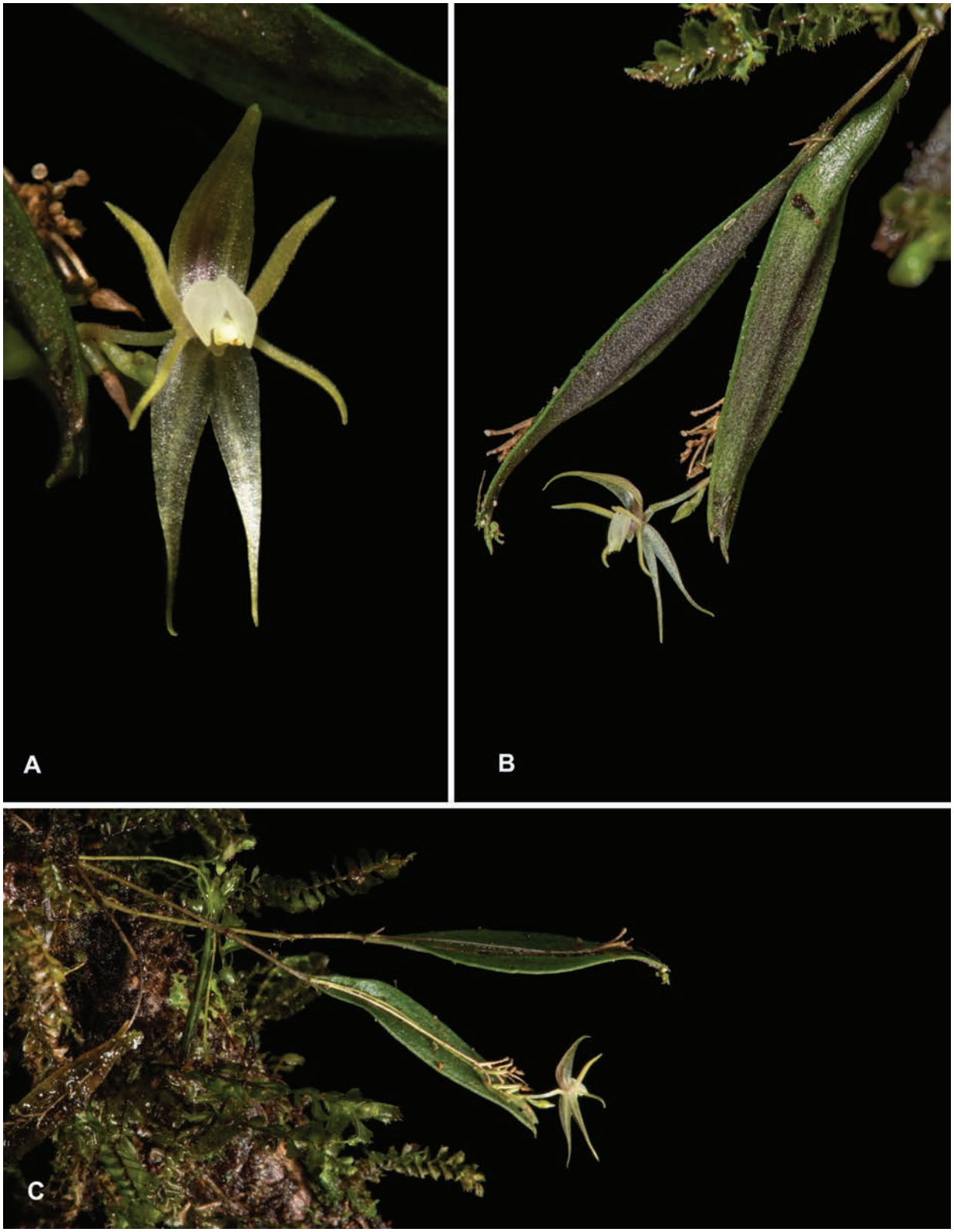


FIGURE 19. In-situ photographs of *Lepanthes nidiagongorana* Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza. **A**, flower, 3/4 view; **B**, leaf and inflorescence; **C**, habit and plant. In-situ photographs by R. Galindo-Tarazona.

sepals for 1.39–2.65 mm. *Lateral sepals* narrowly ovate, acuminate, 2-veined, 3.75–4.06 × 0.72–0.88 mm, connate for 0.92 mm. *Petals* microscopically pubescent, bifurcate, acute, upper lobe 2.47–2.55 mm long, lower lobe 1.98–2.14 mm long and 0.2–0.28 wide; both lobes linear, lower lobe falcate, acute, 3-veined. *Lip* microscopically pubescent, slightly depressed in the middle, bilaminate, blades narrowly oblong, upper end rounded, overlapping, lower end acutely angled on the inner margin with a narrowly obtuse apex, 1.19–1.42 × 0.39–0.48, supported by cuneate connectives; body broad, adnate to the base of the column, sinus rounded with a short microscopically pubescent, semicircular, concave appendix. *Column* terete, 0.82–1.24 mm long, anther dorsal and stigma ventral. *Anther cap* cordate, cucullate, 0.4 mm wide. *Pollinia* 2, yellow, pyriform, narrowly obovoid, 0.37 mm long.

Eponymy: The new species is named in honor of Nidia Góngora, an influential singer-songwriter and founder of the musical band Canalón de Timbiquí, lead voice of Ondatropica, Pacifican Power, and co-founder of the musical project Quantic and Nidia Góngora from Colombia. Hailing from Santa Bárbara de Timbiquí, in the Cauca region, Nidia has devoted her life to promoting and preserving the traditional music of the Colombian Pacific and the Afro-Colombian cultural heritage. As a pioneering female figure in a musical genre, Nidia serves as an inspiration for many, especially women aspiring to make a mark in various fields. Nidia sees music not just as an art form, but also as a means to keep culture and tradition alive. Her role as a woman in the music industry amplifies the significance of this dedication, highlighting the importance of female representation and leadership in all sectors. She aims to ensure that future generations can experience and appreciate the cultural richness of her native region by weaving bridges between the traditional music of her land and other genres around the world.

Lepanthes nidiagonogorana is a new species that can be recognized easily by the combination of: medium size plants with the inflorescences held appressed to the adaxial surface of the leaf, surpassing the leaf and flowering close to the apex; narrowly ovate and long acuminate sepals with transversely bilobed linear petals; and a short semi-circular concave appendix. Only one species from Colombia and Ecuador, *Lepanthes filamentosa* (Fig. 20B), has similar sepals and petals. The new species can be recognized from the latter mainly by its medium-size plants, for *Lepanthes*, up to 3 cm tall (vs. minute-size plants, 4–10 mm long),

FIGURE 20. Comparison with the most similar species. **A**, *Lepanthes nidiagongorana* Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza; **B**, *Lepanthes filamentosa* Luer & Hirtz. Photographs by R. Galindo-Tarazona (A) and J. S. Moreno (B).

narrowly ovate leaves, 1.73–1.97 × 3.6–4.16 cm (vs. small, elliptical leaves, 3–7 × 2.5–5.0 mm), loose and slender inflorescences held appressed to the adaxial surface of the leaf by a filiform, terete peduncle, 1.1–1.4 cm long (vs. erect to suberect inflorescences that surpass the flowers vertically or horizontally with the peduncle up to 1.8 cm long), the linear petals (vs. filiform), and the lip as mentioned above in the diagnosis.

7. Lepanthes nubiamuñozana J.S. Moreno, Gal.-Tar., & Zuluaga *sp. nov.*
TYPE: COLOMBIA, Valle del Cauca, Cali, Minas del Socorro, Parque Nacional Natural Farallones de Cali, 3390 m, 28 June 2020, *R. Galindo-Tarazona, A. Fierro, G. Rodriguez, M. Espitia, & G. Marín 1474* (Holotype: CUVC). Fig. 21–23A.

Lepanthes nubiamuñozana is most similar to *Lepanthes kokonuko* J.S. Moreno & Pisso-Florez, but it differs from the latter mainly by its ovoid lip blades (vs. ovate-lanceolate) and an obtuse, pubescent, and slightly bifid appendix (vs. bipartite appendix composed of two linear, clavate processes).

Plant epiphytic, caespitose, 9.2–11.8 cm tall; *roots* slender, flexuous, filiform, 0.68 mm in diameter. *Ramicauls* erect to suberect, slender, 7.1–8.8 cm long, enclosed by 4–5 acuminate, minutely pubescent lepanthiform sheaths, with a dilated and minutely ciliate ostia. *Leaves* erect, coriaceous, lanceolate, acute, 5.5–6.5 × 1.7–2.6 cm, apex emarginate with an abaxial apiculum in the middle, base cuneate contracted into a petiole, 1.1–1.7 mm long. *Inflorescence* congested, pendant, distichous raceme, 18–22[–many], successively flowered, up to 2.5–3.5 cm long including the peduncle, loose, distichous, slender, held appressed to the adaxial surface of the leaf by a filiform, terete peduncle, 1.1–1.4 cm long; *floral bracts* conical, acuminate, minutely scabrous, 0.9–1.3 mm long; *pedicels* terete, 2.1–2.5 mm long. *Ovary* terete, costate, 3.48 mm long. *Flower* with sepals yellow with the center orange-yellow, petals with the upper lobe orange to red, lower lobe orange; lip orange suffused with red and the column purple. *Dorsal sepal* narrowly ovate, acute, 3-veined, 4.8–4.9 × 5.5–5.6 mm, connate to the lateral sepals for 1.49 mm. *Lateral sepals* minutely pubescent, narrowly ovate, oblique, acute, strongly revolute in natural position, 2-veined, 5.5–6.6 × 3.2–3.9 mm, connate for 2.6 mm. *Petals* microscopically pubescent, transversely bilobed, acute, 1-veined, 1.6–1.7 × 3.7 mm; lobes subequal, triangular, obtuse, sometimes acuminate in the upper lobe. *Lip* minutely pubescent, ovoid, bilaminate, blades narrowly oblong, upper and lower ends rounded, the lower lobe with the apices narrowly obtuse, 2.5 × 0.9–1.1 mm, supported by cuneate connectives; body broad, adnate to the base of the column, sinus broad with a short, obtuse, pubescent, and slightly bifid appendix. *Column* terete, 2.09 mm long, anther dorsal and stigma ventral. *Anther cap* cordate, cucullate, 0.62 mm wide. *Pollinia* 2, yellow, pyriform, narrowly obovoid, 0.3 mm long.

Eponymy: The new species honors Nubia Amparo Muñoz Calero, a renowned Colombian medical scientist who has been a cornerstone in epidemiological research. She was nominated for the Nobel Prize in 2008 by the International Epidemiological Association, due to her groundbreaking advancements in the study of a vaccine against the human papillomavirus (HPV). Her work has not only had a significant impact on global public health, particularly in preventing cervical cancer among women, but has also earned her the Order of Boyacá in 2011, which is the highest honor that the Colombian Government awards to distinguished citizens for their service to the country and stands as a testament to the transformative impact of her work. Nubia Muñoz serves as a role model for female scientists in Colombia, demonstrating that women's leadership in science can lead to significant, life-saving advancements.

Lepanthes nubiamuñozana is a new species that can be easily recognized by its lanceolate leaves and its racemose, loose, and long pendant inflorescences. It is probably related to the other racemose species: *Lepanthes biloba* Luer & R. Escobar, *Lepanthes guanacasensis* Luer & R. Escobar, *Lepanthes kokonuko* J.S. Moreno & Pisso-Florez, *Lepanthes muscula* Luer & R. Escobar and *Lepanthes osiris* Luer & R. Escobar (Luer and Thoerle, 2012; Moreno et al., 2020). But the most similar species is undoubtedly *Lepanthes kokonuko* (Fig. 23B), which shares strongly revolute lateral sepals with the new species, but differs by its elliptical leaves (vs. lanceolate), transversely bilobed petals with the upper lobe narrowly triangular and recurved and the lower lobe shorter than the upper lobe, ovate to triangular and slightly falcate (vs. the petals with the lobes similar in size and triangular), and a bilaminate lip as compared in the diagnosis.

8. Lepanthes paolaalzateana Gal.-Tar., J.S. Moreno, & Zuluaga *sp. nov.*
TYPE: COLOMBIA, Valle del Cauca, Cali, Minas del Socorro, Parque Nacional Natural Farallones de Cali, 3200 m, 29 June 2020, *R. Galindo-Tarazona, A. Fierro, G. Rodriguez, M. Espitia, & G. Marín 1477* (Holotype: CUVC). Fig. 24–26A.

Lepanthes paolaalzateana is most similar to *Lepanthes microprosartima* Tobar & M.J. Gavil., but the new species can be distinguished by its petals with a lanceolate, falcate, caudate, upper lobe that is longer than the lower lobe and an ovate-lanceolate, strongly falcate, caudate lower lobe (vs. a narrowly triangular upper lobe with revolute margins and a broadly triangular and obtuse lower lobe), and a narrowly oblong-ovate lip (vs. ovate) with a short appendix with a minute apiculum in the middle (vs. oblong-lanceolate).

Plant epiphytic, caespitose, 13.4–19.1 cm tall; *roots* slender, flexuous, filiform, 0.7–1.0 mm in diameter. *Ramicauls* horizontal to pendent, slender, 9.0–12.3 cm long, enclosed by 9–10 acuminate, minutely ciliate lepanthiform sheaths, with a dilated and ciliate ostia. *Leaves* spreading, on the adaxial surface dark green, glossy, on the abaxial surface dark purple, thick and coriaceous, with pronounced margins, ovate-lanceolate, acuminate 4.2–5.3 × 1.00–1.27 cm, apex emarginate with an abaxial apiculum in the middle, base cuneate contracted into a petiole, 1.1–3.1mm long.

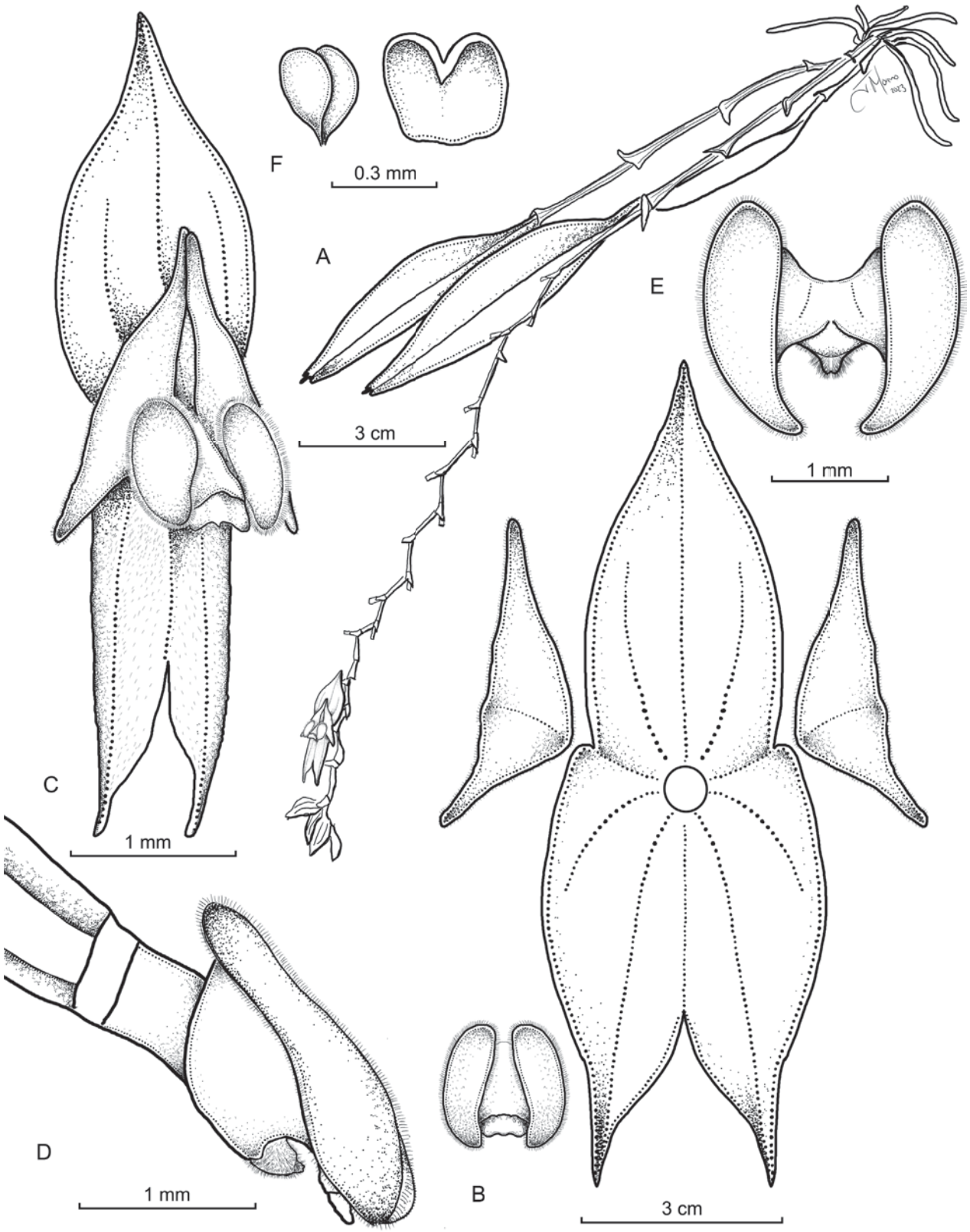


FIGURE 21. *Lepanthes nubiamuñozana* J.S. Moreno, Gal.-Tar., & Zuluaga. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded; **F**, pollinia and anther cap. Drawing by J. S. Moreno based on the holotype.

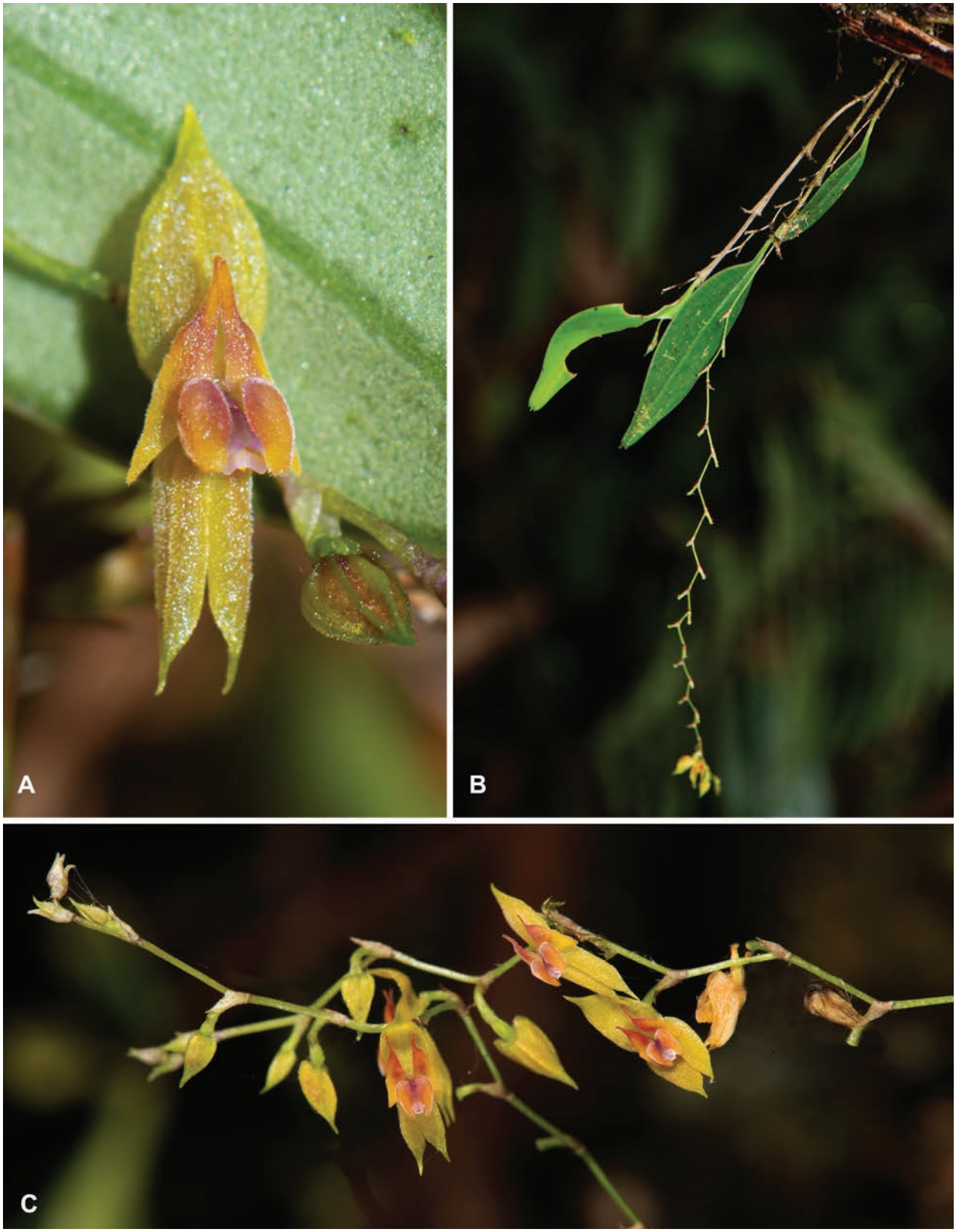


FIGURE 22. In-situ photographs of *Lepanthes nubiamuñozana* J.S. Moreno, Gal.-Tar., & Zuluaga. **A**, flower, 3/4 view; **B**, habit, plant, and inflorescence; **C**, inflorescence. In-situ photographs by A. Zuluaga.

Inflorescence congested, distichous raceme, 10–18[–many] successively flowered, up to 2.5–7.3 cm long including the peduncle, loose, distichous, slender, held appressed to the abaxial surface of the leaf by a filiform, terete peduncle, 1.5–1.8 cm long; *floral bracts* ovate, acuminate, papyraceous, 0.7–1.1 mm long; *pedicels* terete, 0.5–0.8 mm long. *Ovary* terete, costate, 2.9 mm long. *Flowers* with dorsal sepal light-yellow, lateral sepals bicolorous longitudinally with the inner half purple-red and the outer half light yellow; petals bicolorous longitudinally with the inner half red and the outer half yellow, apex of the upper lobe red, lip red-orange with margins purple-red and column purple. *Dorsal sepal* ovate to subtriangular, carinate, acute, 3-veined, 5.9–8.1 × 3.6–4.9 mm, connate to the lateral sepals for 1.7–2.4 mm. *Lateral sepals* minutely pubescent, elliptic-lanceolate, oblique, carinate, short-papillate along the margins, 2-veined, 5.2–7.4 × 2.4–3.3 mm, connate for 2.7–4.0 mm. *Petals* microscopically pubescent, transversely bilobed, 1-veined, 5.6–8.7 × 1.1–1.7 mm; upper lobe lanceolate, falcate, caudate, longer than the lower lobe; lower lobe ovate-lanceolate, strongly falcate, caudate. *Lip* minutely pubescent, slightly oblique in relation to the column axis, with ciliated margin, bilaminate, blades narrowly oblong-ovate, both lobes with rounded ends, 1.5–3.2 × 0.4–1.0 mm, supported by wide, subquadrate, cuneate connectives; body broad, adnate to the base of the column, appendix short, strongly pilose, with a minute apiculum in the middle. *Column* terete, 2.1–3.8 mm long, anther dorsal and stigma ventral. *Anther cap* not seen. *Pollinia* not seen.

Eponymy: The new species honors Paola Alzate, a park ranger and an environmental leader in the National Natura Park Los Farallones de Cali. She has worked in the institution for more than fourteen years in topics related to conservation and protection of the natural resources within

FIGURE 23. Comparison with the most similar species. **A**, *Lepanthes nubiamuñozana* J.S. Moreno, Gal.-Tar., & Zuluaga; **B**, *Lepanthes kokonuko* J.S. Moreno & Pisso-Florez. Photographs by A. Zuluaga (A) and J. S. Moreno (B).

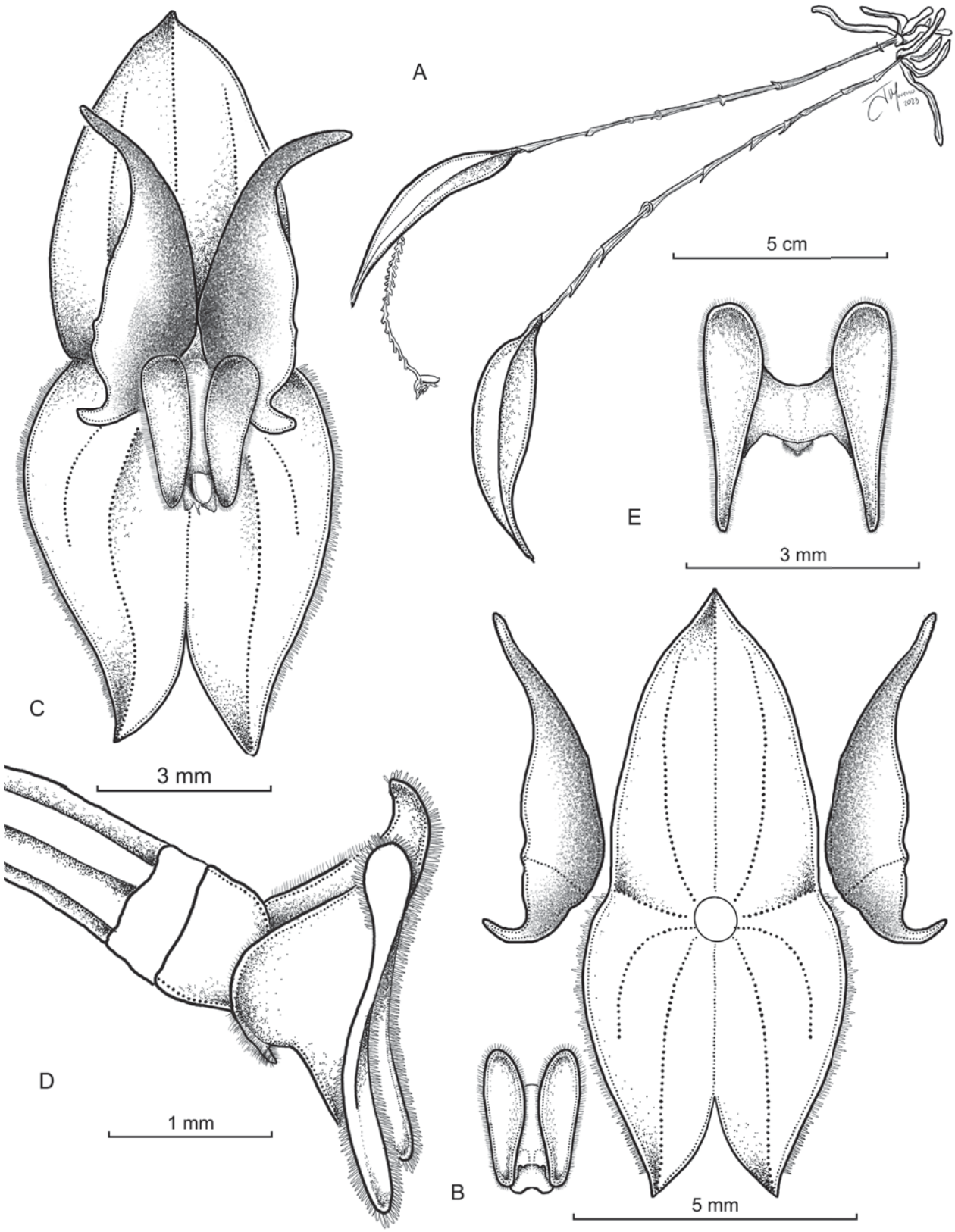


FIGURE 24. *Lepanthes paolaalzateana* Gal.-Tar., J.S. Moreno, & Zuluaga. **A**, habit and plant; **B**, flower; **C**, dissected perianth; **D**, lip, column and ovary; **E**, lip expanded. Drawing by J. S. Moreno based on the holotype.

FIGURE 25. In-situ photographs of *Lepanthes paolaalzateana* Gal.-Tar., J.S. Moreno, & Zuluaga. **A**, flower, 3/4 view; **B**, flower, lateral view; **C**, habit and plant. In-situ photographs by R. Galindo-Tarazona.

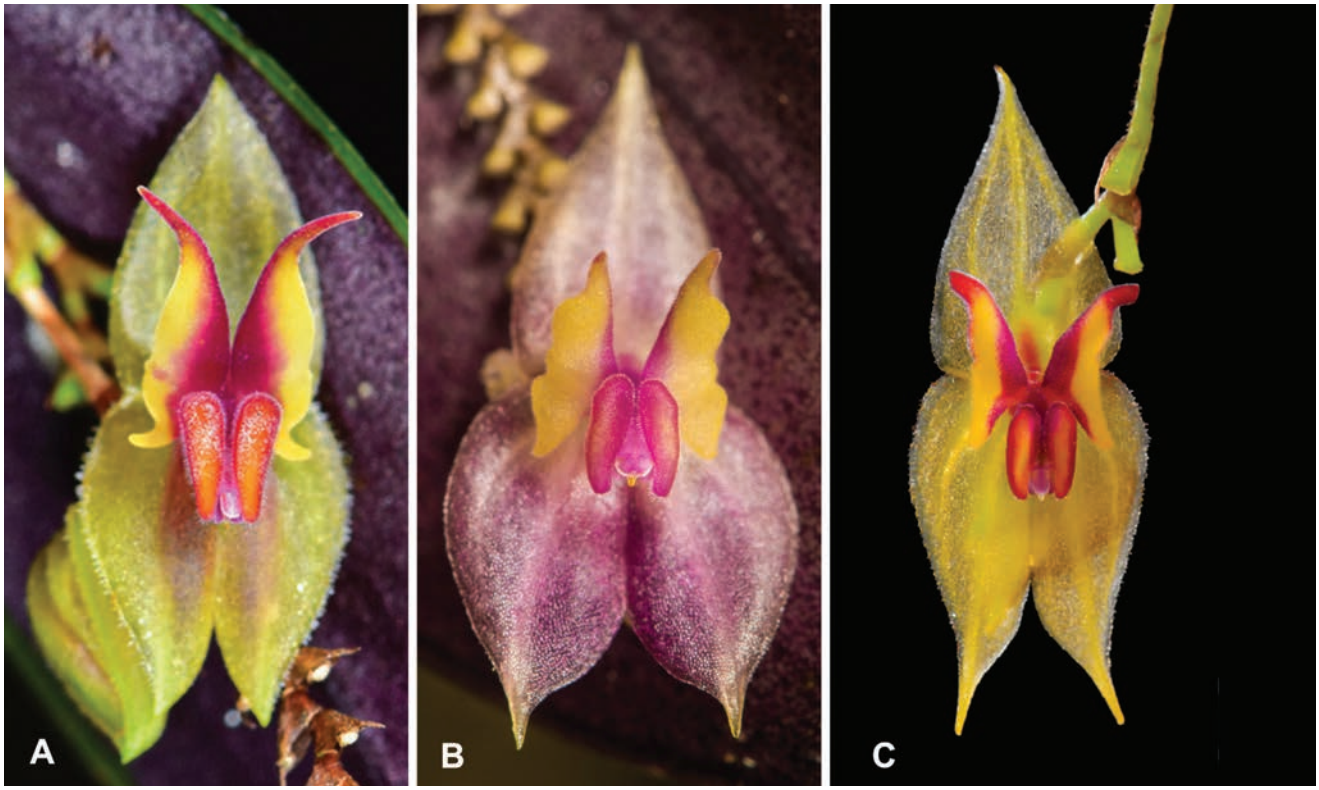


FIGURE 26. Comparison with the most similar species. **A**, *Lepanthes paolaalzateana* Gal.-Tar., J.S. Moreno, & Zuluaga; **B**, *Lepanthes dunstervilleorum* Foldats; **C**, *Lepanthes microprosartima* Tobar & M.J. Gavil. Photographs by R. Galindo-Tarazona (A), J. S. Moreno (B) and Francisco Tobar (C).

the park. Her empirical knowledge of plants and animals lead her to fall in love with orchids. Paola has carried out several projects related to the establishment of orchid nurseries in the department of Valle del Cauca.

Lepanthes paolaalzateana is a new species that can be easily identify by its strongly falcate lobes of the petals with the upper lobe much longer than the lower, as stated in the diagnosis. The most similar species are *Lepanthes dunstervilleorum* Foldats (Fig. 26B), *Lepanthes mirador* Luer & Hirtz, and *Lepanthes microprosartima* (Fig. 26C) (Tobar et al., 2021). It can be distinguished from *Lepanthes dunstervilleorum* by its petals with the upper lobe lanceolate, falcate and the lower lobe ovate-lanceolate, strongly falcate (vs. the upper lobe oblong with the apex variable from rounded to contracted on the medial half and the lower lobe obtuse triangular). Also, the blades of the lip in *L. paolaalzateana* are narrowly oblong-ovate (vs. oblong) with a short appendix, with an apiculum in the middle (vs. more or less oblong with modifications). It is different from *Lepanthes mirador*, which has oblong blades in the lip (vs. narrowly oblong-ovate) and an oblong appendix with a bilobed apical segment. *Lepanthes microprosartima* is undoubtedly the most similar species by sharing similar flowers superficially, but *L. microprosartima* is a larger, terrestrial, prolific plant up to 40 cm tall (vs. epiphytic and caespitose, with plants up to 19 cm tall) with ramicauls that can reach 25 cm long (vs. up to 12.3 cm long). The leaves of *L.* microprosartima are oblong-ovate, up to 9.4 cm long (vs. ovate-lanceolate, up to 5.3 cm long); the petals and lip are compared above in the diagnosis.

Habitat and ecology: *Lepanthes dianatrujilloana*, *L. dianauribeana*, *L. margaritamarinoana*, and *L. nidiagongorana* were found in Cerro Tokio, Queremal, Valle del Cauca, in secondary forests along the road in secondary premontane to montane rainforest transition. The forest is constantly under the influence of clouds that create a humid environment that is ideal for bryophytes. The canopy is low, less than 15 m, and the understory is dominated by Araceae and Cyclanthaceae. *Lepanthes gloriagaleanoana* was found in cloud forests inside secondary forests growing next to *Lepanthes speciosa* Luer & Hirtz and *Dracula chimaera* (Rchb.f.) Luer. *Lepanthes laurarestrepoana*, *L. nubiamuñozana*, and *L. paolaalzateana* were found growing on dense sub-paramo vegetation, with shrubs and small trees less than 4 m.

Conservation status: Most of the eight new species are known only from their type locality and some of them from one more locality but nonetheless located in the buffer zone of the National Natural Park. Due to their position within the park, and assuming their constant protection, the IUCN classification is data deficient (DD), because we lack adequate distribution and population information to make an assessment (IUCN Standards and Petitions Subcommittee, 2017; IUCN, 2023).

Literature Cited

Baquero, L. E., R. Galindo-Tarazona, D. Haelterman, and A. Zuluaga. 2021. A new *Lepanthes* (Pleurothallidinae) from southwestern Colombia. Lankesteriana, 21(3): 341–349. doi: http://dx.doi.org/10.15517/lank.v21i3.49410

Beentje, H. 2012. The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms. Royal Botanic Gardens, Kew. Kew Publishing, Richmond, UK.

Bogarín, D., K. Eberhard, and M. Díaz-Morales. 2019. *Lepanthes elusiva*—a new Species of *Lepanthes* (Orchidaceae: Pleurothallidinae) from Tapantí area in Cartago, Costa Rica and a Glance to Other Species of the Genus in a Small Area Around the Río Grande de Orosi in Costa Rica. Die Orchidee 5(03): 17–28.

Damián, A., and B. Larsen. 2017. Three new species of *Lepanthes* (Pleurothallidinae: Orchidaceae) from Amazonas, Peru. Phytotaxa 291(2): 149–156. doi: https://doi.org/10.11646/phytotaxa.291.2.6

Galindo-Tarazona, R., D. Haelterman, A. Zuluaga, and J. S. Moreno. 2020. Orquídeas de Farallones de Cali: del Páramo a la selva húmeda. Santiago de Cali. D.C. Colombia.

Galindo-Tarazona, R., D. Haelterman, D. L. Mora Aguilar, & A. Zuluaga. 2021. A new *Masdevallia* from south-western Colombia (Orchidaceae: Pleurothallidinae). Phytotaxa 502(3): 277–282.

Guedes, P., F. Alves-Martins, J. M. Arribas, S. Chatterjee, A. M. Santos, A. Lewin, L. Bako, P. W. Webala, R. A. Correia, R. Rocha, and R. J. Ladle. 2023. Eponyms have no place in 21st-century biological nomenclature. Nature Ecology & Evolution 7: 1157–1160. https://doi.org/10.1038/s41559-023-02022-y

IUCN Standards and Petitions Subcommittee. 2017. Guidelines for using the IUCN red list categories and criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. vailable at: http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf (accessed September 10, 2023).

IUCN. 2023. The IUCN red list of species. 2018. Available at: https://www.iucnredlist.org (accessed April 3, 2023).

Jost, L., M. H. Yanez-Muñoz, J. Brito, C. Reyes-Puig, J. P. Reyes-Puig, J. M. Guayasamín, S. R. Ron, C. Quintana, G. Iturralde, L. Baquero, M. Monteros, A. Freire-Fierro, D. Fernández, G. Mendieta-Leiva, J. F. Morales, A. P. Karremans, J. A. Vázquez-García, G. A. Salazar, E. Hágsater, R. Solano, G. C. Fernández-Concha, and M. Arana. 2023. Eponyms are important tools for biologists in the Global South. Nature Ecology & Evolution 7(8): 1164–1165. https://doi.org/10.1038/s41559-023-02102-z.

Karremans, A. P., J. S. Moreno, K. Gil-Amaya, N. Gutiérrez Morales, F. Espinosa, S. Mesa, E. Restrepo, M. Rincón-González, A. Serna, M. Sierra-Ariza, and S. Vieira-Uribe. 2023. Colombian Orchidaceae: A Catalogue of the Pleurothallidinae. Lankesteriana 23(2): 181–400.

Luer, C. A. 1996. Icones Pleurothallidinarum, XIV: The genus *Lepanthes*, subgenus *Lepanthes* in Ecuador. Monographs in Systematic Botany from the Missouri Botanical Garden, 61: 1–255.

Luer, C. A, and L. Thoerle. 2012. Icones Pleurothallidinarum XXXII: *Lepanthes* of Colombia (Orchidaceae). Missouri Botanical Garden Press, St. Louis, Missouri.

Moreno, J. S., S. Vieira-Uribe, and A. P. Karremans. 2017. A new Species of *Lepanthes* (Orchidaceae: Pleurothallidinae) from Colombia with a large and protruding column. Lankesteriana 17: 193–202. doi: http://dx.doi.org/10.15517/lank.v17i2.29928

Moreno, J. S., G. A. Pisso-Florez, and S. Vieira-Uribe. 2020. Discoveries in indigenous territories: Two new species of *Lepanthes* (Orchidaceae: Pleurothallidinae) in southwestern Colombia. Lankesteriana 20(2): 229–239. doi: http://dx.doi.org/10.15517/lank.v20i2.43358

Moreno, J. S., R. Galindo-Tarazona, M. Alegría-Valencia, M. Wilson, and A. Zuluaga Tróchez. 2023. A new species of *Pleurothallis* (Pleurothallidinae) from the southwestern Andes of Colombia in the National Natural Park Farallones de Cali. Lankesteriana 23(2): 401–407. doi: http://dx.doi.org/10.15517/lank.v23i2.56290

Parra-Sánchez, E. P., E. Restrepo, M. Alegría-Valencia, J. S. Moreno, and R. Galindo-Tarazona. 2023. *Lepanthes cordillerana* (Orchidaceae) a new species and the landscape threats to its wild populations. Phytotaxa 603(1): 69–80.

Pethiyagoda, R. 2023. Policing the scientific lexicon: The new colonialism?. Megataxa 10(1): 20–25. https://doi.org/10.11646/megataxa.10.1.4

Pupulin, F., H. Medina, and D. Bogarín. 2011. Two *Lepanthes* (Orchidaceae: Pleurothallidinae) with strongly reduced corolla. Orchideen Journal 1(1): 31–35.

Swartz, O. 1799. Dianome Epidendri generis Linn. Nova Acta Regiae Societatis Scientiarum Upsaliensis 2nd ser. 6: 61–88.

Slabin, U. 2023. Should Eponyms Be Kept? Emphatic Yes. Journal of Baltic Science Education 22(2): 188–191.

Stearn, W. T. 1992. Botanical Latin (4th ed.). Timber Press, Portland, Oregon, U.S.A.

Tobar, F., M. F. López, M. J. Gavilanes, M. F. Monteros, T. García, and C. H. Graham. 2021. Three new endemic species of *Lepanthes* (Orchidaceae, Pleurothallidinae) from the highlands of Ecuador. Phytokeys 180: 111–132.

UAESPNN, Unidad Administrativa Especial del Sistema de Parques Nacionales Naturales. 2023. Plan de Manejo Parque Nacional Natural Farallones de Cali. (2021–2027). Dirección Territorial Pacífico. Santiago de Cali.

Wilson, M., B. Larsen, J. S. Moreno, R. Ward, J. A. G. Riksen, L. Piña, M. A. Sierra-Ariza, M. Jiménez, M. Rincón-González, R. Galindo-Tarrazona, H. Garzón Suárez, and D. Haelterman. 2022. New species of *Pleurothallis* (Orchidaceae: Pleurothallidinae), a new country record, and labellar morphology in the *P. cardiostola-P. lilijae* complex of subsection *Macrophyllae-Fasciculatae*. Harvard Papers in Botany 27(2): 187–220.

Page 694 intentionally left blank.

A NEW ENDEMIC SPECIES FROM THE GUIANA SHIELD, *SMILAX BREVIPEDUNCULATA* (SMILACACEAE)

THOMAS H. MURPHY,[1,2,3] SANTOS MIGUEL NIÑO,[4] AND LUCAS C. MAJURE[1]

Abstract. Ongoing taxonomic revision of the genus *Smilax* is revealing that species diversity is underestimated in the Neotropics. While reviewing specimens from the Guiana Shield, a relatively poorly studied region of *Smilax* diversity, we found multiple specimens possessing a consistent combination of morphological characters that do not match any described species. Here, we describe these specimens as a new species known only from the Guiana Shield, *Smilax brevipedunculata sp. nov.*, based on herbarium specimens. This new species has previously been confused with a morphologically similar taxon from the Guiana Shield, *S. lasseriana*, and bears resemblance to the Amazonian species, *S. magnifolia*. An illustration and distribution map of *S. brevipedunculata* are provided along with detailed comparison with similar species. *Smilax brevipedunculata* is only known from six collections, the most recent of which were collected more than three decades ago, making it of conservation concern.

Keywords: endemic species, Guiana Shield, Neotropics, new species, *Smilax*

Resumen. La revisión taxonómica en curso del género *Smilax* está revelando que la diversidad de especies se subestima en el Neotrópico. Mientras revisábamos especímenes del Escudo de Guayana, una región de diversidad de *Smilax* relativamente poco estudiada, encontramos varios especímenes que poseen una combinación consistente de caracteres morfológicos que no coinciden con ninguna especie descrita. Aquí, describimos estos especímenes como una nueva especie conocida solo del Escudo Guayanés, *Smilax brevipedunculata sp. nov.*, basado en especímenes de herbario. Esta nueva especie se había confundido previamente con un taxón morfológicamente similar del Escudo Guayanés, *S. lasseriana*, y se parece mucho a la especie amazónica, *S. magnifolia*. Se proporciona una ilustración y un mapa de distribución de *S. brevipedunculata* junto con una comparación detallada con especies similares. *Smilax brevipedunculata* solo se conoce de seis colecciones, la más reciente se recolectó hace más de tres décadas, por lo que es motivo de preocupación para la conservación.

Palabras claves: especies endémicas, Escudo de Guayana, neotrópico, *Smilax*

Smilax L. is the sole genus that comprises Smilacaceae and exhibits widespread and near-global distribution, occupying tropical to temperate regions. Estimates of the number of the *Smilax* species has varied from ca. 200–350 (Andreata, 1997; Cameron and Fu, 2006; Ferrufino-Acosta, 2010; Qi et al., 2013). The uncertainty in species diversity is due to both the lack of taxonomic research and difficulty inferring species limits in the genus. This taxonomic uncertainty, as partly noted by Cameron and Fu (2006), is likely driven by: 1) a high degree of morphological variation within species, populations, and individuals, 2) lack of adequate collections in herbaria leading to incomplete knowledge of morphological variation, especially in lower stems and reproductive structures, and 3) sexual dimorphism, associated with dioecy, is another possible source of complexity–-one that has not been systematically assessed in *Smilax* but is clearly an important factor to consider in other dioecious groups, such as *Clusia* L. (Clusiaceae; Luján, 2019), *Leucadendron* L. (Proteaceae), and *Sagittaria* L. (Alismataceae; Barrett and Hough, 2012).

Phylogeny, inferred from plastid and nuclear ribosomal DNA, has recovered a well-supported New World clade, in which all neotropical species are putatively placed (Qi et al., 2013, 2023). Neotropical *Smilax* is widely distributed and is ubiquitous throughout its range, consisting of around 100 species (T. Murphy, unpubl. data), but basic knowledge about species limits remains highly uncertain and is in need of intensive study. Taxonomic and phylogenetic knowledge of the neotropical species lags behind what is known of East Asian and North American taxa, as seen in the most recent phylogeny by Qi et al. (2023), which included 23 species from the Neotropics. In addition to lack of taxon sampling in published phylogenies, preliminary research on neotropical *Smilax* has shown that basic information on morphological variation is lacking. As we conduct fieldwork in new areas and review specimens, morphological variation not previously documented for named taxa is being uncovered. Species limits are poorly resolved with numerous undescribed species and species complexes in need of further study.

In the New World, the Guiana Shield is arguably the most poorly understood, taxonomically, for *Smilax*. Taxonomic treatments are available for smaller regions within the Guiana Shield, such as Central French Guiana (Mitchell, 1997), Suriname (Sipman, 1979), and Venezuelan Guayana (Gaskin and Berry, 1998, 2005). Regional treatments of

Fieldwork associated with *Smilax* of the Guiana Shield was supported by funds from the American Society of Plant Taxonomists awarded to TM. Travel to F, MO, and NY was made possible by awards to TM from the Gapenski Endowment by the Florida Museum of Natural History. Travel to F was also supplemented by support provided by Weston Testo. The following people made visits and examination of specimens possible for TM: Mary Merello and Jordan Teisher of MO, Matthew Pace of NY, Iwan Molgo and Eliza Zschuschen of BBS, and Lucia Kawasaki and Matt von Konrat of F. We are grateful to J. Esteban Jiménez for assistance with assembling Fig. 3. Kelly Ho illustrated Fig. 1. We thank the editor, Gustavo Romero, for comments that improved the manuscript.

[1] University of Florida Herbarium (FLAS), Florida Museum of Natural History, Gainesville, FL 32611, U.S.A.
[2] Department of Biology, University of Florida, Gainesville, FL 32611, U.S.A.
[3] Corresponding author: thm52126@gmail.com
[4] Herbario Universitario (PORT), INBIO-UNELLEZ, Carretera Nacional vía Biscucuy, Mesa de Cavacas, Portuguesa 3323, Venezuela

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 695–702.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n5, Published online: 31 December 2023

Smilax outside of the Guiana Shield (Andreata, 1997; Botina-Papamija., 2008; Ferrufino-Acosta, 2010) have substantially contributed to understanding species limits in the Neotropics. Still, taxonomic treatments and herbarium specimen determinations indicate a great amount of conflict in interpretation of species limits, nomenclatural priority, and application of names. A modern and comprehensive treatment of *Smilax* of the Guiana Shield is needed to capture the complexities and nuances of morphological variation and for application of a consistent species concept.

While reviewing herbarium specimens, the authors found six collections, represented by eight specimens, that exhibited a unique morphology not known in any other *Smilax* species in the Neotropics but which had previously been mistaken as several species that are known from the Guiana Shield. Subsequently, we found the treatment of *Smilax* for Suriname by Sipman (1979) also noted this as a distinct but unnamed taxon "*Smilax* sp. II," which represents the second species that we independently discovered (Murphy et al., in press) from herbarium specimens also noted by Sipman. Due to its morphological distinctiveness, based on multiple vegetative and reproductive characters in *Smilax*, we describe these specimens as a new species, *S. brevipedunculata sp. nov*.

Materials and Methods

We examined physical specimens from BBS, F, FLAS, IVIC, JBSD, MER, MO, NY, PMA, PORT, and USM and photos of specimens from CAY, HOXA, U, and US (acronyms follow Thiers, continuously updated). All measurements were made with a digital caliper from dry herbarium specimens except for flowers and fruits, which were rehydrated prior to measurement. Rehydration entailed boiling water with dish soap in a beaker and placing material in the solution for two minutes. We then removed the material and placed it in a petri dish with a small amount of the soap water solution to keep it from drying out during examination, collecting measurements, and photographing. We compared the new species to species it has previously been determined as, *S. lasseriana* Steyerm., and the morphologically similar taxon, *S. magnifolia* Macbr., which included examination of the type specimens of these species.

The distribution of the species described herein was mapped with R 4.1.2 (R Core Team, 2021), implemented in RStudio 2021.09.1 (RStudio Team, 2021), using the packages 'cowplot' (Wilke, 2020), 'ggplot2' (Wickham, 2016), 'ggsn' (Baquero, 2019), and 'rnaturalearth' (South, 2017). International Union for Conservation of Nature (IUCN) Red List assessments were conducted by calculating extent of occurrence (EOO) and area of occurrence (AOO) to assess threatened categories under Criterion B1, which is based on geographic range. We used the R package 'red' (Cardoso, 2020) to calculate EOO and AOO. When EOO and AOO inferred different threatened categories, we chose the more severe category.

Here, we apply a phenetic species concept (Judd, 2007). This was applied by assigning species based on a combination of characters while also considering secondary evidence from distributions and habitat. We did extract DNA from specimens for sequencing, but the DNA was too degraded to recover usable sequence data, likely due to field preservation techniques using ethanol. Tissue sampled from specimens from the wet tropics tend to yield the poorest quality sequence data based on multiple metrics (Brewer et al., 2019).

For specimens cited below, numbers in brackets refer to unique identifiers, either accession numbers or barcodes. For specimens cited from BBS, MO, and PORT, numbers refer to accession numbers. For specimens cited from NY and U, numbers refer to barcode numbers.

Taxonomy

Smilax brevipedunculata T. Murphy & S. M. Niño, *sp. nov.*, Fig. 1.

TYPE: VENEZUELA. Bolívar: selva pluvial del Río Ikabaru, cerca del Campo Diamantífero de Uai[-P]arú, 400–450 m, 16 abril 1957, (fr), *A. L. Bernardi 6561* (Holotype: NY [barcode 04204354]).

Smilax brevipedunculata is similar to *S. lasseriana* Steyerm. with its peduncles shorter than the petioles and a textured stem, but differs by its stem being lightly verrucose-tuberculate with inconspicuous projections (vs. distinctly verrucose-tuberculate with conspicuous projections), single basal cataphyll (vs. two overlapping basal cataphylls), reniform-shaped receptacles (vs. globose to broadly ovoid), receptacle scales papery and rounded (vs. stiff and acuminate), and anthers 0.5–0.6 mm (vs. [0.6–]0.7–1.0 mm) that are shorter than the filaments (vs. longer than the filaments).

Dioecious climbing vines. Stems to 4 mm wide, unarmed. Branches terete in cross section, surface densely verrucose-tuberculate with inconspicuous and short projections covering the surface, one cataphyll on axial side of basal internode of lateral branches, weakly flexuous to straight on terminal fertile branches, basal internodes of branches 13.1–35.4 mm, shorter than following internodes 17.2–39.7 mm, ratio of basal to following internode length 0.36–1.14. Leaves 9.6–17.2 (–25.0) cm × 2.8–7.7(–12.3) cm, length to width ratio 2.1–3.7, coriaceous, light brown to yellow when dry, glabrous; narrowly elliptic to elliptic, rarely ovate in shape; bases cuneate to rounded, rarely subcordate, apices short-acuminate to apiculate; apex angle obtuse, rarely; adaxial surface lustrous with distinctly raised primary, secondary, and first-order tertiary veins, and higher order veins visible but becoming immersed and somewhat obscured, 4–6 first-order tertiary veins branching directly from midrib in middle 5 cm segment, 7.3–17.9 mm apart; abaxial surface with all vein orders conspicuously raised; venation comprised of midrib with four secondary lateral veins and two additional outer secondary intramarginal veins; petiole 10.0–30.5 mm, darker than lamina when dry, gradually tapering from lamina to petiole. Inflorescences

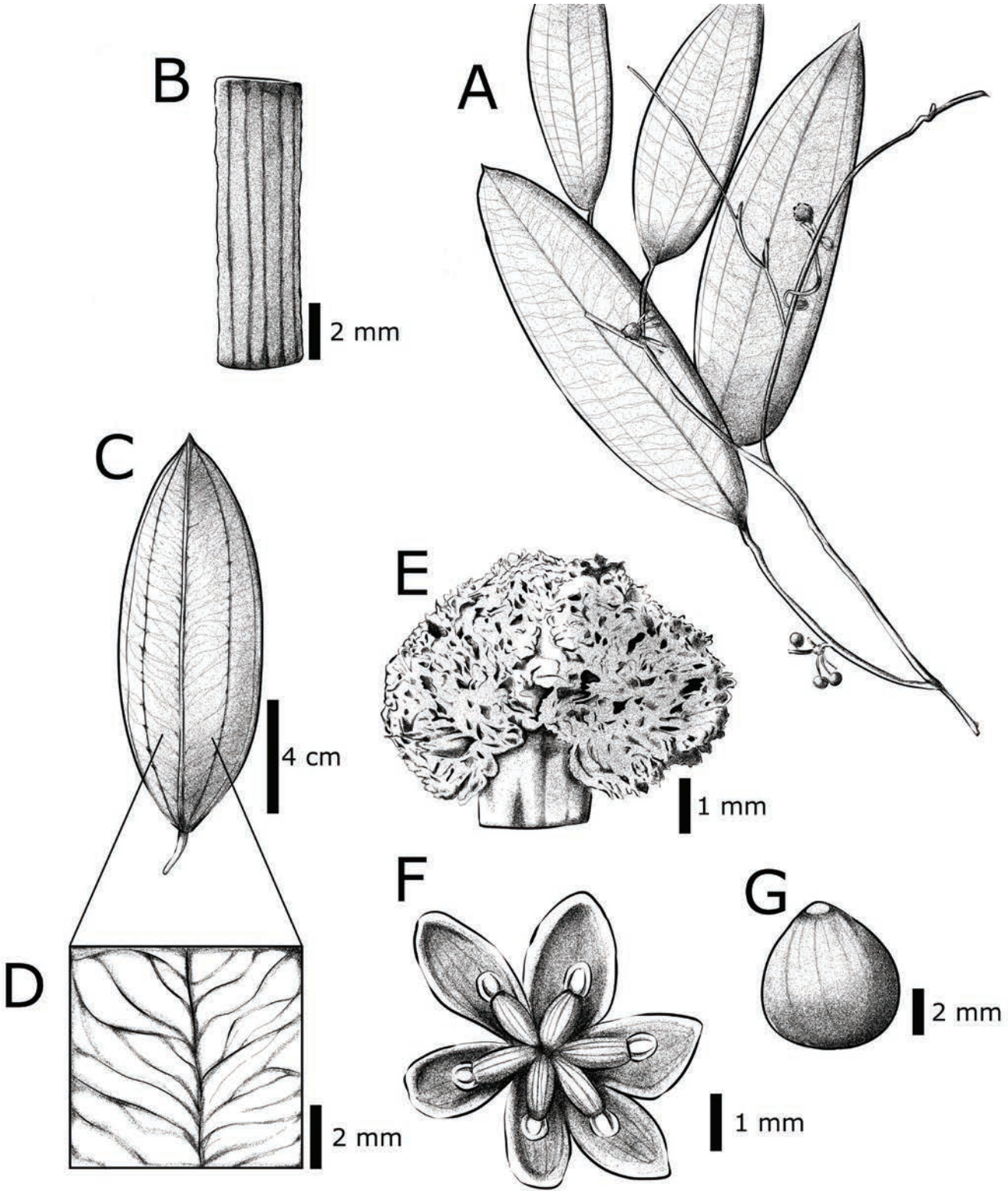


FIGURE 1. Illustration of *Smilax brevipedunculata* T. Murphy & S. M. Niño. **A**, habit; **B**, stem; **C** and **D**, leaf; **E**, receptacle; **F**, staminate flower; **G**, seed. A, C, D, and G drawn from *Bernardi 6561* (NY); B and E drawn from *Bernardi s.n.* (NY); F drawn from *Field No. F1453/ Record No. 4189* [NY]. Illustrations by Kelly Ho.

solitary axillary umbels; peduncles 2.5–12.2 mm long, to ca. 3 mm wide, always shorter than subtending petioles, peduncle to petiole ratio 0.12–0.53 (–0.82), conspicuously flattened, surface verrucose-tuberculate; receptacles distinctly reniform, 2.2–6.2 mm × 4.0–10.8 mm, always wider than long, length to width ratio 0.46–0.78; receptacle scales papery and obtuse, surface smooth; pedicels 7.8–12.1 mm long, surface smooth. Staminate flowers ellipsoid in immature bud, with six tepals divided into two whorls, each consisting of three tepals, tepals oblong-lanceolate, larger tepals 2.3–2.6 mm × 1.2–1.8 mm, smaller tepals ca. 2.0 mm × 0.9–1.0 mm wide with distinct wings, ca. 0.3 mm wide, apices acuminate; stamens 1.4–1.7 mm long, filaments 1.0–1.2 mm × 0.4 mm, anthers 0.4–0.5 mm × 0.5 mm, distinctly shorter than filaments. Carpellate flowers not seen. Fruit a 1- or 2-seeded berry, color unknown, globose, 6.6–8.3 mm long, 6.5–11.7 mm wide, the 2-seeded berries wider than long and the 1-seeded berries ca. as wide as long, seeds ovoid to ellipsoid, 5.8–6.9 mm long, 4.2–5.9 mm wide.

Etymology: The epithet refers to the relatively short peduncles that never exceed the petioles in length which, in part, is a distinguishing character for this species.

Distribution and habitat: *Smilax brevipedunculata* is known from six collections, four of these from Bolívar, Venezuela, one from the region disputed between Guyana and Venezuela, and one from Suriname (Fig. 2). Considering the proximity to the Brazil-Venezuela border, *S. brevipedunculata* may also be found in Brazil. Efforts to locate a population based on the only known specimen from Brokopondo District, Suriname (*Donselaar 2983*, [BBS, NY]) was not successful during fieldwork in 2022. Considering the paucity of collections, this may indicate that it is locally rare, despite its distribution covering a widespread area. Habitats where *S. brevipedunculata* has been collected have been described as high, pluvial, or riverine forests at elevations of 100–850 meters. The most recent collections, *Fernández 4300* (PORT) and *Stergios 12123* (MO, PORT, US), were made in 1988, about 35 years ago. Additional fieldwork is needed to determine if *S. brevipedunculata* is still extant.

The EOO of *S. brevipedunculata* is 56,331 km^2, and the estimated area of occupancy (AOO) is 24 km^2. Under IUCN Criterion B1 (geographic range), the AOO would classify *S. brevipedunculata* as endangered with an AOO < 500 km^2.

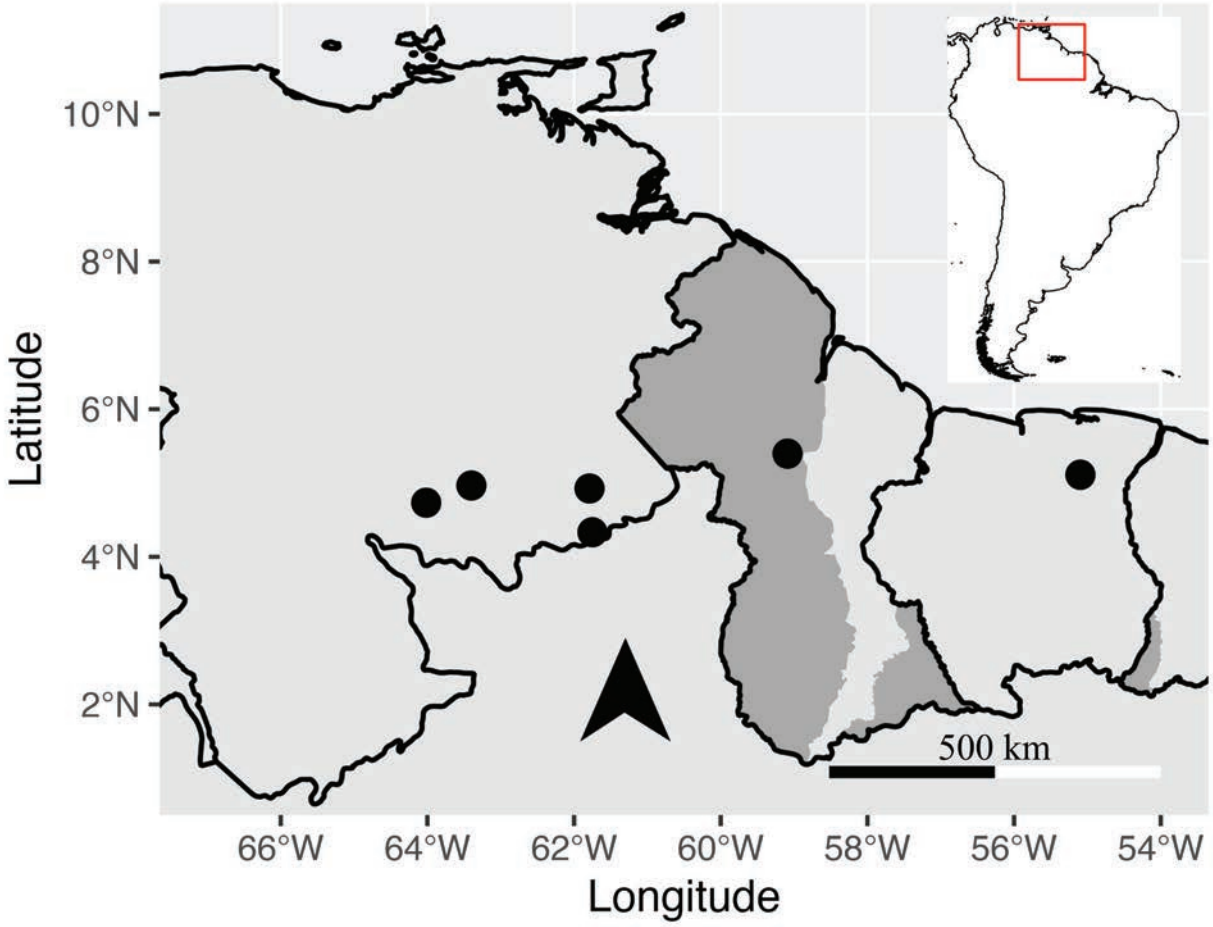


FIGURE 2. Distribution of *Smilax brevipedunculata* T. Murphy & S. M. Niño. Black dots indicate known localities based on herbarium specimens. Disputed territories are shown in dark grey.

The EOO, however, would not classify *S. brevipedunculata* under any of the threatened categories with an EOO>20,000 km^2. Under criterion for B2, *S. brevipedunculata* would fulfill, in part, the requirements for vulnerable status based solely on the number of known occurrences being six. However, there is no data to assess decline or fluctuations, so there is not enough data for the assessment under Criterion B2. Considering there are just six known populations, the most recent population was documented more than three decades ago, and the AOO indicates IUCN endangered status, *S. brevipedunculata* should be considered for conservation efforts and planning.

Phenology: A single specimen with mature fruit, the holotype (*Bernardi 6561* [NY]), was collected in April, and a single specimen with mature flowers was collected in November (*Field No. F1453/ Record No. 4189* [NY]). Three other specimens, *Donselaar 2983* (BBS, NY, U), *Stergios 12123* (MO, PORT, US), and *Fernández 4300* (PORT), bear immature flower buds and were collected in the months of January and April.

Additional specimens examined: Disputed Region Between Guyana and Venezuela. Bartica-Potaro Road, 107 m, 12/11/43, *Field No. F1453/ Record No. 4189* (NY [barcode 04204353]); Suriname. Brokopondo: between villages Afobaka and Brownsweg, high forest, 11 January 1966, *J. van Donselaar 2983* (BBS [accession 0031466], NY [barcode 04204340], U [photo; 2 sheets; barcodes 0072279 and 0072280]); Venezuela. Bolívar: región de los ríos Icabaru, Hacha y cordillera sin nombre a 280˚ de las cabeceras del Río Hacha, 450–850 mts s.n.m., selva pluvial o sabana natural, 23 diciembre 1955–15 de enero 1956, *A.L. Bernardi s.n.* (NY [barcode 04204341]); selvas ribereñas del Río Caura, aprox. 2 km abajo del Caño Guacamaya (Guaya), 04˚44'N 064˚01'W [4.7333333, -64.0166667], 13 al 26 de abril 1988, *Basil Stergios 12123* (MO [accession 05090734; barcode MO-1320221], PORT [accession 52666], US [barcode 00889871]); Municipio Raúl Leoni, bosque a 25 km al Norte del Macizo Ichun Alto Río Paragua, alt. 350 m.s.n.m., 04˚58'N 063˚24'W [4.966667, -63.400000], April 1988, *Ángel Fernández 4300* (PORT [accession 39226])

Smilax brevidpunculata has previously been confused with species that are documented in the Guiana Shield, including *S. jauaensis* Steyerm. & Maguire, *S. lasseriana*, *S. maypurensis* Humb. & Bonpl. ex Willd., *S. riedeliana* A. DC., and *S. siphilitica* Humb. & Bonpl. ex Willd. The species could be confused with the morphologically similar taxon, *S. magnifolia*, which is known from the Amazon of Peru. We focus our discussion on comparisons with *S. lasseriana* and *S. magnifolia*, which is also summarized in Table 1.

Smilax lasseriana has previously been treated as a morphologically variable taxon in herbaria. Gaskin and Berry (1998, 2005) included *S. lasseriana* as a heterotypic synonym of *S. staminea* Griseb. *Smilax staminea* is now accepted as a heterotypic synonym of *S. domingensis* Willd. (Ferrufino-Acosta, 2010). *Smilax lasseriana* is different from *S. domingensis* by the presence of two (vs. one) cataphylls at the base of lateral branches, verrucose-tuberculate (vs. smooth) stems, and shorter tepals (Murphy et al., in press). Additionally, phylogenetic relationships inferred from five plastid loci recover *S. domingensis* forming a clade with North American species, *S. laurifolia* Small and *S. smallii* Morong, and are distantly related to *S. lasseriana* and known close relatives (Murphy et al., in press). Considering the available morphological and molecular phylogenetic evidence, *S. lasseriana* should be recognized as a distinct species. *Smilax brevipedunculata* has been mistaken as *S. lasseriana*, probably due to the verrucose-tuberculate stems, coriaceous, lustrous leaves, and short peduncles. Taxonomic investigations are revealing that what has previously been determined as *Smilax lasseriana* represents multiple distinct species (Sipman, 1979; Murphy et al., in press). *Smilax lasseriana* has stems that possess verrucose-tuberculate projections that are conspicuously raised (vs. dense verrucose-tuberculate projections that are inconspicuously raised; Fig. 3A vs. 3B), leaves that are generally narrowly ovate to ovate with evenly tapered acute to obtuse apices (vs. short-acuminate to apiculate), leaves with tertiary veins conspicuously raised on the adaxial surface, forming a densely reticulate network (vs. with tertiary obscured and immersed, forming a lax reticulate network; Fig. 3D vs. 3E), receptacle shape ovoid (vs. reniform; Fig 3G vs. 3H), receptacle scales of stiff texture and apices acute (vs. papery texture and apices obtuse; Fig 3G vs. 3H), anthers that are of equal or almost equal length of filaments (vs. anthers of conspicuously shorter length than filaments; Fig. 3J vs. 3K).

Smilax brevipedunculata may also be confused with *S. magnifolia* because of its relatively short and wide peduncles, reniform receptacles (Fig 3G and 3I), and single basal cataphyll. *Smilax magnifolia* can be readily distinguished by multiple vegetative characters, including smooth stems (vs. lightly verrucose-tuberculate in *S. brevipedunculata*; Fig. 3A vs. 3C), leaves with tightly-spaced tertiary veins branching at a near-perpendicular to perpendicular angle from the midrib (vs. branching at distinctly acute angle in *S. brevipedunculata*; Fig. 3D vs. 3F), leaves with all vein orders conspicuous, and first lateral pair of secondary veins branching from the midrib above basal portion (vs. first lateral pair of secondary veins branching at the base of the midrib in *S. brevipedunculata*). The stems of *S. magnifolia* also differ in that they are subquandrangular, while stems of *S. brevipedunculata* are terete. Unfortunately, *S. magnifolia* flowers are not currently known, so we cannot make floral comparisons. The paucity of specimens with flowers is a recurring issue with neotropical *Smilax*, which would be ameliorated with further collecting efforts. *Smilax magnifolia* lacks a modern description, and appropriate circumscription of the species remains uncertain given the current lack of knowledge (T. Murphy, unpubl. data). *Smilax magnifolia* is known, with certainty, from the department of Loreto, Peru, mainly in the Maynas Province and one specimen examined from the Ucayali Province (*Valenzuela G. 35828* [MO]). Other specimens from Brazil, Peru, and Venezuela have been determined as *S. magnifolia* but may represent distinct but related species (T. Murphy, unpubl. data). Even when *S. magnifolia* and its allied segregates are considered for comparison with *S. brevipedunculata*, it remains morphologically diagnosable.

TABLE 1. Comparison of morphology, distribution, and habitat between *S. brevipedunculata* T. Murphy & S. M. Niño, *S. lasseriana* Steyerm., and *S. magnifolia* Macbr. sensu lato.

	SMILAX BREVIPEDUNCULATA	*SMILAX LASSERIANA*	*SMILAX MAGNIFOLIA*
Stem cross-section shape	Terete	Broadly quandrangular to quandrangular	Broadly quandrangular
Stem texture	Inconspicuously verrucose-tuberculate	Conspicuously verrucose-tuberculate	Smooth
Stem prickles[a]	Absent	Mostly absent, rarely present	Present
Number of cataphylls on axial side at base of branch	1	2	1
Leaf blade shape	Ovate to narrowly elliptic with short-acuminate to apiculate apex	Ovate to narrowly elliptic with rounded to acute apex	Narrowly oblong to narrowly elliptic with rounded to short-acuminate apex
Adaxial leaf surface	Higher order tertiary veins, reticulate, obscured, and immersed under blade surface	All veins conspicuously raised, forming a dense reticulate network	Higher order veins conspicuously raised, first-order tertiary veins branching from midrib at a near-perpendicular to perpendicular angle
Median (range in parentheses) number of first-order tertiary veins in middle 5 cm segment of leaf adaxial	4 (4–6)	3 (3–4)	10 (6–15)
Length between first-order tertiary veins on adaxial in middle	7.3–17.9 mm	12.2–28.0 mm	3.5–13.9 mm
Receptacle shape	Reniform, always wider than long	Broadly ovoid to globose	Reniform, always wider than long
Receptacle dimensions (length × width/length: width ratio)	2.2–6.2 mm × 4.0–10.8 mm/0.5–0.8	2.0–5.2 mm × 3.1–6.6 mm/0.5–1.1	8.0–13.0 mm × 13.0–17.0 mm/0.6–0.8
Receptacle scale texture and shape	Papery, rounded	Stiff, acute	Papery, rounded
Relative anther length	Shorter than filaments	Ca. as long as or longer than filaments	Unknown
Distribution/habitat	Guiana Shield/high, pluvial, and riverine forests	Guiana Shield/various but mainly lowland to upland forests associated with white sand	Amazon of Peru/lowland forest

[a] Stem prickles can be a problematic when comparing *Smilax* species because lower stems are often not well-collected or -documented (T. Murphy, pers. obs.), so what we describe here is based on limited data which is subject to change with additional fieldwork and documentation.

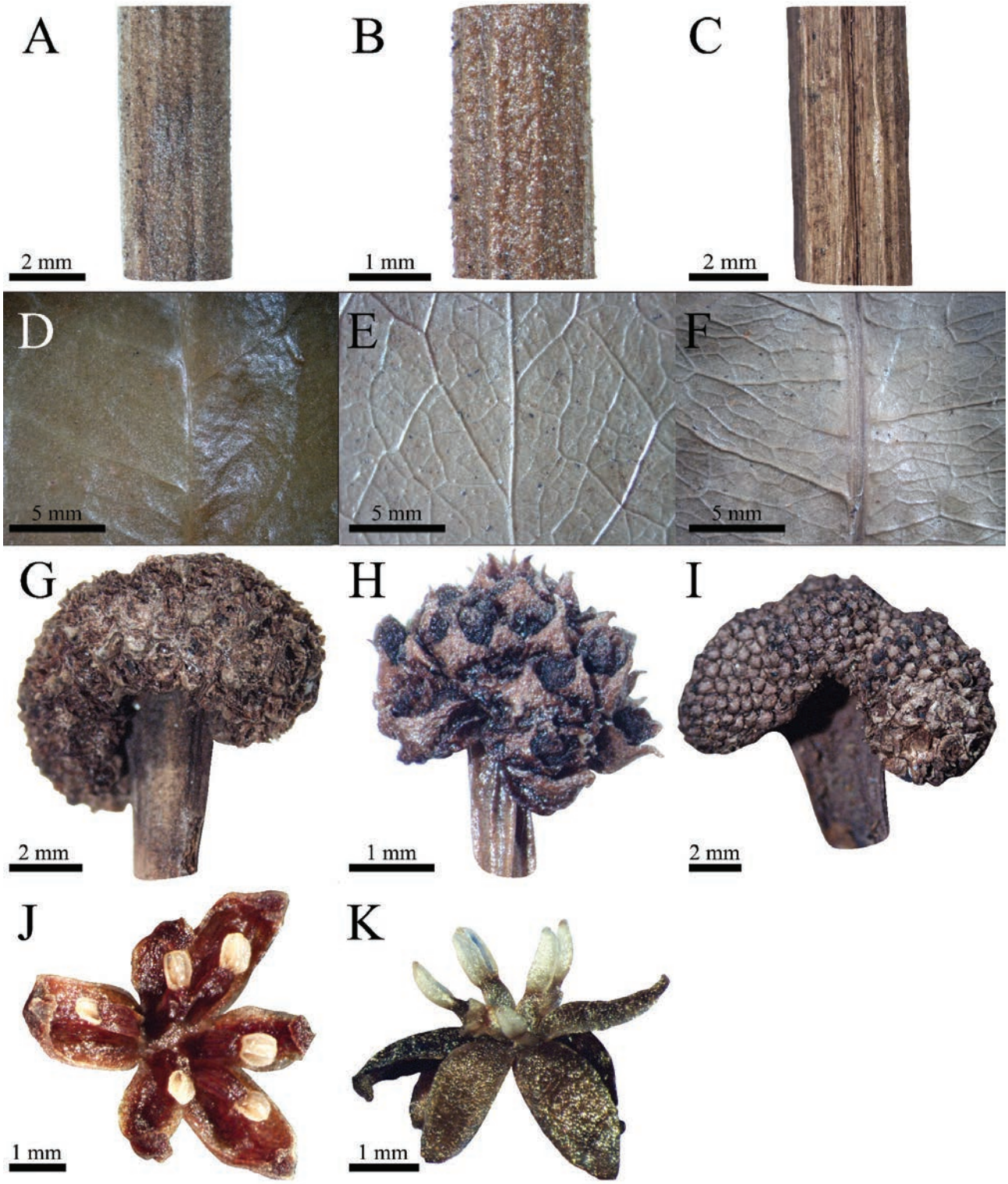


FIGURE 3. Comparison of key morphological features between *S. brevipedunculata* and morphologically similar species. Stems: **A–C**, leaf adaxial: **D–F**, receptacles: **G–I**, and staminate flowers: **J** and **K**. *Smilax brevipedunculata*: A, D, G, and J; *S. lasseriana* Steyerm.: B, E, H, and K; *S. magnifolia* Macbr.: C, F, and I. Note that photos of staminate flowers of *S. magnifolia* are not shown, because they are not known. A and G from *Bernardi s.n.* (NY); B from *Donselaar 2983* (MO); J from *Field No. F1453/ Record No. 4189* (NY); B and H from *Maas 3551* (NY); E from *Maas 3488* (NY); K from *Jansen-Jacobs 1029* (NY); C and I from *Ortiz 54* (MO); F from *Rimachi Y. 6503* (MO).

Literature Cited

Andreata, R. H. P. 1997. Revisão das espécies brasileiras do gênero *Smilax* Linnaeus (Smilacaceae). Pesquisas, Bot., 47: 1–243.

Baquero, O. S. 2019. ggsn: North Symbols and Scale Bars for Maps Created with 'ggplot2' or 'ggmap'. R package version 0.5.0 https://CRAN.R-project.org/package=ggsn

Barrett, S. C. H. and J. Hough. 2012. Sexual dimorphism in flowering plants. J. Exp. Bot., 64(1): 67–82. https://doi.org/10.1093/jxb/ers308

Botina-Papamija, J. R. 2008. Revisión taxonómica y fitogeografía del genero *Smilax* L. (Smilacaceae) en Colombia. Masters thesis. Universidad del Valle, Santiago de Cali, Valle del Cauca, Colombia.

Brewer, G. E., J. J. Clarkson, O. Maurin, A. R. Zuntini, V. Barber, S. Bellot, N. Biggs, R. S. Cowan, N. M. J. Davies, S. Dodsworth, S. L. Edwards, W. L. Eiserhardt, N. Epitawalage, S. Frisby, A. Grall, P. J. Kersey, L. Pokorny, I. J. Leitch, F. Forest, and W. J. Baker. 2019. Factors affecting targeted sequencing of 353 nuclear genes from herbarium specimens spanning the diversity of angiosperms. Front. Plant Sci., 10: 1102. doi.10.3389/fpls.2019.01102

Cameron, K. M. and C. Fu. 2006. A nuclear rDNA phylogeny of *Smilax* (Smilacaceae). Aliso, 22: 598–605. doi.10.5642/aliso.20062201.47

Cardoso, P. 2020. red: IUCN Redlisting Tools. R package version 1.5.0. https://CRAN.R-project.org/package=red

Ferrufino-Acosta, L. 2010. Taxonomic revision of the genus *Smilax* (Smilacaceae) in Central America and the Caribbean Islands. Willdenowia, 40(2): 227–280. https://doi.org/10.3372/wi.40.40208

Gaskin, J. F., and P. E. Berry. 1998. New synonymy and useful taxonomic characters in *Smilax* (Smilacaceae) from the Venezuelan Guayana. Novon, 8(4): 364–370.

———. 2005. Smilacaceae. Pages 184–193 in Volume 9 of P. E. Berry, K. Yatskievych, and B. K. Holst, eds., *Flora of the Venezuelan Guyana*. St. Louis: Missouri Botanical Garden Press.

Judd, W S. 2007. Revision of *Miconia* sect. *Chaenopleura* (Miconieae, Melastomataceae). Systematic Botany Monographs, 81: 1–235.

Luján, M. 2019. Playing the taxonomic cupid: matching pistillate and staminate conspecifics in dioecious *Clusia* (Clusiaceae). Syst. Bot. 44(3): 1–12. https://doi.org/10.1600/036364419X15620113920590

Mitchell, J. D. 1997. Smilacaceae. Pages 362–365 in S. A. Mori, G. Cremers, Gracie, C., de Granville J.-J., Hoff, M., and J. D. Mitchell, eds., *Guide to the Vascular Plants of Central French Guiana*. Memoirs of the New York Botanical Garden Vol. 76, Part 1: 1–422.

Murphy, T. H., N. M. Heaton, I. E. Molgo, K. Ho, and L. C. Majure. 2023. A new endemic *Smilax* (Smilacaceae) from Tafelberg, Suriname, supported by morphometric and phylogenetic evidence. Syst. Bot., in press.

Qi, Z., K. M. Cameron, P. Li, Y. Zhao, S. Chen, G. Chen, and C. Fu. 2013. Phylogenetics, character evolution, and distribution patterns of the greenbriers, Smilacaceae (Liliales), a near-cosmopolitan family of monocots. Bot. J. Linn. Soc., 173(4): 535–548. https://doi.org/10.1111/boj.12096

Qi, Z., P. Li., J. Wu., A. Gamisch, T. Yang, Y. Zhao, W. Xu, S. Chen, K. M. Cameron, Y. Qiu, and C. Fu. 2023. 2023. Climatic niche evolution in Smilacaceae (Liliales) drives patterns of species diversification and richness between the Old and New World. J. Syst. Evol., 61(5): 733–747. https://doi.org/10.1111/jse.12998

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

RStudio Team. 2021. RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA. http://www.rstudio.com/.

Sipman, H. 1979. Liliaceae. Pages 442–456 in Volume 5, part 1 of A. L. Stoffers and J. C. Lindeman, eds., *Flora of Suriname*. Van Eeden-fonds, Netherlands.

South, A. 2017. rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0. https://CRAN.R-project.org/package=rnaturalearth

Thiers, B. (continuously updated). Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium, https://sweetgum.nybg.org/science/ih/ (accessed June 15, 2023).

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilke, C. O. 2020. cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 1.1.1 https://CRAN.R-project.org/package=cowplot

OURATEA CHEPELII (OCHNACEAE), UNA NUEVA ESPECIE Y ASPECTOS FITOGEOGRÁFICOS DEL GÉNERO EN LA REGIÓN ANDINA DE VENEZUELA

Santos M. Niño,[1,2] Laurence J. Dorr,[3] y Daniela S. Canelón[1]

Resumen. Se describe e ilustra *Ouratea chepelii*, a la presente conocida en los Andes venezolanos. Se discute su distribución geográfica y datos ecológicos para el género *Ouratea* en los Andes de Venezuela. *Ouratea chepelii* parece estar relacionada con *O. larae* por su distribución fitogeográfica ya que ambas están restringidas a los Andes venezolanos. La primera especie es morfológicamente similar a *O. caracasana*, que se conoce de la Cordillera de la Costa y se reporta de los Andes, donde aún no se ha confirmado su presencia. *Ouratea chepelii* se puede distinguir fácilmente por sus inflorescencias paniculadas laterales con racimos basales de 1–3.5 cm de largo, y su carpóforo (torus) rojo brillante, semejando una pirámide alargada e invertida, casi siempre 4–5 angulado con 1–2.5 cm de largo. Actualmente, la nueva especie se conoce sólo de la vertiente norte del Parque Nacional Guaramacal y su zona de amortiguamiento entre 1800 y 2000 msnm. Sólo tres especies de *Ouratea*, incluyendo *O. chepelii*, han sido encontradas o reportadas encima de 1000 msnm en los Andes venezolanos, dos de las tres claramente endémicas.

Palabras claves: Andes, bosque andino, Guaramacal, Ochnaceae, Venezuela

Abstract. *Ouratea chepelii* found only in the Venezuelan Andes is described and illustrated. Geographical distribution and ecological data are discussed for the genus *Ouratea* in the Andes of Venezuela. *Ouratea chepelii* seems to be related to *O. larae* due to its phytogeographic distribution since both are restricted to the Venezuelan Andes. The first species is morphologically similar to *O. caracasana*, which is known from the Coastal Mountains of Venezuela, and is also reported from the Andes, where its presence has not yet been confirmed. *Ouratea chepelii* can be distinguished easily by its lateral paniculate inflorescences with basal racemes 1–3.5 cm long, and its bright red 1–2.5 cm long carpophore (torus) that is almost always 4–5 angled and resembles an inverted elongated triangular pyramid. At present, the new species is known only from the northern slope of Guaramacal National Park and the park's buffer zone at 1800–2000 m. Only three species of *Ouratea*, including *O. chepelii*, have been found or reported to occur above 1000 m in the Venezuelan Andes, two of the three clearly endemic.

Keywords: Andes, Andean forests, Guaramacal, Ochnaceae, Venezuela

La Flora de Guaramacal (Dorr et al., 2000; Dorr, 2014) es un proyecto del Museo Nacional de Historia Natural (Instituto Smithsoniano) y la Universidad Experimental de los Llanos (UNELLEZ) en Venezuela, que se desarrolla en una porción de la Cordillera de los Andes conocida como el Ramal de Guaramacal. En esta región se vienen haciendo colecciones botánicas y estudiando su flora y vegetación desde hace más de 40 años (Ortega et al., 1987; Cuello, 1999; Cuello et al., 2010), pero aún continúan apareciendo nuevas especies para la ciencia. Dorr et al. (2000) enumeraron 33 taxones de plantas vasculares descritas a partir de material recolectado en el Parque Nacional Guaramacal. En esta compilación se pasó por alto una especie de orquídea (Köniğer, 1994). Desde 2000 entonces se han descrito 30 taxones adicionales (Romero y Carnevali, 2000: 1131; Taylor, 2002; Dorr y Stergios, 2003, 2009, 2014; Stergios y Dorr, 2003, 2004; Stanĉik, 2004; Hágsater, 2005; Niño et al., 2005; Almeda y Dorr, 2006; Strong, 2006, 2007; Cuello y Aymard, 2008; van der Werff, 2013; Cuello y Santamaría-Aguilar, 2015; Karremans et al., 2015; Stergios et al., 2015; Croat y Delanny, 2017; Niño y Dorr, 2018, 2019; Canelón et al., 2020, 2022).

A pesar de la recolección intensiva, continuamos encontrando géneros y familias de plantas no incluidas en la lista más reciente de plantas vasculares encontradas en Guaramacal (Dorr et al., 2000). Uno de nuestros nuevos descubrimientos es en Ochnaceae. La única especie descubierta pertenece claramente a *Ouratea* Aubl., pero este género es poco común en los Andes venezolanos y nuestras muestras no coinciden con ninguna especie descrita. *Ouratea* es un género de unas 200–300 especies neotropicales (Sastre, 2003, 2004b, 2008; Amaral y Bittrich, 2014; Schneider et al., 2021a, 2021b) con unas 72 en Venezuela (Sastre, 2008), cuyo endemismo se destaca por incluir al menos 65 especies en el macizo de la Guyana venezolana (Sastre, 2003). Se caracteriza por sus hojas pecioladas, raramente sésiles y cuya lámina posee venas secundarias subiguales, fuertemente curvadas a lo largo del margen o desiguales, algunas arqueadas y ascendentes, finas, paralelas y rectas; las inflorescencias pueden ser terminales, axilares o caulinares, en espigas o panículas; los pétalos son frecuentemente amarillos; el ovario es 5–10 carpelado (pseudo-apocárpico), cada carpelo 1-ovulado; el fruto en dos partes (carpóforo y carpelos) con el carpóforo (torus) generalmente carnoso y rojizo y los carpelos (mericarpos) negruzcos al madurar, cada uno con una semilla (Yamamoto, 1989; Sastre, 2003, 2004a).

Aunque la circunscripción de especies en *Ouratea* suele ser difícil ya que el género incluye muchos complejos confusos (Yamamoto, 1989; Yamamoto et al., 2008), algunas

Los autores agradecen a Alice R. Tangerini (US) por la elaboración de la ilustración, a Rose A. Gulledge (US) por preparar las láminas fotográficas y al Sr. Ramón Caracas por su apoyo en campo.

[1] INBIO-UNELLEZ, Herbario PORT, Mesa de Cavacas, Guanare, estado Portuguesa, Venezuela; Instituto Venezolana de Investigaciones Científicas (IVIC), Caracas, Venezuela

[2] Autor de correspondencia: santosmiguelnino@gmail.com

[3] Department of Botany, MRC-166, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington DC 22013-7012, U.S.A.; dorrl@si.edu

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 703–709.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n6, Published online: 31 December 2023

especies endémicas tienen características diagnósticas que las hacen claramente sobresalientes. La especie andina del Ramal de Guaramacal en Venezuela es uno de esos casos. Sastre (1988, 1995) propuso una clasificación infragenérica que finalmente dio cuenta de seis secciones. Según su sistema, nuestra nueva especie está dentro de la sección *Ouratella* (Tiegh.) Sastre, definido por poseer flores con cinco sépalos bien diferenciados, flores con cinco carpelos, los frutos sin restos de la corola y la inflorescencia axilar (Sastre, 1988, 1995). Investigaciones moleculares de Schneider et al. (2021a, 2021b), sin embargo, ponen en duda la clasificación infragenérica de Sastre (1988, 1995) y aunque sus estudios encontraron seis linajes distintivos (subclados) dentro de un *Ouratea* monofilético, *O*. sect. *Ouratella* es polifilético (Schneider at al., 2021a, 2021b). Schneider et al. (2021b) señaló además que existe una fuerte discordia sobre la composición y las relaciones entre los principales clados de *Ouratea* utilizando datos de plastomas en lugar de datos nucleares (Schneider et al., 2021a), un conflicto que también es difícil de resolver desde una perspectiva morfológica. Ni los datos nucleares ni los del plastoma infieren las relaciones esperadas según la clasificación infragenérica actual de Sastre (1995). De todas formas, ninguna de las especies andinas venezolanas ha sido muestreada en estudios moleculares.

Ouratea chepelii S.M. Niño, Dorr, & Canelón, *sp. nov.*
TYPE: VENEZUELA. Trujillo: Municipio Boconó, Zona de amortiguación del Parque Nacional Guaramacal, caserío Laguna de los Cedros, en relicto boscoso formando parte del estrato medio del bosque, Coord. UTM 19: 365,505E; 1,022,608N, 1916 msnm, 3 noviembre 2021, *S. M. Niño & D. Canelón 6668* (Holotipo: PORT; Isotipos: IVIC, US [01184500]). Fig. 1, 3.

Ouratea chepellii can be distinguished by its lateral inflorescences (7–8 cm long); basal racemes (1–3.5 cm long) that are never sessile with 3–10(–12) flowers; and inverted, elongated pyramidal carpophore (torus) that is almost always 4–5 angled; versus *O. caracasana* that always has terminal inflorescences (3–5 cm long); sessile or subsessile basal racemes (0.3–0.5 cm long) with 1–3(–5) flowers; and globose, turbinate to ovoid, never angled carpophore (torus).

Árbol ca. 4–10 m de alto, con ramas mediales glabras, estriadas y cilíndricas, las terminales estriadas casi siempre cuadrangulares o anguladas con stípula cónica de 5–7 mm de longitud, caducas. *Hojas* con peciolo glabro, de 3–5 × 1.5–2 mm, aplanado o semicilíndrico, acanalado; lámina elíptica a obovada, 6–12 × 2.5–4.7 cm, ápice y base obtusa, margen liso o crenulado desde la parte media hasta el ápice, glabra, verde claro por el envés, vena principal sobresaliendo cerca del pecíolo hacia el ápice en ambas superficies, venas secundarias 8–16, arqueadas hacia el ápice de la hoja, sobresaliendo ligeramente o casi no visibles en la superficie superior, subparalelas de la parte media hacia el ápice, venas terciarias y venas secundarias en una red muy densa, colgante (Fig.3D), coriácea. *Inflorescencias* paniculadas, péndulas, glabras, siempre laterales en ramas terminales, 7–8 cm de longitud, racimos basales 1–3.5 cm de largo; *pedúnculo* de inflorescencia aplanado, 1–2.5 cm de largo; *pedicelo floral* verde durante floración y rojo en fructificación, 8–13 mm largo; 3–12 *flores* en los racimos, solitarias o en grupos de 2–3 a lo largo del racimo; *sépalos* 5, verdosos en el exterior y amarillentos en su parte interna, subiguales, coriáceos, ligeramente fusionados en la base, 5–7 × 2.5–3 mm; pétalos 5, espatulados, iguales, ca. 8–11 × 4–6 mm, membranosos, amarillos, caedizos; *estambres* 10, iguales, 5–6 × 0.9–1 mm, sésiles, curvados ligeramente hacia adentro, amarillos o casi naranja; *carpelos* 5, ca. 2–2.5 mm de longitud, soldados y sobresalientes en el ápice de un ginóforo de ca. 0.5 mm de altura; *estilo* de ca. 3–3.5 mm de longitud, curvo y generalmente retorcido en el ápice. *Fruto* compuesto con carpóforo (torus) pirámidal triangular alargada invertida, casi siempre 4–5 angulado, 1–2.5 cm de largo, ápice 5–7 mm de ancho, base 1.5–2 mm de ancho, rojo brillante; carpelo elíptico, globoso, o ovalado, ca. 9–11 × 5–6 mm, verde brillante y negro al madurar (planta viva), colgante (Fig. 3D); *semilla* ovalada, 6–8 × 3–4 mm, muy dura.

Etimología: El epíteto "*chepelii*" corresponde al nombre familiar del Pastor José Canelón (1959–2021), quien dedicó su vida a la obra de Dios, y como menciona Salmos (1:3) "fue como árbol plantado junto a arroyos de agua, que da su fruto en su tiempo y su hoja nunca cae."

Distribución y hábitat: Hasta el presente solo conocida del Ramal de Guaramacal, principalmente en la zona de amortiguación Parque Nacional Guaramacal, en el Municipio Boconó (Fig. 2). Es un arbolito siempreverde, poco frecuente y las poblaciones encontradas lo muestran asociado a bosques subandinos con un dosel que alcanza 15–25 m, dominados por *Croizatia brevipetiolata* (Secco) Dorr y *Wettinia praemorsa* (Willd.) Wess. Boer comprendidos entre 1700 y ca. 2300 msnm en el Ramal de Guaramacal (Cuello y Cleef, 2009). *Ouratea chepelii* se encuentra en la capa media del bosque nublado (5–10 m), y es muy llamativa tanto en flor como en fruto; el primero amarillo (Fig. 3C) y el segundo rojo (Fig. 3D–G). En ocasiones se encuentra en el borde del bosque, pero en general los elementos arbóreos de mayor porte encuentran en el interior del bosque donde pueden alcanzar hasta de 10 m de alto. La floración es muy corta (noviembre-diciembre) y ocurre durante la temporada de menos lluvias en la región, siendo muy notoria la fragancia agradable que atrae diversos insectos polinizadores, principalmente abejas y avispas, mientras que la fructificación se presenta iniciando la temporada de lluvias (marzo-mayo), y los dispersores son principalmente aves. Sin embargo, su floración no es constante y se ha notado que en periodos de tres o cuatro años las plantas permanecen estériles, por lo que será necesario investigar si se trata de sensibilidad a cambios climáticos (observ. en campo).

Observaciones y consideraciones fitogeográficas: *Ouratea chepelli* se distingue de dos especies cercanas tanto morfológicamente como geográficamente, estas son *O. caracasana* (Planch.) Engl. y *O. larae* Sastre. Aunque *O. larae* es la más cercana desde el punto de vista fitogeográfico, pues se ha reportado en la región andina del estado Lara (El Tocuyo y Humocaro) a alturas similares, sin embargo, morfológicamente son algo distintas pues esta especie posee una inflorescencia racimosa y hojas sésiles o subsésiles (pecíolo 1–2 mm de largo) mientras *O. chepelii*

FIGURA 1. *Ouratea chepelii* S.M. Niño et al., *sp. nov*. **A**, Hábito, mostrando rama con inflorescencias y hojas reflejas. **B**, Flor que muestra sépalos, anteras y punta de estilo (sin pétalos). **C**, Flor que muestra ginóforo y estilo (se eliminan dos sépalos y tres pétalos). **E**, Pétalo. **F**, Infrutescencia. **G**, Fruto maduro, que muestra un carpóforo (torus) con cuatro carpelos globosos (A–E, *Niño y Canelón 6668*; F, G, *Niño y Canelón 6519*).

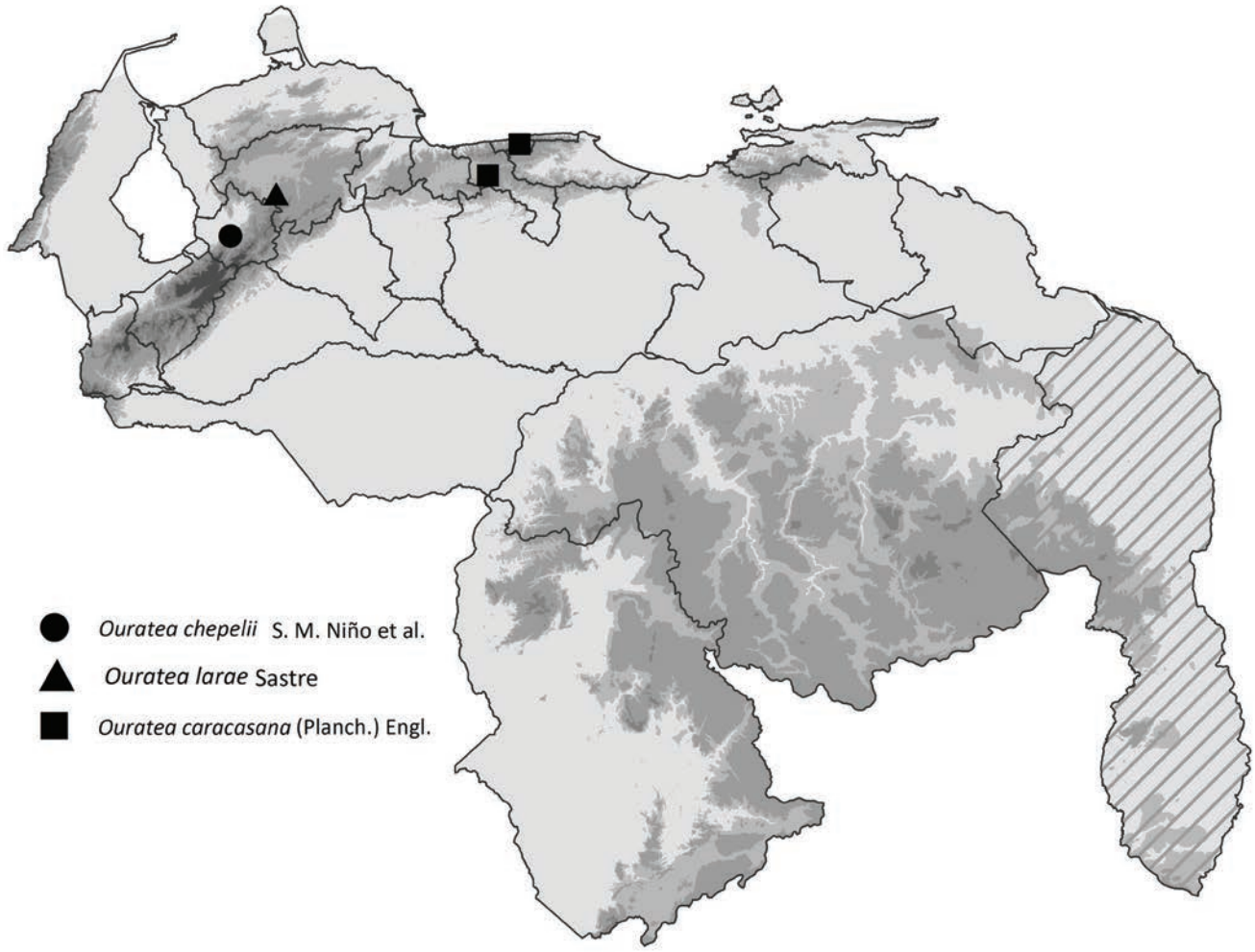


FIGURA 2. Distribución de *Ouratea chepelii* S.M. Niño et al. (●), *O. larae* Sastre (▲), y *O. caracasana* Engl. (■) en los Andes y la Cordillera de la Costa de Venezuela.

es paniculada y peciolada (pecíolo 3–5 mm de largo). De *O. larae* se tienen pocos datos ecológicos por sus escasas colecciones, la floración ocurre entre septiembre-octubre y los frutos entre noviembre-diciembre. Hasta ahora, esta especie solo se conoce de estos sitios que corresponden a montañas calizas de bosques premontanos de la cuenca del rio Tocuyo (600–1200 msnm). A pesar de que los bosques han sido estudiados florísticamente por Alvarado Álvarez (2009, 2010) y Alvarado Álvarez y Mondragón-Izquierdo (2015) no se reporta en sus análisis, seguramente por la escasa distribución. Por ahora se considera una especie endémica "rara" del estado Lara, que se debe incluir en planes de conservación. Es notoria la cercanía morfológica de *O. larae* con *O. guildingii* (Planch.) Urb. sin embargo esta última se restringe al escudo guayanés (200–250 m) y ambas se alejan de *O. chepelli* principalmente por sus inflorescencias racimosas.

Por otra parte, aunque el basónimo de *Ouratea caracasana* fue descrita de la Cordillera de la Costa (Caracas), Sastre (2008) indicó su presencia en Mérida y Yaracuy. Sin embargo, en los herbarios examinados (COL, IVIC, PORT, US), no se encontraron evidencias certeras de su presencia en los andes. Se presentan muy pocas colecciones que muestran la planta con frutos, siendo las de Pittier (*15234* y *15619*) de los años 1946 y 1947 respectivamente, en el hoy Parque Nacional Henry Pittier (estado Aragua), donde se observa el fruto con un carpóforo (torus) obcónico o turbinado de 6–12 mm y el carpelo globoso de 2.5–4 mm, siendo esto una marcada diferencia morfológica con *O. chepelii*, además de la inflorescencia con racimos sésiles o subsésiles, pero siempre muy cortos (0.3–0.5 cm de largo) respecto a *O. chepellii*. En la Tabla 1 se presenta un cuadro sinóptico de las características morfológicas de cada especie y luego una clave para separar entre ellas.

Clave para las Especies de *Ouratea* Encontradas por encima de 1000 msnm en los Andes y la Cordillera de la Costa de Venezuela

1a. Inflorescencias en espigas; láminas de hojas de 1.5–4.5 cm de largo . . . . . *O. larae* Sastre

1b. Inflorescencias en panículas; láminas de hojas de 5–12 cm de largo 2

2a. Hojas crenuladas desde 1/3 de la base hasta el ápice; inflorescencias siempre terminales 3–5 cm de largo; racimos basales sésiles o subsésiles de 0.3–0.5 cm de largo con 1–3(–5) flores; carpóforo globoso, turbinado hasta ovoide, nunca angulado . . . . . *O. caracasana* (Planch.) Engl.

2b. Hojas crenuladas desde la parte ½ o más hasta el ápice; inflorescencias laterales 7–8 cm de largo; racimos basales nunca sésiles de 1–3.5 cm de largo con 3–10(–12) flores; carpóforo piramidal alargado invertido, casi siempre 4–5 angulado . . . . . *O. chepelii* S.M. Niño et al.

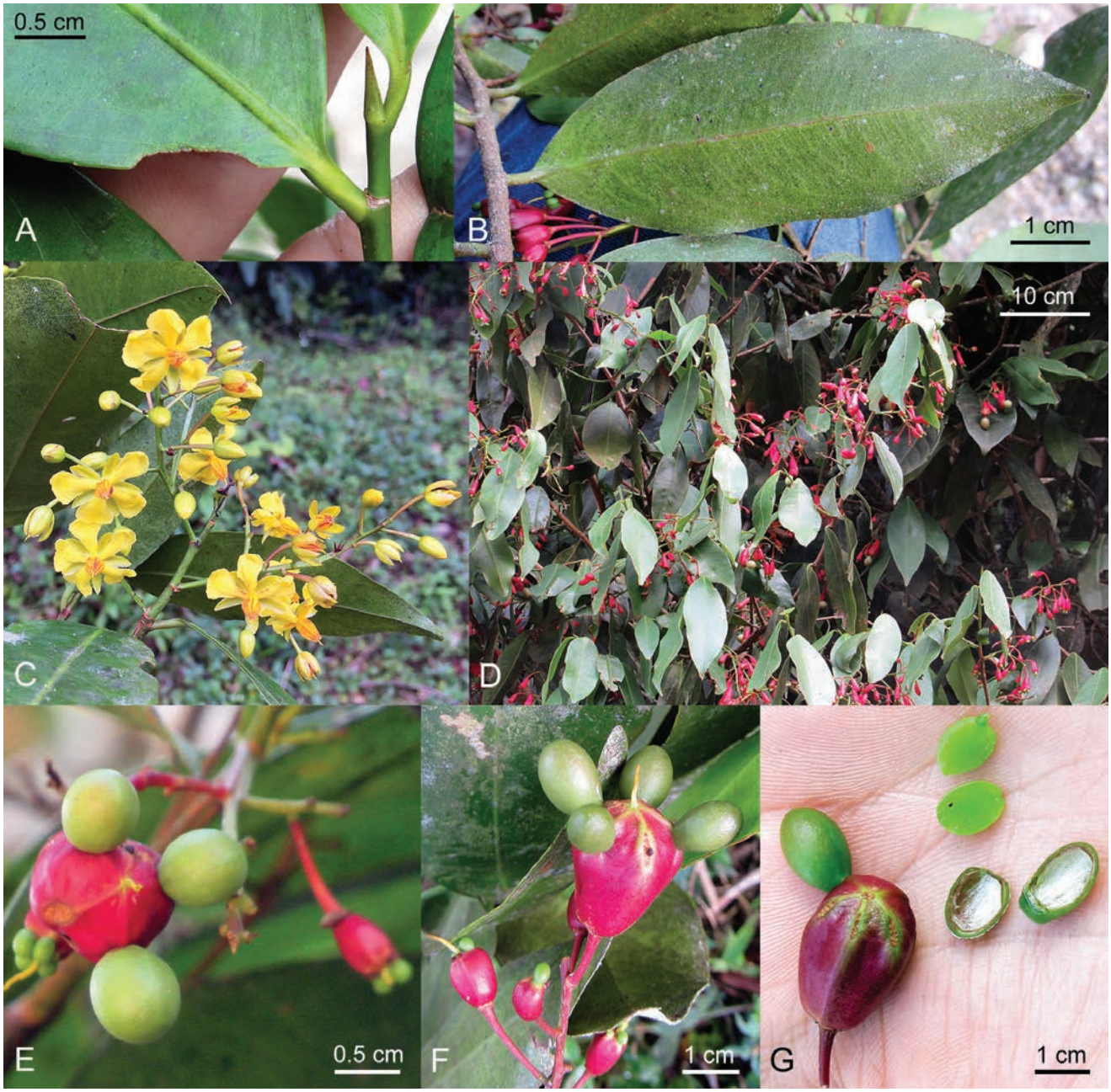


Figura 3. Algunos detalles de *Ouratea chepelli* S.M. Niño et al. en vivo. **A**, Detalle de la stípula en ramas terminales. **B**, Hoja y peciolo por envés. **C**, Inflorescencia con estambres que resaltan por su color naranja (*Niño y Canelón 6668*). **D**, Lámina de las hojas y la infrutescencia colgantes. **E**, Carpóforo (torus) (rojo brillante) desde arriba con carpelos globosos (verde brillante). **F**, Carpóforo (torus) desde el lado con estilo persistente y carpelos (en vida el carpóforo esta colgante). **G**, Carpóforo (torus) con un carpelo o adjunto y otro carpelo dividido para mostrar la semilla (*Niño y Canelón 6519*).

Tabla 1. Tabla comparativa de las especies de *Ouratea* encontradas por encima de los 1000 m en los Andes y la Cordillera de la Costa de Venezuela.

	O. chepelii	*O. caracasana*	*O. larae*
Hoja (lámina)	6–12 × 2.5–5 cm	5–10.5 × 2–4.5 cm	1.5–4.5 × 0.7–2.5 cm
Peciolo	3–5 mm de largo	3–6 mm de largo	1–2 mm de largo
Stípula terminal	5–7 mm de largo	2–2.5 mm de largo	1–2.5 mm de largo
Inflorescencia (tipo)	Panícula lateral	Panícula terminal	Racimo
Inflorescencia (longitud)	7–8 cm de largo	3–7 cm de largo	1–5(–6) cm de largo
Racimos basales	Raquis secundario nunca sésil 1–3.5 cm de largo	Raquis secundario sésil o subsésil 0.3–0.5 cm de largo	—
Fruto (carpóforo)	Piramidal (4–5 angulado) alargada invertida; 1–2.5 cm de largo	Globoso, ovoide, obconico o turbinado, no angulado; 0.6–1.2 cm de largo	Subcónico; 0.5–0.6 cm de largo, no angulado
Fruto (carpelo)	Elíptico, globoso, o ovalado; ca. 9–11 × 5–6 mm	Globoso; 2.5–4 mm de largo	Elipsoide; 3 × 1.5 mm

Especímenes adicionales examinados: *Ouratea caracasana* (Planch.) Engl. VENEZUELA. Aragua: Fila Paraíso, Parque Nacional Henri Pittier, 1400–1450 msnm, 21 octubre 1995, *A. Cardoso et al. 2377* (P [05466302]); Selvas de Guamitas, Parque Nacional, 800 msnm, August 1946 (fl), *H. Pitter 15234* (US [03388341]); Quebrada de Guamitas, Parque Nacional, 900 msnm, September 1947 (fl), *H. Pittier 15566* (US [03388356]); La Regresiva del Diablo, Parque Nacional, 30 October 1947 (fr), *H. Pittier 15619* (US [03388385]). Distrito Capital: Caracas, January–April 1842 (fl), *J. Linden 4* (Holotipo de *Gomphia caracasana* Planch.: K [000382214]; Isotipos: F [V0066129F], G [00341182], G [00341183], P [00582169]); Parque Nacional El Ávila, Cerro el Ávila, vertiente sur, carretera Caracas-Galipán, entre Boca de Tigre y puesto de guardaparques Clavelitos, 1800–1900 msnm, 10° 33'N, 66°54'O, 11 febrero 2006 (fl), *W. Meier 13099* (US [03388189], VEN).

Ouratea chepelii S.M. Niño et al. VENEZUELA. Trujillo: Municipio Boconó, Zona de amortiguación del Parque Nacional Guaramacal, relicto boscoso en el caserío Laguna de los Cedros, Coord. UTM 19: 365,396E; 1,022,598N, 1850 msnm, 20 marzo 2021 (fr), *S. M. Niño & D. Canelón 6519* (IVIC, PORT).

Ouratea larae Sastre. VENEZUELA. Lara: Humocaro, 1100 msnm, 25 September 1922 (fl), *A. Jahn 1195* (US [03388344]); Cerro de la Cantera, El Tocuyo, 1931 (fr), *F. Tamayo 10* (US [03388345], VEN); Cerro de la Cantera, El Tocuyo, August 1937 (fl), *F. Tamayo 260* (Holotipo: VEN [146939]; Isotipo: US [03389255]).

Literatura Citada

Almeda, F. y L. J. Dorr. 2006. *Miconia amilcariana* (Melastomataceae: Miconieae), a new species from the Venezuelan Andes with notes on the distribution and origin of dioecy in the Melastomataceae. Proc. California Acad. Sci., ser. 4, 57(19): 549–555.

Alvarado Álvarez, H. R. 2009. *Flora y Vegetación Ribereña de la Cuenca del río Tocuyo, estados Lara y Falcón, Venezuela*. Tesis Doctoral, Departamento de Ciencias Ambientales y Recursos Naturales, Universidad de Alicante, Alicante, España.

———. 2010. Caracterización estructural y florística de un bosque ribereño de la Cuenca del rio Tocuyo (Tocuyo Occidental), Estado Lara, Venezuela. Ernstia 20(1):1–20.

———. y A. A. Mondragón-Izquierdo. 2015. Riqueza florística de angiospermas del estado Lara depositadas en el Herbario "José Antonio Casadiego" (UCOB), Venezuela. Biota Colombiana 16(1):11–19.

Amaral, M. C. E. y V. Bittrich. 2014. Ochnaceae. Páginas 253–268 en K. Kubitzki, ed., *The Families and Genera of Vascular Plants*. Vol. 11. Springer, Berlin.

Canelón, D., S. M. Niño, L. J. Dorr, y M. Caraballo. 2020. Two new species of *Dendrophthora* (Viscaceae) from the Venezuelan Andes. PhytoKeys 140: 1–10.

———., ———, ———. y ———. 2022. *Dendrophthora kuijtiana* (Santalaceae: Visceae), una nueva especie y adiciones para el género en Venezuela. Brittonia 75(1): 69–78.

Croat, T. B. y X. Delanny. 2017. A revision of *Xanthosoma* (Araceae). Part 4: New species from Venezuela and other Caribbean countries Aroideana 40(2): 649–690.

Cuello A., N. L., editor. 1999. *Parque Nacional Guaramacal*. UNELLEZ – Fundación Polar, Caracas.

———. y G. A. Aymard C. 2008. *Ilex guaramacalensis* (Aquifoliaceae), a new species from the Ramal de Guaramacal in the Venezuelan Andes. Novon 18(3): 319–324.

———. y A. M. Cleef. 2009. The forest vegetation of Ramal de Guaramacal in the Venezuelan Andes. Phytocoenologia 39: 109–156.

———., ———, y G. Aymard. 2010. Phytogeography of the vascular páramo flora of Ramal de Guaramacal (Andes, Venezuela) and its ties to other páramo floras. Anales Jard. Bot. Madrid 67(2): 177–193.

———. y D. Santamaría-Aguilar. 2015. A new species of *Freziera* (Pentaphylacaceae) from the Venezuelan Andes. Harvard Pap. Bot. 20(2): 147–150.

Dorr, L. J. 2014. Flora of Guaramacal (Venezuela): Monocotyledons. Smithsonian Contr. Bot. 100: i–xiv, 1–289.

———. y B. Stergios. 2003. A new species of *Dioscorea* (Dioscoreaceae) from the Andes of Venezuela. Sida 21(3): 1007–1013.

———. y ———. 2009. A new species of *Schefflera* (Araliaceae) from the Venezuelan Andes. J. Bot. Res. Inst. Texas 3(2): 605–608.

———. y ———. 2014. Four new species of Andean *Pilea* (Urticaceae), with additional notes on the genus in Venezuela. PhytoKeys 42: 67–76.

———., ———. A. R. Smith, y N. L. Cuello A. 2000 [2001]. Catalogue of the vascular plants of Guaramacal National Park, Portuguesa and Trujillo states, Venezuela. Contr. U.S. Natl. Herb. 40: 1–155.

Hágsater, E. 2005. *Epidendrum guaramacalense* Hágsater. Icon. Orchid. 7: t. 740.

Karremans, A. P., F. Pupulin, y B. Gravendeel. 2015. *Specklinia dunstervillei*, a new species long confused with *Specklinia endotrachys* (Orchidaceae: Pleurothallidinae). PLoS ONE 10(7): e0131971.

Köniğer, W. 1994. New species of the genera *Cyrtochilum*, *Masdevallia*, *Odontoglossum*, *Oncidium* and *Sigmatostalix*. Arcula 2: 28–57.

Niño, S. M. y L. J. Dorr. 2018. Dos nuevas especies de *Piper* (Piperaceae) de los Andes de Venezuela. Harvard Pap. Bot. 23(1): 9–14.

———. y ———. 2019. Una nueva especie de *Hedyosmum* (Chloranthaceae) para los Andes de Venezuela. Harvard Pap. Bot. 24(2): 269–273.

———., ———, y F. W. Stauffer. 2005. Una nueva especie de *Aiphanes* (Arecaceae) de la Cordillera de Mérida, Venezuela. Sida 21(3): 1599–1606.

Ortega, F., G. Aymard, y B. Stergios. 1987. Aproximación al conocimiento de la flora de las montañas de Guaramacal, Estado Trujillo, Venezuela. BioLlania 5:1–60.

Romero, G. A. y G. Carnevali Fernández-Concha. 2000. *Orchids of Venezuela: An Illustrated Field Guide*, 2nd ed. Vol. 3. Armitano Editores, Caracas.

Sastre, C. 1988. Studies on the Flora of the Guianas 34. Synopsis generis *Ouratea* Aublet (Ochnaceae). Bull. Mus. Natl. Hist. Nat., sér. B, Adansonia 10(1): 47–67.

———. 1995. Novelties in the neotropical genus *Ouratea* Aublet (Ochnaceae). Novon 5(2): 193–200.

———. 2001. New *Ouratea* species (Ochnaceae) from Venezuela and adjacent countries. Novon 11(1): 105–118.

———. 2003. Ochnaceae. Páginas 124–161 en P. E. Berry, K. Yatskievych, y B. K. Holst, eds., *Flora of the Venezuelan Guayana*. Vol. 7. Missouri Botanical Garden, St. Louis.

———. 2004a. Ochnaceae. Páginas 274–275 en N. P. Smith, S. A. Mori, A. Henderson, D. W. Stevenson, y S. V. Heald, eds., *Flowering Plants of the Neotropics*. New York Botanical Garden and Princeton University Press, Princeton, N.J.

———. 2004b. Une nouvelle espèce d'*Ouratea* (Ochnaceae) du Venezuela. Adansonia, sér. 3. 26(1): 129–131

———. 2008. Ochnaceae. Páginas 530–534 en O. Hokche, P. E. Berry, y O. Huber, eds., *Nuevo Catálogo de la Flora Vascular de Venezuela*. Fundación Instituto Botánico de Venezuela Dr. T. Lasser, Caracas, Venezuela.

———. y B. Offroy. 2016. Révision nomenclaturale des binômes du genre néotropical *Ouratea* Aublet (Ochnaceae) décrits par van Tieghem. Adansonia, sér. 3, 38(1): 55–98.

Schneider, J. V., T. Jungcurt, D. Cardoso, A. M. Amorim, M. Töpel, T. Andermann, O. Poncy, T. Berberich, y G. Zizka. 2021a. Phylogenomics of the tropical plant family Ochnaceae using targeted enrichment of nuclear genes and 250+ taxa. Taxon 70(1): 48–71.

———., J. Paule, T. Jungcurt, D. Cardoso, A. M. Amorim, T. Berberich, y G. Zizka. 2021b. Resolving recalcitrant clades in the pantropical Ochnaceae: Insights from comparative phylogenomics of plastome and nuclear genomic data derived from targeted sequencing. Front. Pl. Sci. 12: 638650.

Stančik, D. 2004. *Festuca dinirica* and *F. guaramacalana* (Poaceae, Loliinae), two new species from the Venezuelan Andes. Novon 14(3): 341–344.

Stergios, B., R. Caracas, L. J. Dorr, y S. M. Niño. 2015 [2017]. A new species of *Puya* (Bromeliaceae) from the Venezuelan Andes. Acta Bot. Venez. 28(2): 159–168.

Stergios, B. y L. J. Dorr. 2003 [2004]. Two new species of *Bomarea* (Alstroemeriaceae) from the Venezuelan Andes. Acta Bot. Venez. 26(1): 31–40.

———. y ———. 2004 [2005]. A new species of *Anthurium* sect. *Calomystrium* (Araceae) from the Venezuelan Andes. Acta Bot. Venez. 27(2): 95–100.

Strong, M. T. 2006. *Rhynchospora guaramacalensis*, una nueva especie de *Rhynchospora* sección *Paniculatae* (Cyperaceae) de Venezuela. Acta Bot. Venez. 29(2): 207–210.

———. 2007. *Scleria tropicalis* (Cyperaceae), a new species from northern Andean South America. Harvard Pap. Bot. 11(2): 199–201.

Taylor, C. M. 2002. Rubiacearum Americanarum magna hama pars X. New species and a new subspecies of *Faramea* (Coussareae) from Central and South America. Novon 12(4): 563–570.

Werff, H. van der. 2013. Studies in Andean *Ocotea* (Lauraceae) II. Species with hermaphrodite flowers and densely pubescent lower leaf surfaces, occurring above 1000 meters in altitude. Novon 22(3): 336–370.

Yamamoto, K. R. 1989. *Morfologia, Anatomia e Sistemática do Gênero Ouratea Aubl. (Ochnaceae): Levantamento preliminar das características de importância taxonômica e avaliação das classificações vigentes*. M.Sc. thesis, Programa de Pós Graduação em Biologia Vegetal. Universidade Estadual de Campinas, São Paulo.

———., R. G. Chacon, G. Proenca, C. Cavalcanti, y T. B. Graciano-Ribeiro. 2008. A distinctive new species of *Ouratea* (Ochnaceae) from the Jalapão Region, Tocantins, Brazil. Novon 18(3): 397–404.

Page 710 intentionally left blank.

AN UPDATE ON *XYLOBIUM* (ORCHIDACEAE: MAXILLAREAE)

PAUL ORMEROD[1]

Abstract. An update on nomenclature and taxonomy within the genus *Xylobium* is provided. The distribution of *Xylobium miliaceum* is extended from western South America to Venezuela. *Xylobium subpulchrum* is treated as a new synonym of *X. stanhopeifolium*. Miscellaneous notes are provided on overlooked transfers, misidentifications, and prior synonymy.

Keywords: *Xylobium,* update, new synonymy, transfers, records

A synopsis of the genus *Xylobium* was provided five years ago (Ormerod 2018) wherein 18 species were recognised, along with three varieties. In the intervening time, literature research has revealed a number of transfers to *Xylobium* that were made by Robert Rolfe in 1896 that had long been overlooked. It has also been discovered that *Maxillaria sulfurina* Lemaire had already been transferred to *Xylobium* by Louis van Houtte in 1848. On the taxonomic front, the realisation that *X. miliaceum* occurs in Venezuela solved a problem around the misapplication of the name *X. truxillense*. Another entity, *X. subpulchrum,* had been weakly differentiated from the earlier *X. stanhopeifolium* solely on leaf petiole length (5 vs. 20 cm). This seems not a feasible difference since material that would be called *X. subpulchrum* from Peru has been found with a 23 cm long leaf petiole. So, it would seem best to combine the two taxa. Thus, there are only 17 species in the genus.

Xylobium bractescens (Lindl.) Rolfe, Kew Hand-list Orch.: 149. 1896.

Basionym: *Maxillaria bractescens* Lindl., Edwards's Bot. Reg. 28: 44, misc. 92. 1842. TYPE: ECUADOR. Loja, *K. T. Hartweg, cult. Hort. Soc. s.n.* (Holotype: K-L, image seen).

Distribution: Ecuador and Peru.

Previously (Ormerod 2018) there was some skepticism about the validity of Kraenzlin's (1908) transfer to *Xylobium,* and the combination was instead attributed to Rolfe (1912). However, the discovery of the earlier combination in the "Hand-list" of 1896 negates any such discussion.

Xylobium colleyi (Batem. ex Lindl.) Rolfe, Gard. Chron. ser. 3, 7: 288. 1890.

Basionym: *Maxillaria colleyi* Batem. ex Lindl., Edwards's Bot. Reg. 24: misc. 161. 1838. TYPE: NOT CITED. [GUYANA. Demerara, *leg. T. Colley, cult. J. Bateman s.n.*] (Holotype: K-L, image seen).

Homotypic synonym: *Lycaste colleyi* (Batem. ex Lindl.) P.N. Don in Donn, Hort. Cantabr. ed. 13: 721. 1845.

Heterotypic synonyms: *Maxillaria brachypus* Rchb.f., Bot. Zeit. 10: 734. 1852. TYPE: GUATEMALA. Without locality, *J. R. Warcewicsz s.n.* (Holotype: W-R [41348], image seen; drawing AMES; Isotype: K-L, image seen).

Xylobium brachypus (Rchb.f.) Hemsl., in Godm. & Salv., Biol. Centr.-Amer., Bot. 3: 252. 1883.

Maxillaria rebellis Rchb.f., Fl. Serres Jard. Eur. ser. 1, 9: 102. 1853–1854; Bonplandia 2: 92. 1 Apr 1854. TYPE: VENEZUELA. Without locality, *H. Wagener, cult. G. Schiller s.n.* (Holotype: W-R [41366], image seen).

Xylobium rebellis (Rchb.f.) Schltr., Orchis 7: 23. 1913.

Distribution: Belize, Guatemala, Costa Rica, Panama, Colombia (?), Venezuela, Trinidad and Tobago, Guyana, and Brazil.

Another synonym of this entity is *Xylobium brachystachyum* Kraenzl. from Brazil. Ormerod (2018) did not list *Maxillaria brachypus* in the synonymy due to the divergent drawing of the lip, showing it to be narrowly clawed with two keels and an expanded apical blade. These differences I now accept are due to the lip rehydrating poorly and thus agree with the placement of the name in synonymy with *Xylobium colleyi*.

The transfer *Lycaste colleyi*, as cited above, properly belongs to *Xylobium colleyi,* not to *Batemannia colleyi* Lindl. as is found in some databases (e.g., POWO).

First publication place of the name *Maxillaria rebellis* has not been ascertained. It has not been possible to discover when the relevant part of *Flore des Serres* was published (possibly mid-1854). However, Reichenbach also published the name in Bonplandia on the first of April in 1854. Here he gives the actual origin (Venezuela) of the species and who collected it (Wagener); these were details previously not cited in 2018.

Xylobium corrugatum (Lindl.) Rolfe, Gard. Chron. ser. 3, 5: 459. 1889.

TYPE: COLOMBIA/VENEZUELA. Between Maracaibo (Venezuela) and Bogota (Colombia), *leg. J. Linden, cult. G. Barker s.n.* (Holotype: K-L, image seen).

I wish to thank the curators of F, MO, NY, and SEL for making material available for study. The kindness and hospitality of herbarium and library staff at HUH (A, AMES, GH) during my visits were also greatly appreciated. Stephane Bailleul (Montreal Botanic Garden) is also thanked for kindly sharing images of material cultivated at the gardens.

[1] P.O. Box 8210, Cairns 4870, Queensland, Australia; wsandave1@bigpond.com

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 711–714.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n7, Published online: 31 December 2023

Basionym: *Maxillaria corrugata* Lindl., Edwards's Bot. Reg. 30: misc. 14. 1844.

Heterotypic synonyms: *Maxillaria wageneri* Rchb.f., Bot. Zeit. 10: 735. 1852. TYPE: VENEZUELA. Federal District, Caracas, *leg. H. Wagener,* cult. in Krollwitz by *Bottyer for C. Keferstein s.n.* (Holotype: W-R [40285], image seen).

Maxillaria corrugata Lindl. var. *wageneri* (Rchb.f.) Rchb.f., in Walp., Ann. Bot. Syst. 6, 4: 508. 1863.

Xylobium corrugatum (Lindl.) Rolfe var. *wageneri* (Rchb.f.) Schltr., Orchis 7: 22. 1913.

Xylobium wageneri (Rchb.f.) Schltr., Repert. Sp. Nov. Regni Veg., Beih. 6: 85. 1919.

Distribution: Colombia, Venezuela, and Ecuador (?).

In the previous synopsis of 2018, the combination *Maxillaria corrugata* var. *wageneri* was overlooked. Also, there was some discussion about the collection *J. Linden 655* (K-L, P) sometimes wrongly treated (e.g., Kolanowska, et al., 2011) as type material of *Maxillaria corrugata*. That collection is correctly assigned to *Xylobium miliaceum* (see below).

Xylobium foveatum (Lindl.) G. Nicholson, Ill. Dict. Gard. 4: 255. 1887.

Basionym: *Maxillaria foveata* Lindl., Edwards's Bot. Reg. 25: misc. 2. 1839. TYPE: GUYANA. Demerara, *imp. & cult. Messrs. Loddiges s.n.* (Holotype: K-L, image seen).

Heterotypic synonyms: *Maxillaria hyacinthina* Rchb.f., Linnaea 22: 855. 1852. TYPE: VENEZUELA. Merida: Rio Chama, December, *J. W. K. Moritz 1084* (Lectotype [proposed by Ormerod 2018: 62]: BM [000533404], image seen; Isolectotype: W-R [41337], image seen).

Xylobium hyacinthinum (Rchb.f.) Rolfe, Kew Hand-list Orch.: 149. 1896.

Distribution: Jamaica, Mexico, Honduras, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, French Guiana, Guyana, Brazil, Ecuador, Peru, and Bolivia.

The citation for the transfer of *Xylobium hyacinthinum* is corrected from Schlechter (1913) to that of Rolfe in 1896. There may also exist an earlier transfer for the name *Xylobium foveatum* (along with *X. decolor* [Lindl.] G. Nicholson, and *X. pallidiflorum* [W.J. Hook.] G. Nicholson) since van Houtte (1847) mentions those names but without reference to the basionyms in a way that would validate the combinations.

Further synonyms of *Xylobium foveatum* such as *Maxillaria chapadensis* Barb. Rodr., *M. concava* Lindl., *Xylobium ecuadorense* Rolfe, *X. filomenoi* Schltr., and *X. modestum* Schltr. are listed in Ormerod (2018). Though this synonymy might reflect the broad distribution of *X. foveatum,* it also points to some interesting variation. Stephane Bailleul of the Montreal Botanic Gardens kindly sent images of two quite different plants. One that was presumed to have been collected by Clarence Horich in Costa Rica in 1958 has rather short leaf petioles (5–8 cm long), and densely flowered, arching inflorescences of whitish-yellow flowers with relatively broad sepals. The other plant (origin unknown) had much longer (7–19 cm) leaf petioles, and erect, subdensely flowered inflorescences of yellow starry flowers with relatively narrow sepals. However, looking at material from the whole range of *X. foveatum*, I have been unable to separate out any of these forms due to the number of intermediate variants.

Xylobium miliaceum (Rchb.f.) Rolfe, Orch. Review 20, 230: 43. 1912.

Basionym: *Maxillaria miliacea* Rchb.f., Xenia Orch. 3: 22. 1878. TYPE: BOLIVIA. La Paz: Larecaja Prov., near Sorata, Cerro de Iminapi, on rocks at the source of the Rio Cacique, 2650 m, December 1859, *G. Mandon 1148* (Holotype: W-R [40279], image seen; Isotypes: G [00355206], image seen, K [000588957], image seen, P [00455853], image seen).

Heterotypic synonyms: *Xylobium buchtienianum* Kraenzl., Orchis 2: 129. 1908. TYPE: BOLIVIA. La Paz: Sud Yungas Prov., Sirypaya, near Yanacachi, 2300 m, 19 December 1906, *O. Buchtien 383* (Holotype: HBG [502090], image seen; Isotypes: AMES [00090696], US [00093927], image seen).

Xylobium medinae Szlach. & Kolan., Phyton (Horn) 54, 1: 74. 2014. TYPE: COLOMBIA. Putumayo: Valle de Sibundoy, Vereda La Cumbre, 2300 m, fl. in cult. 29 November 2012, *R. Medina 817* (Holotype: HPUJ, not seen; photo.: MEDEL, not seen).

Xylobium miliaceum (Rchb.f.) Rolfe var. *patens* Ormerod, Harvard Pap. Bot. 23, 1: 65. 2018 *syn. nov.* TYPE: PERU. Amazonas: Bongara Prov., on the road to La Rioja, 5 km N of the N end of Lake Pomacocha, 2000 m, 8 October 1964, *P. C. Hutchinson & J. K. Wright 6793,* 5 October 1968, *cult. Univ. Calif. Bot. Gard., Acc. No. 64.1634* (Holotype: NY).

Usage synonyms: *Maxillaria scabrilinguis auct. non* (Lindl.) Lindl., Edwards's Bot. Reg. 30: misc. 71, no.66. 1844; Orch. Linden.: 19. 1846.

Xylobium truxillense auct. non (Rchb.f.) Rolfe, Dunsterv. & Garay, Venez. Orch. Illustr. 6: 444, f. 1976.

Xylobium variegatum auct. non (Ruiz & Pav.) Garay & Dunsterv., Fernandez, Orquid. Nat. Tachira: 238, ph. 2003.

Xylobium corrugatum auct. non (Lindl.) Rolfe, Kolan., Perez Escobar, Parra Sanchez & Szlach., Illustr. Field Guide Orch. Yotoco For. Res.: 272. 2011 *pro parte* (quoad type citation).

Distribution: Colombia, Venezuela, Ecuador, Peru, and Bolivia.

Additional specimens examined: VENEZUELA. Merida, 1525 m, June 1842, *J. Linden 655* (K-L, P, images seen); 2000 m, 26 April 1949, *O. Renz 5353* (RENZ, image seen); 2000 m, 1 March 1949, *O. Renz 5133* (RENZ, image

seen); 1600 m, 1 March 1949, *O. Renz 5306* (RENZ, image seen). Trujillo, 1800 m, 14 April 1948, *O. Renz 5539* (RENZ, image seen).

This species has long been known from Venezuela but never correctly identified. Part of the problem was the availability of material to study and confusion with forms of *X. undulatum* (Ruiz & Pav.) Rolfe. Judging from the above cited images of specimens showing intermediate floral position (patent to erect), it seems not justifiable to recognize the variety *patens*, and it is thus reduced to synonymy here.

Xylobium stanhopeifolium Schltr., Repert. Sp. Nov. Regni Veg., Beih. 27: 84. 1924.

TYPE: COLOMBIA. Putumayo: near Mocoa, 550 m, May 1921, *W. Hopp 79* (Holotype: B, destroyed).

Heterotypic synonym: *Xylobium subpulchrum* Dressler, Orquideologia 21, 3: 310. 2000 *syn. nov.* TYPE: PERU. Huanuco: Tingo Maria, *leg. E. Jara,* purchased by *H. Hills,* fl. in cult. June 1999, *R. L. Dressler s.n.* (Holotype: MO [197288], image seen; Isotypes: FLAS [207882], image seen, FLAS [228861], image seen, SEL [001132], image seen, USM [000664], image seen).

Usage synonyms: *Xylobium colleyi auct. non* (Batem. ex Lindl.) Rolfe, C.H. & P.M. Dodson, Icon. Pl. Trop. ser. 2: t. 600. 1989; R. Escobar R., Nat. Colomb. Orch. 4: 600, ph. 700. 1992; Bennett & E. A. Christenson, Icon. Orch. Peruv.: t. 198. 1993; Zelenko & Bermudez, Orch. Sp. Peru: 372. 2009.

Xylobium hyacinthinum auct. non (Rchb.f.) Rolfe, Fernandez, Orquid. Nat. Tachira: 237. 2003.

Distribution: Colombia, Venezuela, Ecuador, and Peru.

Additional specimen examined: PERU. Junin: Satipo, Distrito Rio Tambo, Communidad Nativa Parijaro, Parque Nacional Otishi, 786–1086 m, 18 November 2013, *L. Valenzuela G., J. Flores, G. Shareva M., E. Cruz Ortiz, & C. Barboza 26993* (MO, image seen).

Xylobium subpulchrum was weakly distinguished from *X. stanhopeifolium* in my prior paper (Ormerod, 2018) by the shorter leaf petiole (5 vs. 20 cm long). However, on the GBIF (Global Biodiversity Information Facility) site, misidentified as *X. colleyi* is the above cited specimen with an accompanying color photograph. This specimen has a leaf petiole about 23 cm long and shows that this character cannot be used to distinguish *X. subpulchrum* from *X. stanhopeifolium*; therefore, the two are treated as synonymous here, with the older name naturally taking precedence.

Possibly the shorter leaf petiole length in the type material of *X. subpulchrum* was partly caused by its cultivation. Though *X. stanhopeifolium* seems to be a unifoliate species, some online images (e.g., from the Atlanta Botanic Garden) have been seen of what appear to be bifoliate plants.

Xylobium sulfurinum (Lem.) van Houtte, Cat. [van Houtte] 35: 31. 1848.Basionym: *Maxillaria sulfurina* Lem., Fl. Serres jard. Eur. ser. 1, 4: 330b. March 1848. TYPE: GUATEMALA. Without locality, *imp. & cult. L. B. van Houtte s.n.* (Holotype: W-R 40251, image seen).

Heterotypic synonyms: *Maxillaria hypocrita* Rchb.f., Hamb. Gart.-Blumenz. 16: 15. 1860. TYPE: ORIGIN UNKNOWN. *Cult. E. Stange s.n.* (Syntype: W-R 40255, image seen); *cult. F. W. G. Lauche s.n.* (Syntype: W-R 40255, image seen).

Xylobium hypocritum (Rchb.f.) Rolfe, Kew Hand-list Orch.: 149. 1896.

Distribution: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama.

Further synonyms (*X. powellii* Schltr., *X. sublobatum* Schltr., and *X. tuerckheimii* Kraenzl.) are listed in my prior account of 2018. Louis van Houtte first transferred *Maxillaria sulfurina* to *Xylobium* in his Autumn catalogue of 1848, thus the transfer of Schlechter in 1918 is an isonym. Furthermore, Rolfe transferred *Maxillaria hypocrita* to *Xylobium* in 1896, not 1912, as previously cited.

Xylobium undulatum (Ruiz & Pav.) Rolfe, Orch. Review 20: 43. 1912.

Basionym: *Maxillaria undulata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 221. 1798. TYPE: PERU. Huanuco: forests of Chinchao and Muna, August/September 1786, *H. Ruiz & J. Pavon s.n.* (Holotype: MA, image seen; Iconotypes: MA [2 paintings], images seen).

Homotypic synonym: *Dendrobium undulatum* (Ruiz & Pav.) Pers., Syn. Pl. 2: 524. 1807.

Usage synonym: *Xylobium coelia auct. non* (Rchb.f. & Warc.) Rolfe, Sambin & Aucourd, Richardiana n.s., 5: 27–33, Fig.1–2. 2021.

Distribution: Costa Rica, Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Ecuador, Peru, and Bolivia.

The extensive synonymy of this species can be found in my 2018 paper. Recently, Sambin and Aucourd (2021) recorded *Xylobium coelia* (Rchb.f. &Warc.) Rolfe from French Guiana, but their plant differs from the latter in having bifoliate (vs. unifoliate) pseudobulbs, yellowish-cream flowers suffused with pinkish red (vs. yellow to orange flowers), and a 5-keeled labellum midlobe hardly wider than long (3.5 × 5.0 mm). In *X. coelia*, the midlobe is reniform and 4.0 × 8.5 mm. The upper half of the lip is five-veined but not (or very weakly) developed into keels. Also, the lip of *X. coelia* is cuneate-flabellate when spread out (not oblong-elliptic as in the French Guiana plant). In my opinion their plant is a form of *X. undulatum,* a quite variable species.

Xylobium wilhelminae Ormerod, Harvard Pap. Bot. 23, 1: 72. 2018. TYPE: SURINAME. Wilhelmina Range, near summit of hill, West Rivier, 4 km S of Juliana Top, 700 m, 1 September 1963, *H. S. Irwin, G. T. Prance, T. R. Soderstrom & N. Holmgren 55297* (Holotype: NY).

Distribution: Suriname.

Additional specimen examined: SURINAME. Near airfield on the Oelemari River, 19 March 1963, *J. G. Wessels Boer 1010* (U [0123867], image seen).

The above collection would appear to be a second herbarium specimen of this species. It shows the unifoliate (a separate pseudobulb is bifoliate) pseudobulbs and 5- to 6-flowered inflorescences that are some of the features that characterize the species. According to Wessels Boer, the plant is epiphytic, and the flowers are yellow with the upper lip lined inside with pink. In the protologue, I could not determine if the flowers were non-resupinate, but Wessels Boer's note about the "upper lip" seems to indicate that they are indeed non-resupinate. The Oelemari River is next to the border with French Guiana, so one could expect *X. wilhelminae* to occur in that country too.

Literature Cited

Kolanowska, M., O. A. Perez Escobar, E. Parra Sanchez, and D. L. Szlachetko. 2011. An illustrated field guide to the orchids of the Yotoco Forest Reserve (Colombia). Fundacja Rozwoju Uniwersytetu Gdanskiego, Gdansk, Poland.

Kraenzlin, F. 1908. Neue und kritische Arten. Orchis 2: 127–129.

Ormerod, P. 2018. A Synopsis of the Genus *Xylobium* (Orchidaceae, Maxillareae). Harvard Pap. Bot. 23, No. 1: 57–75.

Rolfe, R. A. 1896. Hand-list of orchids cultivated in the Royal Gardens. Royal Botanic Gardens, Kew.

———. 1912. The Genus *Xylobium*. Orch. Review 20, No. 230: 43.

Sambin, A., and M. Aucourd. 2021. Premier enregistrement de *Xylobium coelia* (Orchidaceae) en Guyane francaise. Richardiana n.s. 5: 27–33.

Schlechter, R. 1913. Die Gattung *Xylobium* Lindl. Orchis 7: 21–24.

van Houtte, L. B. 1847. Prix Courant de Louis van Houtte, Horticulteur No. 31. Horticulteur a Gand, Ghent, Belgique.

NOTES ON SOME MALESIAN ORCHIDACEAE VI

Paul Ormerod[1,2] and Lina Juswara[3]

Abstract. Continuing herbarium and literature research on Malesian orchids has identified seven new synonyms, the necessity for two combinations, and one new record. The new transfers are *Dyakia cruikshankii* and *Oberonioides latifiana*.

Keywords: Malesia, orchids, synonymy, *Dyakia, Oberonioides*

This paper continues our studies (e.g., Ormerod and Juswara, 2023) of Malesian orchids with the intent of updating floristic knowledge of the region. As per usual most of the taxa dealt with occur in Indonesia, though *Oberonioides latifiana* is endemic to Peninsular Malaysia.

Bulbophyllum Thouars, Hist. Orchid. Iles Austral. Afr.: tabl. esp. 3 et tt. 93–110. 1822.
Type species: *Bulbophyllum nutans* Thouars *typ. cons.*

A genus of about 2020 accepted species, found in Central and South America, Africa, Madagascar, India through Malesia to Tahiti, south to New Zealand, and north to Japan. The plants are predominantly epiphytes that have single-noded pseudobulbs topped by one or two leaves, basal inflorescences of one to many flowers, and flowers most often with a hinged labellum. *Bulbophyllum* is the second largest orchid genus in Indonesia with about 622 species, 320 of which are endemic.

Bulbophyllum flammuliferum Ridl., J. Bot. (London) 36: 211. 1898. TYPE: MALAYSIA. Selangor, Gua Batu [= Batu Caves], 305 m, December 1896, *H. N. Ridley s.n.* (Lectotype [here designated]: SING [01300805, image seen]); without origin, bought at a sale, January 1897, *cult. Hort. Bot. Singapor. s.n.* (Syntype: SING [0131556, image seen]).
Heterotypic synonym: *Bulbophyllum rhodosepalum* Schltr., Notizbl. Konigl. Bot. Gart. Berlin 4: 171. 1905 *syn. nov.*
TYPE: INDONESIA. Sumatra, 1900, imported and collected *G. Schneider, cult. Berlin Botanic Garden s.n.* (Holotype: B, destroyed).

Distribution: Malaysia; Indonesia (Sumatra, Kalimantan).

This taxon is a distinctive member of section *Desmosanthes* (Blume) J.J. Sm., recognised by its erect, sublax racemes (vs. congested heads) of flowers with mostly red, lanceolate-caudate sepals (with a yellowish basal part). It had not been recognised as occurring in Sumatra until Comber (2001) reported it based on his own find. The description of *B. rhodosepalum* completely coincides with the known variation of *B. flammuliferum,* and, thus, we have no hesitation in reducing the former to synonymy.

Dendrobium Swartz, Nova Acta Regiae Soc. Sci. Upsal. ser. 2, 6: 82. 1799 *nom. cons.*
Type species: *Dendrobium moniliforme* (L.) Swartz *typ. cons.*

A large genus of about 1530 species distributed from Sri Lanka and India to Tahiti. The plants are primarily epiphytes, but some taxa are terrestrial (especially in New Caledonia) or can often be found growing lithophytically (e.g., *D. speciosum* J.E. Sm. in Australia). It is the largest orchid genus in Indonesia with about 685 species, 405 of which are endemic.

Dendrobium hymenocentrum Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 567. 1 Oct 1912. TYPE: PAPUA NEW GUINEA [as Kaiser-Wilhelms-Land]. Near Pro, 15 m, August 1909, *R. Schlechter 20000* (Holotype: B, destroyed; Isotypes: AMES [00090108], E [000394206, image seen], G [00165515, image seen], GH [00090107], L, not found, NSW [926675], S [S-G-1932, image seen].
Homotypic synonyms: *Aporum hymenocentrum* (Schltr.) Rauschert, Feddes Repert. 94, 7–8: 439. 1983.
Ceraia hymenocentra (Schltr.) M.A. Clem., Telopea 10, 1: 291. 2003.
Heterotypic synonyms: *Dendrobium humboldtense* J.J. Sm., Repert. Sp. Nov. Regni Veg. 11: 131. 20 Oct 1912 *syn. nov.* TYPE: INDONESIA. Papua Prov., Humboldt Bay, Hollandia [now Jayapura], 50 m, July 1911, *K. Gjellerup 574* (Holotype: BO [0032530]).
Aporum humboldtense (J.J. Sm.) Rauschert, Feddes Repert. 94, 7–8: 439. 1983.
Ceraia humboldtensis (J.J. Sm.) M.A. Clem., Telopea 10, 1: 291. 2003.

Distribution: Indonesia (Papua); Papua New Guinea.

The first author would like to thank the herbarium and library staff at BRI, HUH (A, AMES, and GH), K, and NSW for their help and hospitality during his visits. The second author would like to thank colleagues at the Directorate of Scientific Collection Management, National Research and Innovation Agency, BO for their ongoing help and advice. We would also like to thank Serena Lee (SING) for arranging the imaging of materials at SING relevant to our studies.

[1] P.O. Box 8210, Cairns 4870, Queensland, Australia
[2] Corresponding author: wsandave1@bigpond.com
[3] Herbarium Bogoriense, Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), KST Soekarno, Jl. Raya Jakarta KM 46, Pakansari, Cibinong, Bogor Regency 16911, West Java, Indonesia; linajuswara@gmail.com

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 715–719.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n8, Published online: 31 December 2023

A characteristic species of section *Aporum* Blume, recognizable by the flowers having a 12 mm long mentum with the lateral sepals flared back, and the lip only weakly quadrilobate near the very apex. Both *D. hymenocentrum* and *D. humboldtense* are identical in their characters, and, therefore, we unite the two. *Dendrobium hymenocentrum* has been recorded from the island of Bougainville by Lewis and Cribb (1991), based on *A. N. Millar & J. Vandenberg NGF 48504* (BRI, K). Examination of the latter collection showed it to be *D. goldfinchii* F. Muell., a common species in the Solomon Archipelago.

Dendrobium leonis (Lindl.) Rchb.f., Ann. Bot. Syst. 6: 280. 1861.

Basionym: *Aporum leonis* Lindl., Edwards's Bot. Reg. 26: misc. 59. 1840. TYPE: SINGAPORE. *Leg. J. Prince in N. Wallich 2018* (Syntype: K-L, not seen; K, drawing, not seen); *leg. H. Cuming, cult. Messrs. Loddiges s.n.* (Syntype: K-L, not seen).

Homotypic synonym: *Callista leonis* (Lindl.) O. Kuntze, Rev. Gen. Pl. 2: 655. 1891.

Heterotypic synonyms: *Dendrobium uniflorum* Teijsm. & Binn., Nat. Tijdschr. Ned. Ind. 24: 313. 1862 *nom. illeg., syn. nov.* (*non* Griff. 1851). TYPE: INDONESIA. Sumatra, Lampong Prov., *J. E. Teysmann s.n.* (Holotype: lost).

Dendrobium monanthum Teijsm. & Binn., Nat. Tidjschr. Ned. Ind. 28: 167. 1865.

Usage synonym: *Aporum indivisum auct. non* Blume, Lindl., Gen. Sp. Orch. Pl.: 70–71. 1830.

Distribution: Vietnam; Laos; Cambodia; Thailand; Malaysia; Singapore; Brunei; Indonesia (Sumatra).

This taxon is a commonly collected and cultivated member of section *Aporum* Blume. Kraenzlin (1910) considered *D. uniflorum* Teijsm. & Binn. (*non* Griff. 1851) as a synonym of *D. prostratum* Ridl., and, thus, if this is correct, then the former would have priority due to its substitute epithet, *D. monanthum*, appearing in 1865. However, the protologues of the two are not compatible, with *D. prostratum* having long-creeping rhizomes, while *D. monanthum* has caespitose stems. Other characters of *D. monanthum*, such as the broad, blunt leaves, a single terminal flower that is tawny-colored with purple spotting on the outside, and an apically emarginate lip, suggest it is rather a synonym of *D. leonis*. Therefore, we treat *D. monanthum* as a synonym of *D. leonis*.

Dendrobium metrium Kraenzl., in Engl., Pflanzenr. IV 50, II B. 21, 45: 221. 1910.

Basionym: *Dendrobium modestum* Ridl., J. Bot. (London) 36: 211. 1898 *nom. illeg.* (*non* Rchb.f. 1855). TYPE: MALAYSIA. Penang Island, top of Penang Hill, 610 m, March 1896, *H. N. Ridley 7238* (Holotype: SING [0047307, image seen]; Isotype: K [001085064, image seen]).

Homotypic synonyms: *Pedilonum metrium* (Kraenzl.) Rauschert, Feddes Repert. 94, 7–8: 461. 1983.

Eurycaulis modestus M.A. Clem., Telopea 10, 1: 287. 2003 *nom. illeg.*

Heterotypic synonyms: *Dendrobium sociale* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 2, 3: 61. 1912. TYPE: INDONESIA. Sumatra, Proeba Toea, *B. Hagen s.n.* (Holotype: BO, not found).

Dendrobium batakense J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 3, 5: 90. 1922. TYPE: INDONESIA. Sumatra, Batak Lands, Siborborong, 1100 m, *cult. W. Groeneveldt 1972* (Holotype: BO, spirit, not seen).

Dendrobium nhatrangense Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) ser. 2, 2: 237. 1930. TYPE: VIETNAM. Nhatrang: N of Ninh Hoa, 1600 m, 17 May 1923, *E. Poilane 6508* (Holotype: P [00408216, image seen]).

Grastidium nhatrangense (Gagnep.) Rauschert, Feddes Repert. 94, 7–8: 451. 1983.

(?) *Dendrobium filicaule* Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) ser. 2, 21: 741. 1950. TYPE: VIETNAM. Annam: Summit of Nui Bach Ma, 1400–1500 m, 8 September 1938, *E. Poilane 27674* (Holotype: P [00407691, image seen]; Isotype: P [00407692, image seen].

(?) *Anisopetala filicaule* (Gagnep.) M.A.Clem., Telopea 10, 1: 283. 2003.

Distribution: Vietnam; Laos; Thailand; Malaysia (Peninsula); Indonesia (Sumatra).

Additional specimen examined: INDONESIA. Sumatra, E coast, Aekanaeli District, Simalaengan, rim of crater on E side of Lake Toba, 1220–1830 m, 1 February 1935, *W. N. Bangham & C. M. Bangham 1279* (AMES).

This species was recently recorded from Laos (Phonepaseuth et al., 2023). They repeated the synonymy found on POWO (Plants of the World Online), which includes, in addition to the names cited above, *D. dalleizettei* Gagnep. from Vietnam. We believe that the latter should be excluded from the synonymy; however, the status of another entity (*D. filicaule*) is rather problematic.

Dendrobium dalleizettei Gagnep. was described from North Vietnamese material (between Laokay and Chapa, *C. d'Alleizette s.n.* [Syntype: P 00408215, image seen]; Lai Chan, San-Tan-Ngai, *E. Poilane 25606* [Syntype: P 00408212, image seen]). Seidenfaden (1985) suspected it was close to *D. sociale*, but noted it differed in the shorter mentum and details of the labellum. In Seidenfaden (1992) he lists it in the synonymy of *D. sociale* without question. However, Seidenfaden's original suspicions about the differences were correct, to which it can be added the plant has thicker stems than *D. metrium*. We believe *D. dalleizettei* to be a synonym of *D. moniliforme* (L.) Sw., a taxon that wasn't known to occur in Vietnam at the time.

Dendrobium filicaule Gagnep. was described from South Vietnamese material. It is similar in habit to *D. metrium* but differs in its unusual flowers with a broader, right-angled to slightly incurved (vs. straight, infundibuliform) mentum, and narrower lip with a distinct depression (possibly an artifact) in the upper half (see Seidenfaden, 1992, for an illustration). On first appearances, the differences appear quite distinct, but Dr. Ba Vuong Truong sent us images of Vietnamese material named *D. metrium* that has a short blunt

mentum (at times with a poorly developed prolongation). This material is somewhat intermediate between typical *D. metrium* and *D. filicaule*. Obviously, more studies are called for, especially into the unique variation to be found in Vietnamese material.

Dendrochilum Blume, Bijdr. Ned. Ind. 8: 398. 1825.

Type species: *Dendrochilum aurantiacum* Blume

A genus of about 270 species distributed from Myanmar to Papua New Guinea. The two centers of speciation are the Philippines and Indonesia. About 122 species are found in Indonesia, of which 94 are endemic. *Dendrochilum* are mostly pseudobulbous epiphytes bearing one or two leaves, and usually have inflorescences of many smallish greenish to whitish flowers.

Dendrochilum gracile (J.D. Hook.) J.J. Sm., Recueil Trav. Bot. Neerl. 1: 69. 1904.

Basionym: *Platyclinis gracilis* J.D. Hook., Fl. Brit. Ind. 5: 708. 1890. TYPE: MALAYSIA. Perak, Larut, 1220–1525 m, August 1882, *G. King's coll. s.n.* (Holotype: K [000482373, image seen]; Isotype: CAL [0000000091, image seen].

Homotypic synonyms: *Acoridium gracile* (J.D. Hook.) Rolfe, Orch. Review 12, 139: 220. 1904.

Coelogyne gracilis (J.D. Hook.) M.W. Chase & Schuit., Phytotaxa 510, 2: 112. 2021.

Heterotypic synonyms: *Dendrochilum krauseanum* Schltr., Orchis 4: 106. 1910 *syn. nov.* TYPE: INDONESIA. Sumatra, Batak Range, 1000 m, *leg. R. Schlechter,* fl. September 1910, *cult. M. von Fuerstenberg s.n.* (Holotype: B, destroyed).

Coelogyne krauseana (Schltr.) M.W. Chase & Schuit., Phytotaxa 510, 2: 115. 2021.

Distribution: Malaysia; Indonesia (Sumatra, Java, Bali, Flores, Sumba, Kalimantan).

Analysis of the protologue of *D. krauseanum,* plus the published floral dissection (Schlechter, 1933), shows it to have all of the characters of *D. gracile*, and, therefore, we find them to be conspecific. The holotype of *Platyclinis gracilis* in Kew has a "King's collector" label, while the isotype in CAL has a *H. Kunstler* label. Also, the CAL specimen has more mature flowers. Further synonymy can be found in Jeff Wood's (2001) monograph of Bornean *Dendrochilum*.

Dyakia E.A. Christ., Orchid Digest 50, 2: 63. 1986.

Type species: *Saccolabium hendersonianum* Rchb.f.

Dyakia is a monospecific genus of Aeridiinae restricted to Borneo. It is an attractive, small-sized orchid, with a glaucous green coloring underneath the leaves, and erect, densely-flowered racemes of pink flowers.

Dyakia cruikshankii (Postans) Ormerod & Juswara, *comb. nov.*

Basionym: *Saccolabium cruikshankii* Postans, Gard. Chron. ser. 2, 2: 83. 18 Jul 1873; Hort., Garden (London, 1872–1927) 6: 63. 18 Jul 1873. TYPE: WITHOUT ORIGIN. Exhibited at the Royal Horticultural Society, 15 July 1873, *Messrs. E. G. Henderson & Sons s.n.* (Holotype: lost).

Heterotypic synonyms: *Saccolabium hendersonianum* Rchb.f., Gard. Chron. ser. 2, 4: 356. 18 Sep 1875 *syn. nov.*

TYPE: BORNEO. *Cult. E. G. Henderson and Sons s.n.* (Holotype: W-R, not seen; Isotype: K [000891619, image seen]).

Ascocentrum hendersonianum (Rchb.f.) Schltr., Die Orchideen ed. 1: 576. 1914.

Dyakia hendersoniana (Rchb.f.) E.A. Christ., Orch. Digest 50, 2: 63. 1986.

Distribution: Malaysia (Sarawak, Sabah); Indonesia (Kalimantan).

The protologue of *Saccolabium cruikshankii* describes it briefly as "…a small plant with short upright spathes of pale rosy flowers." A little more detail was published simultaneously in The Garden, "…a pretty rosy-flowered *Saccolabium,…* it has erect spikes, and drooping fleshy leaves of a glaucous green colour." While the description is brief, it is valid, and we believe representative of the taxon later named *Saccolabium hendersonianum* by Reichenbach based on material from the same company. Reichenbach (1875) admitted that "The plant has been known among the *crème* of intelligent English Orchidists, for I believe, two or three years 'as the new Bornean *Saccolabium'* and highly appreciated…." He also suspected that Messrs. E. G. Henderson and Sons were the only ones to flower it.

Saccolabium cruikshankii was rarely mentioned later, except for a report by H. C. Murton that was quoted by William Robinson (1875) in The Garden, that the species was naturalised on trees in the Singapore Botanic Gardens. Hooker (1876) quoted Reichenbach as telling him that *Saccolabium hendersonianum* was said to have been introduced into England by Messrs. Low in 1862, but so far no proof has been found to support this statement.

Liparis L.C. Rich., De Orchid. Eur. 21, 30, 38. 1817 *nom. cons.*

Type species: *Ophrys loeselii* L.

If treated in the broad sense, this is a genus of about 500 species distributed around the world. In the narrow sense, there about ten species in Indonesia, of which nine seem to be endemic. The Indonesian plants are mostly terrestrial with conduplicate leaves and have yellowish to purplish flowers in terminal racemes.

Liparis montana (Blume) Lindl., Gen. Sp. Orch. Pl.: 29. 1830.

Basionym: *Malaxis montana* Blume, Bijdr. Fl. Ned. Ind. 8: 388. 1825. TYPE: INDONESIA. Java. Mt. Gede, fl. June, *C. L. Blume s.n.* (Holotype: lost). Neotype [here designated]: Java, Mt. Megamedong, *C. L. Blume 475* (Holoneotype: L [0061508, image seen]; Isoneotype: L [0061509, without collector number, image seen]).

Homotypic synonyms: *Leptorkis montana* (Blume) O. Kuntze, Rev. Gen. Pl. 2: 671. 1891.

Heterotypic synonyms: *Malaxis atropurpurea* Blume, Bijdr. Fl. Ned. Ind. 8: 390. 1825. TYPE: INDONESIA. Java, Mt. Salak, fl. October, *C. L. Blume 634* (Holotype: L [0061507], image seen).

Platystylis atropurpurea (Blume) Lindl., Gen. Sp. Orch. Pl.: 18. 1830.

Microstylis atropurpurea (Blume) Miq., Fl. Ned. Ind. 3: 625. 1859.

Liparis repens Ridl., J. Linn. Soc., Bot. 22: 279. 1886.

Leptorkis atropurpurea (Blume) O. Kuntze, Rev. Gen. Pl. 2: 671. 1891.

Chlorosa gracilis Blume, Bijdr. Fl. Ned. Ind. 8: 420. 1825 *syn. nov.* TYPE: INDONESIA. Java, Mt. Burangrang, fl. July, *C. L. Blume 1456* (Holotype: L [0063330, image seen]).

Spiranthes gracilis (Blume) Hassk., Catal. Pl. Hort. Bogor.: 47. 1844 *nom. illeg.* (*non* Beck 1833).

Distribution: Indonesia (Java).

Blume (1858) reported that his *Chlorosa gracilis* belonged in the genus *Liparis*. However, after this the species is absent from major accounts of the Javanese orchid flora (Smith, 1905; Comber, 1990). We believe J. J. Smith did discover the identity of *Chlorosa gracilis* but likely forgot about it. Its type material is filed with *Liparis montana* and correctly identified as such. Therefore, we publish the synonymy of the two, so that another obscure name can be removed from the Javanese flora.

Type material of *Malaxis montana* from Mt. Gede has not been located. Therefore, we designate as neotype another Blume collection from Mt. Megamedong (now Megamendung) that has been annotated as *Malaxis montana* by him. There is a probable concurrent historical collection from Mt. Gede of *Liparis montana* in L, but we believe it was collected by Alexander Zippelius (L [1522431, image seen]), and it is not annotated by Blume.

Oberonioides Szlach., Fragm. Fl. Geobot., Suppl. 3: 134. 1995.

Type species: *Malaxis oberoniiflora* Seidenf.

A genus of seven (now eight) terrestrial herbs with short pseudobulbs, a single, usually cordate, conduplicate leaf, often minute flowers (sepals usually ca. 2 mm long, but rarely up to 12 mm long), a simple to bilobed, often ciliate-margined labellum, and short column. One more recently described species is transferred here.

Oberonioides latifiana (P.T. Ong) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis latifiana* P.T. Ong, Malesian Orch. J. 24: 54. 2020. TYPE: MALAYSIA. Kedah: cult. Cameron Highlands Montane Park, 27 April 2015, *S. C. Ng FRI 80716* (Holotype: KEP, spirit, not seen; Isotype: K, not seen).

Distribution: Malaysia (Kedah).

Phaius Lour., Fl. Cochinch. 2: 517, 529. 1790.

Type species: *Phaius grandifolius* Lour.

A genus of terrestrial herbs with either pseudobulbs or stems bearing a few pleated leaves, with erect (or occasionally, short axillary) inflorescences of mid-sized to large, often quite attractive flowers. Cribb and Stone (2017) monographed the genus accepting 41 species distributed from Africa to Tahiti.

Phaius tankervilleae (Banks) Blume, Mus. Bot. Lugd.-Bat. 2: 177. 1856.

TYPE: Icon of *Limodorum tankervilleae* drawn in 1787 by *J. Sowerby* (Lectotype [Mabberley 2011: 476]: BM, not seen).

Basionym: *Limodorum tankervilleae* Banks, plate of *Limodorum tankervilleae* distributed in 1788.

Distribution: India, Myanmar, China, Vietnam, Laos, Thailand, Malaysia, Philippines, Taiwan, Japan, Indonesia, Papua New Guinea, Australia, Vanuatu, New Caledonia, Fiji, Tonga, and Samoa.

Mabberley (2011) pointed out that the basionym of this species was effectively published by Joseph Banks, who distributed a plate drawn by James Sowerby in 1788. This a common, widespread, attractive species which is amenable to horticulture.

Phaius tankervilleae var. ***papuanus*** J.J. Sm., Nova Guin. 12, 3: 203. 1915. TYPE: INDONESIA. Papua Prov., Humboldt Bay (?), *leg. K. Gjellerup, cult. Hort. Bogor. 466* (Lectotype [here designated]: L [0061882, image seen]; Isolectotype: U [1462298, image seen]).

Heterotypic synonym: *Phaius tankervilleae* (Banks) Blume var. *devogelii* Cribb & Stone, Lady Tankerv. Legacy: 115. 2017 *syn. nov.* TYPE: PAPUA NEW GUINEA. Oro Prov., Kokoda Valley, Kowelo, 5 km W of Kokoda, 450 m, *cult. Hort. Leiden 20031931,* January 2008, *leg. E. F. de Vogel & A. Vogel s.n.* (Holotype: L [1518775, image seen]; Isotype: L [23924, spirit, not seen]).

Distribution: Indonesia (Sulawesi, Papua); Papua New Guinea.

Phaius tankervilleae var. *papuanus* was not illustrated by Smith when he published it, but Smith's unpublished drawing can be found on the Orchids of New Guinea website. This drawing does not show the ovate, apiculate labellum midlobe said to characterise the variety *devogelii*, but type material of variety *papuanus* does have the aforementioned characters. Therefore, we regard the two taxa as the same. The authors of variety *devogelii* overlooked Smith's variety. Considering the overall variation of *Phaius tankervilleae*, we doubt that the variety *papuanus* can be maintained, but this will need further studies.

We were unable to find any preserved material of variety *papuanus* in the dried or spirit materials housed at BO; therefore, the sheet in Leiden is chosen as the lectotype.

Plocoglottis Blume, Bijdr. Fl. Ned. Ind. 8: 380. 1825.
Type species: *Plocoglottis javanica* Blume.

A genus of about 38 terrestrial species distributed from India (Andaman Islands) and Thailand to the Solomon Islands. Most species have yellow flowers variously marked with reddish-brown, but there are some taxa that have pink to purple flowers, or yellow flowers with bright pink to purple lateral sepals. An interesting feature of the flowers is that the lip has basal elastic hinges that act as a sort of trap when triggered by a visiting insect, pushing it against the column.

Plocoglottis quadrifolia J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 3, 8: 36. 1926. TYPE: INDONESIA. Sumatra: Agam, Bukit Batu Banting, *cult. W. Groeneveldt 873* (Holotype: L, spirit, not seen; Isotype: L [0062347, image seen]).

Distribution: Vietnam; Thailand; Malaysia; Indonesia (Sumatra, Kalimantan).

Specimens examined: MALAYSIA. Sabah: Tenom District, Crocker Range Forest Reserve, 17 April 1970, *A. Gibot SAN 66772* (L [1525147], image seen). INDONESIA: Kalimantan. NE of Muara Uja, 3 km from Djaro, Batu Kumpai, 140 m, 20 February 1971, *E. F. de Vogel 935* (BO, L [1525117, image seen]); ca. 10 km NE of Muara Uja, Batu Kumpai, Djaro Dam, 350 m, 15 October 1972, *E. F. de Vogel 1627* (L [1525104, image seen], L [1525105, image seen]).

This species is here recorded from Borneo for the first time; it occurs in both the Indonesian and Malaysian parts of the island. It is easily recognised by its stems that apically have four to six leaves, basal inflorescences, and flowers with a subquadrate, ciliate-margined lip. The superficially similar *P. gigantea* (J.D. Hook.) J.J. Sm. has much taller stems, often with 10–12 leaves or more, and the flowers have a lip with glabrous margins.

Literature Cited

Blume, C. L. 1858. Collection des Orchidees les plus remarquables L'Archipel Indien et du Japon. C. G. Sulpke, Amsterdam.

Comber, J. B. 1990. Orchids of Java. Royal Botanic Gardens, Kew.

———. 2001. Orchids of Sumatra. Royal Botanic Gardens, Kew.

Cribb, P. J., and J. Stone. 2017. Lady Tankerville's Legacy. A Historical and Monographic Review of *Phaius* and *Gastrorchis*. Natural History Publications (Borneo), Kota Kinabalu, in association with Royal Botanic Gardens, Kew.

Hooker, J. D. 1876. *Saccolabium hendersonianum*. Curtis's Bot. Mag. 102: t. 6222.

Kraenzlin, F. 1910. Orchidaceae-Monandrae-Dendrobiinae Pars 1. In A. Engler, Das Pflanzenreich. Regni vegetabilis conspectus IV. 50, II. B. 21, 45: 1–382.

Lewis, B. A., and P. J. Cribb. 1991. Orchids of the Solomon Islands and Bougainville. Royal Botanic Gardens, Kew.

Mabberley, D. J. 2011. A note on some adulatory botanical plates distributed by Sir Joseph Banks. Kew Bull. 66, 3: 475–477.

Ormerod, P., and L. Juswara. 2023. Notes on Some Malesian Orchidaceae V. Harvard Pap. Bot. 28, No. 1: 93–98.

Phonepaseuth, P., K. Souvannakhoummane, S. Xayyasith, C. Keovongsy, K. Soulida, and P. Souladeth. 2023. Two new distribution records of *Dendrobium* (Orchidaceae), with an updated checklist of *Dendrobium* for Laos. Thai Forest Bull. Bot. 51, No. 1: 24–35.

Reichenbach *f*., H. G. 1875. New Garden Plants. Gard. Chron. ser. 2, 4: 356.

Robinson, W. [editor]. 1875. Notes of the Week. The Garden (London, 1872–1927) 8: 362.

Schlechter, R. 1933. Blutenanalysen neuer Orchideen. IV. Indische und malesische Orchideen. Repert. Sp. Nov. Regni Veg., Beih. 74: tafel 1–85.

Seidenfaden, G. 1985. Orchid Genera in Thailand XII. *Dendrobium* Sw. Opera Botanica 83: 1–295.

———. 1992. The Orchids of Indochina. Opera Botanica 114: 1–502.

Smith, J. J. 1905. Die Orchideen von Java. Flora von Buitenzorg 6: 1–672. E. J. Brill, Leiden.

Wood, J. J. 2001. *Dendrochilum* of Borneo. Natural History Publications of Borneo, in association with Royal Botanic Gardens, Kew.

Page 720 intentionally left blank.

A NEW RECORD FOR THE FLORA OF VENEZUELA AND THE RIO NEGRO BASIN: *DOURADOA CONSIMILIS* (XIMENIACEAE)

Gustavo A. Romero-González[1,2] and Gerardo A. Aymard-Corredor[3,4]

Abstract. A new record for the flora of Venezuela and the Rio Negro Basin, *Douradoa consimilis*, is reported herein. It was collected in the Ekeweni river, a major tributary of the San Miguel River, itself a tributary of the Guainía river that eventually becomes the Rio Negro after its confluence with the Casiquiare canal. It was collected in vegetation subject to immersion, partially or totally, during the rainy season.

Keywords: Amazonia, *Douradoa*, Rio Negro basin, San Miguel River, Venezuela, Ximeniaceae

The largest tropical forest in the world is located in the Amazon basin and the Guiana Shield region (Myster, 2016; Antonelli et al., 2018). This area covers ca. 40% of South America and harbors 10% of the world's plant species (ca. 50,000); including ca. 16,000 taxa estimated to be trees (ter Steege et al., 2013, 2020; Cazzolla Gatti et al., 2022). One the most relevant issues observed in the last decade is that only 1.4% (227 ssp.) of the tree species are extremely common. This subset of disproportionately common trees has been dubbed the "hyperdominants" (ter Steege et al. 2013).

More than 25,000 plant species are endemic to the region (Science Panel for the Amazon, 2021). Such high plant diversity is presumably due to changes in climatic, hydrological, edaphic, and geological conditions that this region has undergone (Latrubesse et al., 2007, 2010, 2017; Tuomisto et al., 2016; Jaramillo, 2023). These changes oscillated extensively during the biogeographical history of Amazonia, allowing the assembly of unique habitats that reached its present geological configuration throughout the Neogene, during the uplift of the Andes (Hoorn et al., 2010, 2017, 2022; Boschman et al., 2021).

The distribution range of some Amazonian tree species extends across the entire Amazon basin, but most are apparently restricted to much smaller areas shared with other rare species (Zizka et al., 2016). A similar imbalance is observed in species:genus ratios; over half of all Amazonian tree species belong to genera with 100 or more species, while the majority of genera (52%) have ten or fewer species (Gentry, 1993; Dexter and Chave, 2016).

The difficult and, in some cases, impossible access (for multiple reasons) to some field sites in Amazonia, especially remote ones (geographically and/or logistically) has hindered botanical exploration; therefore, the Amazon flora remains inadequately studied (Hopkins, 2007; Aymard et al., 2016; Arellano et al., 2019).

The Rio Negro basin, in particular, shows considerable variation in floristic composition and forest structure along local and regional environmental gradients; it comprises a mosaic of unique vegetation types, particularly sclerophyllous forests on oligotrophic and acid soils, known as "caatinga Amazónica" (Venezuela). The area also harbors small to extensive areas of savannas, shrubby savannas, and scrublands growing on white sands. Additionally, these white-sand forests are established through an ecological and floristic transition between *terra-firme* forests commonly found on peneplain red-yellow clay soils, and flooded forest communities on alluvial plains called *igapó* and *varzéa* (for a review see Arellano-Peña et al., 2023). Sporadic reports of new distributions for Amazonian tree species have been published recently, such as the first report of *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber (Rhabdodendraceae) for the flora of Colombia and the upper Rio Negro (Aymard et al., 2016; Arellano et al., 2019) and a new report of *Schoeffia clarkii* Steyerm. (Schefiaceae) within the Rio Negro basin (Farroñay et al, 2019).

The species reported here is another notable example. The genus *Douradoa* Sleumer and *D. consimilis* Sleumer (Ximeniaceae), described by Sleumer (1984: 136), were based on two collections made in 1968, *Silva 1082* and *Oliveira 4134*, and a third one made in 1976, *Rosa 1374* (the latter sterile; see additional specimens examined). All three collections were gathered in the general area of Monte Dourado, along the border of the states of Amapá and Pará, Brazil. Another collection from the same area, made in 1982, *Silva 5288*, was not examined by the author of the species. Two additional collections from Brazil were reported more recently, *Maas et al. 9176*, made in 2001in the state of Acre, and *Zartman 5547*, made in 2006 in the state of Amazonas.

The collection reported here was made, serendipitously, in the context of an orchid inventory project in southern

The senior author thanks the Harvard University Herbaria and the Orchid Society of Arizona for providing financial support for his expeditions in southern Venezuela, the Sandalio Camico and Aragua families in Maroa and the personnel of TFAV in Puerto Ayacucho for their logistic support, and his field companions, C. Gómez, O.-Gómez, J. Aragua, and E. Cayupare, without whom his work could not have been completed. The authors thank H. Arellano-Peña for preparing the distribution map.

[1] Orchid Herbarium of Oakes Ames, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 20138, U.S.A.
[2] Corresponding author: romero@oeb.harvard.edu
[3] UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, estado Portuguesa 3350, Venezuela
[4] Current address: Compensation International Progress S.A. Ciprogress–Greenlife, Bogotá, D.C., Colombia; cuyuni24@hotmail.com

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 721–726.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n9, Published online: 31 December 2023

Venezuela. Due to limitations in the weight and volume that could be carried in a small plane, collections were restricted to Orchidaceae, and few other families were collected unless they appeared rare or exceptional to the senior collector (one of us, GAR-G). *Douradoa consimilis* was collected after an eight-hour journey by boat departing from Maroa (2°43'12"N, 67°33'46"W), on the eastern side of the Guainía River, navigating up the San Miguel river and "caño" Ekeweni, to a camp site near Sabana Tinaja (see coordinates below). The collection was made at night, when we sampled the vegetation around the camp site using flashlights. It was identified by the junior author based on a small sample from a hand press (Fig. 1). It was first reported for the Venezuelan Rio Negro basin in Romero-González et al. (2019: 98). Again, surprisingly, this new locality is ca, 1850 km from the ones reported in the protologue, ca. 1430 km from the locality in Amazonas, Brazil, and approximately 1300 km from the locality in Acre, Brazil.

We report herein *Douradoa consimilis* for the flora of Venezuela and the Rio Negro basin. We present photographs, amend the description of floral parts, and provide new data on geographic distribution and ecology.

Douradoa consimilis Sleumer, Fl. Netrop. 38: 136. 1984. TYPE: BRAZIL. Pará: [lower] Rio Jarí, Monte Dourado [0°51'51"S 52°32'25"W], Planalto A., mata de terra firme, árvore de 38 m, botão verde, 2 October 1968, *N. T. Silva 1082* (Holotype: IAN, not seen; Isotypes: NY [00285458 & 00285459], L [0038961, image seen]. Fig. 1–3.

Additional specimens examined: BRAZIL. Acre: Município Cruzeiro do Sul, 364 near comunidade Assis Brasil, Ramal do Pentecoste, Km 10, 7°31'17"S, 72°51'15"W, forest on white sand, tree 25 m tall, 40 cm in diam., pedicels pink, ovary green, tepals pale green, 23 October 2001, *P. J. M. Mass, H. Mass-van de Kamer, J. Prado, D. P. Gomes Silva, R. L. Maia, E. C. Oliveira, & J. R. Bandeira 9176* (NY [00868494], MO [1791025]). Amapá: Município Mazagão, área do Felipe V, floresta de terra firme, 0°6'54"S, 51°17'22"W, tronco cilíndrico, DAP 35 cm, altura commercial 12 m, copa 08 m, total 20 m, 23 February 1982 (fr), *N. T. Silva 5288* (MG [124357_2, image seen]); Porto Platon-Serra do Navio, 0°59'N; 52°03'W, 10 October 1976 (st.), *N. A. Rosa 1374* (MG, not seen]. Amazonas: Apuí, Rio Sucunduri acampamento, Floresta riparia na beira do Rio Sucunduri, 8°00'S, 59°40'W, 26 June 2006, *C. E. Zartman 5547* (INPA). Pará: Rio Jarí, Monte Dourado, Planalto, mata alta, T. firme, árvore de 22–25 m, 0°52'S; 52°31'W, 28 January 1968, *E. Oliveira 4134* (NY [02259736]); same locality, Planalto A., mata de Terra firme, árvore de 30–35 m, flôr esverdeada, 10 September 1968, *N. T. Silva 929* (NY [02259737]). VENEZUELA. Amazonas: Municipio Autónomo Maroa, cuenca del río San Miguel, margen oeste del caño Ekeweni, en los alrededores del Puerto de Tinaja, 2°44'11"N, 66°47'42"W, árbol de 7 m, flores verdes, en el ápice blancas, único individuo visto en la orilla del caño, 28 August 2008 (fl), *G. A. Romero, C. Gómez, O. Gómez, E. Yuriyuri, & J. Aragua 4013* (GH, MO, TFAV, VEN [×2]).

Common name: "Pau curupira" (based on *Silva 5288*).

Distribution and ecology: Brazil (Acre, Amapá, Amazonas, and Pará) and Venezuela (Amazonas; Fig. 3). In the type locality, found on *terra firme*; in Acre, found in forest on white sand; in Venezuela, found in seasonally flooded forest, along a black-water river, growing on white sand.

Iconography: Sleumer (184: 137, Fig. 19), reproduced in Kuijt and Hansen (2015: 188, Fig. 71).

The material from Venezuela, although apparently referable to *Douradoa consimilis*, differs from the original description in some features (Fig. 2). First of all, it is much more floriferous, ranging from 18 to 27 flowers per inflorescence (versus "*8–10 florae*" in Sleumer, 1984: 138), and the petals are reflexed and, consequently, the stamens are exposed (versus "*stamina… inclusa*" in Sleumer, 1984: 138; Fig. 2D herein).

The full collection of *Romero et al. 4013*, five sets, destined for, in the following order, VEN [×2], GH, TFAV, and MO, are in storage at TFAV, where they were dried, are yet to be distributed.

Literature Cited

Antonelli, A., A. Zizka, F. A. Carvalho, and F. L. Condamine. 2018. Amazonia is the primary source of Neotropical biodiversity. Proceedings of the National Academy of Sciences of the United States of America 115: 6034–6039.

Arellano-P H., G. Bernal-Gutiérrez, A. Calero-Cayopare, F. Castro-Lima., A. Lozano, D. S. Bernal-Linares, C. Méndez-R., and G. A. Aymard-C. 2019. The first botanical exploration to the upper Cuiarí (Cuyarí) and Isana rivers, upper Río Negro basin, Guainía department, Colombia. Harvard Papers in Botany 24, No. 2: 83–102.

Arellano-Peña, h., D. cárdenas-López, J. Stropp, N. Castaño, G. Romero-González, F. Castro-Lima, A. Lozano, M. C. Montilla, H. ter Steeege, and G. A. Aymard Corredor. 2023. The forests of the upper Rio Negro (north-western Amazon) and adjacent south-western Orinoco basins: a phytosociological classification. Pages 55–109 in J. A. Zinck, O. Huber, P. García and E. Medina, eds., Psammic Peinobiomes: Nutrient-Limited Ecosystems of the Upper Orinoco and Rio Negro Basins. Springer-Verlag, Cham, Switzerland.

Aymard, G., H. Arellano, V. Minorta-C., and F. Castro-Lima. 2016. First report of Rhabdodendraceae for the vascular flora of Colombia and the Upper Río Negro basin, with comments on phytogeography, habitats, and distribution of *Rhabdodendron amazonicum*. Harvard Papers in Botany 21, No. 1: 5–21.

Boschman, L. M., F. A. Cassemiro, L. Carraro L, J. de Vries, F. Altermatt, O. Hagen, C. Hoorn, and L. Pellissier. 2021. South American fresh-water fish diversity shaped by Andean uplift since the Late Cretaceous. bioRxiv https://doi.org/10.1101/2021.05.14.444133

Cazzolla Gatti, R. et al. [more than 100 coathors] 2022. The number of tree species on earth. Proceedings of the National Academy of Sciences of the United States of America 119, No. 6: 1–11. https://doi.org/10.1073/pnas.2115329119

Dexter, K., and J. Chave. 2016. Evolutionary patterns of range size, abundance and species richness in Amazonian angiosperm trees. PeerJ 4: e2402. https://doi.org/10.7717/peerj.2402.

CONTINUED ON PAGE 726

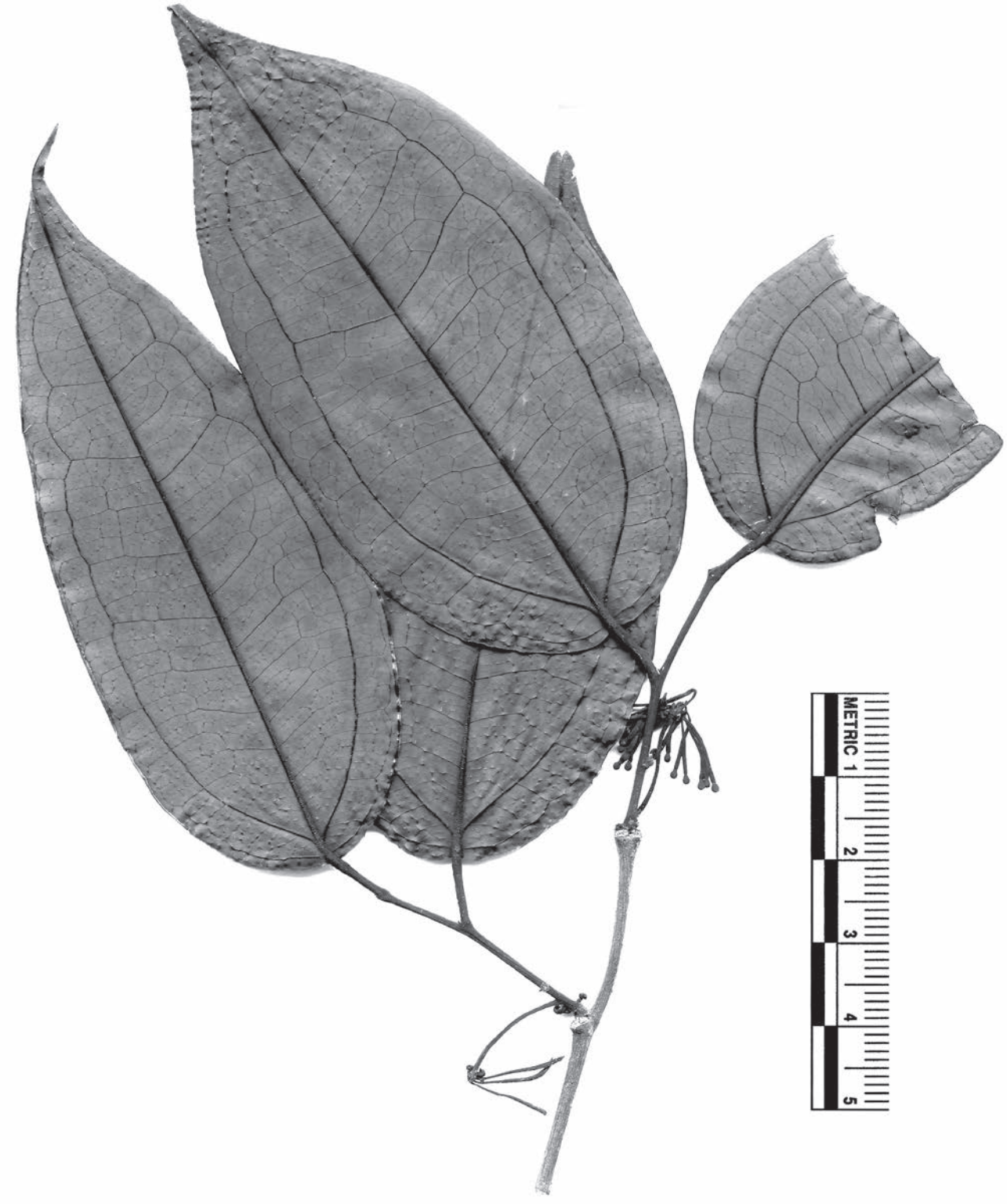


FIGURE 1. *Douradoa consimilis* Sleumer. Based on *Romero et al. 4013* (TFAV). Photographs by G.A. Romero-González.

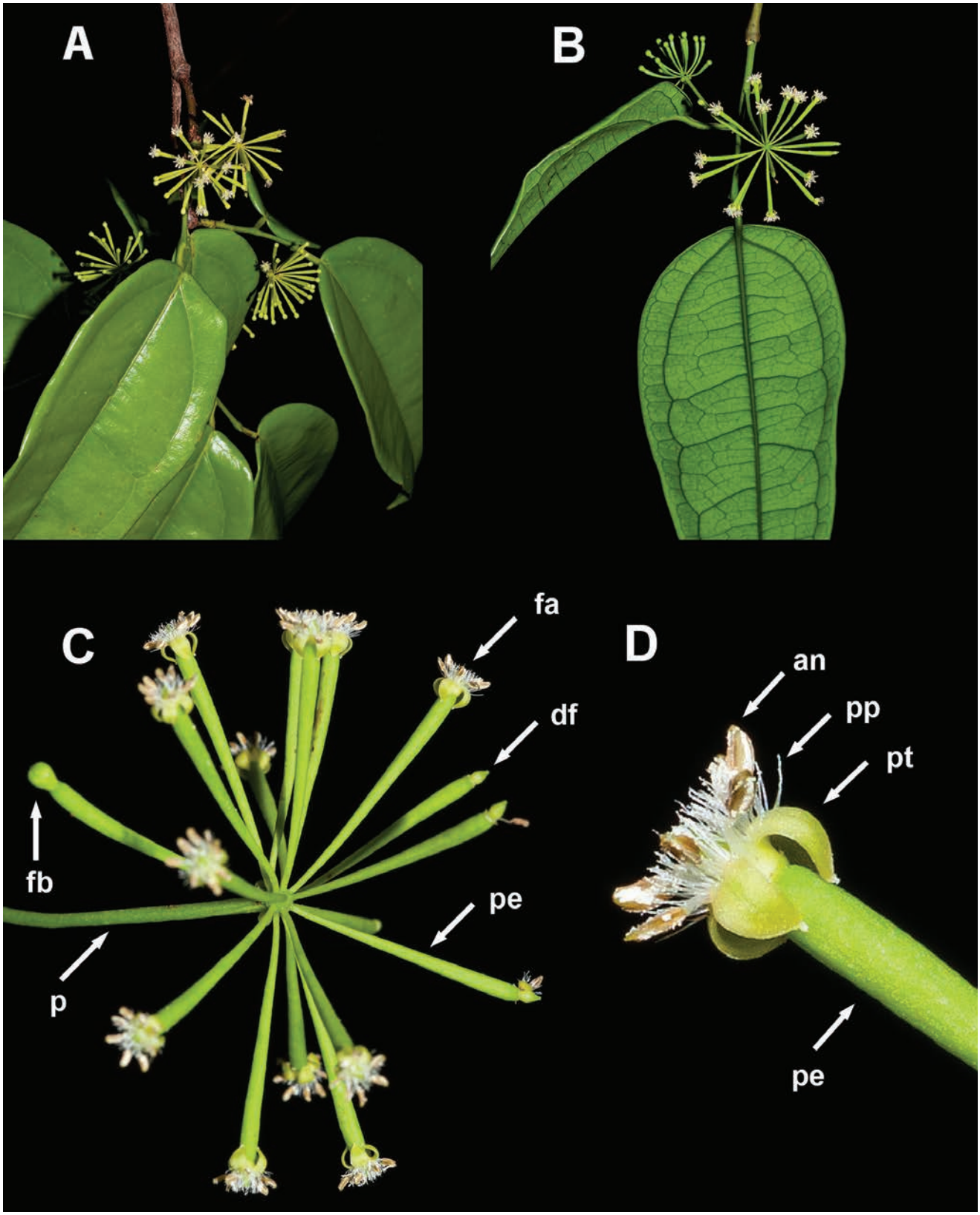


FIGURE 2. *Douradoa consimilis* Sleumer from the Venezuelan Rio Negro basin. **A**, branch showing adaxial side of leaves and several inflorescences; **B**, branch showing abaxial side a leaf, one immature inflorescence and one at anthesis; **C**, inflorescence, showing the peduncle (p), pedicels (pe), a flower bud (fb), flowers at anthesis (fa), and three developing fruits (df); **D**, flower at full anthesis showing the pedicel (pe), the reflexed petals (pt), the trichomes on the inner surface of the petal (pp), and the anthers (an). Photographs by G.A. Romero-González.

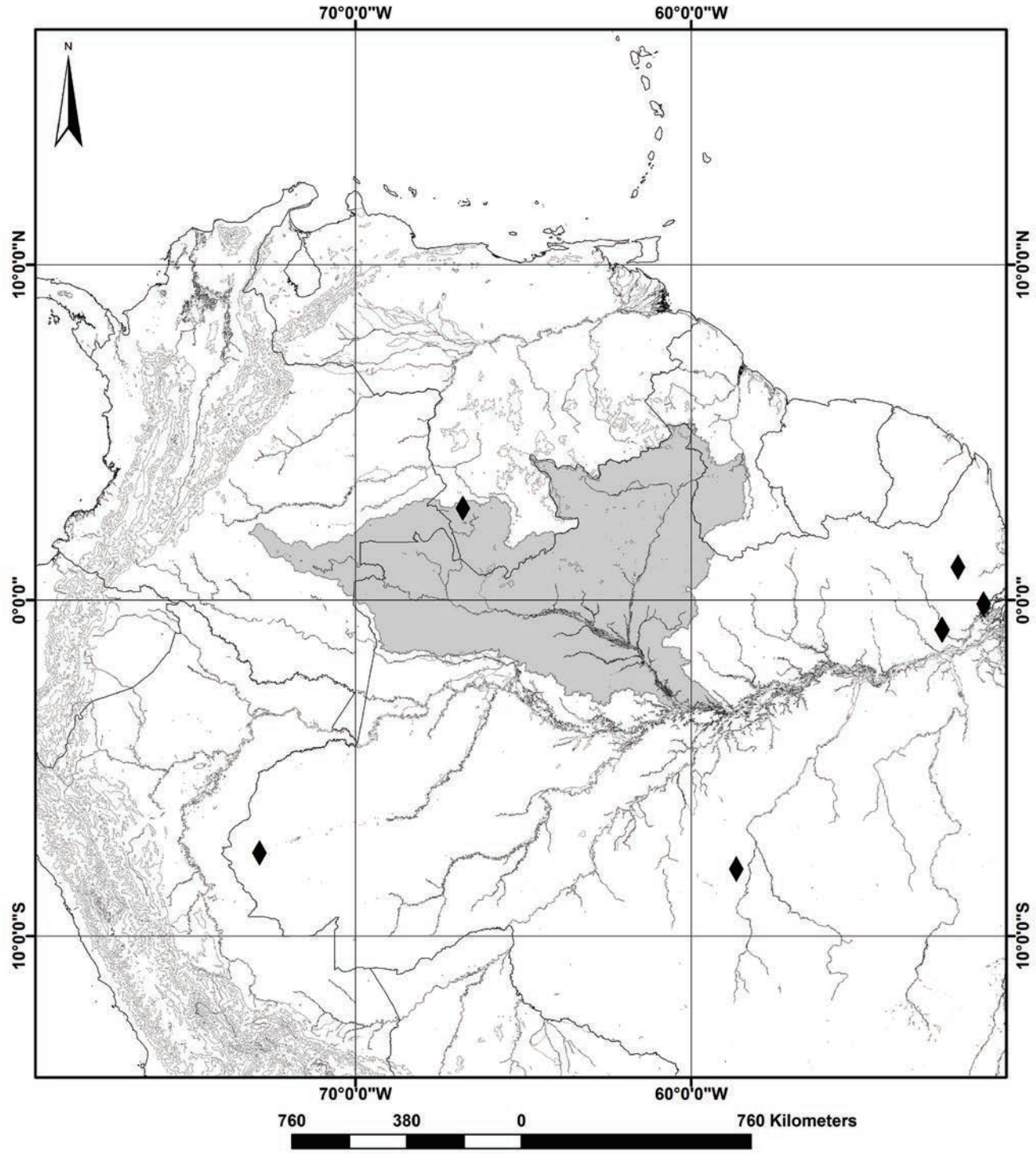


FIGURE 3. Geographical distribution of *Douradoa consimilis* Sleumer in the Amazon basin (the Rio Negro basin shaded). Prepared by H. Arellano-Peña.

Literature Cited cont.

Farroñay, F., R. De Oliveira Perdiz, F. Magalhães Costa, E. Magalhães Borges Prata, and A. Vicentini. 2019. A new record and emended description of a rare Amazonian white-sand species: *Schoepfia clarkii* (Schoepfiaceae). Brittonia 71, No. 3: 312–317.

Gentry, A. 1993. Diversity and floristic composition of lowland forest in Africa and South America. Pages 500–547 in P. Goldblatt, ed., Biological Relationships between Africa and South America. Yale University Press, New Haven, Connecticut, U.S.A

Hoorn, C., F. P. Wesselingh, H. ter Steege, M. A. Bermudez, A. Mora et al. 2010. Amazonia through time: 0Andean uplift, climate change, landscape evolution, and biodiversity. Science 330, No. 6006: 927–31.

Hoorn, C., G. R. Bogotá-A., M. Romero-Baez, E. I. Lammertsma, S. G. Flantua, E. L. Dantas, R. Dino, D. A. do Carmo, and F. Chemale Jr. 2017. The Amazon at sea: onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. Global and Planetary Change 153: 51–65.

Hoorn, C., L. M. Boschman, T. Kukla, M. Sciumbata, and P. Val. 2022. The Miocene wetland of western Amazonia and its role in Neotropical biogeography. Botanical Journal of the Linnean Society 199, No. 1: 25–35. https://doi.org/10.1093/botlinnean/boab098

Hopkins, M. J. G. 2007. Modelling the known and unknown plant biodiversity of the Amazon basin. Journal of Biogeography 34, No. 8: 1400–1411.

Jaramillo, C. 2023. The evolution of extant South American tropical biomes. New Phytologist 239: 477–493. doi:10.1111/nph.18931.

Kuijt, J., and B. Hansen, B. 2015. Ximeniaceae. Pages 187–189 in K. Kubitzki, ed., The Families and Genera of Vascular Plants 12. Springer, Cham, Heidelberg.

Latrubesse, E. M., S. A. Da Silva, M. Cozzuol, and M. L. Absy. 2007. Late Miocene continental sedimentation in south-western Amazonia and its regional significance: biotic and geological evidence. Journal of South American Earth Sciences 23, No. 1: 61–80.

Latrubesse, E. M., M. Cozzuol, S. A. Da Silva-Caminha, C. A. Rigsby, M. L. Absy, and C. Jaramillo. 2010. The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. Earth-Science Reviews 99, N. 3–4: 99–124.

Latrubesse, E. M., E. Y. Arima, T. Dunne, E. Park, V. Baker, F. d'Horta, et al. 2017. Damming the rivers of the Amazon basin. Nature 546: 369. doi: 10.1038/nature22333

Myster, R.W. 2016. Forest Structure, Function and Dynamics in Western Amazonia. Wiley-Blackwell, Oxford, UK.

Romero-González, G. A., C. A. Gómez Dahuema, and G. A. Aymard-Corredor. 2019. La Exploración botánica del río San Miguel. Pages 95–104 in G. A. Romero-González, C. A. Gómez Dahuama, O. González Ñañez, and G. Aymard Corredor, Las Cuatro "Yavitas." Boletín de Historia de las Geociencias en Venezuela No. 131: 1–133.

Science Panel for the Amazon. 2021. Executive Summary of the Amazon Assessment Report. United Nations Sustainable Development Solutions Network, New York. https://www.theamazonwewant.org/wp-content/uploads/2022/06/220717-SPA-Executive-Summary-2021-EN.pdf

Sleumer, H. O. 1984. Olacaceae. Flora Neotropica No. 38. New York Botanical Garden, New York.

Ter Steege, H. et al. [more than 100 additional coauthors]. 2013. Hyperdominance in the Amazonian tree Flora. Science 342, No. 6156: 1243092. https://doi.org/10.1126/scien ce.1243092

Ter Steege, H. et al. [more than 100 additional coauthors]. 2020. Biased corrected richness estimates for the amazonian tree flora. Scientific Reports 10: 10130. https://rdcu.be/dooOy

Tuomisto, H., G. M. Moulatlet, H. Balslev, T. Emilio, F. O. G. Figueiredo, D. Pedersen, and K. Ruokolainen. 2016. A compositional turnover zone of biogeographical magnitude within lowland Amazonia. Journal of Biogeography 43: 2400–2411.

Zizka A, H. ter Steege, M. Do Céo, R. Pessoa, and A. Antonelli. 2016. Finding needles in the haystack: where to look for rare species in the American tropics. Ecography 41, No. 2: 321–330. https://doi.org/10.1111/ecog.02192

A NEW SPECIES OF *KEFERSTEINIA* (ORCHIDACEAE: ZYGOPETALINAE), WITH PECULIAR NON-RESUPINATE FLOWERS

Mario Alexei Sierra-Ariza[1,3] and Patricia Harding[2]

Abstract. In this study, a new species of the genus *Kefersteinia* is described and illustrated. This species was discovered in the forests of the Tolima department of Colombia. Details about its distinctive morphology are provided, along with a comparison with the closest species in the same genus. Additionally, information regarding its distribution, habitat, and phenology is also furnished.

Keywords: Orchid, Resupination, Systematics, Taxonomy, University of Tolima

Resumen. En este estudio, se describe y se ilustra una nueva especie del género *kefersteinia*, que se descubrió en los bosques del departamento del Tolima, Colombia. Se proporcionan detalles sobre su morfología distintiva y se establece una comparación con las especies más cercanas dentro del mismo género. Se proporciona información sobre su distribución, hábitat y fenología.

Palabras claves: Orquídea, Resupinación, Sistemática, Taxonomía, Universidad del Tolima

In 1852, the eminent German botanist, Heinrich Gustav Reichenbach, established the taxonomic foundation of the genus *Kefersteinia* Rchb.f., naming it in recognition of Mr. Keferstein, an influential 19th-century German orchid horticulturist (Reichenbach, 1852). Within the scope of *Kefersteinia*, a diverse taxonomic range is evident, encompassing an estimated 60 to 70 recognized species to date (Pupulin et al., 2009; POWO. 2023).

Species of *Kefersteinia* have a broad distribution, extending from southern Mexico to Panama and countries in South America, including Venezuela, Colombia, Suriname, Ecuador, Peru, and Bolivia. The presence of this genus is notable in the mountainous enclaves of Central America, from southern Mexico reaching as far as Costa Rica. In the range from Guatemala to southern Mexico, the diversity of this genus sharply decreases, with *K. tinschertiana* Pupulin and *K. lactea* (Rchb.f.) Schltr. being the only recorded species in that region. Furthermore, *Kefersteinia* exhibits a limited presence in the Amazon's lowlands and the Guiana region (Carnevali et al., 2007; Carnevali et al., 2015; Pupulin and Merino, 2008). In Colombia, 22 species from this genus have been identified so far, six of which are endemic (Ministerio de Ambiente y Desarrollo Sostenible and Universidad Nacional de Colombia, 2015).

From a morphological perspective, species of *Kefersteinia* are typically small-sized plants without pseudobulbs. They have slender, mostly pendant inflorescences, and a flower with a basal, and generally bilobed, callus. The column often bears a laminar ventral plate and a central keel (Pupulin, 2001).

Within the nomenclature of the genus, several authors have traditionally distinguished two morphologically distinct groups. The first group corresponds to species with flowers structurally similar to *Kefersteinia graminea* (Lindl.) Rchb.f., the type species of the genus, that is mainly found in the Andes. These species are characterized by having a very pronounced lateral fold in the middle of the lip blade and a sessile callus that is generally low and laminar. The second group, primarily distributed in Central America, with some species located along the Pacific coast of Colombia and Ecuador as well as in western Venezuela, includes species with a straight lip blade and a solid raised callus, as seen in *Kefersteinia wercklei* Schltr. However, molecularly, both groups do not form monophyletic entities, which hinders their formal recognition (Whitten et al., 2005).

Subtribe *Zygopetalinae*, within Orchidaceae, represents a natural group that spans throughout the entire American tropics, ranging from southern Mexico to northern Argentina, comprising 38 genera (Pupulin et al., 2009; pers. comm. to Sierra-Ariza, 2023). Morphologically, both in vegetative and floral aspects, this group exhibits astonishing diversity. While it is evident that resupinate flowers are a predominant feature in the subtribe, it is important to note that a few species, such as those belonging to the genus *Chaubardiella* Garay, *Benzingia hirtzii* Dodson, and *Kefersteinia carolorum* Carnevali & Cetzal, have non-resupinate flowers. In this context, we present a description and illustration of a new species of *Kefersteinia*, which is characterized by having non-resupinate flowers.

We want to express our most sincere gratitude to the distinguished researchers Franco Pupulin and Sebastian Moreno for their invaluable comments on the genus *Kefersteinia* and for generously sharing their deep knowledge on the taxonomy and study of orchids. Likewise, we extend our gratitude to the researchers Germán Carnevali, W. R. Cetzal-Ix, J. L. Tapia-Muñoz, and Gustavo A. Romero-González for allowing us to access to their texts, fugures, and herbarium material. These resources have been fundamental to the development of our research work and have contributed significantly to the quality and precision of our scientific article. Additionally, we wish to express our gratitude to the dendrology section of the TOLI Herbarium at the University of Tolima for receiving the type material of the new species. Their collaboration and support have been fundamental to our research.

[1] Grupo de Investigación Schultes, Fundación Ecotonos, 760001, Valle del Cauca, Cali, Colombia.
[2] Independent researcher
[3] Corresponding author: mrsierraariza80@gmail.com

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 727–733.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n10, Published online: 31 December 2023

Materials and Methods

The new species was discovered in October 2021 during a supplementary expedition for the research project titled "Síntesis de las orquídeas del río Azufrado, Tolima-Colombia". In this project, six new orchid species were discovered and published with the following names: *Acianthera villahermosae* Sierra-Ariza, Rinc.-González & Karremans, *Oncidium tolimense* Sierra-Ariza & A. Albino-Bohórquez, *Pleurothallis petroana* Sierra-Ariza, *Pleurothallis villahermosae* Sierra-Ariza, Rinc.-González, & Villanueva, *Epidendrum villahermosaense* Sierra-Ariza & Hágsater, and *Epidendrum rioazufrense* Sierra-Ariza, Hágsater & E. Santiago.

Images of the type specimen were captured using a Nikon D5300 camera equipped with a NIKKOR AF 105 mm f/2.8 D Micro lens. The specimen was preserved by storing its vegetative structures in newspaper soaked with 75% ethanol. Floral structures were kept in an equal mixture of glycerin and ethyl alcohol. The collected material was dried at a temperature of 75C for a period of 14 hours and subsequently incorporated into the collection of the Herbario TOLI at the University of Tolima.

A digital composite plate (LCDP) was generated using Adobe Photoshop® CS6. The drawings were created using the Procreate illustration application on a seventh-generation Apple iPad device.

Taxonomic Treatment

Kefersteinia universitatis-tolimae Sierra-Ariza, *sp. nov.* TYPE: COLOMBIA. Tolima, Casabianca municipality, Hoyo Caliente vereda, 1790 m, 8 October 2021, *M. A. Sierra-Ariza 440* (holotype, TOLI). Fig. 1–3.

The species most similar to *Kefersteinia universitatis-tolimae* is *K. carolorum* Carnevali & Cetzal. However, it can be distinguished from the latter by having a nearly square-shaped callus on the lip when viewed from above (vs. slightly pandurate) with two rounded apical teeth (vs. acute) and no teeth on the lateral margins (vs. having approximately two teeth around the middle length).

Plant 7–19 cm tall, epiphytic, inclined, caespitose, stems very short and totally enveloped by leaf-sheaths, each shoot provided with 2–3 leaves and 2–4 acute basal sheaths. Roots terete, thick, white. *Leaves* 11–19 × 0.8–1.8 cm, linear-oblong, acute, narrowing at base to a conduplicate petiole. *Inflorescence* 2.5–3.0 cm long, 1-flowered, slender, suberect to arcuate-pendent, peduncle terete, green, with 2 internodes and with one peduncle bract at base 5 × 4 mm, a more distal one of 4 × 3 mm; floral bract double, the outer one broadly ovate, short acuminate, 5.0 × 3.5 mm, subopposite internal bractlet smaller, oblong-lanceolate, acuminate, 3.5 × 1.8 mm. *Ovary* terete-subclavate, triangular in section, valves deeply grooved to 6 mm long including the pedicel. *Flowers* non-resupinate, sepals pale green and petals occasionally with scarlet dots at the base, lip marked with small, clustered claret blotches, callus white with claret spots, column white, with a few small light claret spots, or without them. *Dorsal sepal* 11.0 × 5.5 mm, elliptic, acute, concave distally, abaxially subcarinate, 7-veined. *Lateral sepals* 13.0 × 5.5 mm, inserted along the margins of the column foot, oblong-elliptic, rounded to subacute, concave basally, dorsally slightly carinate along the mid-nerve, 7-veined, veins branched. *Petals* 11.5 × 6.5 mm, elliptic, acute to apiculate, irregularly erose, 7-veined, veins branched, dorsally slightly carinate along the mid-vein. *Lip* 14.5 × 17.0 mm, deeply concave at base, the apical half geniculate in natural position, suborbicular to slightly unguiculate when flattened, emarginate, apical margins erose and slightly undulate; callus 5.6 × 3.8 mm, emarginate directly from the base of the lip, subquadrate in general outline with upturned lateral margins narrow when viewed from above, apically forming two elliptic teeth, slightly flattened, rounded. *Column* 8.8 × 4.1 mm, including the foot, elongate, slender, lateral margins protruding at half-length to 2 semi-rounded wings, adaxial surface with an infrastigmatic keel, thin and long, sub-concave, abaxial and adaxial surfaces scabrous, ventral surface and foot with dark green trichomes. *Anther cap* cucullate, broad ovate, 2-celled. *Pollinia* 4 in two pairs of different sizes, obovate, on a triangular, folded stipe; viscidium hyaline, indistinct.

Etymology: The term "Universitatis-Tolimae" translates as "Of the University of Tolima." Its origin lies in two Latin words: "universitatis," which indicates possession or belonging to the university, and "Tolimae," which is the singular genitive of "Tolima," signifying the connection with the Tolima department in Colombia. The name honors and expresses gratitude for the remarkable history of the University of Tolima, which, for nearly eight decades, has provided higher education to both the Tolima department's community and individuals from other regions of Colombian territory. (Fig. 4A).

Distribution and ecology: *Kefersteinia universitatis-tolimae* Sierra-Ariza was discovered in a fragment of montane understory forest (bmh-MB or "bosque muy húmedo montano bajo") located in the Azufrado River basin, between the municipalities of Casabianca and Villahermosa, at the northernmost tip of the Tolima department in Colombia. This species grows at altitudes ranging from 1700 to 2000 meters above sea level as an epiphytic plant rooted in the understory of trees that exhibit a notable presence of bryophytes and limited exposure to direct sunlight. It's worth noting that this orchid shares its distribution with other species of the genus, such as *K. laminata* Rchb.f., *K.* aff *taggesellii* Neudecker, and *K. tolimensis* Schltr., all of which have been found in the Azufrado River basin.

Of particular interest is the chromatic variability observed within the same population of *K. universitatis-tolimae* Sierra-Ariza. Some of its plants have flowers with a greenish-white hue adorned with numerous scarlet-colored dots, while others exhibit pale white flowers with a few dots in a claret tone. This intrapopulation phenomenon of chromatic variation adds an intriguing aspect to the understanding of this species (Fig. 4B–C).

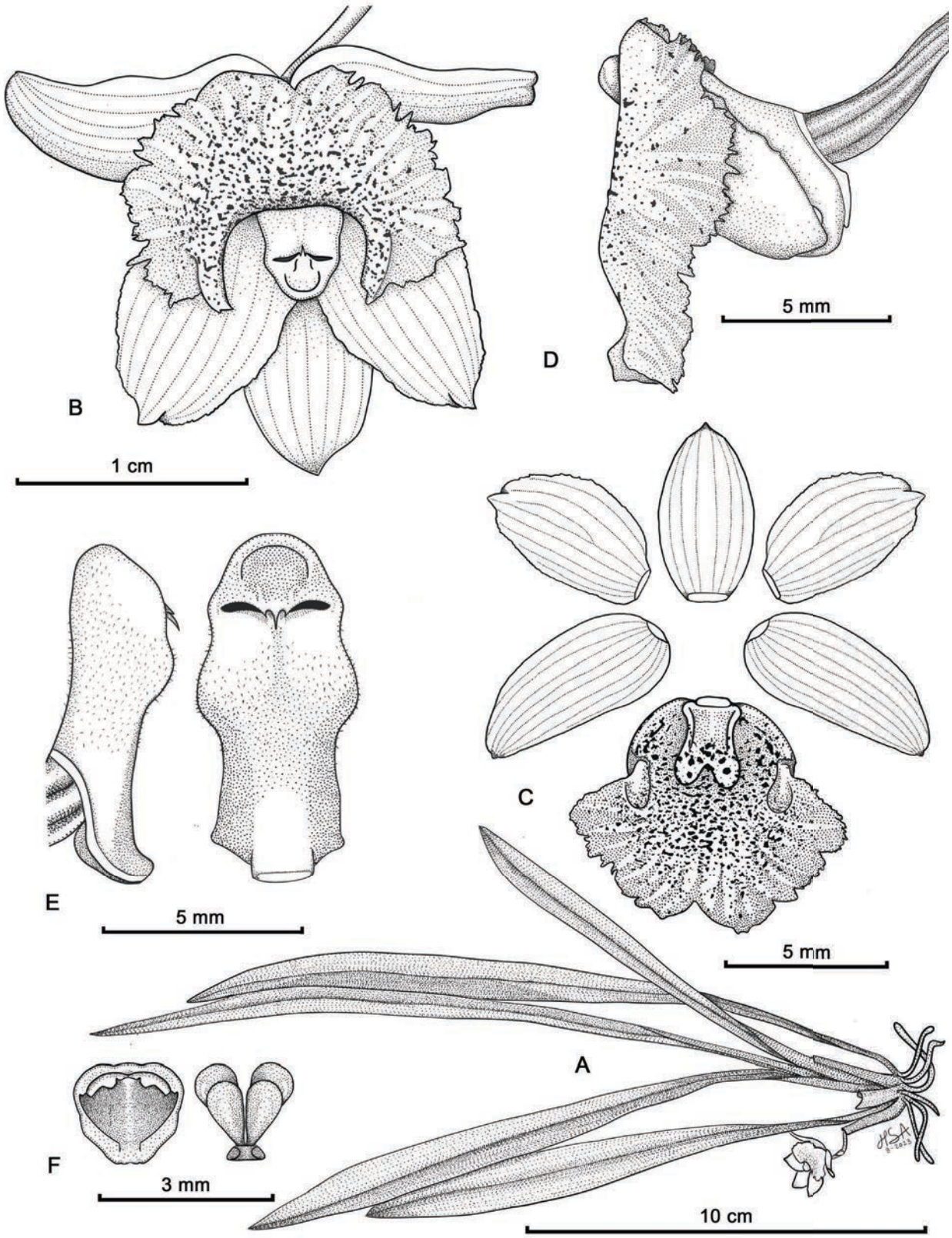


FIGURE 1. *Kefersteinia universitatis-tolimae* Sierra-Ariza. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip and column lateral view; **E**, column, **F**, anther and pollinia. Illustration by M. A. Sierra-Ariza based on the holotype.

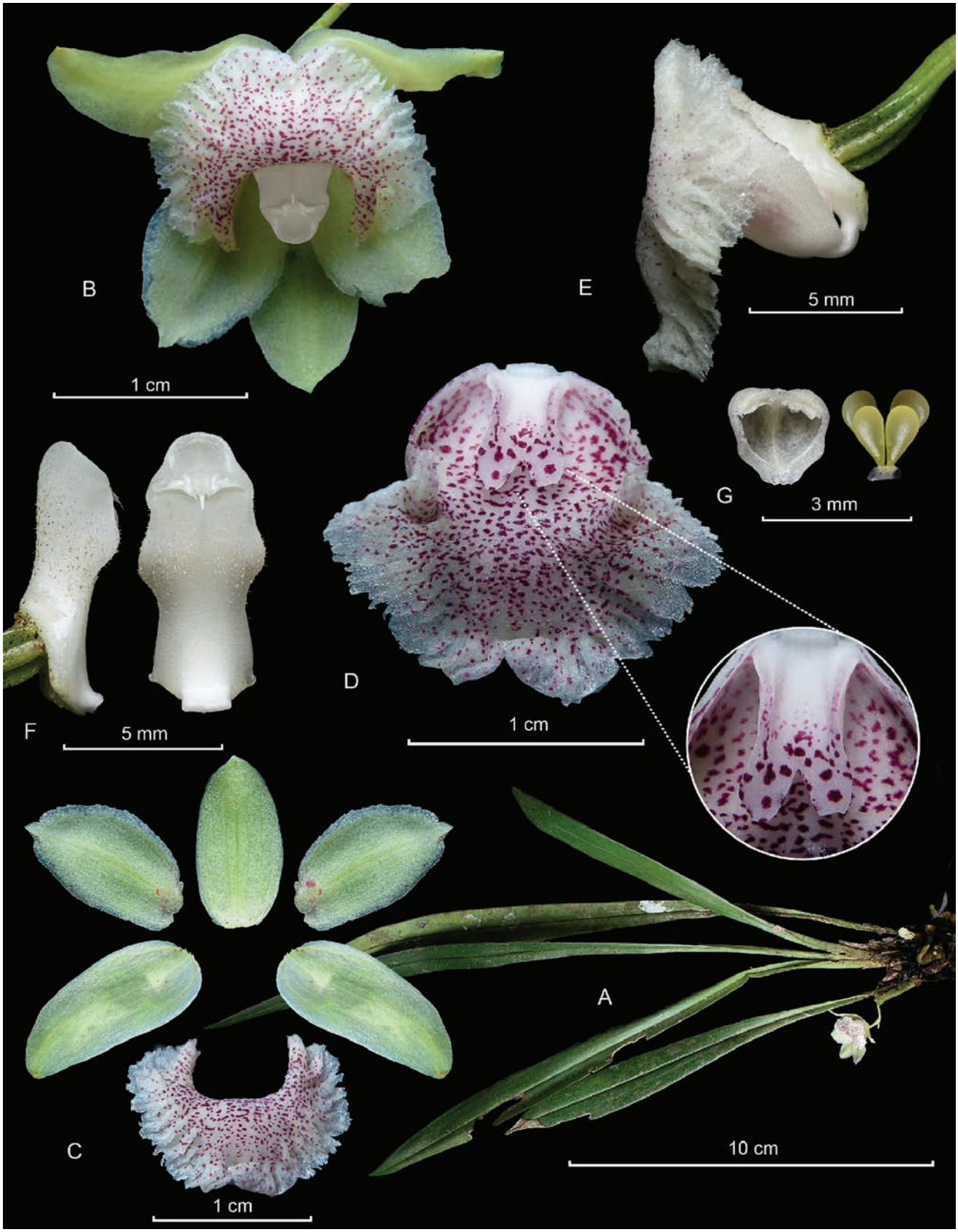


FIGURE 2. *Kefersteinia universitatis-tolimae* Sierra-Ariza. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip; **E**, lip and column lateral view; **F**, column; **G**, anther and pollinia. LCDP by M. A. Sierra-Ariza, based on the holotype.

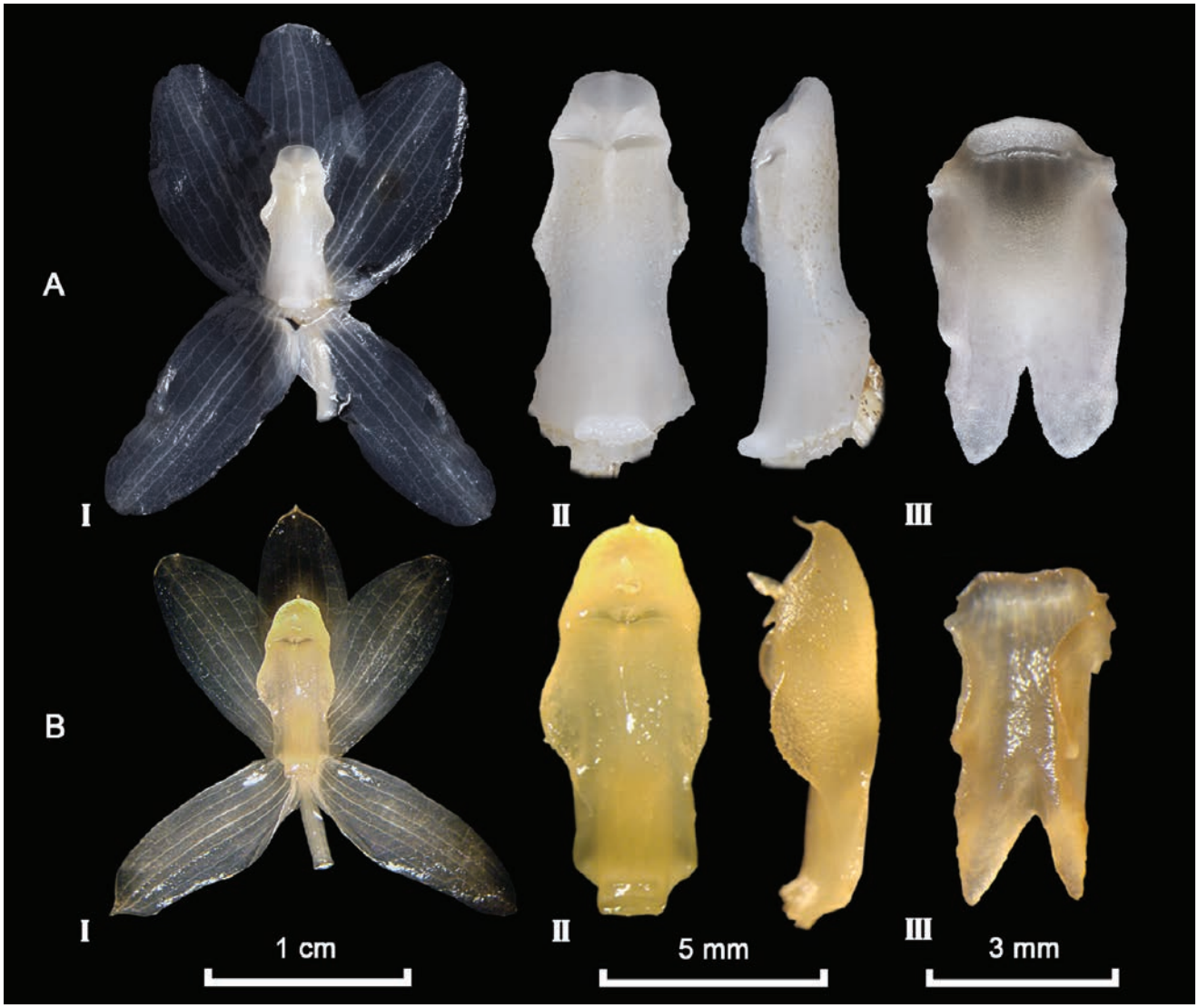


FIGURE 3. Comparison with the most similar species. **A**, *Kefersteinia universitatis-tolimae* Sierra-Ariza; **B**, *Kefersteinia carolorum* Carnevali & Cetzal. **I**, sepals and petals with column; **II**, column; **III**, callus of the lip. Prepared by M. A. Sierra-Ariza. A based on the holotype (TOLI), B on the holotype, *García Esquivel & Bello s.n.* (VEN). Fig. 3B previously published in Carnevali et al., 2015).

Kefersteinia universitatis-tolimae Sierra-Ariza and *K. carolorum* Carnevali & Cetzal (Venezuela) share the characteristic of having non-resupinate flowers. However, the new species is distinguished by several distinctive morphological features. Its flowers are slightly larger, with broad petals that have irregularly eroded edges. The lip is suborbicular to slightly unguiculate, and the lip callus has a nearly square shape when viewed from above, with two rounded apical teeth and lacks teeth on the lateral margins. Additionally, its column is slender and scabrous, with smaller and thinner wings. In contrast, *K. carolorum* is characterized by having thin petals with entire margins, an orbicular lip, a slightly pandurate callus with pointed apical teeth and an additional pair of teeth on the lateral margins, a thick and papillose column, and large, wide wings (Fig. 3A vs. 3B).

The flowers of *K. universitatis-tolimae* share similarities with other species of *Kefersteinia*; however, these are characterized by having resupinate flowers. In turn, *K. escalerensis* D.E.Benn. & Christenson (Peru) stands out with its ovate-elliptical petals, a suborbicular lip, and an ovate callus with two sharp and close apical teeth, as well as a thick column with broad wings that bend forward. *Kefersteinia lactea* (Rchb.f.) Schltr. (Mexico to Panama) is characterized by a wide, ovate lip and an ovate callus with pointed teeth, along with a slender column with triangular wings located above the halfway point of its length. *Kefersteinia alba* Schltr. (Costa Rica and Panama) has the distinctive feature of a wide, rhombic to suborbicular lip, accompanied by a lyre-shaped callus and slightly pointed apical teeth, while the column exhibits narrow triangular wings situated above the halfway point of its length. *Kefersteinia microcharis* Schltr. (Costa Rica) has a wide, ovate lip, with an obovate callus when viewed from above, apical teeth that are slightly rounded and separated, and the column lacks wings.

The species *K. sanguinolenta* Rchb.f (found from Venezuela to Bolivia) and *K. klabochii* (Rchb.f.) Schltr. (Colombia) can also potentially lead to confusion with the new species. To address these two species in the current work, an interpretation has been made based on the original descriptions and illustrations provided by Reichenbach f. *Kefersteinia sanguinolenta* has been considered a morphologically variable species with a wide distribution. It is characterized by a cuneate or narrow, obovate lip with strongly undulated margins, a ligulate callus, and column wings that project forward. *Kefersteinia klabochii* is distinguished by its broad, elliptical, transversely-shaped lip, a ligulate callus, pointed apical teeth, and a pair of teeth on the lateral margins.

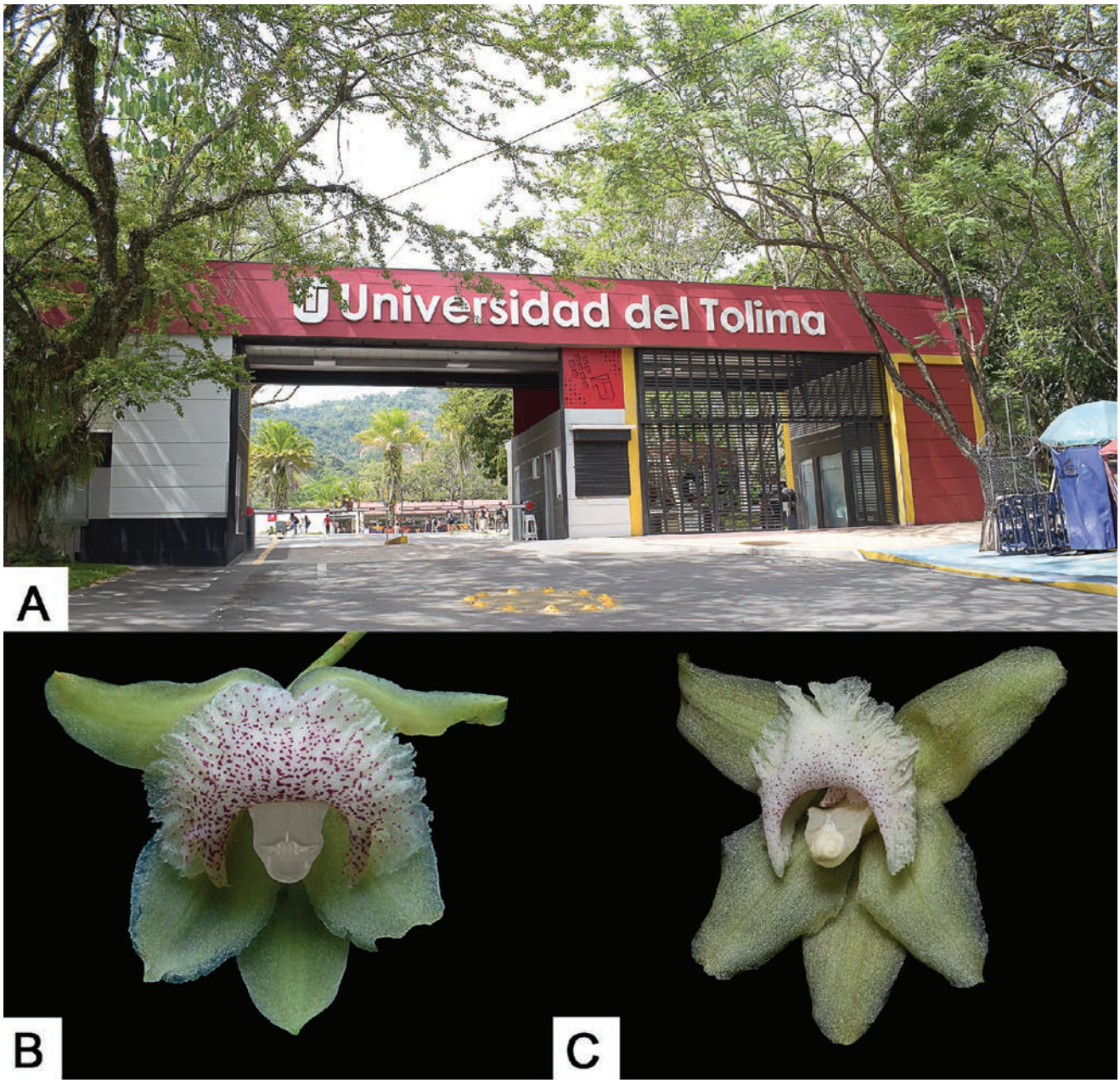


FIGURE 4. **A**, main gate of the University of Tolima; **B**, flowers with a greenish-white hue adorned with numerous scarlet-colored dots; **C**, flowers with a pale white hue adorned with few dots in a claret tone. Prepared by M. A. Sierra-Ariza.

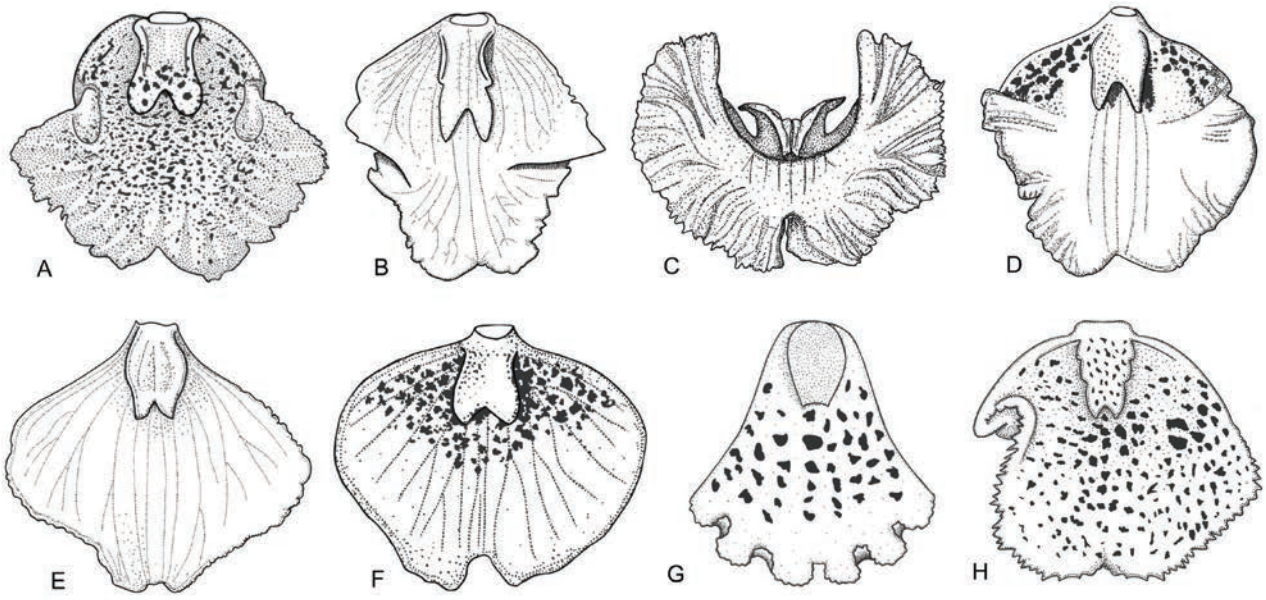


FIGURE 5. Comparison of the adaxial view of the lip of *Kefersteinia* species allied to the new species. **A**, *Kefersteinia universitatis-tolimae* Sierra-Ariza; **B**, *Kefersteinia carolorum* Carnevali & Cetza; **C**, *Kefersteinia escalerensis* D.E.Benn. & Christenson; **D**, *Kefersteinia lactea* (Rchb.f.) Schltr.; **E**, *Kefersteinia alba* Schltr.; **F**, *Kefersteinia microcharis* Schltr.; **G**, *Kefersteinia sanguinolenta* Rchb.f.; **H**, *Kefersteinia klabochii* (Rchb.f.) Schltr. Redrawn by M. A. Sierra-Ariza based on A (holotype, TOLI); B (holotype, VEN); C (holotype, USM); D (*F. Pupulin 2431*, USJ); E (from the lectotype at AMES by F. Pupulin); F (*F. Pupulin 252*, USJ); G (from Xenia Orchid. I, 1854: tab. 25I); H (holotype, W).

LITERATURE CITED

CARNEVALI, G., E. CHRISTENSON, E. FOLDATS, I. M. RAMÍREZ-MORILLO, G. A. ROMERO-GONZÁLEZ, C. A. VARGAS, AND M. WERKHOVEN. 2007. Checklist of the plants of the Guiana Shield, Orchidaceae. Pages 118–149 in V. FUNK, T. HOLLOWELL, P. BERRY, C. KELLOFF, & S. N. ALEXANDER, EDS., Checklist of the Plants of the Guiana Shield. Contributions from the United States National Herbarium. Washington.

CARNEVALI, G., W. R. CETZAL-IX, J. L. TAPIA-MUÑOZ, AND G. A. ROMERO-GONZÁLEZ. 2015. The world upside down: The first *Kefersteinia* (Orchidaceae: ZYGOPETALINAE) with non-resupinate flowers. Phytotaxa 239(2): 165–173; https://doi.org/10.11646/phytotaxa.239.2.5

MINISTERIO DE AMBIENTE Y DESARROLLO SOSTENIBLE Y UNIVERSIDAD NACIONAL DE COLOMBIA. 2015. Plan para el estudio y la conservación de las orquídeas en Colombia. Texts by: Betancur, J., H. Sarmiento-L., L. Toro-González, y J. Valencia. Ministerio de Ambiente y Desarrollo Sostenible, Colombia. Universidad Nacional de Colombia, Bogotá D.C.

POWO. 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew (accessed September 10, 2023). http://www.plantsoftheworldonline.org/

PUPULIN, F. 2001. Contributions to a reassessment of Costa Rican Zygopetalinae (Orchidaceae). The genus *Kefersteinia* Rchb.f. Annalen des Naturhistorischen Museums in Wien 103B: 525–555.

PUPULIN, F. AND G. MERINO. 2008. Two new species of *Kefersteinia* (Orchidaceae: Zygopetalinae). Willdenowia 38: 187–193.

PUPULIN, F., A. M. PRIDGEON, N. C. VEITCH, R., J. GRAYER, AND M. BLANCO. 2009. Subtribe Zygopetalinae. Pages 456–546 in A. M. PRIDGEON, P. J. CRIBB, M. W. CHASE, AND F. N. RASMUSSEN, EDS., Epidendroideae (Part 2). Genera Orchidacearum 5. Oxford University Press, Oxford.

REICHENBACH, H. G. 1852. Gartenorchideen. Botanische Zeitung 10: 633–640.

WHITTEN, W. M., N. H. WILLIAMS, R. L. DRESSLER, G. GERLACH, AND F. PUPULIN. 2005. Generic relationships of Zygopetalinae (Orchidaceae: Cymbideae): Combined molecular evidence. Lankesteriana 5(2): 87–107.

Page 734 intentionally left blank.

A NEW SPECIES OF *CEDRELA* (MELIACEAE) FROM A COLOMBIAN DRY FOREST AND AN UPDATED KEY FOR THE SPECIES OF THE GENUS

Boris Villanueva-Tamayo,[1,2] María Eugenia Morales-Puentes,[3] Omar Melo Cruz,[4] and Gerardo A. Aymard-Corredor[5]

Abstract. A new species of cedar (*Cedrela gonzalopalominoi)* is described and illustrated, and its morphological relationships with other similar species are discussed. *C. gonzalopalominoi* is found in dry forest remnants in the Western Andean foothills and on the slopes of the Central Cordillera of Colombia. This is a region composed of low hills and plains systems inside inter-Andean valleys in the upper Magdalena River in the Department of Tolima. The new species is a tree up to 20 m tall and shares features with two species, *C. odorata* and *C. weberbaueri*. However, it can be distinguished by the leaflet numbers, pubescence, size and shape, inflorescences, pedicels, calyx, fruit size, and corolla lobes that are short pilose externally and fused to the androgynophore from the middle up. A morphological description, taxonomic comments, an illustration, and information about its current conservation status are presented. An updated key of 21 neotropical species of *Cedrela* is provided.

Keywords: Dry forest, inter-Andean valleys, upper Magdalena River, timber species, CITES, *Cedrela*, Meliaceae

Resumen. Una nueva especie de cedro (*Cedrela gonzalopalominoi*) es descrita, ilustrada y sus relaciones morfológicas con sus especies afines son discutidas. *C. gonzalopalominoi*, se encuentra en remanentes de bosques secos sobre pendientes y pie de monte del sector occidental de la Cordillera central de Colombia. Esta región posee un sistema de lomeríos y planicies situadas en los valles interandinos, en el alto río Magdalena, departamento del Tolima. Esta nueva especie es un árbol de hasta 20 m de altura, que presenta similitudes morfológicas con dos especies (*C. odorata* y *C. weberbaueri*). Sin embargo, se distingue de estas especies en el número, pubescencia, tamaño y forma de los folíolos, en el tamaño de las inflorescencias, pedicelos, calíz y frutos, los lóbulos de la corola son pilosos externamente, los cuales están fusionados al androginóforo arriba de la mitad. Se presenta una descripción morfológica, comentarios taxonómicos, una ilustración e información acerca de su estado actual de conservación. Se incluye una clave de las 21 especies de *Cedrela* presentes en el Neotrópico.

Palabras clave: Bosques secos, valles interandinos, alto río Magdalena, especies maderables, CITES, *Cedrela*, Meliaceae

Cedrela P. Browne (Meliaceae) is a genus endemic to the Neotropics, found from 22 degrees north latitude in Mexico through Central America, Colombia, Venezuela, Guianas, Ecuador, Perú, Brazil, Bolivia, Paraguay, and Argentina (Pennington and Muellner, 2010; Muellner et al., 2010). The genus has 21 species, including the new species described herein. It is an important timber tree genus in Meliaceae, a pantropical family, that comprises trees and shrubs that are widely distributed throughout the tropics and subtropics, and occasionally in temperate zones (Muellner-Riehl and Rojas-Andrés, 2022). This family includes ca. 740 species in 58 genera, of which eight genera and ca. 202 species are present in the Neotropics (Muellner-Riehl and Rojas-Andrés, 2022). A great number of taxa occur in rain forests, with some species extending to seasonally dry forests and mangrove swamps (Pennington et al., 1981). Ten genera (two cultivated: *Azadirachta* A. Juss. and *Melia* L.) and ca. 80 species are found in Colombia (Bernal, 2016).

Recent phylogenetic studies support the monophyly of *Cedrela* and *Toona* (Endl.) M. Roem. Both taxa belong to the tribe *Cedreleae* DC. (also monophyletic), subfamily *Cedreloideae* Arn. (Muellner et al., 2003, 2009; Pennington and Muellner, 2010). Genetic and morphological differences are supported by the geographical disjunction of the genera, with *Cedrela* confined to the Neotropics and *Toona* occuring in Indo-Malasya and Australia (Koenen et al., 2015).

Cedrela is characterized, and differs from the other Meliaceae genera, by its five free stamens adnate to an androgynophore, which is adnate to the petals in its lower half by a central adaxial keel. The genus is also characterized by its alternate and paripinnate leaves, deeply fissured bark on the trunk (except in *C. kuelapensis* T.D. Penn. & Daza),

The authors are grateful to the Bogotá Flora Group of "Jardín Botánico de Bogotá" and to the Biological Systematic Group of "Universidad Pedagógica y Tecnológica de Colombia" for kindly allowing the use of their laboratory facilities and herbaria (JBB, UPTC). The authors especially thank Mateo González and Diego Moreno-Gaona for their laboratory assistance, Alejandro Rodríguez and Percy Hernández for their field assistence, and D. Rodríguez for his help with the GeoCat conservation assessment tool. The first author is grateful to the University of Tolima for their financial support that allowed the discovery of the new species through setting up permanent plots and survey trails over the last decade. This work would not be possible without the International Plant Names Index (https://www.ipni.org/), JSTOR Global Plants (https://plants.jstor.org/), and TROPICOS (http://legacy.tropicos.org/Home.aspx)

[1] Jardín Botánico de Bogotá José Celestino Mutis, Cl. 63 #68-95, Bogotá DC., Colombia.

[2] Corresponding author: bvillanueva@jbb.gov.co

[3] Universidad Pedagógica y Tecnológica de Colombia, Av. Central del Norte, 39-115, Edificio Centro de Laboratorios, 1r. piso LS-142, Campus Universitario, Tunja, Boyacá, Colombia; maria.morales@uptc.edu.co

[4] Universidad del Tolima, Barrio Santa Helena parte alta, Bloque 30, Laboratorio de Biodiversidad, Ibagué, Tolima, Colombia; omelo@ut.edu.co

[5] UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, estado Portuguesa 3350, Venezuela; Compensation International Progress S.A. Ciprogress–Greenlife, Bogotá, D.C., Colombia; Jardín Botánico de Bogotá José Celestino Mutis, Cl. 63 #68-95, Bogotá DC., Colombia.

Harvard Papers in Botany, Vol. 28, No. 2, 2023, pp. 735–743.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n11, Published online: 31 December 2023

fruit a septifragal capsule, lenticelate, loculi multiovulate, and seeds with a thin papery wing below, attached to the distal end of the columella (Pennington and Styles, 1975; Pennington et al., 1981; Mabberley, 2011).

Pennington et al. (1981) published a revision of *Cedrela*, and, subsequently, Pennington and Muellner (2010) presented a full monographic treatment of the genus with extensive morphological and molecular data, accompanied by data from new fieldwork. As a result, the genus was separated into four clades that formed genetically distinct units, and 17 species were recognized, four of which were new to science. Two of the 17 species (*C. odorata* L. and *C. fissilis* Vell.) are very variable lowland species, occurring in both rain forests and dry forests, with local ranges scattered through Central and South America (Pennington and Muellner, 2010; Cárdenas-López et al., 2022).

These results provided evidence indicating that three genetically distinct entitites in *C. odorata* were not separated morphologically. These entities are morphologically cryptic and require a great deal more investigation to delimit their ranges (Muellner et al., 2009). Therefore, the molecular data rejected the *C. odorata* wide species concept, indicating instead that at least three species are "cryptic" under this name (Muellner et al., 2010). In addition, most *Cedrela* species have a localized distribution, which allows for delimitation of their geographical ranges. Since these contributions, three new species have been described (Köcke et al., 2015: Palacios et al., 2019, 2023).

The wood of *Cedrela* and *Swietenia* Jacq. is the most sought after and appreciated lumber in the world, mainly because of excellent properties and relative ease of cultivation in plantations (Morales-Puentes, 1997; López and Cárdenas, 2002; Muellner et al., 2009; Blanco, 2020). The Meliaceae timber species are currently catalogued as some of the most threatened species (Hills et al., 2022; published, 2023). To prevent the decline of population sizes, all *Cedrela* taxa have been incorporated into Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2021; https://cites.org/esp/node/57207). *Cedrela* is subject to overexploitation and excessive logging for domestic and international trade, habitat loss, genetic erosion, and significant illicit cutting and illegal trade (Llerena et al., 2018; Araujo-Murakami et al., 2020; Cotrina-Sánchez et al., 2021).

The present contribution increases to five the number of *Cedrela* species known from Colombia, of which three have been recorded in Colombian dry forests. In Colombia, two species, *C. odorata* (which is found in lowland forests) and *C. montana* Moritz & Turcz. (from highland areas), are the species with the highest number of records in the country's herbaria (Morales-Puentes, 1997). The new species, *C. gonzalopalominoi,* was found during fieldwork supported by the "Universidad de Tolima," while setting up permanent plots and conducting general botanical collections in dry forests located in the upper Magdalena riven basin, Tolima department, Colombia. These studies were conducted in forest remnants in one of the largest dry forest reserves (ca. 150 ha) known as "Bosque Los Limones," a region on the western edge of Magdalena River.

Materials and methods

During field work in 2017, permanent plots were established in the locality of "vereda Salto Nuevo o bosque Los Limones," Venadillo municipality, Tolima department. Specimens were collected, pressed, dried, studied, and deposited in the herbarium TOLI (herbarium codes after Thiers, 2019). The specimens of the new species were compared with the *Cedrela* collections deposited in the following herbaria: Herbario Nacional Colombiano (COL), Jardín Botánico de Bogotá (JBB), Universidad Distrital (UDBC), Instituto SINCHI (COAH), and Universidad de Tolima (TOLI). Additionally, *Cedrela* collections hosted by virtual herbaria, including those maintained by the Field Museum (F; http://emuweb.fieldmuseum.org/botany/taxonomic.php), Missouri Botanical garden (MO; http://https://tropicos.org/home), and the New York Botanical Garden (NY; https://sweetgum.nybg.org/science/vh/) were consulted. Type specimens of *Cedrela* species involved in this study were examined using online images from JSTOR Global Plants (https://plants.jstor.org/).

The new species was described from fresh and dried material. Buds and flowers were rehydrated with liquid soap dissolved in warm water to carry out dissections and measurements. Details of morphological structures were examined using a LEICA Dm750 microscope and a LEICA EZ4 HD stereoscope with Software LAS EZ v3.0 2013. Reproductive structures of the herbarium samples were rehydrated as indicated above. The quantitative characters included in the descriptions were measured using digital calipers. Data concerning the plant habit and the colors of the floral parts were derived from the labels and *in situ* observations.

The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Stearn (2004), and Pennington and Muellner (2010). To determine the conservation status (IUCN, 2022), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Bachman et al., 2011), which is continually updated (https://geocat. kew.org/). GeoCAT is an open source, browser-based tool that performs rapid geospatial analysis for Red List assessment. The EOO is defined by the IUCN (2022) as the minimum convex polygon encompassing all known occurrences of a species. Additionally, AOO is the area within the EOO, which is comprised of 2 × 2 km grid cells containing known occurrence records.

Taxonomy

Cedrela gonzalopalominoi Villanueva & M.E. Morales, *sp. nov*.

TYPE: COLOMBIA. Tolima: Venadillo, vereda Salto Nuevo o bosque Los Limones, vía hacia el Totare por Palmarosa, desvío por Los Limones, 253 m, 4°40'32.93"N; 74°49'17.61"O, 11 Octubre 2017 (fl), *Boris Villanueva Tamayo & Omar Melo 3985* (Holotype: TOLI [018963]). Fig. 1–2.

Cedrela gonzalopalominoii resembles *C. odorata* and *C. weberbaueri* Harms but can be differentiated from these species by having 2–4 pairs of leaflets, 1.6–5.8 × 2.2–10.3 cm, elliptic to ovate, (basal broadly elliptic to broadly ovate), papillate and glabrous on the lower surface, except along the midrib and the secondary veins, where they are covered by scattered yellow trichomes (ca. 0.2 mm long); inflorescences 18.0–18.5 cm long, pedicels 0.7–1.2 mm long; calyx 3.0–3.16 mm long, bell-shaped, puberulous outside, lobes triangular to ovate; corolla lobes short pilose externally, fused to the androgynophore from the middle up; fruit ellipsoid to ovoid, 3.6–3.8 cm long, apex rounded to slightly acute and base acute to rounded.

Tree up to 20 m tall, stem, branches and branchlets strongly fissured, with simple, minute trichomes, scattered to glabrescent when mature. Outer bark rough and fissured, gray to whitish. *Leaves* compound, paripinnate, 10–19 cm long, petioles 2.4–5.0 cm long, rounded, glabrous; rachis rounded to semiterete, 10–15 cm long, glabrous, petiolules ca. 1 mm long, glabrous. *Leaflets* opposite (basal subopposite), 2–4 pairs, elliptic to ovate (basal broadly elliptic to broadly ovate), 3.8–5.8 × 6.9–10.3 cm long (basal 1.6– 3.2 × 2.2–4.0 cm), membranous, yellow-green, apex acute to acuminate, base asymmetric, glabrous on the upper surface, except along the midrib and the secondary veins, where they are covered by very scattered trichomes, along the midrid and secondary veins, glabrescent when mature, weakly glossy, glabrous and papillose on the lower surface, except along the midrib and the secondary veins, where they are covered by scattered yellow trichomes (ca. 0.2 mm long), acarodomatia present on the axils of secondary veins on the lower surface, 0.2 × 0.1 mm, triangular, trichomes unbranched, elongate, hyaline; primary veins eucanthodromous, midrib flat on the upper surface and prominent on the lower surface; secondary veins 9–15 pairs (6–8 pairs in basal leaflets), flat above and prominent below, ascending, parallel; intersecondary veins conspicuous; tertiary veins reticulate. *Inflorescences* terminal, compound panicle, dense, erect, 18.0–18.5 cm long, rhachis with minute, simple trichomes, scattered to glabrous when mature. *Flowers* pentamerous, unisexual, yellow with red glands at the base of the corolla internally, onion-scented; pedicels 0.7–1.2 mm; calyx 5-merous, bell-shaped, 3.0–3.16 × 2.7–3.1 mm, fused to 3/4 of its length, membranous, with marked and irregular veins, puberulous; calyx lobes, 1.10–1.18 mm long, triangular to ovate, with irregular margin, onion-scented; petals 5, free, imbricate to imbricate-quincuncial, linear to elliptic-linear, 6.33–7.50 × 1.4–1.5 mm, white to creamy-white, pilose; trichomes short, lax, simple externally, with a middle vein, and small reticulate veins, fused to the androgynophore from the middle up; stamens 5, attached to base of ovary, free for 2/3 of length, 3.5–4.0 mm; filaments glabrous, attached to form an androgynophore; anthers oblong, 0.80–1.20 × 0.74–0.96 mm, light yellow to brown, glabrous, longitudinally dehisced; ovary elongate, glabrous; style tapered, 1.60–1.72 mm; stigma subglobose, keeled, 0.56–0.60 mm tall, 1.00–1.06 mm wide. *Fruits* septifragal capsules, ellipsoid to ovoid, 3.6–3.8 × 2.5–3.0 cm, apex rounded to slightly acute, base acute to rounded, epicarp olive green to brown with beige, prominent, amorphous, glabrous, with numerous pale lenticels; valves 5, 3.6–3.8 × 2.5–3.0 cm, central column keeled, 5-angled. *Seeds* winged, 2.0–2.2 × 0.7–0.8 cm (includes wing and embryo), wing membranous, reticulate, brown, glabrous, smooth, shiny, embryo dark brown.

Phenology: This new species was collected with flowers in October and November (flowers in different ripening stages), and with fruit in January and June (the capsules had already opened).

Etymology: *Cedrela gonzalopalominoii* is named after professor Gonzalo Palomino Ortíz (1936–2018), a prominent ecologist from the University of Tolima. He was a pioneer of environmentalism in Colombia. Since the 1970s, he led an environmental movement that, among many objectives, envisaged the threat to tropical dry forests. In 1988, he was awarded the Global 500 Prize by the United Nations (UN) in a ceremony held in London, which was attended by "El Comandante," as he was known among his friends and colleagues. In 2011, he was awarded by the newspaper, El Colombiano, with the "El Colombiano Ejemplar," an award in the environment category. These and 13 other distinctions were awarded to him by different entities and organizations (https://es.wikipedia.org/wiki/Gonzalo_Palomino_Ortiz).

Common names: The names "Cedro" and "Cedro cebollo" were recorded during the field work.

Distribution and ecology: *Cedrela gonzalopalominoii* is known to occur in Armero-Guayabal and Venadillo municipalities, Tolima department. This is a region of dry forest on low hills and plains systems inside inter-Andean valleys, located at the western bank of the upper Magdalena river, between 250–300 m elevation. These forests have a maximum slope of 45%, and the hills have an array of intermediate plains areas in the middle of them. They are compact, non-fragmented forests, some of which can be flooded in the rainy season. Besides the new species described here, and despite the larger botanical explorations in the upper and middle Magdalena valley at Cundinamarca and Tolima departments, so far only *C. odorata* has been recorded in this portion of the Madgalena valley (i.e., north of Honda and Mariquita municipalities).

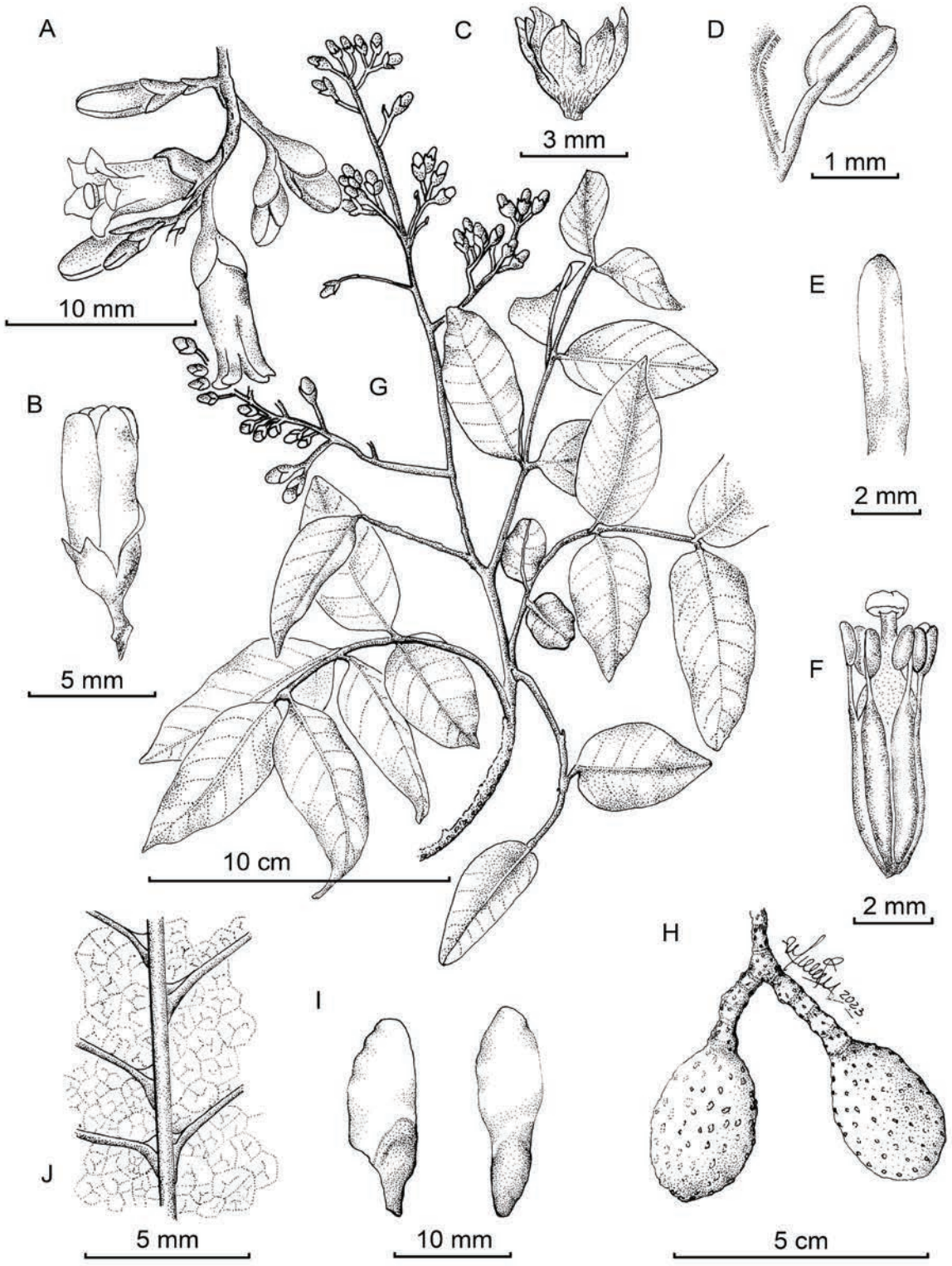


FIGURE 1. *Cedrela gonzalopalominoi* Villanueva & M.E. Morales. **A**, inflorescence branch; **B**, flower in lateral view; **C**, calyx in lateral view; **D**, anther in lateral view showing the connective at the base of the anther; **E**, petal; **F**, flower in cross section showing the staminal tube and gynoecium; **G**, habit showing the floral branch; **H**, immature fruits; **I**, seeds; **J**, leaf abaxial side showing the acarodomatia. A–F based on the holotype; H–I based on *Mendoza-C. 1054* (COL). Drawn by María E. Morales-Puentes.

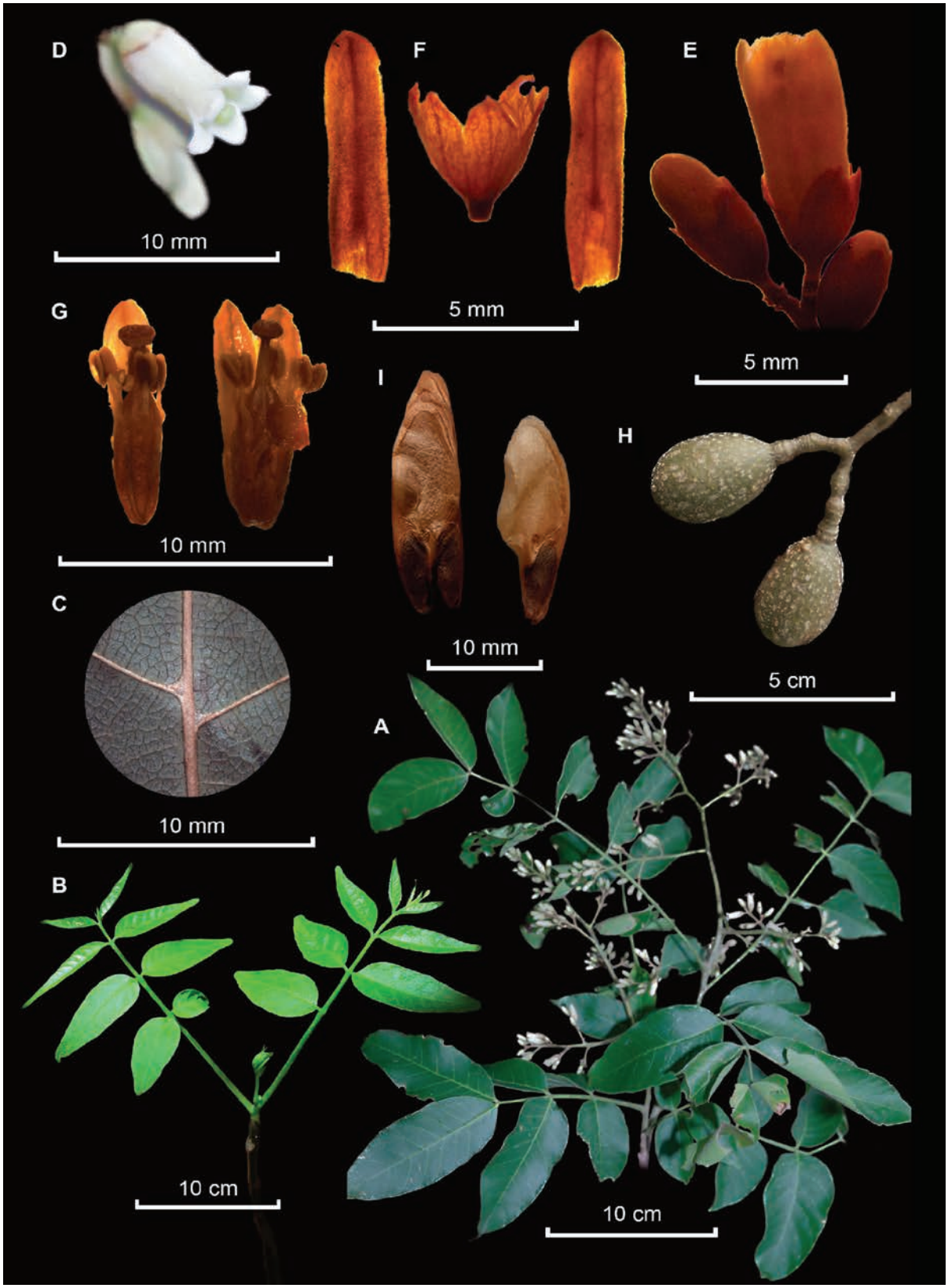


FIGURE 2. *Cedrela gonzalopalominoi* Villanueva & M.E. Morales. **A**, habit showing the floral branch; **B**, leaf branch; **C**, leaf abaxial side showing the acarodomatia; **D, E**, flowers in lateral view; **F,** calyx and petals in lateral view; **G**, flower in cross section showing the staminal tube and gynoecium; **H**, immature fruits; **I**, seeds. A–G based on the holotype; E–G from re-hydrated herbarium material; H–I based on *Mendoza-C. 1054* (COL). Photographs C, E, F, G, and I by Mateo González and Diego Moreno-Gaona; A, B, D, and H by Boris Villanueva Tamayo.

The dry forests from the upper Magdalena valley are characterized by endemic species, such as *Trichilia carinata* M.E. Morales (Meliaceae), *T. oligofoliolata* M.E. Morales (Meliaceae), *Ampelocera* sp. nov. (Ulmaceae), *Bulnesia carrapo* Killip & Dugand (Zygophyllaceae), *Picramnia apetala* Tul. (Picramniaceae), and *Mascagnia violacea* (Triana & Planch.) Nied. (Malpighiaceae), among others.

Additional specimens examined: COLOMBIA. Tolima, Venadillo: Vereda Salto Nuevo, bosque los Limones, 4°40'32.93"N; 74°49'17.61"O, 09 June 2019 (fr), *Boris Villanueva 4957* (TOLI). Armero, 01 January 1941 (fl), *Jesús M. Duque-Jaramillo 3992* (COL, two sheets: 66835, 75175). Armero, Guayabal, 5°05'3.17"N; 74°45'8.12"O, 300 m, 19 November 1995 (fr) *Humberto Mendoza-C. 1054* (COL, TOLI).

Conservation status: At present, *Cedrela gonzalopalominoi* is known from four collections; two from the type locality, and two from ca. 30 km North of the type locality (see the additional specimens). In the type locality, 12 permanent plots, 50 × 50 m (3 ha), were installed, and all individuals with DBH greater than 10 cm were recorded. In this area, with a slope close to 36%., 1305 individuals were measured, but only nine trees belong to the new species. In the same plots, seed rain sampling was done during one year, using a network of 12 fall meshes. The sampling recorded only one C. *gonzalopalominoi* capsule. No seeds were found inside the meshes, indicating lower seed rainfall values under the tallest individuals. Likewise, 25 1 × 1 m plots were created for monitoring seedlings with fortnightly censuses. Seedlings were found on high slopes and were recorded in 20% of the plots.

Under IUCN (2022) guidelines, there are not sufficient data (DD) to accurately determine the conservation status of the new species. However, it should be regarded as Critically Endangered (CR B1a) according to our calculations that estimate its Area of Occupancy (AOO) to be 8.000 km^2 and its Extent of Occurrence (EOO) to be 0.000 km^2 (following guidelines in IUCN, 2022). These guidelines estimate the EOO as the minimum convex polygon that includes all known occurrences of any taxon, and the AOO as the region inside the EOO that is occupied by the species (using a grid of 2 × 2 km). For threatened species, the AOO value recommended by IUCN is above 10,000 km^2 (IUCN, 2022). Although conservation status assessments can be made for species with such small numbers of collections (Rivers et al., 2011), it may be difficult to determine whether the appearance of rarity in a species is due to the lack of, or outdated, data, collection artifact, loss of habitat, or to its actual rarity (Verspagen and Erkens, 2022).

Additionally, the conservation of these dry forests is at

Table 1. Comparison of diagnostic morphological characters of *Cedrela gonzalopalominoi* Villanueva & M.E. Morales and closely related species.

Characters	*C. gonzalopalominoi*	*C. odorata*	*C. weberbaueri*
Leaves	Petiole and rachis: 10–19 cm long	Petiole and rachis: 25–50 cm long	Petiole and rachis: 18–20 cm long
Leaflets	2–4 pairs, 1.6–5.8 × 2.2–10.3 cm, elliptic to ovate, broadly elliptic to broadly ovate, glabrous on the lower surface, or with scattered trichomes, acarodomatia present, secondary veins 6–15 pairs	7–11 pairs, 8 × 2.5–15 × 4.5 cm, somewhat falcate, lanceolate to oblong-lanceolate, glabrous or very rarely puberulous on the lower surface, acarodomatia present, secondary veins 9–14 pairs	4–5 pairs, 7.5–10.8 × 4.5–6.0 cm, ovate, tomentose with pale brown hairs on lower surface, acarodomatia absent, secondaries 12–14 pairs
Inflorescences	18.0–18.5 cm long, flowering when in leaf, pedicel 0.7–1.2 mm long	15–40 cm long flowering when in leaf, pedicel 1–2 (–3) mm long	15–17 cm long, flowering when leafless, pedicel 1–2 mm long
Calyx	3.00–3.16 mm long, bell-shaped, puberulous outside, lobes triangular to ovate	1.5–2.0 (–2.5) mm long, cup-shaped or cupulate, glabrous or, rarely, sparsely puberulous outside, lobes obtuse	1.5–2.0 mm long, cup-shaped, villose outside, lobes shallow triangular acute
Corolla	Short pilose externally, fused to the androgynophore from the middle up	Densely appressed puberulous to sericeous externally, fused to the androgynophore in the lower third or middle	Sericeous externally, fused to the androgynophore in the lower middle
Fruit	Ellipsoid to ovoid, 3.6–3.8 cm long, apex rounded to slightly acute, base acute to rounded	Ellipsoid to oblong, rarely obovoid, 3.0–4.5(–5.0) cm long, apex and base rounded	Obovoid, 8–9 cm long, apex rounded, tapering gradually to an acute base
Distribution	Central Colombia	Mesoamerica, the Caribbean, South America to northern Argentina	Central Peru

risk due the continuous deforestation and degradation of the upper Magdalena valley. The area where *C. gonzalopalominoi* occurs is unprotected by "Sistema de Parques Nacionales Naturales de Colombia". However, the region "Bosque Los Limones," currently is a primary forest (150 ha) and is well protected by regional initiatives.

The plot data and the EOO and the AOO calculations are coherent with the hypothesis raised by Brown et al. (2023). These authors indicated that species with small ranges and/or population sizes are less likely to be encountered in the wild (and thus less likely to be described) and more likely to be threatened (Gaston, 2003).

Because of the size of its fruit and its geographical distribution, *C. gonzalopalominoi* is related to the South American *C. odorata* clade based on sequences from Brazil and Venezuela, according to the cladograms in Muellner et al. (2009) and Pennington and Muellner (2010).

The new species can be recognized by the number of its leaflets (less than five pairs), papilose and glabrous on the lower surface, except along the midrib and the secondary veins, where they are covered by scattered yellow trichomes (ca. 0.2 mm long), the margin ciliate; the flowers with a zygomorphic calyx, the calyx-corolla ratio of 1:4.

Cedrela gonzalopalominoi is morphologically related to two taxa: *C. odorata* and *C. weberbaueri*. It differs from *C. odorata* by its smaller fruit and geographical distribution; it differs from *C. weberbaueri* by the number and size of leaflets (smaller in *C. weberbaueri*), shape of the calyx, and its geographical distribution (see Table 1). Nonetheless, *C. gonzalopalominoi* differs from these two species and others of this genus in the characters discussed in the diagnosis, in Table 1, and in the following key.

Key to the species of Cedrela

The following key is based on Pennington and Muellner (2010), the fruit images available on the Field Museum of Chicago website, and the descriptions of new species published since 2015 (Köcke et al., 2015; Palacios et al., 2019, 2023).

1a. Leaves paripinnately; calyx regularly 5-lobed, lobes often imbricate at base, petal margins free to the base 2

1b. Leaves paripinnate; calyx shallowly or irregularly lobed and often split down one side to the base; petal margins adnate (except some *C. balansae*) 3

2a. Leaflets 3–6 cm wide, usually oblong to oblong-lanceolate, apex acuminate, base rounded, truncate to slightly cordate, pubescent on the lower surface, with brownish hairs to glabrous; calyx lobes sparsely pubescent; petals fused to the androgynophore for one-third to one-half their length; capsule (3–)4–6 cm long . . . . . *C. montana* (Venezuela to northern Peru)

2b. Leaflets 2.0–3.5 cm wide, usually lanceolate, apex caudate, base acute to rounded, glabrous; calyx lobes sparsely appressed puberulous to subglabrous; petals adnate to the androgynophore in the lower one-third; capsule 2.5–4.0 cm long . . . . . *C. angustifolia* (southern Ecuador to Bolivia)

3a. Leaflets 3–6(–7) pairs (usually with fewer than 7) 4

3b. Leaflets (7–)8–20 pairs (sometimes 21–24) 13

4a. Lower leaflet surface essentially glabrous, with scattered trichomes or minutely puberulous on the midrib, secondary veins and the leaf margin 5

4b. Lower leaflet surface uniformly pubescent to tomentose 9

5a. Petiolule 7–13 cm long, leaflet apex caudate, capsule 2.5–4.2 cm long . . . . . *C. dugesii* (central Mexico)

5b. Petiolule 1–5 mm long, leaflet apex acute-acuminate, capsule 3.6–8.0 cm long 6

6a. Lower leaflet surface minutely puberulous on the midrib and secondary veins . . . . . *C. ngobe* (Costa Rica, Panama)

6b. Lower leaflet surface essentially glabrous, or with scattered trichomes on the midrib and secondary veins 7

7a. Lower leaflet surface with scattered trichomes on the veins and the leaf margin; petiolule ca. 1 mm long; capsule 3.6–3.8 cm long . . . . . *C. gonzalopalominoi* (central Colombia)

7b. Lower leaflet surface essentially glabrous; petiolule 2–5 mm long; capsule 6–8 cm long 8

8a. Bark smooth; calyx ± glabrous; corolla pinkish red; capsule 6.0–6.5 cm long . . . . . *C. kuelapensis* (southeastern Ecuador and northwestern Peru)

8b. Bark fissured; calyx puberulous; corolla greenish-cream: capsule 7–8 cm long . . . . . *C. molinensis* (northwestern Peru)

9a. Plant flowering when leafless; inflorescence lateral on old wood 10

9b. Plant flowering when in leaf; inflorescence terminal 11

10a. Leaflets 4–5 pairs, ovate, apex acute; capsule 8–9 cm long . . . . . *C. weberbaueri* (central Peru)

10b. Leaflets 6–7 pairs, broadly oblong, apex rounded or obtuse; capsule 8–14 cm long . . . . . *C. salvadorensis* (Mexico to Costa Rica)

11a. Secondary veins mostly 16–18 pairs; capsule 5–8 cm long . . . . . C. *tonduzii* (Mexico to Panama)

11b. Secondary veins mostly 10–16 pairs; capsule 3–4 cm long 12

12a. Leaflets 5–12 pairs, 11.5–20.0 × 4.5–7.5 cm; capsule pendulous . . . . . *C. saltensis* (southern Peru to northern Argentina)

12b. Leaflets 5–7 pairs, 6–11 × 3–6 cm; capsule erect . . . . . *C. oaxacensis* (southern Mexico)

13a. Leaflets on the lower surface with persistent pubescence, easily visible with the naked eye or a hand lens 14

13b. Leaflets glabrous, or if pubescent on the lower surface, then indumentum confined to midrib and veins, or leaflets discolorous and with minute, white, appressed indumentum visible only with a dissecting scope (30x) 16

Key to the species of Cedrela cont.

14a. Leaflets 10–17 pairs, 2.0–4.5(–5.0) cm wide, 3–4 times as long as broad, oblong-lanceolate or narrowly lanceolate; capsule obovoid with a straight, tapering cuneate base, 5.5–9.0(–11.0) cm long . . . . . *C. fissilis* (Bolivia, Paraguay, southern Brazil to Colombia)

14b. Leaflets (4–) 5–12 pairs, 5–8 cm wide, 2–3 times as long as broad, ovate to broadly lanceolate; capsule ellipsoid, base convex, 3–8 cm long 15

15a. Leaflets oblong-lanceolate, less frequently lanceolate, secondary veins mostly 16–18 pairs; calyx 2–2.5 mm long, ; petals pale tomentose to sericeous outside, scattered coarse pubescence inside; capsule 5–8 cm long . . . . . *C. tonduzii* (Mexico to Panama)

15b. Leaflets broadly lanceolate, ovate, elliptic or oblong-lanceolate, secondary veins mostly 10–15 pairs; calyx 1.5–3 mm long; petals sericeo-tomentose outside; sparse woolly indumentum inside in the lower half; capsule 3–4 cm long . . . . . *C. saltensis* (southern Peru to northern Argentina)

16a. Leaflets discolorous, lower surface with minute, appressed white hairs confined to the interstices of the veins (requires magnification of 30x–40x) 17

16b. Leaflets not discolorous, glabrous, or indumentum, if present, spreading and visible with a 10x hand lens 18

17a. Petiolule 2–4 mm long, leaflet base acute, not, or only slightly, asymmetric, corolla sericeo-tomentose outside . . . . . *C. discolor* (northwestern Mexico)

17b. Petiolule 6–13 mm long, leaflet base strongly asymmetric, acute to obtuse on one side, rounded to truncate on the other, corolla finely sericeous . . . . . *C. longipetiolulata* (Amazonian Peru)

18a. Leaflets with domatial cavities usually present in axils of secondary veins on lower surface 19

18b. Leaflets with domatial cavities absent 21

19a. Leaflets mostly 4–8 cm wide, domatium amorphous and inflated (blister-like); corolla purple-red . . . . . *C. domatifolia* (eastern Ecuador)

19b. Leaflets mostly 2.5–4.5 cm wide, domatium not inflated (flap-like); corolla white or cream 20

20a. Leaflets falcate and glabrous, petal margins adnate, densely appressed puberulous to sericeous outside . . . . . *C. odorata* (Mesoamerica, the Caribbean, South America to northern Argentina)

20b. Leaflets not, or only slightly, falcate, with some pubescence along the midrib and secondary veins below, petal margins often free, finely sericeous outside . . . . . *C. balansae* (Bolivia, Paraguay, southern Brazil, northwestern Argentina)

21a. Corolla puberulent outside; capsule narrowly obovoid, base acute, 1.4–1.8 cm in diameter. . . . . *C. angusticarpa* (northwestern Ecuador)

21b. Corolla sericeous or sericeo-tomentose outside; capsule ellipsoid to slightly obovoid, base obtuse-rounded to rounded; 2.0–2.2 cm in diameter 22

22a. Corolla sericeo-tomentose, capsule valves opening at maturity and slightly reflexed . . . . . *C. nebulosa* (Ecuador and Peru)

22b. Corolla sericeous, capsule valves remaining ± closed at maturity, not reflexed . . . . . *C. monroana* (Guatemala, El Salvador)

Literature Cited

Araujo-Murakami, A., F. S. Zenteno-R., y K. A. Paredes-V. 2020. Biogeografía, taxonomía y nuevos registros de *Cedrela* en Bolivia. Revista de la Sociedad Boliviana de Botánica 11(1): 10–27.

Bachman, S., J. Moat, A. W. Hill, J. de la Torre, and B. Scott. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool ZooKeys 150: 117126.

Blanco, J. 2020. Caracterización de las 30 especies forestales maderables más movilizada en Colombia provenientes del bosque natural. Organización de las Naciones Unidas para la Alimentación y la Agricultura, Ministerio de Ambiente y Desarrollo Sostenible y Unión Europea. Bogotá, Colombia (Producto elaborado en el Marco del Convenio 481 de 2019, entre Minambiente-FAO para la Asistencia Técnica para la Implementación del Modelo de Forestería Comunitaria e impulso a la economía forestal).

Bernal, R. 2016 (continuously updated). Meliaceae. Pages 1664–1671 in R. Bernal, S. R. Gradstein, and M. Celis, eds., *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (accessed August 15, 2023). www.catalogoplantasdecolombia.unal.edu.co.

Brown, M. J. M., S. P. Bachman, and E. N. Lughadha. 2023. Three in four undescribed plant species are threatened with extinction. New Phytologist 239. https://nph.onlinelibrary.wiley.com/doi/full/10.1111/nph.19214.

Cárdenas-López, D. N. Marín-C., W. Vargas, S. Sua Tunjano, J. Betancur, y N. Castaño-Arboleda. 2022. Diversidad florística del departamento del Guianía. Pages 90–101 in J. S. Usma Oviedo, F. Trujillo, and L. G. Naranjo, eds., Diversidad biológica y cultural del departamento de Guainía. Gobernación de Guainía, WWF Colombia, Corporación para el Desarrollo Sostenible del Norte y el Oriente Amazónico –- CDA & Instituto Amazónico de Investigaciones Científicas SINCHI, Bogotá, Colombia.

CITES (Convention on International Trade in Endangered Species of Wild Flora and Fauna). 2021. La inclusión de especies valiosas de holoturias y cedros en el Apéndice II de CITES entra en vigor (accessed August 15, 2023).

Cotrina-Sánchez, A., N. B. Rojas-Briceño, S. Bandopadhyay, S. Ghosh, C. Torres Guzmán, M. Oliva, B. K. Guzman, and R. Salas López. 2021. Biogeographic distribution of *Cedrela* spp. genus in Peru using MaxEnt modeling: a conservation and restoration approach. Diversity 13(6): 261. https://doi.org/10.3390/d13060261

Font-Quer, P. 2001. Diccionario de Botánica. Ediciones Península, Barcelona, España.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, U.K.

IUCN. 2022. Guidelines for using the IUCN Red List Categories and Criteria. Version 12. Prepared by the Standards and Petitions Subcommittee (accessed August 18, 2023). https://www.iucnredlist.org/

Hill, R., M. Barstow and M. Rivers. 2022 [2023]. The Red List of Timber Trees. Botanic Gardens Conservation International, Richmond UK.

Köcke, A. V., A. N. Muellner-Riehl, O. Cáceres, and T. D. Pennington. 2015. *Cedrela ngobe* (Meliaceae), A new species from Panama and Costa Rica. Edinburgh Journal of Botany 72(2): 225–233.

Koenen, E. J. M., J. J. Clarkson, T. D. Pennington, and L.W. Chatrou. 2015. Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. New Phytologist 207: 327–339.

Llerena, S. A., N. Salinas, L. S. de Oliveira, M. Jadán-G., and C. Segovia-S. 2018. Distribution of the genus *Cedrela* in Ecuador. RUDN Journal of Ecology and Life Safety 26(1): 125–133.

López-C., R. y D. Cárdenas-L. 2002. Manual de identificación de especies maderables objeto de comercio en la Amazonia colombiana. Instituto Amazónico de Investigaciones Científicas, SINCHI, Bogotá, D.C.

Morales Puentes, M. E. 1997. Estudio de la familia Meliaceae y su potencial de uso para Colombia. Tesis de Maestría. Universidad Nacional de Colombia. Bogotá. Colombia.

Mabberley, D. J. 2011. Meliaceae. Pages 185–211 in K. Kubitzki, ed., The Families and Genera of Vascular Plants 10. Springer, Berlin, Germany.

Muellner, A. N., R. Samuel, S. A. Johnson, M. Cheek, T. D. Pennington, and M. W. Chase. 2003. Molecular phylogenetics of Meliaceae (Sapindales) based on nuclear and plastid DNA sequences. American Journal of Botany 90:471–480.

Muellner, A. N., T. D. Pennington, and M. W. Chase. 2009. Molecular phylogenetics of Neotropical *Cedreleae* (mahogany family, Meliaceae) based on nuclear and plastid DNA sequences reveal multiple origins of "*Cedrela odorata*". Molecular Phylogenetics and Evolution 52: 461–469.

Muellner, A. N., T. D. Pennington, A. V. Koecke, and S. S. Renner. 2010. Biogeography of *Cedrela* (Meliaceae, Sapindales) in Central and South America. American Journal of Botany 97: 511–518.

Muellner-Riehl, A. N. and B. M. Rojas-Andrés. 2022. Biogeography of Neotropical Meliaceae: geological connections, fossil and molecular evidence revisited. Brazilian Journal of Botany 45: 527–543.

Palacios, W.A., J. Santiana, and J. Iglesias. 2019. A new species of *Cedrela* (Meliaceae) from the eastern flanks of Ecuador. Phytotaxa 393: 84–88.

Palacios, W.A., M. de L. Torres, M. A. Quintana, P. Asadobay, J. Iglesias, R. Quillupangui, E. Rojas, J. Santiana, A. Sola, and G. Rivas-Torres. 2023. A new species and a new record for *Cedrela* (Meliaceae, Sapindales) in Ecuador: morphological, molecular, and distribution evidence. Phytotaxa 595(2): 127–138.

Pennington, T. D. and B. T. Styles. 1975. A generic monograph of the Meliaceae. Blumea 22: 419–540.

Pennington, T. D., B. T. Styles, and D. A. H. Taylor.1981. Meliaceae, with accounts of *Swietenioideae* and chemotaxonomy. Flora Neotropica 28. New York Botanical Garden, New York.

Pennington, T. D. and A. N. Muellner-Riehl. 2010. A monograph of *Cedrela* (Meliaceae). dh Books, Milborne Port, DT, England.

Rivers, M. C., L. Taylor, N. A. Brummitt, T. R. Meagher, D. L. Roberts, and E. N Lughadha. 2011. How many herbarium specimens are needed to detect threatened species? Biological Conservation 144(10): 2541–2547.

Stearn, W. T. 2004. Botanical Latin. Fourth Edition. Timber Press. Portland, Oregon, U.S.A.

Thiers, B. 2019 (continuously updated). Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium (accessed August 22, 2023). http://sweetgum.nybg.org/ih/

Verspagen, N. and R. H. J. Erkens. 2022. A method for making Red List assessment with herbarium data and distribution models for species-rich plant taxa: Lessons from the Neotropical genus *Guatteria* (Annonaceae). Plants, People, Planet 5: 536–546.

Page 744 intentionally left blank.

INDEX TO NEW NAMES AND COMBINATIONS

Harvard Papers in Botany, Vol. 28, No. 2, 2023, p. 745.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.n12, Published online: 31 December 2023

Page 746 intentionally left blank.

Harvard Papers in Botany was initiated in 1989 to consolidate the following journals published by the Harvard University Herbaria: *Botanical Museum Leaflets—Harvard University* (vols. 1–30, 1932–1986), *Contributions from the Gray Herbarium of Harvard University* N.S. (nos. 1–214, 1891–1984), and *Occasional Papers of the Farlow Herbarium of Cryptogamic Botany* (nos. 1–19, 1969–1987). Starting with no. 8, it incorporates the *Journal of the Arnold Arboretum* (vols. 1–71, 1920–1990) and the *Journal of the Arnold Arboretum Supplementary Series* (1, 1991).

Harvard Papers in Botany was published as individually paginated issues up to number 10 (April 1997). Starting with the next issue, it has been published in volumes, each volume consisting of two numbers with continuous pagination. Number 1–10, published between May 1989 and April 1997, constitute Volume 1. Volume 1, number 10, includes a cumulative, comprehensive index for the first volume. Print Copies for most volumes 1 through 18 are available. Please contact papers@oeb.harvard.edu for more information.

This issue of *Harvard Papers in Botany* was composed by Barbara Kroner Morra, using Adobe InDesign for the Macintosh. The body of the text is set in 10-point Times Roman on 11 points of leading.

Harvard Papers in Botany

Volume 28, Number 2 December 2023

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

Harvard Papers in Botany

Volume 28, Number 2 December 2023

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

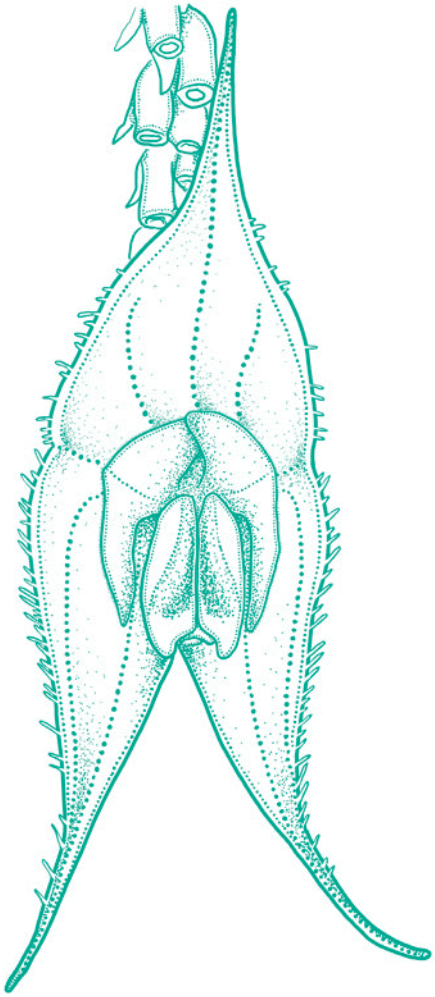
Arnold Arboretum

Botanical Museum

Farlow Herbarium

Gray Herbarium

Oakes Ames Orchid Herbarium



Harvard Papers in Botany, Vol. 28, No. 2, 2023, Front matter, Table of Contents, End matter.

ISSN: 1938-2944, DOI: 10.3100/hpib.v28iss2.2023.fmem, Published online: 31 December 2023