NEW REPORTS OF *GALEANDRA* (ORCHIDACEAE) FROM MEXICO

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Abstract. Here we report two species as new for Mexico, *G. arundinis* and *G. sobralioides*, and discuss the report of *G. batemanii* for the state of Tabasco. A discussion of possible diagnostic characters of this genus and a key to the Mexican species also are presented.

The field of orchidology has been plagued by catch-all names for more than 200 years. These are species, usually described early on, which have become sorts of trash baskets where many other similar species, described or not, have been placed by convenience or because the group has not been carefully evaluated. Examples abound in the literature (e.g., *Cyrtopodium punctatum* (L.) Lindl., *Encyclia oncidioides* (Lindl.) Schltr., and *Epidendrum nocturnum* Jacq.). *Galeandra* Lindl. is not an exception: all Mexican galeandras were referred mistakenly to *Galeandra baueri* Lindl. until Rolfe (1892) recognized the obviously different *Galeandra batemanii* Rolfe (see also Pollard, 1974; Siegerist, 1983). More than a hundred years later Warford (1994) described *G. greenwoodiana*, a distinctive species that in the past had been confused with both *G. baueri* (Paxton, 1848) and *G. batemanii* (Linden, 1901; see Warford, 1994). Likewise, in Central America, plants of *Galeandra arundinis* G.A. Romero & Garay have been misidentified multiple times.

Galeandra arundinis was first described from Costa Rica, although it was known already from Belize to Panama but, not surprisingly, mostly confused with other species of the genus (see discussion below). Hitherto, the species had not been fully documented in Mexico.

Galeandra batemanii, according to one of the most recent accounts of the species (Warford, 1994), was thought to be "endemic to Mexico on the Gulf slope of the state of Oaxaca at an elevation of ca. 750 m" (see also Soto-Arenas and Salazar, 2004: 291). All well documented reports of this species, including the type, were collected in a relatively small area of the state of Oaxaca, west of the isthmus of Tehuantepec; photographic records (Beutelspacher Baigts, 2008, 2013; Beutelspacher Baigts and Moreno Molina 2018: 476) indicate its presence in Chiapas. Nonetheless, two of the authors (CMB and MAG) have documented flowering plants apparently referable to this same species in the state of Tabasco (González A. and Burelo R., 2012; see discussion below).

We were surprised when a plant collected in Municipio San Miguel de Chimalapa, in the Mexican state of Oaxaca, turned out to be, then, yet another previously unknown, undescribed species. It was first collected in Mexico in 1985 by Gerardo Salazar and cultivated by one of the authors (GC) starting in 1996. From this plant originated the image published in Hágsater et al. (2005: 145; see iconography below). Photographic plates and a line drawing were prepared to describe it but, in the interim, it was described as *Galeandra sobralioides* Archila & Chiron based on a plant collected in Guatemala.

The goal of the present contribution is to formally report the presence of *Galeandra arundinis* and *G. sobralioides* in Mexico, and to discuss the presence of *G. batemanii* in the state of Tabasco. We also discuss a possible case of introgression between *G. arundinis* and *G. batemanii* in the state of Tabasco and include a discussion of possible diagnostic characters and a key to the Mexican species of *Galeandra*.

Materials and Methods

Systematic work.

The study was conducted at the Oakes Ames Orchid Herbarium and the Centro de Investigación Científica de Yucatán, A.C. (CICY). Plants and materials in the field in Mexico were obtained under scientific permits (SGPA/DGVS/008421/18 and SGPA/DGGFS/712/2913/17) issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) to researchers at CICY.

Conservation assessment.

The conservation status of the *Galeandra* species was assessed using the IUCN Red List Criteria (IUCN, 2012). Because population data of these species was not available beyond casual observations, we relied mostly on the B criteria, geographical distribution assessed both as B1 (Extent of Occurrence) or B2 (Area of Occupancy), as implemented in GeoCAT (Bachman et al. 2011). We complemented these assessments with our own field experience, published data, and iconography, whenever available.

We thank the staff of AMO, JBL, MO, NY, and SEL for their invaluable help, B. Angell for her drawings, I. Ramírez-Morillo (CICY) for her comments on an earlier version of the text and for scrutinizing the final version, F. Hernández N. (CHIP) for allowing us to use his data and photographs, and G. A. Salazar (MEXU) for supplying a live plant of *G. sobralioides*. We are fortunate to have available the extraordinary drawings of Natalie Warford (1927–2013), many of which we publish here for the first time, her notes, and some of her preserved material of *Galeandra*.

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Galeandra arundinis G.A. Romero & Garay, Vanishing Beauty I: 326. 2005. TYPE: COSTA RICA. Alajuela: San Carlos, Guatuso, collected by Carlos Cambronero, August 1997, flowered in cultivation at the Lankester Botanical Garden, 12 October 2000, *sub M. Blanco 1639* (Holotype: USJ). Fig. 1–9.

Synonyms: *Galeandra archilae* Chiron, Revista Guatemalensis 15, No. 2: 11. 2012. TYPE: GUATEMALA. Alta Verapaz: Laguna Lachuá, *ex Hort*. Estación de Orquídeas de Guatemala, *F. Archila s.n*. (Holotype: BIGU, not seen).

Galeandra garifunae Archila & Chiron, Revista Guatemalensis 15, No. 2: 10. 2012. TYPE: GUATEMALA. Izabal: sobre palmeras a la orilla del mar Caribe, 3 m, December 2007, *F. Archila s.n*. (Holotype: BIGU, not seen).

Field and herbarium recognition: Plants epiphytic, found from Mexico (Tabasco, expected in Chiapas, Campeche, and Quintana Roo) to Panama (expected in Colombia), along Atlantic slopes, mostly in lowlands, often growing on "tasiste" (*Acoelorrhaphe wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc., Arecaceae) and other palms (e.g., "Suyate," *Brahea dulcis* (Kunth) Mart.; Pérez Mungía, 2015: 111); pseudobulbs narrowly fusiform, cane-like, in herbarium specimens up to 25 cm long; flower color varies from sepals and petals dark reddish-brown, the labellum externally yellowish striped dark burgundy, internally dark yellow, the apex dark reddish burgundy (the type, from Costa Rica), to sepals and petals yellowish-brown, stripped red toward the base, the labellum externally yellowish green, often stripped reddish brown toward and including the upturned spur, light pink toward the apex, internally yellowish-white at the base, including the upturned spur, light pinkish-red toward the apex (in most of its geographical range). The labellum has a distinct, narrowly triangular color pattern at the apex, which varies in color: it maybe undistinguishable in flowers with a dark labellum, but clearly discernable in the ones with a lighter tone. It is even more conspicuous in flowers with little or no pink pigmentation. As circumscribed here, all plants bearing narrowly fusiform to arundinoid pseudobulbs found from Mexico to Panama are referrable to *G. arundinis*. Here we present a series of drawings of flowers collected from Belize to Panama showing slight variations in the size and ornamentation of the labellum (see discussion below).

Etymology: From the Latin *Arundo*, reed, cane, and the Latin adjectival suffix *-inus*, indicating resemblance, in reference to the cane-like pseudobulbs.

Distribution: Along Atlantic slopes from Mexico (Tabasco, expected in southern Campeche, northern Chiapas, and southern Quintana Roo) to Panama.

Phenology: Herbarium records indicate that this species flowers from May to December. In cultivation, it flowers from July to January.

Additional material examined: BELIZE. Belize: originally and allegedly collected in the vicinity of Rockville Quarry, seasonally flooded savanna and low forest, 20 m; obtained in Chetumal, Quintana Roo *ex Hort*. G. Carnevali *sub G. Carnevali 7996* (AMES, CICY [fragment])]. El Cayo: Mountain Pine Ridge, San Agustin, on tree in pine uplands, epiphyte, fls. brownish, with margin of corolla purplish, July-August 1936, *C. L. Lundell 6691* (MICH). Toledo: Monkey River, near Cow Pen, in pine ridge, flowers pinkish, on tree in hammock, 17 September 1942, *P. H. Gentle 4154* (MICH). Sibun River, 2 February 1935, *P. H. Gentle 1510* (MICH). Stann Creek: Stann Creek Railway, on palm, sepals reddish brown, lip wine red shading to yellow, December 1939, *W. A. Schipp 878* (AMES, F); All Pines, handsome "epiphyte" more often to be found growing on *Acoelorrhaphe* palms, flowers brown, yellow, and pale mauve, occasional, 7 December 1930, *W. A. Schipp 590* (AMES, GH, MICH, NY); near Gracie Rock, 21 September 1936, *H. O'Neill 8347* (AMES, MICH, NY). **COSTA RICA.** Alajuela: vicinity of Los Chiles, Río Frio, 30–40 m, 1 August 1949, *R. W. Holm and H. H. Iltis 819* (A, AMES, MICH, P, U); without additional locality data, "sépalos y pétalos café rojizo, labelo blanco con borde rosado, con líneas café rojizo desde el nectario [spur] hasta 2/3 del labelo, olor a rancio," *ex Hort*. Lankester Botanical Garden *sub J. Warner s.n*. (drawing, AMES). Guanacaste: Parque Nacional Guanacaste, La Cruz, Estación Pitilla, sendero Evangelista, 700 m, epífita, flores moradizas con rayas amarillas, *P. Ríos Castro 205* (INB); Area de Conservación La Cruz, Estación Pitilla, 700 m, epífita a 3 m, raices blancas esponjosa[s], sépalos pardo-claro, pétalos morados opaco, 11 September 1990, *C. Moraga 13* (INB). **GUATEMALA.** Alto Verapaz: Laguna Lachuá [type locality of *G. archilae*], "pseudobulbs slender, fusiform, tinged purple, sepals and petals yellow suffused and striped brown, lip whitish suffused with brown, apical third reddish-purple," 20 February 1990, *ex Hort. W. del Pinal s.n. sub G. Salazar 5146* (AMES [drawing], AMO [spirits]). **HONDURAS.** Comayagua: Custeca, Siguatepeque, open mountain forest, epiphyte, 3700 ft [ca. 1120 m], petals and sepals bronze, lip light purple [at the apex], white shading to dark bronze [toward the spur], spur green, 15 October 1932, *J. B. Edwards 284* (AMES); El Tablón, San Luis, 2500 ft [ca. 758 m], epiphyte in palm tree, in dense palm thickets, petals and sepals bronze or greenish lavender, lip ruffled, tip lavender shading to bronze, at base, column white with vert. lavender stripes on under side, 30 May 1933, *J. B. Edwards 421* (AMES); Copán: vicinity of Santa Rosa de Copán, sepals and petals olive, lip limb pale rose purple, throat whitish, spur striped olive, 31 July 1978, collected *F. Mathews ex Hort*. Marie Selby Botanical Gardens 20-74-536 *sub J. D. Ackerman 1274* (F, SEL); same locality, "sepals and petals green-brown, lip pin kish, spur brown," *F. Mathews s.n., ex Hort*. Marie Selby Botanical Gardens, flowered 10 June 1975 (SEL 016837); same locality, "tepals brownish rose, spur green, lip white with rose border," *F. Mathews s.n., ex Hort*. Marie Selby Botanical Gardens, flowered September 1985 (SEL 055083); same locality, "sepals and petals yellow green, lip pink with spur stripws with maroon, column white" *F. Mathews s.n., ex Hort*. Marie Selby Botanical Gardens, flowered 6 August 1976 (SEL 016474); same locality, "sepals and petals greenish brown, lip light pink, with darker pink at edges, spur stripped with green and brown," *F. Mathews s.n., ex Hort*. Marie Selby Botanical Gardens, flowered 12 August 1976 (SEL 017712); Francisco Morazán: El Hatillo, "sepals and petals brown, lip white, edge tinged lavender, spur brown," *F. Mathews s.n., ex Hort*. Marie Selby Botanical Gardens, flowered 16 July 1976 (SEL 016505); Valle de los Ángeles, unos 3 km

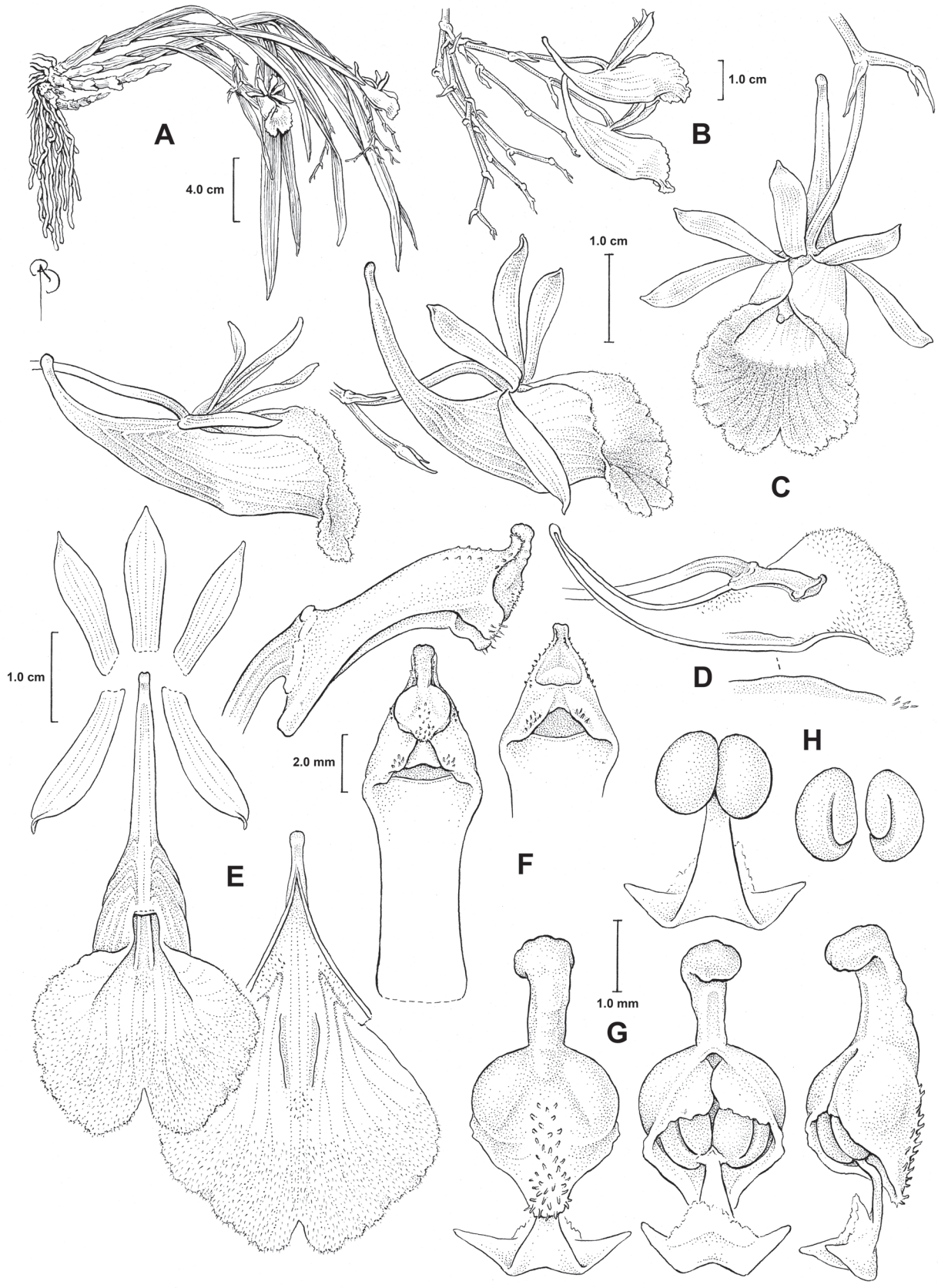

FIGURE 1. *Galeandra arundinis* G.A. Romero & Garay from Belize. **A**, Habit; **B**, inflorescence; **C**, views of the flower; **D**, sagittal section of the labellum; **E**, floral segments; **F**, column; **G**, views of the anther with pollinarium; **H**, pollinarium and pollinia. Drawn by B. Angell from material in spirits based on *Carnevali 7996* (CICY).

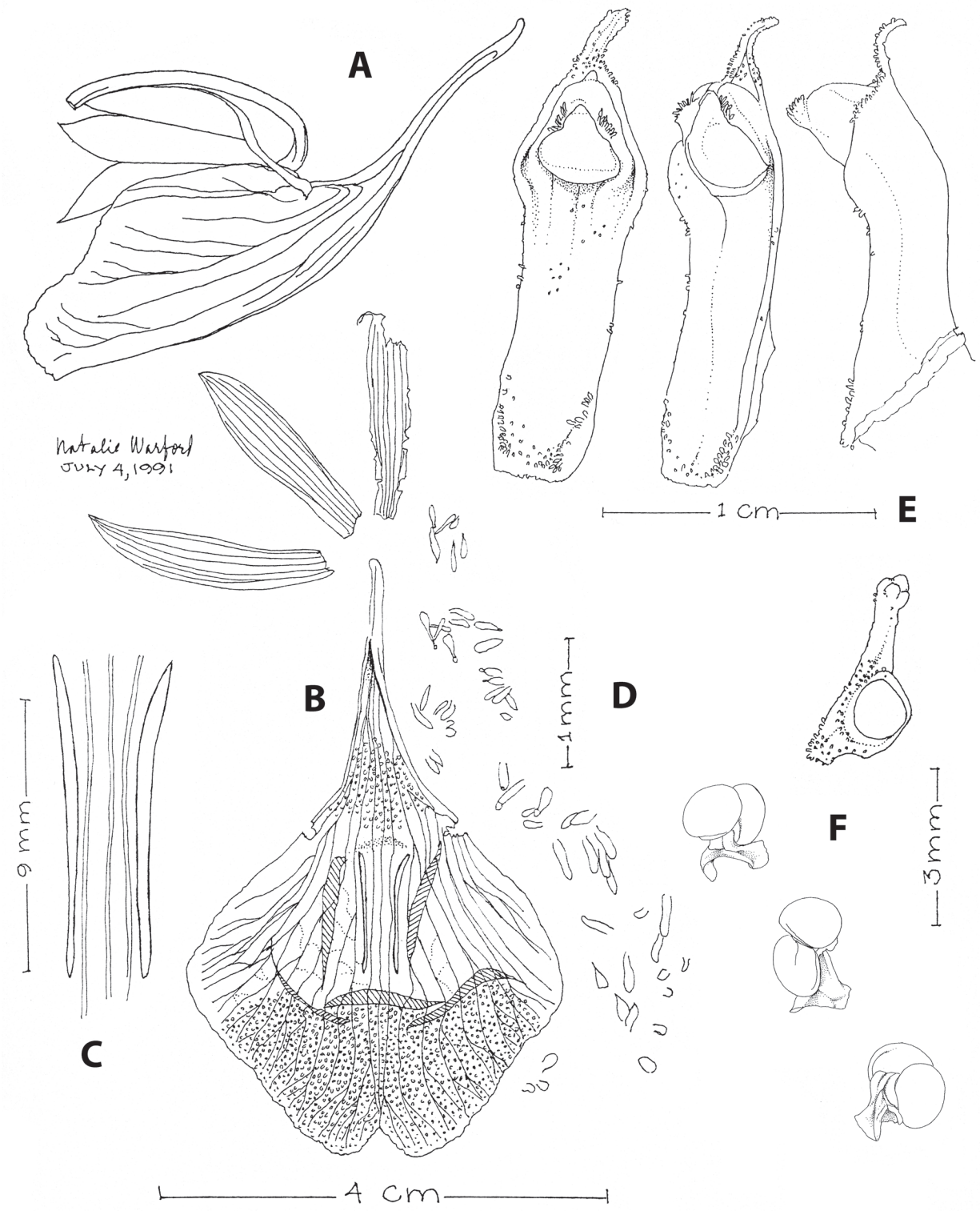

FIGURE 2. *Galeandra arundinis* G.A. Romero & Garay from Laguna Lachuá, Guatemala, type locality of *G. archilae* Chiron. **A**, flower profile; **B**, flower segments; **C**, keels and the three central nerves; **D**, trichomes; **E**, column; **F**, anther and views of the pollinarium. Drawn by N. Warford from material in spirits based on *Salazar 5146* (AMO).

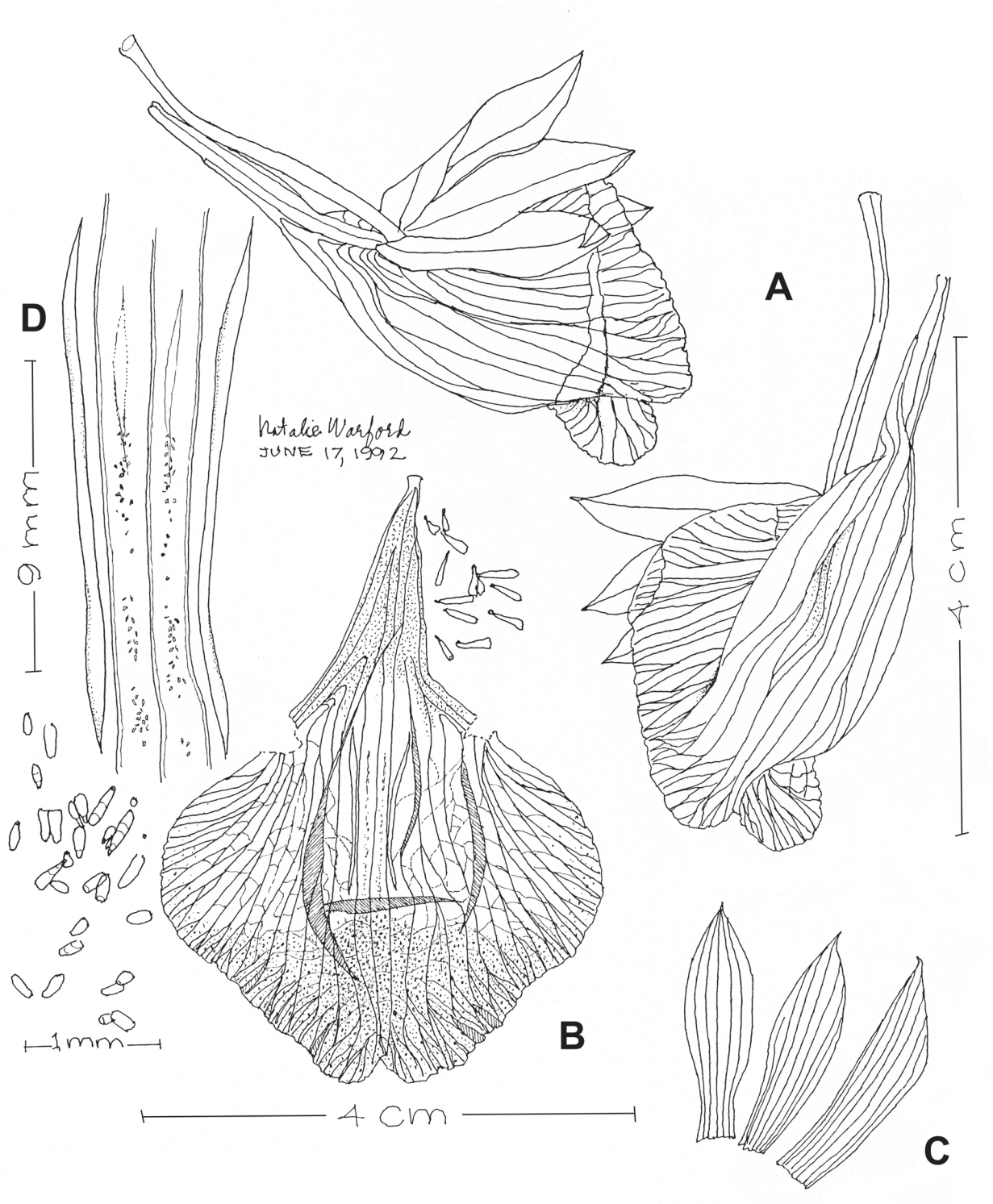

FIGURE 3. *Galeandra arundinis* G.A. Romero & Garay from Nicaragua. **A**, views of the flower; **B**, labellum, flattened; **C**, sepals and petal; **D**, keels and central nerves. Drawn from a hydrated flowers by N. Warford based on *Moore s.n.* (SEL).

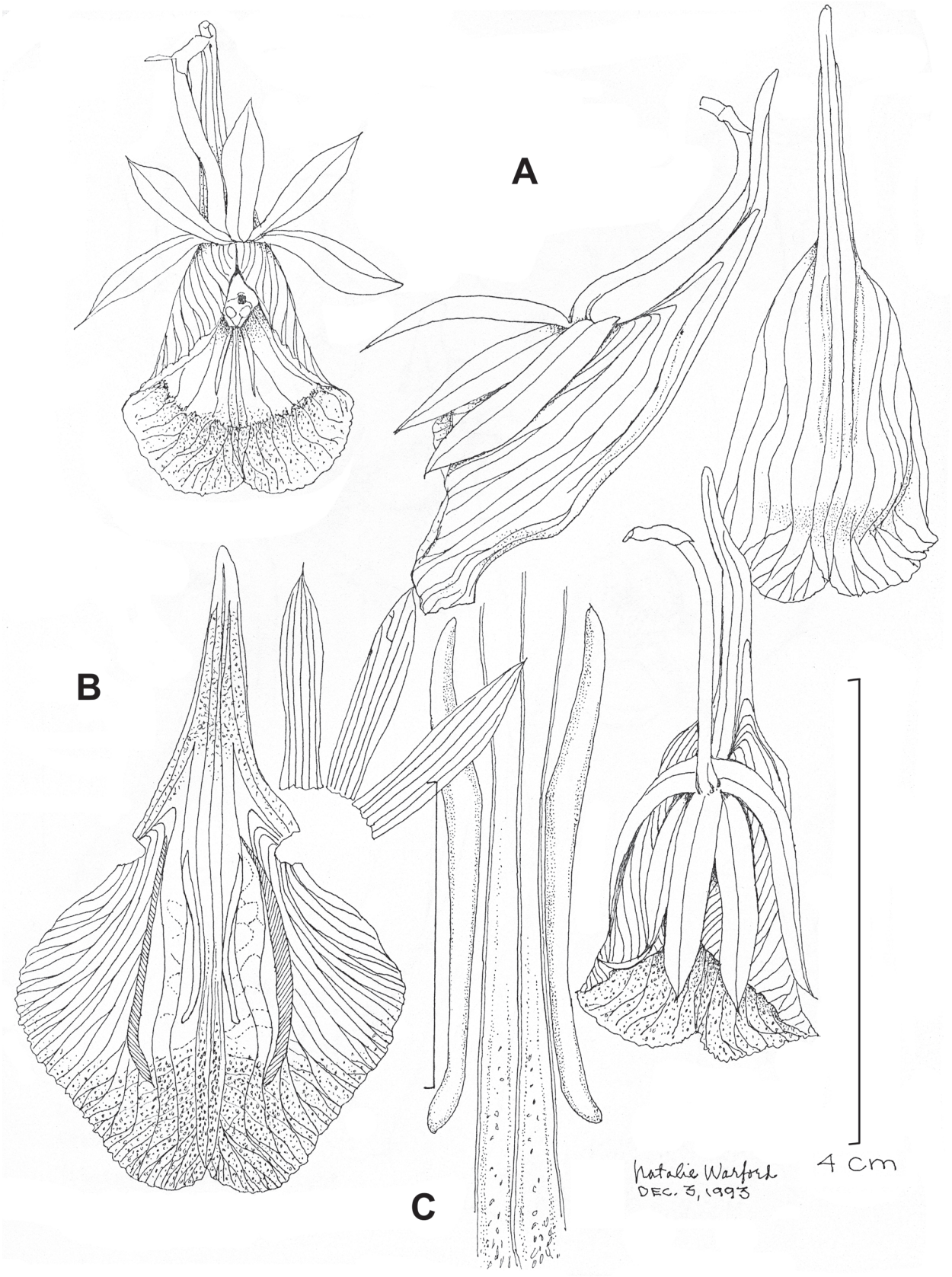

FIGURE 4. *Galeandra arundinis* G. A. Romero & Garay from Costa Rica. **A**, views of the flower; **B**, floral segments; **C**, keels and central nerves (scale 9.0 mm). Drawn from a flower in spirits by N. Warford based on *Warner s.n.* (voucher not preserved).

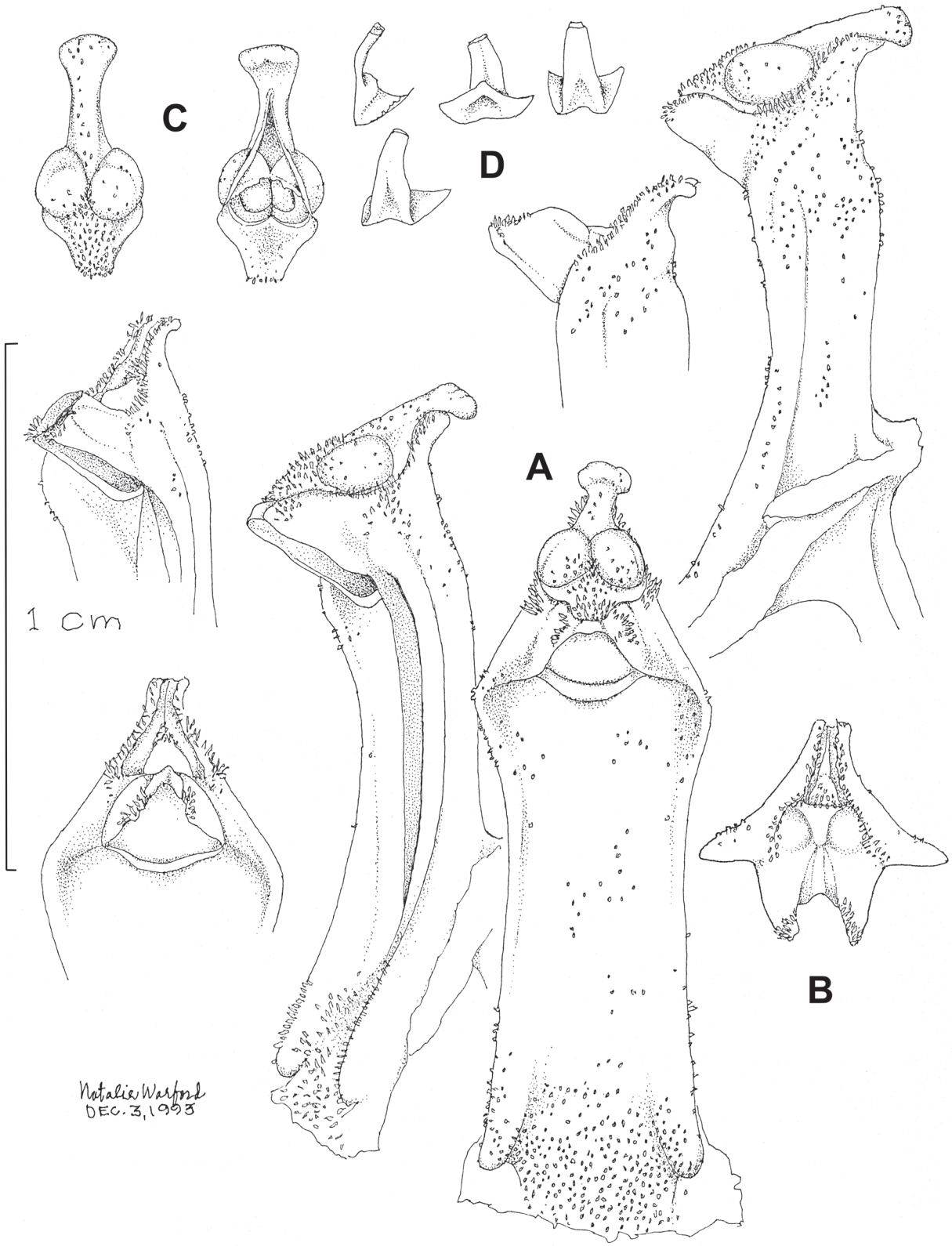

FIGURE 5. *Galeandra arundinis* G. A. Romero & Garay from Costa Rica. **A**, views of the column, with and without the anther in place; **B**, clinandrium; **C**, anther; **D**, views of stipe and viscidium. Drawn from a flower in spirits by N. Warford based on *Warner s.n.* (voucher not preserved).

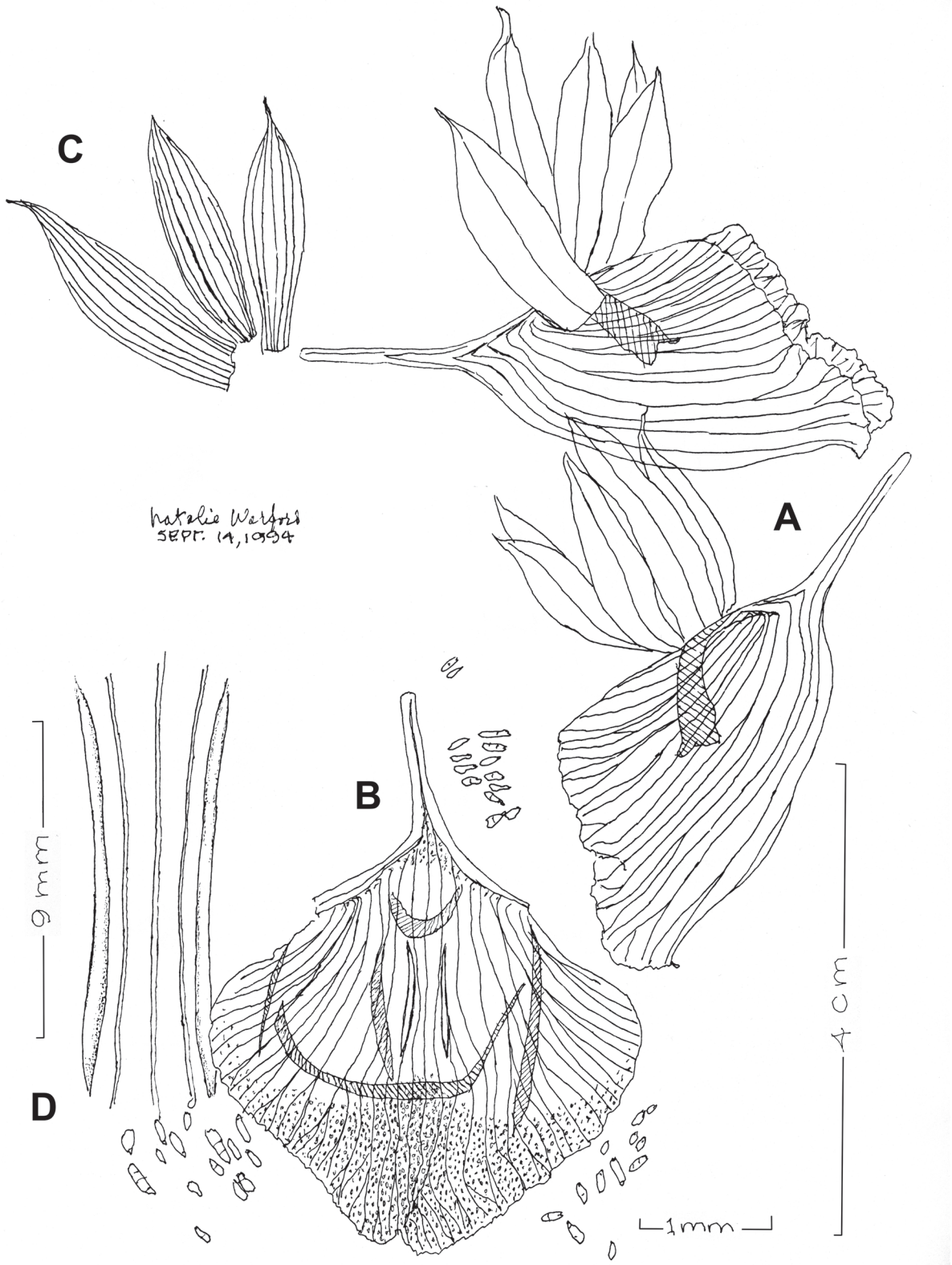

FIGURE 6. *Galeandra arundinis* G. A. Romero & Garay from Panama. **A**, views of the flower; **B**, labellum, flattened; **C**, sepals and petals; **D**, keels and central nerves. Drawn from a hydrated flower by N. Warford based on *von Wedel 2712* (AMES).

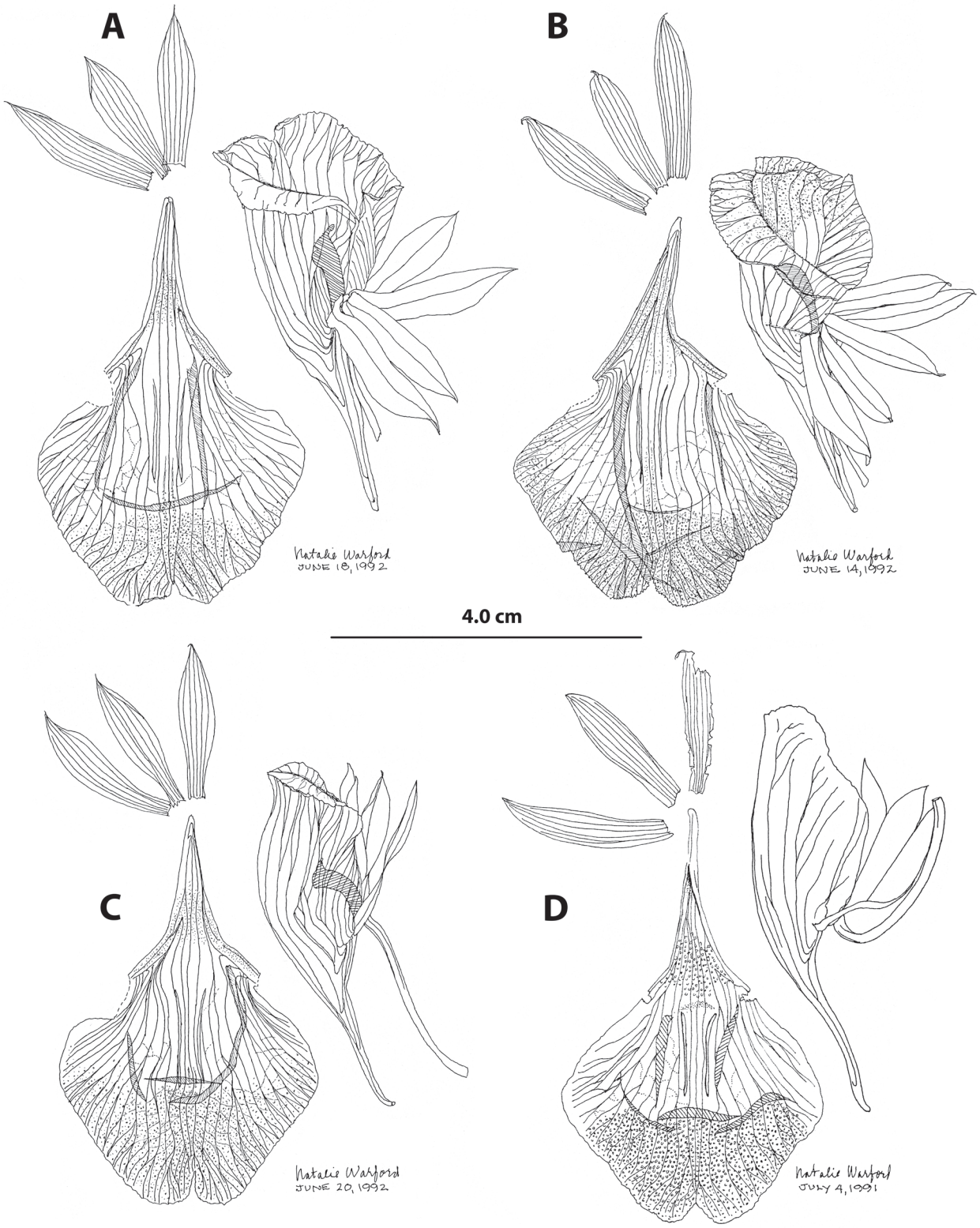

FIGURE 7. Labellum and floral profile of *Galeandra arundinis* G.A. Romero & Garay. Drawn by N. Warford from hydrated flowers based on **A**, Honduras, *Mathews s.n.* (SEL 055083); **B**, Honduras, *Mathews s.n.* (SEL 017712); **C**, Honduras, *Mathews s.n.* (SEL 016505); **D**, Guatemala, *Salazar 5146* (AMO).

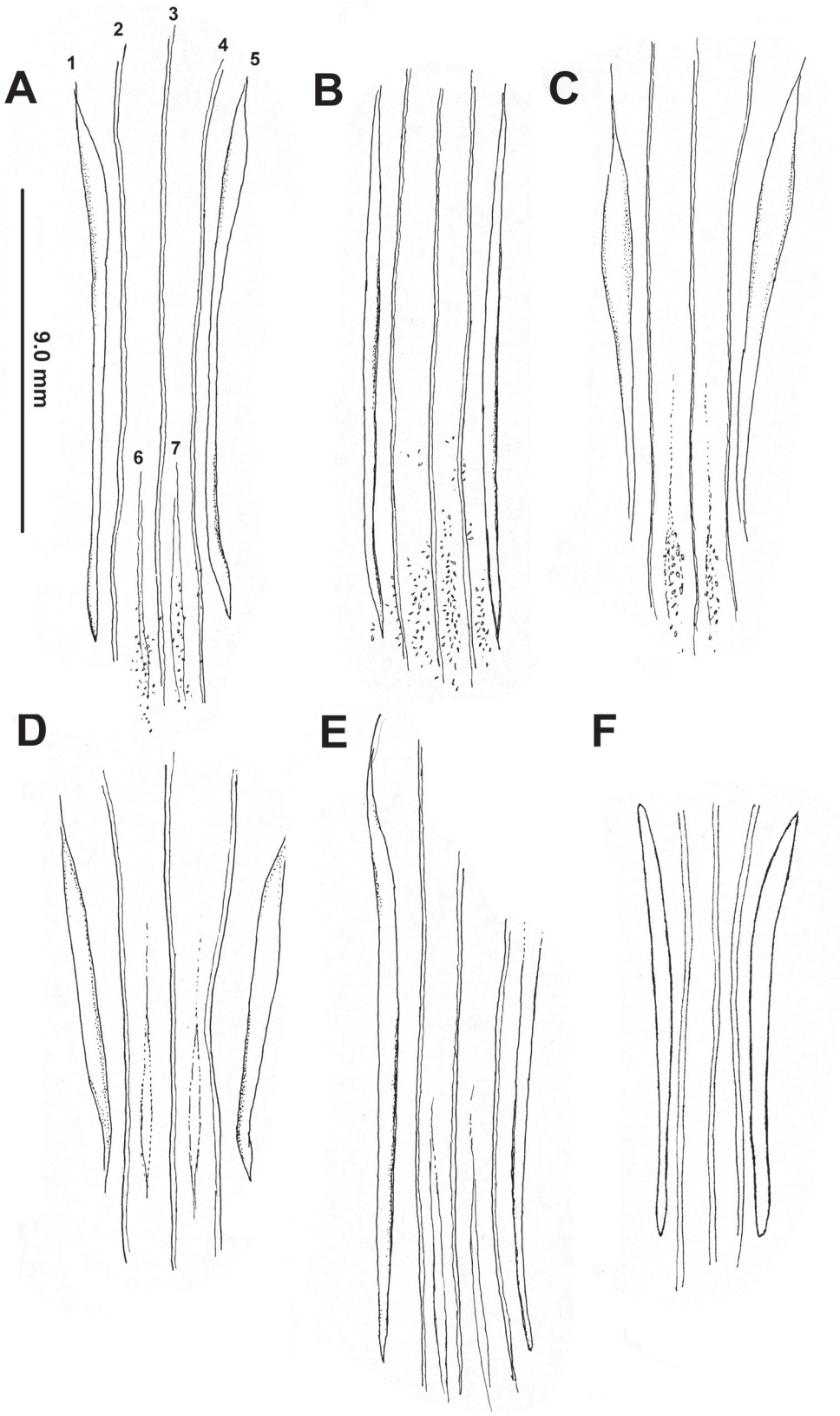

FIGURE 8. Keels of *Galeandra arundinis* G.A. Romero & Garay. Drawn by N. Warford based on **A**, Honduras, *Mathews s.n.* (SEL 055083); **B**, Honduras, *Mathews s.n.* (SEL 017712); **C**, Honduras, *Mathews s.n.* (SEL 016474); **D**, Honduras, *Mathews s.n.* (SEL 016837); **E**, Honduras, *Mathews s.n.* (SEL 016505); **F**, Guatemala, *Salazar 5146* (AMO). Numbers in A: 1, 5, keels; 3, labellum central nerve; 2, 4, first lateral nerves; 6, 7, lamellae.

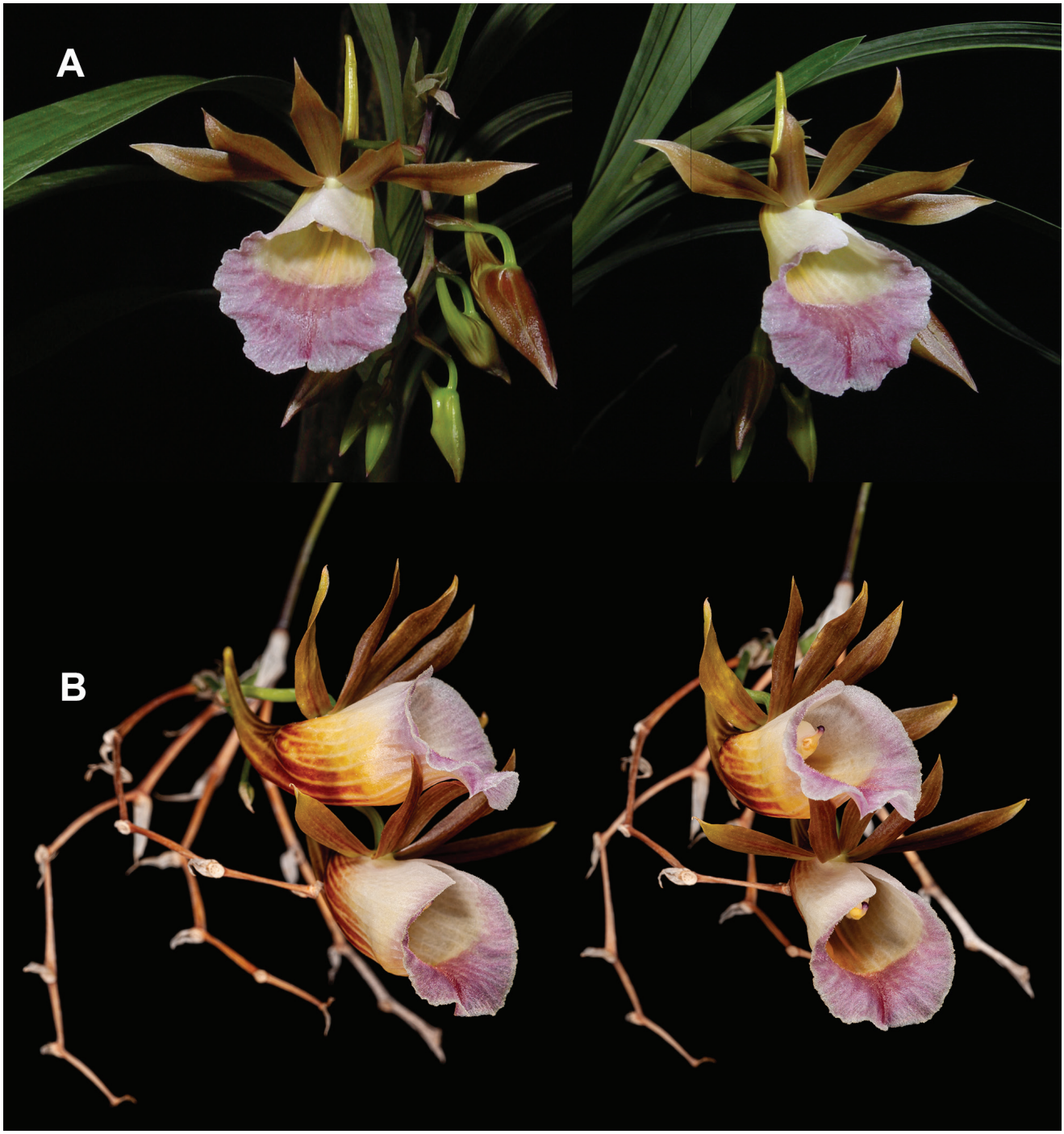

FIGURE 9. *Galeandra arundinis* G.A. Romero & Garay from Belize. **A**, early flowers (July 2013); **B**, late flowers two years later (December 2005). Notice changes in flower shape and color between seasons in flowers produced by the same plant; notice also the old inflorescence branches in B. A photographs by G. Carnevali; B by G. A. Romero-González. Based on *Carnevali 7996* (CICY). For scale, see Figure 1 herein.

al E del parque central, 1300–1350 m, 23 July 2009, *G. Carnevali & O. Moreno 7492* (CICY). Yoro: Concepción, 2500 ft [ca. 758 m], epiphyte, open mountain forest, petals and sepals light brown, lip light lavender, bag light brown with dark brown vertical stripes, column light brown, 14 August 1933, *J. B. Edwards 491* (AMES). **MEXICO.** Tabasco: [precise locality omitted], 8 m, *M. A. González & C. Burelo 50* (CICY, UJAT). **NICARAGUA.** Atlántico Norte: vicinity of junction of road Alamikamba with road between El Empalme and Limbaika, pine savanna and gallery forest, locally common on tips of *Acoelorrhaphe* trunks, leaf sheaths and bracts purple-spotted, pseudobulb round in cross-section, perianth except lip pale brown, all held erect above lip, mouth of lip pale purple, tube pale yellow, spur pale yellow with pale brown stripes, apparently scentless, 4 July 1982, *D. W. Stevens 21692* (MO); Atlántico Sur: Monkey Point, desembocadura del Caño El Pato, en el lado derecho, 1–10 m, 24 October 1981, *P. P. Moreno & J. C. Sandino 12316* (MO); Matagalpa: mountains E of Santa María de Ostuma, *A. H. Heller 1106* (drawing, SEL); Nueva Segovia: 7.6 km N of Ocotal-San Fernando highway along road toward Hacienda Las Brisas on Cerro Mogotón, E fork of road, along Caño El Zapote, 1095 m, pine forest on granite, broadleaf trees along steam, epiphyte, pseudobulb round in section, flowers dull brown and purple, 5 June 2014, *W. D. Stevens & O. M. Montiel 34707* (MO); Zelaya: sepals and petals brown, lip pink, spur striped with brown, column white, *E. Moore s.n., ex Hort*. Marie Selby Botanical Gardens, flowered 7 September 1976 (SEL). **PANAMA.** Bocas del Toro: Shepherd Island, vicinity of Chiriquí Lagoon, epiphyte, flowers maroon-red with purple edges, 20 September 1941, *H. von Wedel 2712* (AMES); in swamp near Almirante, 20 August 1962, *Hugo Nash 1962* (AMES).

Selected iconography: Williams (1946: 334, Fig. 147, as *Galeandra baueri*); Ames and Correll (1953: 473, Fig. 128, same illustration in Williams, 1946, again as *G. baueri*); Halcrow and Halcrow (ca. 1968: 71, as *G. baueri*); Hammer (1983, 1988, illustrating a plant from Nicaragua, as *G. batemanii*); Mora and Atwood (1992, illustrating a plant from Costa Rica, as *G. baueri*); McLeish et al. (1995: reverso of plate between pages 62–63, photograph 46; 64, Fig. 26, as *G. batemanii*); Nelson S. (2008: 1518, Fig. 743, as *G. batemanii*); van den Berghe and van den Bergue (2009: A72, as *G. dives* Rchb.f.); Pérez Munguía (2015: 110–111, as *G. batemanii*).

Conservation assessment: LC. The species has an EOO of 292,876.9 km^2 (that would qualify it as LC) and an AOO of 100.00 km^2 (which would qualify it as an EN). *Galeandra arundinis* is widespread, ranging for NE Panama into southeastern Mexico in Tabasco. Judging from the collection record, the species is apparently rare, and the populations are isolated and widely apart, but it is seldom vouchered and collected plants are most often brought into cultivation because of their horticultural appeal, and thus lost from scientific documentation. Collectors often mention that the plants are locally common and when not in flower they are fairly inconspicuous, contributing to its perceived rarity. There are many photographs uploaded on the WWW featuring this species, mostly identified as *G. batemanii* or *G. baueri* that witness to its being commoner that the formal record suggests. *Galeandra arundinis* tends to grow on *Acoelorrhaphe* palms that often occur in dense stands on soils flooded with brackish water or in other coastal or riparian ecosystems. However, several other collections come from other types of forests, including pine forests. It ranges from sea level to elevations of up to 1350 m, but it is more common below 500 m. Thus, being widespread, of a broad ecological range, and often occurring in mostly undisturbed ecosystems, we asses this species as Least Concern (LC).

Galeandra arundinis had been confused with at least two species before its formal description by Romero and Garay (2005), perhaps more often than any other species in the genus. It was first cited for Panama as *G. baueri* (Williams, 1939: 284; 1946: 332; 334, Fig. 147), thought to occur in Guatemala and Belize, without citing specimens, again, confused with *G. baueri* (Ames and Correll, 1953: 472, 474; 473, Fig. 128), from Honduras and Costa Rica, misidentified as *G. dives* Rchb.f. & Warsz. (see Siegerist, 1983; Puplin, 2013, respectively, the latter citing what would later be designated as the holotype of *G. arundinis*), from Mexico to northern South America as *G. baueri* (Mora and Atwood, 1992), and from Belize, again confused with *G. baueri* (Halcrow and Halcrow, ca. 1968: 70, figure on page 71) and later with *G. batemanii* (McLeish et al. 1995: 63, photograph 46; Bridgewater et al., 2006). Hammer (1883) reported it from Belize, Honduras, and Nicaragua, illustrating a specimen from Nicaragua (*Heller 10125*, SEL), as *G. baueri*. Later, in his comprehensive field guide to the orchids of Central America, Hammer (1988), extended its range to Mexico and Guatemala (and, surprisingly, to "The West Indies"), using the same illustration (*Heller 10125*, SEL), as *G. batemanii*. More recently, Nelson S. (2008: 816–817) reported three species of *Galeandra* for Honduras but, based on the references he cited, they all referred to *G. arundinis*; the same author (Nelson, 2010 [2013]) reported *G. arundinis* for Honduras, citing *Edwards 243* at AMES; van den Berghe and van den Bergue (2009: 63–64) reported it from Nicaragua as *G. dives* Rchb.f.; Bogarin et al. (2014), cited it correctly for Panama.

Ossenbach et al. (2007: 66) reported *Galeandra arundinis* for Costa Rica, and *G. dives* for Panama, Nicaragua, Honduras, Guatemala, Belize, and Mexico. Although it is possible that the latter could be found in Panama, since it was described from neighboring Colombia (no type locality reported in the protologue, but "Neu-Granada" and "N. Granada" in Reichenbach f., 1856: 323 and 1857: 35, respectively), it would appear that the reports for the rest of Central America are referable to *G. arundinis*. Plants of *G. dives* bear yellowish flowers, with a patch of parallel reddish bands that merge near, yet not reaching the margin of the labellum, as shown in Hooker (1853; Fig. 10 herein; also in Bateman, 1867), as *G. baueri* var. *floribus luteis*, and in Escobar (1972: 161) and Ospina and Dressler (1974: Fig. 143), in the latter two cases as *G. leptoceras* Schltr. There is also a specimen at K (*L. Schlim 994*, see appendix herein), also from Colombia, the flowers of which faintly, yet unambiguously show the same pattern of coloration. Sheet 26543 in "Reichenbach: Herb. Orchid." (W; see link in the appendix) shows a sketch of a flower with a "blotch" in the labellum central lobe but, again, well separated from the margin, and with speckles on the side lobes. In contrast, all the herbarium material and iconography from these countries (i.e., from Mexico to Panama), examined by the authors, show flowers with the labellum apex solid

FIGURE 10. *Galeandra dives* Rchb.f. & Warsz. as *G. baueri* var. *floribus luteis* (Hooker, 1853).

dark red (as in the type) to light purplish-red all along the margins of the labellum (in most of its geographical range); exceptionally, as mentioned before, the apex of the labellum can have little or no pigmentation at all.

Examining the specimen *Salazar 5148* (AMO), from the type locality of *Galeandra archilae*, we find no morphological features to distinguish it from *G. arundinis*. Based on the information furnished in the protologue of *G. archilae*, we are confident that both taxa are one and the same species. Furthermore, although we have not seen any actual material referable to *G. garifunae* or the type, based on the protologue and its type locality, we do not hesitate to place it in the synonymy of *G. arundinis*.

The labellum keels of *Galeandra arundinis* are fairly constant; the lamellae, however, can vary in herbarium specimens, either pressed and dried or kept in spirits (Fig. 1–8; see discussion below). We encouraged researchers to study this variation in the field, capturing detailed images *in vivo*. Flower color can vary tremendously, again, from dark to light pigmentation, even in the same plant in different years or flowering season, presumably as a response to light exposure and physiological status of the plant (Fig. 9; see discussion below).

Galeandra batemanii Rolfe, Gard. Chron. ser. 3, 12: 431. 1892. TYPE: MEXICO. Oaxaca: Kisatipa, 10 leagues from Melatepec ["apparently Quezaltepec... in the hills north of Tehuantepec, some 10–15 km west of Malacatepec," *fide* McVaugh, 1985: 125, most likely San Miguel Quetzaltepec], *J. Ross ex Hort. G. Barker* (Holotype: K). Fig. 11–17.

For comprehensive descriptions, see Warford (1994) and Soto-Arenas and Solano Gómez (2007).

Field and herbarium identification: Plants epiphytic or occasionally lithophytic or subterrestrial, growing on forest litter, often growing on pines (*Pinus oocarpa* Schiede ex Schltdl., Pinaceae), in Oaxaca, or on *Acoelorrhaphe wrightii* in Tabasco; pseudobulbs thickened at the base, ovoid to piriform, flowers with a labellum "… rich ruby burgundy or slightly duller at the apex, usually with a narrow white margin or not…" (Warford, 1994: 46). Both in the field and the herbarium, flowers of *G. batemanii* are larger than the flowers of *G. arundinis* (Fig. 1–7 versus Fig. 11). However, if herbarium flowers have lost their rich burgundy pigmentation in the apex of the labellum and/or are not properly hydrated, and without pseudobulbs or precise locality, flowers of *G. batemanii* are almost indistinguishable from those of *G. arundinis* (see discussion below). *In vivo*, however, the two species can be easily distinguished by the color of the leaves (see key below).

Etymology: Named after James Bateman (1811–1897), naturalist, horticulturalist, and garden designer, who developed pioneer methods to grow orchids. He also was author of *The Orchidaceae of Mexico and Guatemala* where *G. batemanii* was depicted for the second time (Bateman, 1840).

Distribution: Hitherto endemic to Mexico, in the gulf drainage of Oaxaca, in Chiapas (Beutelspacher Baigts, 2008, 2013; Beutelspacher Baigts and Moreno Molina 2018: 476), and Tabasco (González Aguilar y Burelo Ramos, 2012); expected in Guatemala, perhaps the plant cited by Archila et al. (2012: 15, note). Bateman (1840), in fact, reported "... specimens more recently discovered by Mr. Skinner in Guatemala". Notwithstanding, the border between Guatemala and Mexico changed considerably in the early 19th century (see Carnevali et al., 2018: 8–9), and it is possible that Skinner collected this species in what is currently Mexican territory.

Phenology: The only reliable reports of this species indicate that plants flower between May and July. The phenology reported by McVaugh (1985: 125), "Aug–Oct," is attributable to *G. greenwoodiana* Warford.

Additional material examined: MEXICO. Chiapas: [precise locality omitted], 1500 m, July 2014, *F. Hernández N. 4530A* (CHIP). Oaxaca: "Talea [de Castro], 4,000 ft. [ca. 1200 m], epip., sepals ochre-violacé, labelle violâtre," 1840s, *H. Galeotti 5271* (BR, K, P [several specimens, some without numbers, but presumably from the same gathering]); same locality, "parasitica in sylvis", August 1842, *F. M. Liebmann 6943* (US); near [Santiago] Choapam, on fallen pine in open pine forest, 750 m, 25 May 1990, *O. Suárez and E. W. Greenwood 1122* sub *N. Warford 594* (AMO, drawings, photograph of flattened flower, AMES). Tabasco: [precise locality omitted], en vegetación riparia, creciendo sobre *Acoelorrhaphe wrightii,* 3 m, 3 May 2013, *M. A. González & C. Burelo 01* (CICY, UJAT).

Selected iconography: Lindley (1840b, as *G. baueri*; Fig. 12 herein); Bateman (1840, as *G. baueri*, Fig. 13 herein);[5] Warford (1994: 47, Fig. 5; 1999: 129, Fig. 2); Day's Book (43, 17 August 1886, unpublished, image at AMES; includes a note from R. A. Rolfe: "is *G. batemanii*, Rolfe"); Paxton (1848,[6] as *G. baueri*, Fig. 14 herein); Warner et al. (1887, as *G. baueri*); Linden (1901, Fig. 15 herein);[6] Wiard, 1987: 175, photographs on the upper right;[7] Beutelspacher Baigts (2013: 69); Beutelspacher Baigts and Moreno Molina (2018: 476).

[5] Reichenbach f. (1863) described Bateman's plate as "*icon phantastica horribile florulenta foliis cauleque minus correctis*." Rolfe (1892) pointed out that "… part of another plant has in some way crept into Mr. Bateman's figure…" Bateman (1840; Fig. 13, herein), in fact, indicated that "… Mr. Barker's plant produced flowers in the autumn of 1839, and from these, assisted by native specimens more recently discovered by Mr. Skinner in Guatemala, Miss Drake prepared the exquisite drawing from whence the accompanying plate is taken." Later, Bateman (1867) admitted that "My vexation will therefore be imagined when—some years afterwards—one of Mr. Skinner's plants flowered and, instead of the *Galeandra*, turned out to be a new *Epidendrum* (*E. lacertinum*), of which, besides being more numerous, the flowers were disposed in a manner totally different from those of the species it had simulated," accounting perhaps for some of the thick, fusiform pseudobulbs depicted in Bateman's plate. The pseudobulbs of *Epidendrum lacertinum* Lindl. are produced sequentially from the upper nodes of older pseudobulbs (E. Hágsater, personal communication to GAR-G, 2021); Lindley (1841), likewise, stated, in the protologue of the species, "it is stated to have the habit of *Galeandra baueri*...." Nevertheless, it should be pointed out that the upper, flowering pseudobulb shown in Bateman (1840), arose not from the basal but from one of the lower nodes of an old decaying pseudobulb, an uncommon but nonetheless documented strategy in plants of Catasetinae, where old, decaying pseudobulbs activate meristems on the nodes, from which normal pseudobulbs develop.

[6] Here we differ from Warford (1994: 46) and assign the early iconography in Paxton (1848; Fig. 14 herein) and Linden (1901; Fig. 15 herein) to *Galeandra batemanii* and not to *G. greenwoodiana*, based on the intense burgundy color of the labellum apex.

[7] The photograph on the upper right, although identified as *G. batemanii*, appears to depict a flower of *G. greenwoodiana*.

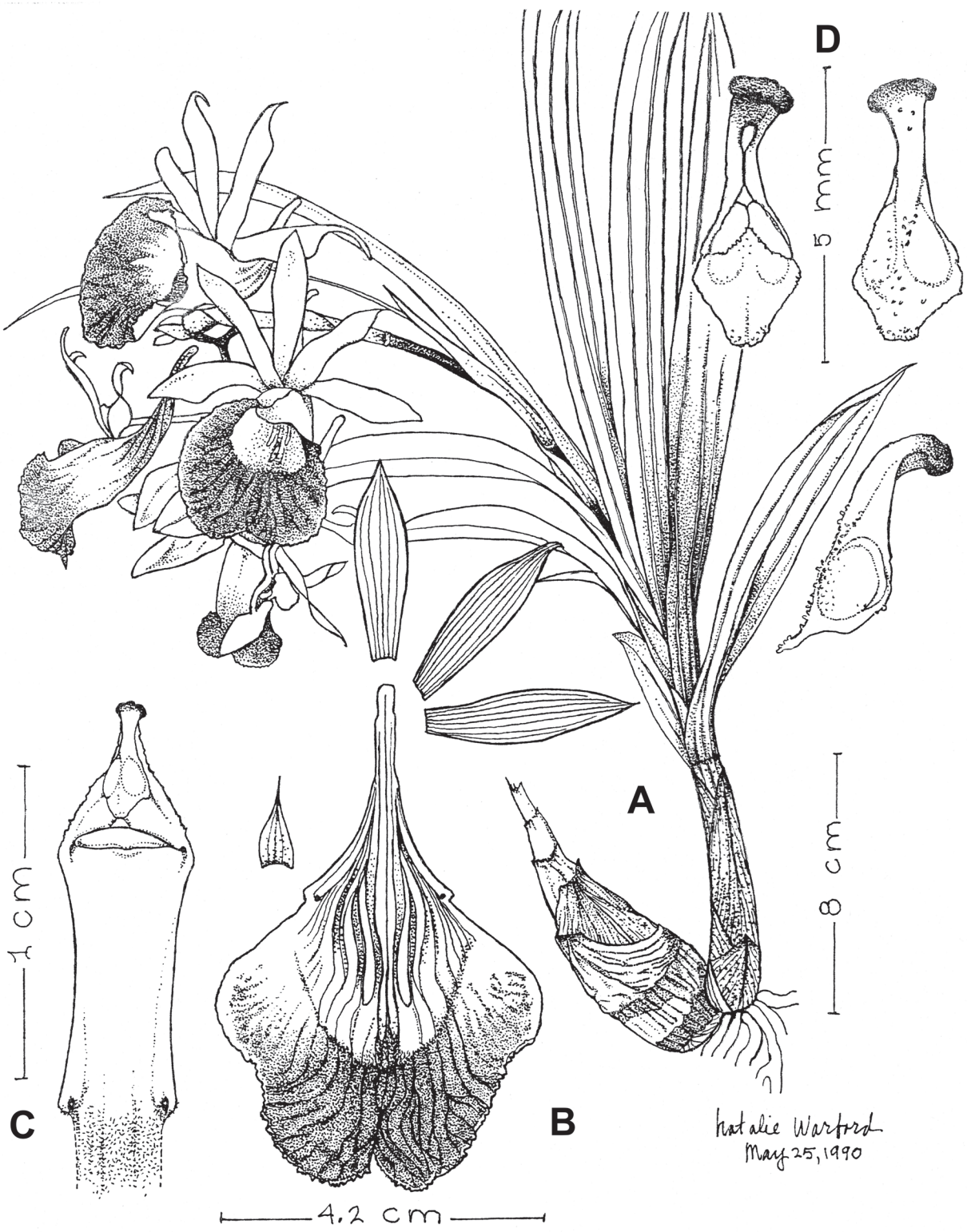

FIGURE 11. *Galeandra batemanii* Rolfe. **A**, Flowering plant; **B**, labellum, flattened, floral bract on the upper left; **C**, abaxial view of the column with pollinarium; **D**, views of the anther. Drawn by N. Warford from material in vivo based on *Warford 594* (AMO).

FIGURE 12. *Galeandra batemanii* Rolfe as *G. baueri* Lindl. (Lindley, 1840b).

FIGURE 13. *Galeandra batemanii* Rolfe as *G. baueri* Lindl. (Bateman, 1840).

FIGURE 14. *Galeandra batemanii* Rolfe as *G. baueri* Lindl. (Paxton, 1848).

FIGURE 15. *Galeandra batemanii* Rolfe (Linden, 1901).

FIGURE 16. Views of *Galeandra greenwoodiana* Warford and *G. batemanii* Rolfe. **A**, *G. greenwoodiana*; **B**, *G. batemanii*. Photographs by N. Warford based on the holotype, *Warford 543* (AMO) and *Warford 594* (AMO), respectively. Colors on this plate do not necessarily match the original colors of the flowers.

FIGURE 17. *Galeandra batemanii* Rolfe from Arroyo Negro, Chiapas, growing subterrestrially. Photograph by F. Hernández N. based on *F. Hernández N. 4530A* (CHIP).

Conservation assessment (IUCN): EN. *Galeandra batemani* has an EOO of 33782.6 km^2 (that would qualify it as NT) and an AOO of 24.0 km^2 (which would qualify it as an EN). The species meets criteria EN B2ab (i, ii) of the IUCN. It is known from five localities, and the AOO is 24.00 km^2. It is a rare species known with certainty from the Atlantic slope of the mountain ranges in and around the isthmus of Tehuantepec. It grows in pine forests, more rarely, as a lithophyte or subterrestrial and, in Tabasco, on *Acoelorrhaphe* palm stands. The habitat of the species is highly fragmented under natural conditions and is also simultaneously being severely threatened by anthropogenic activities, mainly slash-and-burn agriculture and extensive cattle ranching. It is also being illegally extracted from the field for horticultural purposes. None of the populations known reside in an area that is under any level of protection. Being such a horticulturally desirably subject, its rarity under cultivation and in the herbarium record witness to its rarity in the field. *Galeandra arundinis*, though with almost identical flowers and cultivation appeal, is much more common in the herbarium and photographic record and it is not under any perceived threat. For other notes on the conservation of this species, see Soto-Arenas and Solano-Gómez (2004).

Galeandra batemanii was long misidentified as *G. baueri* (e.g., Lindley, 1840b; Bateman, 1840; Paxton, 1848; Warner et al., 1887), until Rolfe (1892) described it, presenting convincing arguments to treat it as a distinct species (see also Bateman, 1867). Nonetheless, in the mid 20th century, Williams (1939) and generic treatments for the flora of Panama (Williams, 1946), Guatemala (Ames and Correll, 1953), and Mexico (Williams, 1951) placed *G. batemanii* under the synonymy of *G. baueri* (see also Klaassen, 1979). It was not until Pollard (1974) called attention to the differences between *G. batemanii* and what he circumscribed as *G. baueri*, which he distinguished based on the shape of the pseudobulbs, color of the lip, flowering time, and distribution:

Pseudobulbs slender, fusiform; lip pale colored, blooms in July; Southern Mexico, Central America, Colombia, Peru, Venezuela and French Guiana . . . . . *G. baueri*
Pseudobulbs round to ovoid; lip with large purple spot at apex; blooms September, October; Nayarit, Mexico . . . . . *G. batemanii*

However, reliable bibliographic and herbarium resources on *Galeandra* were then scarce and, while solving the *G. baueri* versus *G. batemanii* puzzle, misinterpreted other species: Pollard's "*G. batemanii*" would eventually be described as *G. greenwoodiana*, and his "*G. baueri*" included several species, including *G. arundinis*. Nevertheless, Pollard's contribution was critical:[8] it brought attention to the fact that species in the *G. batemanii* group were distinct and coherent: they currently conform a relative well supported subclade, sister to all other epiphytic galeandras except for *G. devoniana* R.H. Schomb. ex Lindl., which is itself sister to all the other member of the genus (Monteiro et al., 2010).

McVaugh (1985: 127) argued that "The plant from Nayarit appears to be conspecific with the one from Oaxaca, which is the true *G. batemanii*;" the plant from Nayarit would eventually be described as *G. greenwoodiana*.

According to Warford (1994, 1999), *Galeandra batemanii* is easily distinguished from *G. greenwoodiana* based on the differences of the labellum lobes *in vivo* (Fig. 16). In iconography, and in herbarium material (in these two last cases not always discernable), when the labellum is flattened, the lobes are almost symmetrical, rounded in the former, versus lobes markedly asymmetrical, one of them much larger than the other and half-rounded at the apex, in the latter (Fig. 17). Other characters that differ between these two species are listed in Table 1. Furthermore, *Galeandra batemanii* and *G. greenwoodiana* have disjunct distributions, the former from highlands in the Atlantic slopes of Oaxaca and Chiapas, east of the isthmus of Tehuantepec, and here reported from Tabasco, the latter from the Pacific slopes of Mexico from Nayarit to NW Oaxaca (see appendix for the southern, easternmost collection of *G. greenwoodiana*).

We include a drawing of a flower from the holotype of *G. batemanii* (Fig. 18), from a flower sent to L. A. Garay in 2004, which is now conserved at K in spirits.

Galeandra sobralioides Archila & Chiron, (as "*sobralioide*"), Revista Guatemalensis 15, No. 2: 12. 2012. TYPE: GUATEMALA. Departamento San Marcos: Bocacosta, sobre palmeras de coyolar [*Acrocomia aculeata* (Jacq.) Lodd. ex Mart.], 150 m, November 1995, *Fredy Archila s.n.* (Holotype: BIGU). Fig. 19–20.

We provide a full description of this species, to complement the one given in the protologue.

Plants epiphytic, vegetatively undistinguishable from its close relatives, *G. batemanii* and *G. greenwodiana*, *pseudobulbs* up to 122 mm long and 28.5 mm in diameter, perhaps the smallest of the group, covered with the *leaf sheaths* that eventually dry out and senesce. *Leaves* 6–7, deciduous, distichous, plicate, articulate; *lamina* linear lanceolate to linear elliptic, to 20 cm long and 2.5 cm wide. *Inflorescence* a multiflowered raceme, emerging from the developing pseudobulb, often flowering later from adventitious branches borne from one or more of the uppermost peduncle nodes; *peduncle* and *rachis* light

TABLE 1. Stable, distinguishing characters of *Galeandra batemanii* Rolfe and *G. greenwoodiana* Warford.[1]

	G. batemanii	*G. geenwoodiana*
Pseudobulbs	To 10 cm high, conic ovoid obclavate	To 25[–72] cm long, conic-ovoid to obclavate
Leaves	Up to 7, to 21 × 3 cm; dark green with a silken sheen	Up to 12, to 50 × 4 cm; medium, matte green
Rachis	Stout, 2 mm in diameter	Wiry, 1 mm in diameter
Peduncle bracts	To 6 cm long	To 14 cm long
Flower bracts	To 1.3 cm long	To 4 cm long
Labellum keels[2]	12–14 mm long	8–10 mm long
Labellum apex	Rich, bright burgundy	Pale, dull burgundy
Column	1 cm long, 4 mm wide[3]	1.2–1.3 cm long, 5 mm wide[3]

[1] From Warford (1991 [unpublished notes at AMES], 1994).
[2] In dry flowers.
[3] Across the wings.

[8] Pollard's contribution also fueled E. D. Greenwood and N. Warford interest in the Mexican galeandras and, in fact, early N. Warford's notes at AMES show that she at first planned to describe her *G. greenwoodiana* as *G. pollardiana*.

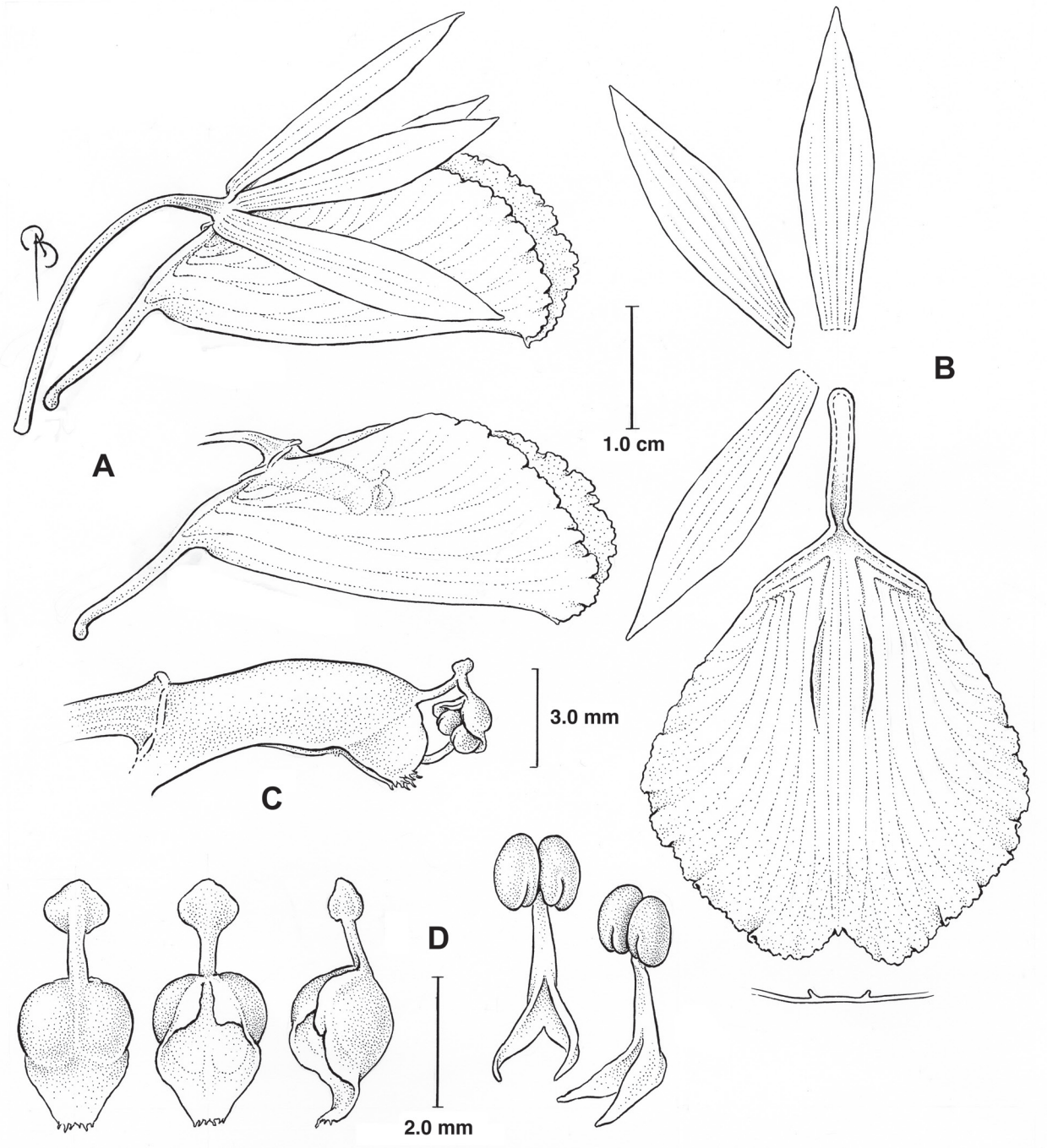

FIGURE 18. *Galeandra batemanii* Rolfe. **A**, side views of the flower; **B**, floral segments; **C**, side view of the column; **D**, views of the anther and pollinarium. Drawn from a hydrated flower by B. Angell based on the holotype (K).

green, often with red pigmentation; peduncle light green, 7.0 cm long, in diameter ca. 2.0 mm at the base, 1.5 mm at the apex; floral bracts 6–7 × 3–4 mm, becoming smaller distally along the rachis, ovate, shortly acuminate. *Flowers* showy, opening in succession, lasting a week to 10 days, and therefore it is often the case that several are at anthesis simultaneously, trumpet-shaped. *Sepals* and *petals* abaxially yellowish-green, suffused brown, adaxially yellowish green, striped brown at the base, suffused brown toward the apex, *dorsal sepal* lanceolate, acute, 21.7 × 6.4 mm, *lateral sepals* lanceolate, falcate, 22.3 × 6.7 mm, *petals* lanceolate, acute, 20.9 × 7.3 mm. *Labellum* saccate, widely infundibuliform, spurred, deeply bilobed, lobes subequal, ovate-subrhombic when spread; excluding the *spur*, in its apical three fifths deep purple, velvety, bearing unicellular trichomes, diminishing in density towards the lighter purple upper sides and absent

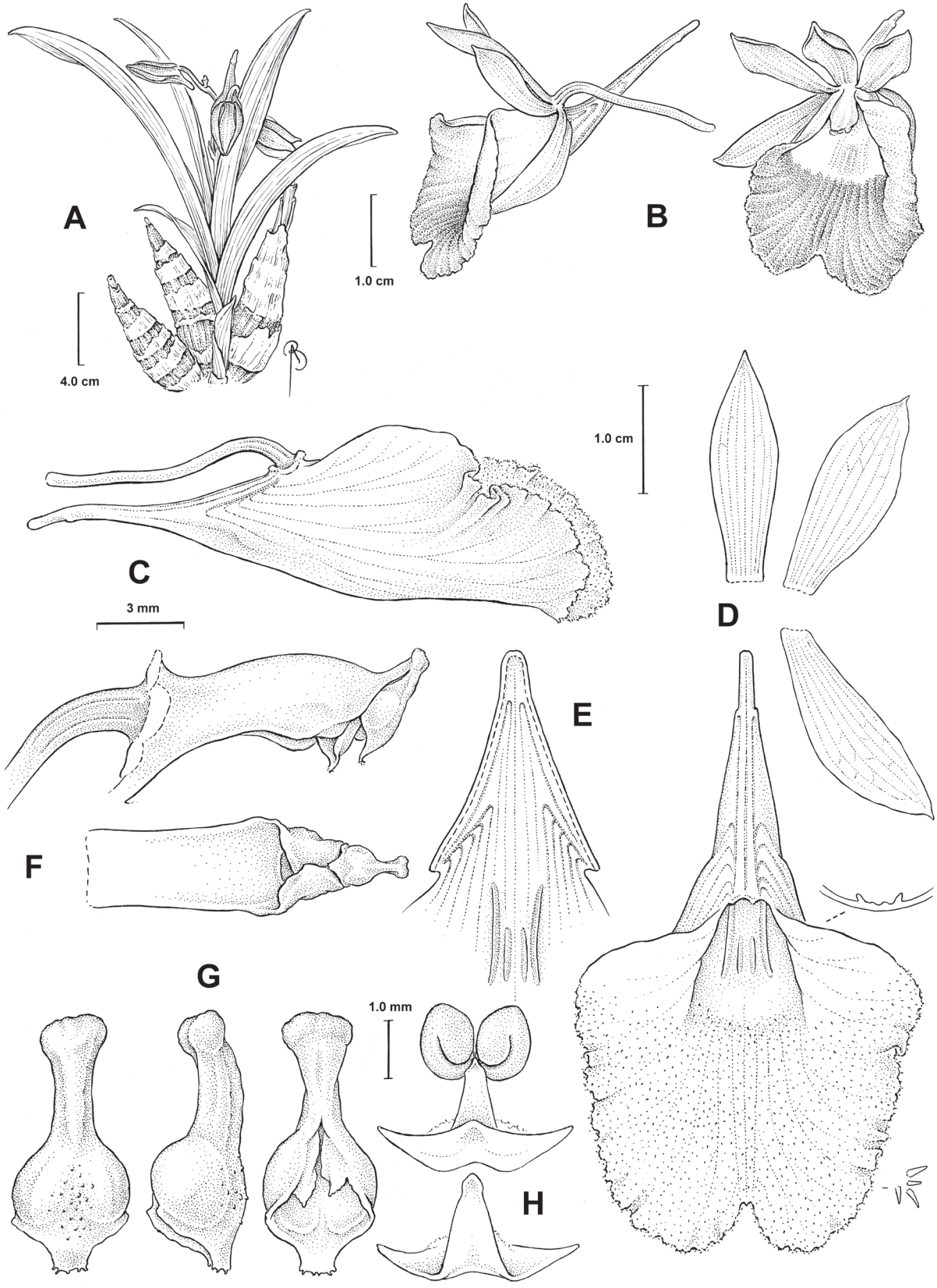

FIGURE 19. *Galeadra sobralioides* Archila & Chiron. **A**, habit, plant with flowers in bud; **B**, views of the flower; **C**, side view of the labellum; **D**, floral segments; **E**, spur, spread; **F**, view of the column; **G**; views of the anther; **H**, views of the pollinarium. Drawn from a flower in spirits by B. Angell based on *Carnevali 8596* (CICY).

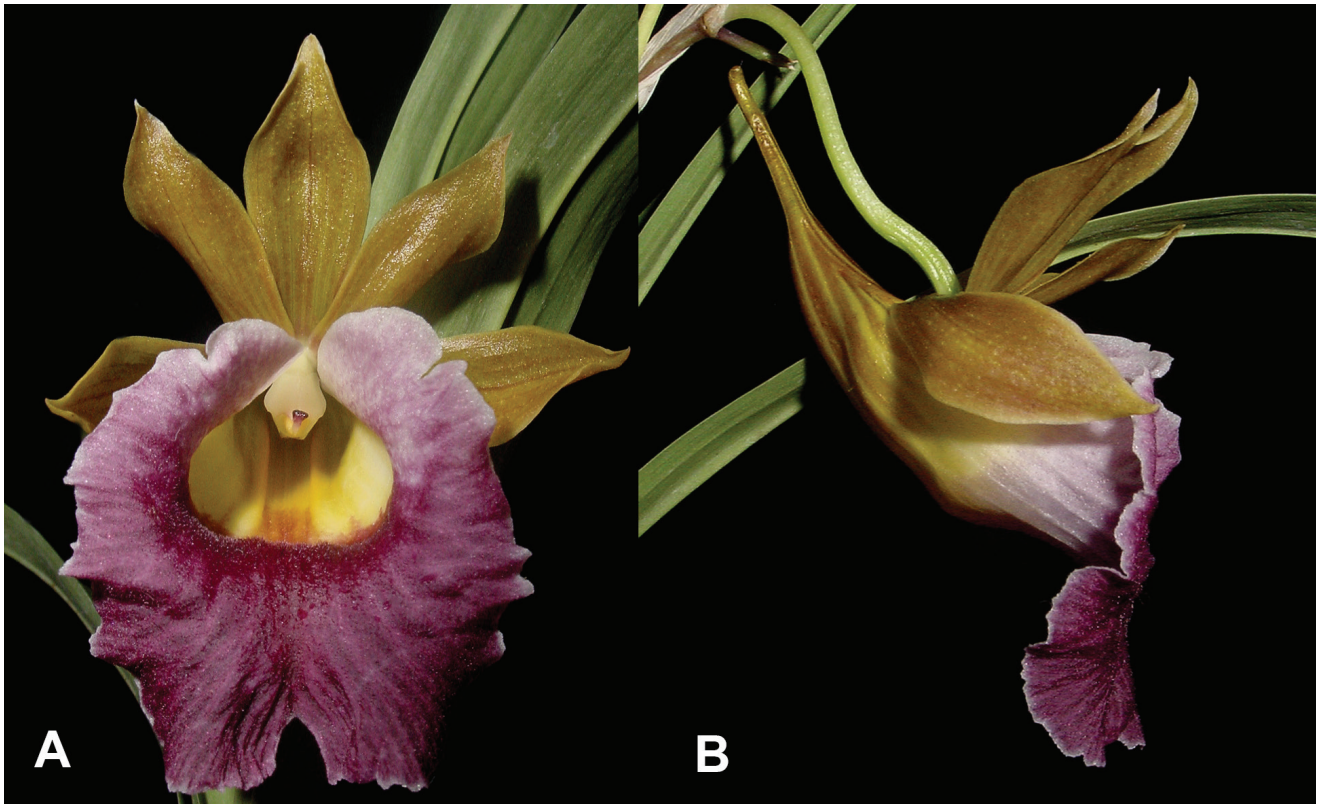

FIGURE 20. *Galeandra sobralioides* Archila & Chiron. **A**, front view; **B**, side view. Photographs by G. Carnevali based on *Carnevali 8596* (CICY). For scale, see Figure 18.

towards the yellow base, the apex strongly flared, the basal portion bearing two outer, conspicuous, yellow, waxy *keels* that curve outward toward the base, less so toward the apex, and two inner, slightly purple *thickenings* between the nerves, not surpassing the outer keels; including the spur and up to the edge of the longest lobe, 57.2 mm long, 31.8 mm at its widest point, *spur* narrowly infundibuliform, rigid, gently upturned or straight, yellowish-green, striped maroon, 18 × 22 mm long. *Column* glabrous, white with a few reddish spots at the base, gently arcuate, 9.5 × 3.5 mm, with a conspicuous foot, winged, clinandrium slightly upturn. *Anther* beaked, 4.6 × 2.1 mm, white, dark purple at the tip, the base scrotiform, the apex slightly bent, clavate, slightly bilobed at the tip. *Pollinarium* with viscidium, stipe, and two pollinia; viscidium subtriangular, white, extending at the sides into triangular hyaline arms; stipe laminar, when dried semi-tubular; pollinia ovoid, longitudinally cleft, yellow, hard, waxy, 1.3 × 1.1 mm. *Capsule* not seen (based on *Carnevali 8596*, CICY and *Carnevali 7356*, CICY, AMES).

Etymology: According to the authors, in reference to flowers of the genus *Sobralia* Ruiz & Pav. (Orchidaceae), and the Latin adjectival suffix *-oides*, indicating resemblance.

Distribution: Hitherto known from Pacific slopes in southern Mexico and northern Guatemala, along southern slopes of the Sierra Madre de Chiapas, west of the isthmus of Tehuantepec, in Oaxaca at 1000–1300 m, in Guatemala at 150 m; expected in the intervening Mexican state of Chiapas.

Phenology: in cultivation in Mérida, Yucatán, Mexico, plants of *Galeandra sobralioides* flowered in April–June. The protologue does not state flowering time.

Additional material examined: MEXICO. Oaxaca: Municipio San Miguel Chimalapa: Arroyo El Caracol, al pie del Cerro Guayabitos al N de Benito Juárez, selva mediana subcaducifolia riparia (ladera arriba hay encinar tropical y *Pinus oocarpa*), ca. 1000–1200 m, única planta vista, en tronco caido sobre el arroyo, ambiente sombreado y húmedo; cerca *Maxillaria variabilis*, *Lycaste aromatica*, *Scelochilus*, *Notylia*, *Stanhopea*, *Catasetum integerrimum*, 25 julio 1996, *G.A. Salazar, S. Maya, O. Rocha & L. Cabrera 5651 ex hort. sub G. Carnevali 8596* (CICY; AMES [fragment]); same locality and genotype, flowering under cultivation, 17 May 2002, *G. Carnevali 7356* (CICY; AMES, fragment); same locality, bosque con mezcla de tropicales (*Bursera*) con elementos de bosque mesofilo (*Cedrela*), pendientes fuertes, suelo amarillo arcilloso, 31 july 1986, *S. Maya 3689* (CHAPA); Cerro de la Division, ca. 5 km al E de Benito Juarez, ca. 39 km en linea recta al NNE de San Pedro Tapanatepec, 1400–1600 m, bosque mesofilo de montaña de *Quercus*, *Calophyllum*, *Podocarpus*, *Liquidambar*, pendiente suave, suelo negro, 4 mayo 1985, *S. Maya 1607* (CHAPA).

Iconography: Hágsater et al. (2005: 145, as *G. aff. batemanii*);[9] Monteiro et al. (2010: Fig. 5F, plant with flowers in bud, photograph by G. Carnevali, based on

[9] The photograph appearing in Hágsater et al. (2005) and Archila et al. (2012) was originally taken by G. Carnevali, see Fig. 19A herein, based on *Carnevali 8596*).

Carnevali 8596, as *G. batemanii*); Archila et al. (2012: verso of plate inserted between pages 18–19, as "*Galeandra sobraliolide* Archila & Chiron").

Conservation assessment (IUCN): EN. *Galeandra sobralioides* has an EOO of 1661.4 km^2 (that would qualify it as EN taxon) and an AOO of 12.0 km^2 (which would qualify it as an EN species). The species meets criteria EN B2ab (i, ii) of the IUCN. It is known from three, possibly only two locations, separated by 310–320 km, one in Guatemala and two in SE Mexico (which are so close to each other as to possibly be considered the same). The species is rare, even at these localities. The intervening area between the Mexican and Guatemalan populations has not been thoroughly explored and with certainty more populations are to be expected. The very imprecise type locality in San Marcos, Guatemala ("Bocacosta") is in an area that has been heavily perturbed by extensive cattle ranching developments and it is hard to assess what the status of the species is there, but judging from the paucity of collections it must also be very rare. The type locality is described by the authors of the species as " … hot subtropical, very wet forests on palms at elevations around 150 meters …. hot growing epiphyte …" The known populations in Mexico occur in medium-height riparian forests and in evergreen tropical forests at 1200–1400 m (Soto-Arenas & Solano, 2007; personal observations). These forests are mostly inaccessible and still fairly well preserved but slash-and burn agriculture and extensive cattle ranching are making inroads in the area. The fact that the species is known from such widely diverging ecological settings suggests that *G. sobralioides* may eventually be found under conditions intermediate between those of the Mexican and Guatemalan populations and has a broader ecological and geographical range. The species has obvious horticultural appeal with its relatively large, showy flowers and if these populations become accessible to "materos," (commercial plant collectors), they are likely to be severely striped from nature.

Galeandra sobralioides is closely related to *Galeandra batemanii* and *G. greenwoodiana* (see distribution of these two species above, under *G. batemanii*). *Galeandra sobralioides* is known only from a few plants collected in the general area of Los Chimalapas, in eastern Oaxaca, in Pacific slopes, where it has been found at altitudes above 1000 m, reaching sometimes 1300 m. The type from Guatemala was collected at a much lower elevation (100 m).

Galeandra batemanii, *G. greenwoodiana*, and *G. sobralioides* share a distinctive vegetative character, ovoid to piriform, relatively heavy pseudobulbs (Warford, 1994, personal observation of the authors, but see Table 1 and discussion below). Furthermore, the leaf sheaths are green when young but later are allegedly speckled with dark red, particularly along the edges and the articulation (as reported in the protologue), a character they share with some South American species (e.g., *G. macroplectra* G. A. Romero & Warford), and with *G. arundinis*. According to Warford (1994), however, "*G. greenwoodiana*… is … generally more robust [than *G. batemanii*] when living plants of the same age are compared, growing to as much as 72 cm versus about half that for *G. batemanii*" (see table 1 herein). One of the authors (GC) cultivated a plant of *Galeandra sobralioides* for five years and this species is apparently even smaller than *G. batemanii*.

Galeandra sobralioides (Fig. 19–20) is most easily distinguished *in vivo* from its closest relatives by its solid dark purple, highly flared, deflexed apex of the labellum (sometimes with faint white stripes, with a narrow white band along the margin; the labellum is only slightly deflexed in *G. batemanii* and *G. greenwoodiana*). Furthermore, it also differs from *G. greenwoodiana*, which also grows in the Pacific slopes of Oaxaca, but further north and apparently at lower elevations, on the western side of the isthmus of Tehuantepec, in the almost symmetrical lobes of the labellum (versus highly asymmetrical in *G. greenwoodiana*) and the gently upturn or straight spur (versus deflexed or hooked in *G. greenwoodiana*). In the herbarium, the relative size of the lobes of the labellum and the spur should be discernible in dry flowers and should easily distinguish *G. sobralioides* from *G. greenwoodiana*; likewise, in re-hydrated and carefully dissected flowers, the two low, inner lamellas, not thickened at the apex and not surpassing the outer keels, and the relatively longer labellum, the shorter sepals and petals, and the slightly falcate lateral sepals should distinguish *G. sobralioides* from *G. batemanii* (compare Fig. 11 and 18 versus 19).

Discussion

The general shape of flowers in *Galeandra* is relatively uniform, with little variation within the clades and subclades recovered by Monteiro et al. (2010). In fact, flower shape is so well conserved within subclades that many closely related species cannot be distinguished without having precise localities, descriptions (including fragrance: see discussion below), color photographs, and carefully done dissections and drawings. Pseudobulb shape is also highly conserved within clades, and, in the one that includes all the epiphytic galeandras, we find two general shapes: narrowly fusiform, cane-like in the South American clade, that presumably includes *G. arundinis*, and enlarged at the base, somewhat piriform (Lindley, 1840b; Bateman, 1840; Paxton, 1848; Warford 1994), ovoid to almost spherical (Warner et al., 1887; Linden, 1901) in the Mexican subclade. The fusiform, cane-like shape is considered the ancestral state, as observed in *Galeandra devoniana*, sister species to all other galeandras (Monteiro et al., 2010).

Williams (1939: 248) questioned, somewhat ambiguously, whether pseudobulb shape (fusiform, cane-line versus enlarged at the base, piriform to ovoid) was a constant, conserved character:

"Rolfe distinguished *G. batemanii* as having 'a short ovoid pseudobulb, and a dull purple lip' and *G. baueri* as having 'a slender fusiform pseudobulb, and a pale-coloured-lip.' Most of the Mexican and British Honduran material examined has slender pseudobulbs, but the shape seems to depend on age, the younger ones being slender, the older ones thicker" (Williams 1939: 284).

It is unclear whether this author had examined material

of the Mexican galeandras: in 1939 he was curator of the Oakes Ames Orchid Herbarium where, at this moment, there are only recently accessioned specimens of this group,[10] or what meant when he said "… the younger ones being slender, the older ones thicker", which is the case in *Galeandra arundinis*: young pseudobulbs, in fact, are *in vivo* generally slender, older ones, can be narrowly fusiform. As for "slender" versus "thicker", the following authors appear to have interpreted them as "narrowly fusiform, cane-like" versus "enlarged at the base, piriform".

Edward W. Greenwood (January 1973, unpublished notes at AMES) wrote "Although I have seen in the field only the Nayarit plant (*G. batemanii*), the sample was sufficiently large to make Williams' suggestion that very young pseudobulbs are slender, older ones are thick, seems most unlikely. Even the very small pseudobulbs at that location were heavy". Pollard (1974: 170) soon followed with the following most perplexing statements: "In 1964, my friend Walter Miller sent me live plants which his men in [San Juan] Juquila Mixes [ca. 16°53'N 95°53'W, 1480 m], Oaxaca, had collected north and east of the village, I later flowered these plants for several years. There were several pseudobulbs on each of the two plants and in no case was there any indication of age producing swelling at the base of the although the back bulbs were of age. All were slender, irrespective of age. These plants I would consider to be *G. baueri* even though 1000 miles from the type locality. During the past year, I have received two more plants from the same area, they also have slender pseudobulbs without any sign of swelling at the base. These plants should bloom in July as they are now in bud." The plants from Nayarit mentioned by Greenwood would eventually be described as *G. greenwoodiana*.

Although Pollard did not give much detail about the plants from the vicinity of San Juan Juquila Mixes and did not give a precise account of the color photographs with which he illustrated his article, Greenwood (July 1977, unpublished notes, AMES) later met with Walter Miller and found out that the plants had been found on pines and rocks. A flower of these gatherings, flattened on paper, is preserved at AMO: the floral segments are described as "sepals and petals yellowish-brown, green on tips, lip purple at front, grading to yellow to brown, column pale green, purple at apex tip." Warford (1994: 49) referred the plants from San Juan Juquila Mixes to *G. batemanii*. Warford drew another flower from San Juan Juquila Mixes, probably from another card sent to her by E. W. Greenwood: her drawing lacks the details of her other work, due to their loss due to the preservation method (floral segments attached to paper using non-archival transparent tape, which yellowed with age and hides the minute detail of flowers preserved in spirits or rehydrated from herbarium material).

Relevant to the topic, Warford (1991, unpublished notes, AMES) wrote "Although *Suarez 1122*, the plant [of *G. batemanii*] sent to Warford in 1989, had produced ovoid pseudobulbs in its habitat [Choapam, Oaxaca], the plant produced a fusiform pseudobulb while in cultivation at sea level in Puerto Vallarta [Jalisco]; a most confounding development, but undoubtedly brought by unnatural cultural conditions. The development must be mentioned as it may be an ancestral, latent manifestation".

Two of the authors (CMB and MAG) collected galeandras in the state of Tabasco, growing on *Acoelorrhaphe wrightii*, that included plants bearing pseudobulbs from piriform to fusiform, cane-like pseudobulbs, bearing flowers typical of *G. arundinis* (labellum apex light rose to light purple, spur bent upwards) or *G. batemanii* (larger flowers, labellum apex dark burgundy, spur bent downwards).

It should be emphasized that plants of *Galeandra arundinis* do not "universally" bear fusiform, cane-like pseudobulbs. Infrequently, one can find pseudobulbs slightly enlarged toward the base, as in *Heller 1106* (SEL), from Nicaragua, the oldest pseudobulb of which apparently was somewhat piriform, the two most recent ones definitely fusiform (Hammer, 1983, 1988), and *O'Neill 8347* (NY), from Belize, which also shows a pseudobulb somewhat enlarged toward the base (see appendix for link to this specimen); however, the specimen from the same gathering at AMES shows fusiform pseudobulbs, as all other specimens from Belize to Panama cited above under *G. arundinis*. A photograph of a plant from Honduras, Puerto Lempira (see link in Appendix 1), no doubt representing *G. arunidinis*, also shows a basally thickened pseudobulb.

Here are two cases of plants that apparently bear *Galeandra arundinis* pseudobulbs but produce *G. batemanii* flowers (the plants from San Juan Juquila Mixes) or *G. batemanii* pseudobulbs that bear *G. arundinis* flowers (the ones from Tabasco), and isolated cases of plants of *G. arundinis*, throughout its range, bearing roundish pseudobulbs.

These discrepancies in pseudobulb shape in *G. arundinis* and *G. batemanii* may be due to any of the following factors, or a combination thereof: 1) that pseudobulb shape is a plastic, not genetically fixed character, and different shapes are triggered by environmental variables, both in nature and in cultivation; or 2) genetic introgression.

The first hypothesis is not supported by the evidence observed in herbarium specimens. "Nature is not perfect," someone must have said. Natural variation is expected, but the overall pattern is clear: *Galeandra arundinis*, as it names implies, tends to have cane-like pseudobulbs, deviating occasionally. However, the pyriform pseudobulbs of the *G. arundinis* population in Tabasco could support the second hypothesis, which should be investigated.

Vegetative, Reproductive, and Ecological Characters in Galeandra

Size of mature, flowering pseudobulbs.

They can vary a great deal. Those of *Galeandra devoniana* can vary from 20 cm to close to two m in height ("… five to six feet high...": R. H. Schomburgk in Lindley, 1840a). Thus, plant height, although does not vary in most species as dramatically as in *G. devoniana*, is not a diagnostic character in this genus.

[10] In fact, other than the recent accessions in AMES, no herbarium in the United States appears to have specimens of species of the Mexican clade, except for *Liebmann 6943* (US, cited above), perhaps a testimony of the rarity of these species in nature (and of the reluctacy from orchid growers to press them.)

Leaf number, size, shape, and color.

Leaf number, length, and width varies a great deal throughout the genus, being relatively numerous, short, and narrow in *G. devoniana,* supposedly the ancestral characters and, in narrowness, shared with the terrestrial species and the South American subclade (based on Monteiro et al. 2010, and the authors' personal observations). although leaf width and average length appears to be closely associated with the age of the plant, and therefore with its reproductive status, the Mexican galeandras, including *G. arundinis*, differ in leaf width and leaf color: both *G. arundinis* and *G. greenwoodiana* have relatively wider leaves, matte green in color, whereas *G. batemanii* and *G. sobralioides* have narrower leaves, dark green with a silken sheen (see key below).

Flower size and color.

Flower size remains more or less constant *in vivo* when comparing what mature, well-grown plants bear, with minimal variation, although depauperate plants in cultivation may produce noticeably smaller flowers. Also, the same inflorescence may carry flowers of different sizes, depending upon de age of the inflorescence, whence the last, most distal flowers tend to be somewhat smaller than earlier, more proximal flowers. In herbarium material, the actual state of the fresh material (flowers not at full anthesis, at full anthesis, or wilting), how it is pressed and dried, and later, how it is hydrated, can affect the size of the flowers considerably.

Flower color can vary somewhat within a species and even in the same plant in the same flowering season or between years (Fig. 9). Nonetheless, overall, over several flowering seasons, it is generally a diagnostic character. Warford (1999: 133; see figure 7 versus 16 therein) reported plants of *Galeandra greenwoodiana* with yellowish flowers, which she attributed to "... age or environmental stress;" the same plant later produced flowers with the expected light burgundy labellum. Two of the authors (GAR-G and GC) also have observed yellowish flowers in *G. macroplectra*, whitish-cream to yellowish green at anthesis, no doubt attributable to age (Romero and Warford, 1995). See Warford (1994: 46) for discussion of trichomes and flower color. Readers are cautioned to carefully consider the color of flowers presented on Internet, as deviations from the "original" colors, for multiple reasons (including monitor settings), are common.

Carinae (keels) versus lamellae.

Keels have a corneous, waxy texture, are inornate, in cross section subtriangular, arquate, marginally acute, in some cases (e.g., *G. blattiodora* G.A. Romero & C. Gómez), apically with a serrate tooth, and are readily discernable in live, alcohol-preserved, and pressed and dried herbarium material. Their number, two in the Mexican species treated here, is fairly constant in most species. In contrast, lamellae are thickenings found along and between the central nerves, often covered and surrounded by trichomes; they are discernable in some species *in vivo*, but may or not persist in re-hydrated, herbarium material. Their presence on the labellum can vary a great deal, from being absent at all to thickenings along and in between the central nerves. However, when comparing fresh flower to flowers kept in spirits or hydrated flowers from herbarium material, it is difficult to assess this variation, which could be caused by the preservation method. We have found ambiguities in description published in protologues and floras: "… *Lip*… with two parallel ridges inside the tube" (McLeish et al., 1995: 63), yet the line drawing (McLeish et al., 1995: 64, Fig. 26) shows four "ridges"; according to Archila and Chiron (2012: 13), the labellum has "… dos protuberancias de la parte media hacia atrás", shown in Fig. 1 (Archila and Chiron 2012: 14), yet, the flower depicted on the color plate inserted between pages 18 and 19 shows two slight thickenings between the keels, also present in *Carnevali 8596* (Fig. 19A, same photograph, by G. Carnevali, at a greater resolution).

Flower fragrance and pollination.

This topic has been little studied in *Galeandra*. According to Dressler (1981: 254), "the pollinaria of *Galeandra* have been found on *Euglossa* and large anthophorid bees." Warford (1991, unpublished notes, AMES) reported the mid-morning fragrance of *G. batemanii* and *G. greenwoodiana* as "... faint floral in both species but with slightly different overtones; odour at night was acidic;" she added: "Neither species... was naturally pollinated in open air cultivation although their pollinaria were removed... on a number of occasions. The plants were watched so closely during the daylight hours that it was suspected that a night flyer was responsible..." Waldo and Roubik (1986: 427, Table 1 therein) reported several genera and species in Anthophoridae[11] from light traps on Barro Colorado Island, and Warford's suspected night flier may be in fact one of these bees, flying at dim-light or darkness (see also Wcislo and Tierney, 2009). Chase and Hills (1992: 44, Table 1), for *Galeandra*, reported both male and female euglossine bee pollinators. Romero and Warford (1995) reported male euglossine bees as pollinators of *G. macroplectra* (*Euglossa ignita* Smith, *E. imperialis* Cockerell, and *Eulaema moczaryi* (Friese)) and *G. magnicolumna* G.A. Romero & Warford (*Eulaema cingulata* (Fabricius), *E. meriana* (Olivier), and *E. nigrita* Lepeletier, in the latter case, both male and female bees). These two species of *Galeandra* have subtle, pleasant fragrances. A population that was at first referred to *G. macroplectra* was later described as *G. blattiodora* (Romero-González and Gómez, 2014). The latter became apparent only after the authors had plants with flowers, which had a distinct, repugnant fragrance; later, diagnoseable morphological characters were documented and the species was formally described (Romero-González and Gómez, 2014); what pollinates this species is unknown. Nonetheless, fragrance, as in other species groups of Catasetinae, may not be a reliable diagnostic character (e.g., all species in *Catasetum* section *Catasetum* have basically

[11] Readers should be aware of changes in the circumscription of this family.

the same fragrance, and attract the same pollinators: genetic isolation is attained *via* differences in phenology and/or geographic isolation).

Variation in the orientation and size of the spur.

Little has been discussed about this character. We have seen abundant collections as well as images of *G. arundinis* from across its broad geographical distribution and are aware of the great deal of variation of this character found within the species. It is rarely completely straight. Usually, it is slightly and gradually upcurved at an angle of ca. 20–30˚ relative to the main body of the labellum, often with the narrowest portion of the apex taking a sharper upcurve or even, bending downwards. In flowers from some plants (e.g., *Carnevali & Moreno 7492*, from Honduras), the whole labellum gradually but sharply bends at a 45–55˚ angle whereas a specimen from Tabasco (photograph by M.A. González) has the labellum sharply upturned until the tip of the spur is facing forward. Nonetheless, we have been unable to detect any pattern to this variation, and it seems to vary even within populations of the species. Warford (1994) described the spur of *Galeandra greenwoodiana* as "typically hooked, occasionally not" and the one of *G. batemanii* as "typically gently curved upward, rarely straight or hooked." Romero and Warford (1995) reported that, in both *Galeandra macroplectra* and *G. magnicolumna*, "the relative size of the spur may vary... from at least twice to more than twice as long as the lamina."

Symmetry of the labellum lobes.

Few *Galeandra* flowers have perfectly symmetrical lobes, especially in the Mexican species: one of the apical lobes is, to some degree, slightly (*G. batemanii* and *G. sobralioides*) to conspicuously longer than the other (*G. greenwoodiana*).

Presence absence of an apiculus.

"An apiculus between the apical lobes may be produced but may be absent during drier periods; it does not seem that, in *Galeandra*, the presence or absence of an apiculus is a dependable taxonomic character" (Warford, 1994: 44). Likewise, the superposition of the sepals and petals can vary a great deal within a population or even between the flowers in the same inflorescence and it does not appear to be a reliable diagnostic character.

Hosts.

Some species show clear host preferences (e.g., *G. devoniana* for palm trees, including *Leopoldinia* spp. and *Mauritia aculeata* H.B.K. according to H. R. Schomburgk in Lindley, 1840a; personal observation, GAR-G). *Galeandra arundinis* has been found growing on *Acoelorrhaphe wrightii* in Belize and other portions of its geographical range, and *G. batemanii*, in Oaxaca, found on pine trees or occasionally as a lithophyte, whereas *G. greenwoodiana* has been found on the palms *Sabal rosei* Bacc. and *Cryosophila nana* (Kunth) Blume. Both *G. batemanii* and *G. sobralioides* have also been collected growing on live or dead pine trunks; *G. batemanii* has even beem found growing on the litter of gently sloped *Pinus*-savanna. However, most *Galeandra* species seem to be, as in other genera of Catasetinae, largely opportunistic as far as hosts are concerned.

The following key should assist in the identification of the four known Mexican galeandras.

Key to the species of Galeandra found in Mexico

1a. Pseudobulbs cane-like, narrow to widely fusiform to cylindrical; labellum, in Mexican plants, light pinkish-red at the apex, plants from the lowlands on the Atlantic slopes in Tabasco, expected in Quintana Roo, Chiapas, and Campeche. . . . . *G. arundinis*

1b. Pseudobulbs ovoid to pyriform, noticeably enlarged toward the base; labellum apex from light to dark burgundy; plants from Tabasco, Chiapas, Oaxaca on the Atlantic and Pacific slopes 2

2a. Leaves, *in vivo*, medium matte green; labellum apex light burgundy, labellum lobes usually distinctly asymmetrical, one being conspicuously longer than the other, not rounded at the apex; spur generally deflexed or hooked, rarely straight; plants from the Pacific slopes of the Sierra Madre del Sur . . . . . *G. greenwoodiana*

2b. Leaves, *in vivo*, dark green with a silken sheen; labellum apex dark burgundy, labellum lobes rounded, symmetrical to only slightly asymmetrical; spur gently upturned or straight, rarely deflexed (but see discussion on orientation of spur above); plants from the Atlantic slopes of Tabasco or the both the Atlantic and Pacific slopes of Oaxaca 3

3a. Apex of the labellum slightly or no deflexed at all, *in vivo*, inner lamellae thickened at the apex and surpassing the outer keels; plants from the Atlantic slopes . . . . . *G. batemanii*

3b. Apex of the labellum strongly deflexed; *in vivo*, inner lamellae not thickened at the apex and never surpassing the outer keels; plants from Pacific slopes . . . . . *G. sobralioides*

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Appendix

Specimens cited but not listed in the text

Galeandra arundinis G.A. Romero & Garay
Puerto Lempira, Honduras, photograph by Delmer Jonathan (as *G. baueri*):
https://www.inaturalist.org/observations/40657788

Belize, *O'Neill 8347*
AMES:
https://s3.amazonaws.com/huhspecimenimages/JPG/02389153.jpg

MICH:
https://www.gbif.org/tools/zoom/simple.html?src=//api.gbif.org/v1/image/unsafe/https%3A%2F%2Fquod.lib.umich.edu%2Fcgi%2Fi%2Fimage%2Fapi%2Fimage%2Fherb00ic%3A1650585%3AMICH-V-1650585%2Ffull%2Fres%3A0%2F0%2Fnative.jpg

NY:
http://sweetgum.nybg.org/science/vh/specimen-details/?irn=4406086

Galeandra batemanii Rolfe
Chiapas, photograph by Diego Manzano:
https://www.inaturalist.org/observations/9265903

Galeandra dives Rchb.f. & Warsz. COLOMBIA ["N^{lle} Grenade"]: S^{ta} Martha…, Minca, 1000 m, "fl. pétales & sépales jaune & pourpre, labelle jaune avec une grande macule pourpre", July 1853, *L. Schlim 994* (K000364037).

This specimen was identified, by R. A. Rolfe, as "No doubt *G. dives* Rchb. f. et Warscew."

Although this species is often cited under the sole authorship of Reichenbach f., this author clearly stated, in his introduction to *Orchideae Warscewiczianae recientores* (Reichenbach f., 1854: 96) "Wir schätzen uns glücklich, hier die Beschreibung einer Anzahl der von unserm Freunde, Herrn J. v. Warscewicz entdeckten Arten unter unserer gemeinschaftlichen Autorität…"; "We are happy to present here the description of a number of species discovered by our friend, Mr. J. v. Warscewicz, under our collective authority."

Galeandra dives Rchb.f. & Warsz. at W:
https://www.gbif.org/occurrence/1230761845

The first page of Bateman (1867) is also shown on this image.

Galeandra greenwoodiana Warford, Lindleyana 9, No.1: 39. 1994. TYPE. MEXICO. Nayarit: near the Pacific coast, epiphytic on Sabal rosei Bacc. palm, 300 m, 24 June 1989, N. Warford & J. C. Amezcua 543 (Holotype: AMO; Isotype: AMES). Oaxaca: near Candelaria [Loxicha], on thorny dwarf palm, 300 m, flowers have somewhat darker pigmentation of the labellum apex (darker dull burgundy but show the distinctive labellum apex of this species: one of the lobes longer; slit-bilobate), 28 January 1993, *O. Suárez, E. W. Greenwwood & N. Warford 1644A* (AMES, AMO); same locality and information, *O. Suárez, E. W. Greenwwood & N. Warford 1644B* (AMES).