

NOTES ON THE CARIBBEAN, MEXICAN, AND CENTRAL AND SOUTH AMERICAN *CARDAMINE* (CARDAMINEAE, BRASSICACEAE)

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Abstract. The present study deals with the native *Cardamine* species of the New World south of the United States, because previous studies failed to clarify their distribution, delimitation, and endemism. The status of 12 species (*C. carrii*, *C. cebollana*, *C. chilensis*, *C. hispidula*, *C. killipii*, *C. marginata*, *C. nana*, *C. obliqua*, *C. pacensis*, *C. pygmaea*, *C. speciosa*, and *C. subterranea*) is discussed. The new name *C. hintonii* and the new combination *Rorippa pygmaea* are proposed. Three species (*C. aschersoniana*, *C. nana*, and *C. obliqua*) are lectotypified, and *C. carrii*, *C. cebollana*, *C. chilensis*, and *Rorippa austroamericana* are reduced to synonymy of *C. macrocarpa*, *C. longipedicellata*, *C. africana*, and *R. pygmaea*, respectively. Mexico has eleven native species (three endemic), Central America has eight (three endemic), and the Caribbean Islands have three (two endemic). A key to the South American species and another to the Mexican, Central American, and Caribbean species are presented.

Keywords: Brassicaceae, *Cardamine*, Caribbean Islands, Central America, Cruciferae, Mexico, South America.

Cardamine L., the second largest genus in the Brassicaceae (Cruciferae) with about 280 species (Šlenker et al., 2021; Marhold et al., 2022) and updated here to 284, is represented by native species on all continents except mainland Antarctica. It includes a number of weedy species, including *C. africana* L., *C. flexuosa* With., *C. hirsuta* L., *C. impatiens* L., *C. occulta* Hornem., and *C. parviflora* L.

In order to determine the number of native species per continent or region, we checked all *Cardamine* names, regardless of their rank, in worldwide databases, including CardaBase (<https://cardamine.sav.sk>), BrassiBase (<https://brassibase.cos.uni-heidelberg.de>), and IPNI (International Plant Name Index: <https://ipni.org>). Our compilation indicates that Africa has the fewest native species (six, or perhaps seven), of which four are endemic, whereas Australia has 13 native species (11 endemic), and New

Zealand has 42 spp., all of which, except a pair that also grows in Australia, are endemic (Heenan, 2017; Heenan and de Lange, 2018). The majority of species, herein compiled, are Eurasian (153), of which 61 (39.8%) are native to Europe and 54 (ca. 28.3%) to China (32 endemic). North America north of Mexico has 37 native species, all of which grow in the United States (14 endemic), Canada (20), and three in Greenland (Al-Shehbaz et al., 2010).

The present study deals with the New World *Cardamine* species from the US-Mexico border southward through the southernmost tip of Patagonia in South America, an area covering a distance of over 9200 air miles (ca. 14,806 km). It aims to resolve the status of several controversial binomials that have been either recognized as distinct species or overlooked in some or all the databases listed above.

SOUTH AMERICAN SPECIES

The native South American species of *Cardamine*, estimated by Al-Shehbaz & Marhold (2023) to be 23 species, are updated to 24 by the recognition of Venezuelan *C. aschersoniana* O.E. Schulz. *Cardamine albertii* O.E. Schulz is not recognized here and has been treated by Al-Shehbaz (2024) as only a trivial variant of the widespread *C. ovata* Benth. The country distribution of all species is presented in Table 1. Chile has 15 species, of which five are endemic, and *C. bonariensis* Pers. is the only species that grows in all countries excluding French Guyana, Guyana, and Suriname that have no native species. This species is by far the most variable in the New World, especially in habit, leaf morphology, and the bracteate part of the raceme.

Although the following species names are based on South American plants, they were recognized, synonymized, overlooked, or remained in obscurity for more than a century (see the three databases above).

1. *Cardamine aschersoniana* O.E. Schulz, Bot. Jahrb. Syst. 32 : 410. 1903. TYPE: VENEZUELA. Tovar, May 1836, J. W. K. Moritz 369 (Lectotype, here designated; B [0-0386988]).

Schulz (1903) cited four syntypes under *Cardamine aschersoniana*. Fendler 23 β (GH) was cited under this species, whereas Fendler 23 was cited as the single type collection of *C. fulcrata* var. *scabra* O.E. Schulz. However, plants of both collections are indistinguishable, and they

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TABLE 1. Country distribution of the native South American species of *Cardamine*. An asterisk (*) indicates presence, and E means endemic to that country. Country abbreviations are: ARG: Argentina; BOL: Bolivia; BRA: Brazil; CHL: Chile; COL: Colombia; ECU: Ecuador; PRY: Paraguay; PER: Peru; URY: Uruguay; and VEN: Venezuela.

SPECIES	ARG	BOL	BRA	CHL	COL	ECU	PRY	PER	URY	VEN
<i>C. armoracioides</i> Turcz.					*					*
<i>C. aschersoniana</i> O.E.Schulz										E
<i>C. bonariensis</i> Pers.	*	*	*	*	*	*	*	*	*	*
<i>C. chenopodiifolia</i> Pers.	*	*	*	*			*		*	
<i>C. cordata</i> Barnéoud	*			*						
<i>C. fulcrata</i> Greene					*					*
<i>C. geraniifolia</i> (Poir.) DC.	*			*						
<i>C. glacialis</i> (G.Forst.) DC.	*			*						
<i>C. hispidula</i> Phil.				E						
<i>C. jamesonii</i> Hook.					*	*				*
<i>C. kruesselii</i> Johow				E						
<i>C. lojanensis</i> Al-Shehbaz						E				
<i>C. marginata</i> Phil.				E						
<i>C. nana</i> Barnéoud	*			*						
<i>C. ovata</i> Benth.		*			*	*		*		*
<i>C. peruviana</i> Al-Shehbaz & Marhold								E		
<i>C. picta</i> Hook.					*	*				
<i>C. rostrata</i> Griseb.				E						
<i>C. speciosa</i> Britton		E								
<i>C. tenuirostris</i> Hook. & Arn.	*			*						
<i>C. tuberosa</i> DC.				E						
<i>C. variabilis</i> Phil.	*			*						
<i>C. volkmannii</i> Phil.	*			*						
<i>C. vulgaris</i> Phil.	*			*						

are clearly synonyms of *C. fulcrata* Greene. *Cardamine aschersoniana* is easily distinguished from the latter by having long-acuminate (vs. acute) leaflets.

2. *Cardamine chilensis* DC., Syst. Nat. 2: 254. 1821. TYPE: CHILE. "Dubia tetradyname siliquosa. Ruiz et Pavón! in Lamb." (Holotype: BM [000583653]).

The examination of the holotype of *Cardamine chilensis* was quite a surprise because it is indistinguishable from, and herein synonymized with, the earlier-published *C. africana*. Unless the type locality of the former was from a different country, Candolle (1821) is the only record to date of *C.*

africana from Chile. We have examined collections of the latter from Argentina, Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela, but none from Chile. Therefore, all other reports of *C. chilensis* from Argentina and Chile in the past two centuries represent a different species recognized below as *C. nana*.

3. *Cardamine hispidula* Phil., Anales Univ. Chile 81: 79. 1892; *Cardamine alsophila* var. *hispidula* (Phil.) Reiche, Anales Univ. Chile 90: 99. 1895. TYPE: CHILE. [Region XVI] Andes of Prov. Ñuble, October 1878, *F. Puga s.n.* (Holotype, not seen).

Schulz (1903) justifiably recognized *Cardamine hispidula* (pp. 452, 453) and examined and indicated that its type is housed at the Museo Nacional in Santiago Chile (cited as H.Ch., presently SGO). However, a search for its type by one of us (IAS) and the curatorial staff of SGO, where the herbarium of Rodolfo Amando Philippi (1804–1904) is housed, did not yield any results (see Al-Shehbaz et al., 2011), and we assume that it is lost.

Except for the following description, hardly anything else is known about *Cardamine hispidula*, a well-defined species easily distinguished from the other South American species by the key below.

Herbs, perennial. *Rhizomes* globose-tuberous, stolon filiform, tuberous at apex. *Stems* 2–15 cm tall, erect, simple or branched at base, flexuous, slender, subangular, sparsely hirsute to glabrescent. *Rhizomal leaves* rosulate, 1.2–3.0 cm long, petiolate, 3-foliolate; terminal leaflet orbicular, base subcordate, obscurely crenate or 6-angled, long petiolulate, 3.5–8.0 × 2.5–8.0 mm; lateral leaflets ovate, entire, short petiolulate; cauline leaves 0.8–2.5 cm long, lower ones 3–5-foliolate; terminal leaflet ovate, strongly 1- or 2-crenate, short petiolulate, 2.5–8.0 × 1.5–6.0 mm; lateral leaflets similar but sessile; upper leaves short petiolate, 3-foliolate, leaflets 1-toothed; uppermost leaves subsessile, simple, lanceolate, entire or 1-toothed; hirsute to long ciliate. *Racemes* ebracteate, ca. 10-flowered, flowers small, ca. 3 mm long. Ovary 20–28 ovuled. Fruit ca. 1.8 cm × 0.7 mm.

4. *Cardamine killipii* O.E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 10: 341. 1928. TYPE: COLOMBIA. Santander, eastern Cordillera, edge of Páramo de las Vegas, 3300–3700 m, 20–21 December 1926, *E. P. Killip & A. C. Smith 15596* (Holotype: B [10-0386986]; Isotypes: F [009295F], GH[00312548], K [000485032], NY [00172742], PH [00000959], S-R [7296], US [00100037]).

With its simple, suborbicular to broadly ovate to subreniform, and entire cauline leaves, the casual observer would believe that *Cardamine killipii* is quite distinct from *C. bonariensis*, the type of which and most of its populations have pinnately compound cauline leaves. However, the latter is extremely variable in leaf morphology, number of lateral leaflets, bracteate portion of the raceme, and habit. The species is adapted to wet habitats (ponds, streams, seepage areas, bogs, moist slopes, wet bluffs, muddy banks, wet paramo, moist turf, gravel, wet grass fields, swales, marshes) and grows at elevations from sea level to 4500 m. Its distribution ranges from Patagonian Argentina and Chile into Central America and Mexico, and as many as 26 species and varieties were described from its entire range. The examination of hundreds of collections from all of the major herbaria of the world clearly demonstrates that all features appearing to be sufficiently distinct are in fact continuous, and it is not possible to maintain any of the variants. A comprehensive molecular phylogenetic study of this complex covering its entire range is much needed and, without that, it is advisable to recognize a single polymorphic species.

5. *Cardamine marginata* Phil., Anales Univ. Chile 27(2): 324. 1865; *C. vulgaris* var. *marginata* (Phil.) O.E. Schulz, Bot. Jahrb. Syst. 32: 545. 1903. TYPE: CHILE. Región VIII, near Chillán, *Manuel Antonio de Solis Obando s.n.* (Lectotype, designated by Al-Shehbaz et al. (2011: 281); SGO [63903]; Isolectotype: SGO [49376]).

Schulz (1903) reduced *Cardamine marginata* to a variety of *C. vulgaris* and examined a single specimen, *Delfin s.n.* (SGO), but this collection definitely belongs to the latter species. *Cardamine marginata* resembles the small-sized forms of *C. vulgaris* by having a tuberous stem base, attenuate styles, and fruit forming a distinct angle with the fruiting pedicels. However, the two species are quite different in flower, infructescence, fruit, and seed morphology. *Cardamine marginata* has smaller flowers (sepals 1.0–1.5 × 0.5–0.7 mm; petals 2.5–3.2 × 0.7–1.0 mm), a flexuous rachis of fruiting racemes, smaller and wider, linear-lanceolate fruit 1.0–1.5(–1.7) cm × 1.8–2.5 mm, fewer ovules (6–10) per ovary, and orbicular to broadly ovate seeds 2.0–2.5 × 1.2–1.5 mm that are winged all around. By contrast, *C. vulgaris* has larger flowers (sepals 2.5–3.5 × 1.0–1.5 mm; petals (5–)6–9 × 2.0–3.5 mm), a straight rachis of fruiting racemes, larger and narrower linear fruits 2.0–3.5(–4.0) cm × 1.0–1.5 mm, more ovules (20–34) per ovary, and ovate, wingless seeds 1.2–1.6 × 0.8–1.2 mm. Unfortunately, *C. marginata* is known thus far only from the type collection and those cited below.

Additional specimens examined: CHILE. Región VII. Ñuble, 2 km E of Chillán on road to El Carmen, 36°37'S, 72°5'W, *Bliss 512* (CONC), *Keeley et al. 25824* (CONC). Región VIII. Bío Bío, Antuco, *Barros 2790* (SI). Región IX. Araucanía, Malleco, Mininco, [37°47'S, 72°28'W], *Montero 5254* (CONC, SI), *Montero 9416* (CONC).

6. *Cardamine nana* Barnéoud in Gay, Fl. Chil. 1: 108. 1846; *C. chilensis* var. *nana* (Barnéoud) O.E. Schulz, Bot. Jahrb. Syst. 32: 445. 1903. TYPE: CHILE. [Región XIV. Los Ríos] Valdivia, 1839, *C. Gay s.n.* (Lectotype, here designated; P [00747619]; Isolectotype: P [00747620]).

Schulz (1903), who reduced the species to a variety of *Cardamine chilensis*, was followed by subsequent authors (e.g., Boelcke & Romanczuk, 1984; Al-Shehbaz & Salariato, 2012), but none examined the types of both species. That confusion persisted to the present, and our examination of both types reveals that the type of *C. chilensis* is indistinguishable from plants of *C. africana* (see above). *Cardamine nana* differs substantially from *C. africana* (including *C. chilensis*) by having simple (vs. trifoliolate) cauline leaves, bracteate (vs. ebracteate) racemes with a flexuous (vs. straight) rachis, and a tuberous (vs. non-tuberous) stem base.

A full description of *Cardamine nana* and citation of Chilean plants are provided herein, but for a complete synonymy and cited Argentinean specimens, the reader should consult Al-Shehbaz & Salariato (2012).

Labels of the type collection of *Cardamine nana* were annotated by Barnéoud, and that of the designated lectotype has Valdivia, the type locality cited in the original publication.

Herbs, perennial, often with a thickened, tuber-like stem base, sometimes rooting from the lower nodes, glabrous or with trichomes 0.1–0.2 mm long. Stems (2–)4–30 cm tall, erect, simple or several from the base, simple or branched above, glabrous or pubescent near the base. *Basal leaves* not rosulate, simple or rarely with 1 or 2 lateral leaflets; *cauline leaves* (0.8–)1.4–4.0(–5.5) cm long, petiolate, not auriculate; petiole (0.4–)0.8–3.0(–3.5) cm long; blade (2–)7–15(–25) × (1–)3–8(–12) mm, oblanceolate to spatulate or obovate to ovate, glabrous or sparsely pubescent, usually minutely ciliate, cuneate to attenuate at the base, entire or repand, rounded to obtuse at the apex. *Racemes* several flowered, bracteate throughout or at least along the proximal half; rachis slightly to strongly flexuous, glabrous; fruiting pedicels (2–)4–10(–17) mm long, ascending, slender, straight. *Sepals* oblong, 1.2–1.5(–2.0) mm long, glabrous, caducous; *petals* white, oblanceolate, 2.5–3.5(–4.0) × 0.7–1.0(–1.5) mm, apex obtuse; filaments 1–2 mm long; anthers ovate, 0.1–0.2 mm long; ovules (16–)20–30 per ovary. *Fruit* 0.7–1.5(–2.0) cm × 0.7–0.8(–1.0) mm; style 0.1–0.5(–1.0) mm long. *Seeds* light brown, oblong to ovate, 0.7–0.9 × 0.5–0.6 mm, usually with a distal wing ca. 0.1 mm wide.

The species grows in seepy sites, streamsides, pond margins, sloughs in dry sandy matorral at sea level to 1000 m. It is distributed in Argentina (Chubut, Nuequén, Río Negro, Salta) and Chile (Región V, Santiago, VI, VII, VIII, IX, X).

Additional specimens examined: CHILE. Región V (Valparaíso): Catapilco, *Philippi* 67 (SGO); Las Láunas, *Jaffuel* 3005 (CONC, GH), *Jaffuel* 3114 (CONC, GH); Olmué, *Garaventa* 2024 (CONC, SI); Cerro de La Campana, 27 Sep. 1962, *Weisser* s.n. (CONC); Quilpué, *Zöllner* 4601 (BACP, SI); Marga, *Zöllner* 7103 (CONC, NA), *Jaffuel & Pirion* 3056 (GH); Limache, *Garaventa* 2230 (BACP, CONC, SI); Viña del Mar, 30 August 1932, *Behn* s.n. (CONC); Concón, *Pöppig* 171 (W); El Pangal, *Garaventa* 4090 (BAA, BACP, SI). Región VI (Santiago): Santiago: Batuco, *Garaventa* 2206 (BAA, CONC, SI); Caro, 0.6 km W of RR crossing in Alcones on road to Pichilemu, *Bliss* 547 (CONC); Mine La Leona, Oct. 1935, *Grandjot* s.n. (MO); Lolol, *Barros* 2797 (CONC, SI); Colchagua, Lolol, *Bliss* 754 (CONC); Rancagua, *Bertero* 145 (GH, P); Leona, *Bertero* 146 (G, MO, NY, P, W). Región VII (Maule): Talca, *Claude-Joseph* 4321 (US); SE Linares along Río Ancoa, along road to Melado and Medina, 38.2 km upstream to Peñasco, *Taylor & Gereau* 10997 (CONC, MO); Itahue, Fdo. “El Colorado,” *Garaventa* 4539 (BACP, CONC, SI); N Colbun, *Bliss* 670 (CONC); 10 km E Cauquenes on road to Parral, *Bliss* 538 (CONC). Región VIII (Bíobío): Ñuble, 5 km W San Nicholas, *Bliss* 850 (CONC); La Posada, *Barros* 2804 (CONC, SI); 2 km S Escuadrón on hwy 160, *Lammers, Baeza, & Peñailillo* 7490 (CONC, MO); Vegas de San Vicente, *Junge* 992 (CONC, SI). Región IX (Araucanía): Biobio, Cabrero, 5–8 km N Salto El Laja, *Bliss et al.* 2005 (CONC); Antuco, *Barros* 2803 (SI); Malleco, Mininco, *Montero* 5253 (CONC, SI); 5–6 km SE Minico

on road to Collipulli, *Bliss* 864 (CONC); Araucanía, Nov. 1887, *Philippi* s.n. (SGO); E Pucón, from the Río Turbio along road to Termas de Huife, *Taylor & Taylor* 10870 (MO). Región X (Los Lagos): Valdivia, *Hohenacker* 275 (G, P), *Buchtein* s.n. (US); Talcahuano, *Pöppig* 168 (P, W); Quinchilca, *Hollermayer* 870 (CONC, SI); Llanquihue, Peulla, *Pennell* 12669 (GH); San Miguel, *Barros* 798 (BACP).

7. *Cardamine pacensis* Díaz Rom., Bol. Direcc. Nac. Estad. Estud. Geogr., La Paz, Segunda Epoca iii. Nos. 25–27: 64. 1920. [as *C. pacense*]. TYPE: BOLIVIA. No collection data were given.

A search for any authentic material of this species did not yield anything, and according to the director of LPB, where such material is most likely to be found, there is no such material, and if it exists, it is either misfiled or lost. Although the species was compared to watercress, *Nasturtium officinale* W.T. Aiton, it was said to resemble *Cardamine andicola* Phil. However, Díaz Romero (1920) provided a detailed species description, all indications of which clearly indicate that the species belongs to a family quite unrelated to the Brassicaceae. Translation of the description from Spanish indicates that: the plants are aquatic with opposite submerged and emergent leaves, axillary aerial inflorescences, a bell-shaped and five-toothed (as quinquedentate), 5-angled calyx, 1–2 cm long intensely yellow flowers with 2 parallel series of small red spots in the throat, and with ovoid, bifurcate silicles. No Brassicaceae species has any of these features and, therefore, it is excluded here from the family. However, we are not in a position to suggest a family to which this species belongs.

8. *Cardamine pygmaea* Dusén

According to Stafleu & Cowan (1976: 712), Dusén’s herbarium is housed at S, and a search for it during an earlier visit by one of us (IAS), as well as a communication with the current director of botany, Mats Wedin, did not yield anything, and it may be misplaced or lost. The original publication included the illustration of two plants but without additional details of the other parts. However, the description and illustration of the fruit clearly exclude the species from *Cardamine*. Schulz (1903) did not examine any material of it, but he suspected (p. 595) that it belongs to *Nasturtium*, a genus he broadly circumscribed to include *Rorippa* Scop. The only diminutive Patagonian species of *Rorippa* that perfectly matches *C. pygmaea* is *R. austroamericana* (see below). Plants of this species can be as minute as 1.5 cm long, with pinnatisect basal and cauline leaves as short as 1.5 cm and with as few as three lateral lobes. These features, as well as the white flowers and oblong fruits, confirm the generic and species assignments. It is the southernmost Patagonian *Rorippa* that also grows elsewhere in Argentina, Chile, and Peru along irrigation canals and edges of ponds at elevations of 2000–4270 m (Al-Shehbaz & Salariato, 2012). Therefore, the following new combination is needed.

Rorippa pygmaea (Dusén) Al-Shehbaz & Marhold, *comb. nov.*

Basionym: *Cardamine pygmaea* Dusén, *Wiss. Ergebn. Schwed. Exped. Magellansl. 1895–1897*, 3(5): 175, pl. 8. 1900.

TYPE: CHILE. [Región de Magallanes y de la Antártica Chilena], Rfo San Martín, *Dusén s.n.* (S, not located).

Rorippa austroamericana Mart.-Laborde, *Parodiana* 2: 73. 1983, *syn. nov.* TYPE: CHILE. [Región V: Vaparaíso.] Los Andes, Potrero Escondido, ca. 3500 m, 22 February 1947, *O. Boelcke 2444* (Holotype: BAA).

9. *Cardamine speciosa* Britton, *Bull. Torrey Bot. Club* 16: 16. 1889; *C. jamesonii* var. *speciosa* (Britton) O.E. Schulz, *Bot. Jahrb. Syst.* 32: 422. 1903. TYPE: BOLIVIA. La Paz, Undavi, 1885, 10,000 ft [3048 m], *H. H. Rusby 1199* (Holotype: NY [00172744]; Isotypes: NY [00172745], US [09919955]).

Schulz (1903) reduced *Cardamine speciosa* to a variety of *C. jamesonii*, but the two are quite distinct morphologically. They are also disjunct by some 1840 air km from the range of the former in Undavi (Bolivia) to that of the latter in the southernmost part of Loja Province (Ecuador). *Cardamine speciosa* can easily be separated from *C. jamesonii* by having ebracteate (vs. bracteate) racemes, entire or repand (vs. crenate, incised-crenate, or serrate leaflets), petiolulate (vs. sessile) lateral leaflets, and leaflets of cauline leaves drastically narrower and smaller (vs. about the same shape and size) as the lowermost leaves.

Cardamine speciosa is very rare, under collected, and known thus far only from the type gathering and the following two collections.

Additional specimens examined: BOLIVIA. La Paz: Undavi, North Yungas, 3300 m, November 1910, *Buchtien 126* (E, F, G, GH, NY), *Buchtien 585* (NY).

10. *Cardamine subterranea* Larrañaga, *Escritos Damaso Antonio Larranaga* 2: 205. 1923. Type indication and diagnosis: “floribus hermaphroditis, terminalibus siliquosis, foemineis siliculososis, subterraneis. Folia simplicibus. Julio 5 de 1809.” TYPE: Not located.

The above brief diagnosis is everything known to date about the species. It is absolutely clear that the above name is a synonym of *Cardamine chenopodiifolia* Pers., a species distributed in Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay. It is most unique in the entire Brassicaceae for having two fruit types: aerial, dehiscent, 12–20-seeded, linear siliques 1.7–4.0 cm long and with seeds 1.8–2.3 mm long, as well as hypogeal (geocarpic), indehiscent, 1–4-seeded, obovoid to fusiform silicles 0.5–1.0 cm long and with seeds 2.5–3.5 mm long (Al-Shehbaz & Salariato, 2012).

In addition to *Cardamine chenopodiifolia*, geocarpic fruits evolved independently in five other tribes of the Brassicaceae. These include the Aphragmeae in one of 13 species of *Aphragmus* Andr. ex DC., Euclidieae in the Himalayan monospecific *Pyconoplinthopsis* Jafri, Eutremeae in two of 44 species of *Eutrema* R. Br., Microlepidieae in monospecific Australian *Geococcus* J. Drumm. ex Harv, and Brassiceae in monospecific *Morisia* J. Gay (Corsica, Sardinia), and both species of Algerian-Moroccan *Raffenaldia* Godr. Unlike *C. chenopodiifolia*, geocarpic plants in these five tribes do not produce fruits on aerial racemes.

KEY TO THE NATIVE SOUTH AMERICAN SPECIES

The Argentinean species of *Cardamine* can be identified in Al-Shehbaz & Salariato (2012), but no updated key is available for the native species of the entire continent. Three naturalized species (*C. africana*, *C. hirsuta*, *C. flexuosa*) are not as widespread in South America as they are in the Caribbean islands, Central America, and Mexico. They are included in the species key of these three areas, but not in the following.

- 1a. Plants annual; fruits heteromorphic, linear siliques on aerial racemes and ovate to oblong silicles on subterranean solitary pedicels *C. chenopodiifolia*
- 1b. Plants perennial; fruit only on aerial stems 2
- 2a. Racemes bracteate at least proximally 3
- 2b. Racemes ebracteate, rarely a basal flower bracteate 13
- 3a. Cauline leaves almost always simple, rarely lowermost minutely trifoliolate 4
- 3b. Cauline leaves compound 6
- 4a. Fruit 3.0–5.5 cm long; leaves lanceolate to ovate, serrate, long acuminate; Colombia, Venezuela *C. armoracioides*
- 4b. Fruit (0.7–)1.5–2.2(–2.8) cm long; leaves entire or repand 5
- 5a. Stem base not tuberous; fruit 1.0–1.5 mm wide; cauline leaves orbicular, broadly cordate to reniform, lowermost with a pair of small leaflets; petiole 1.5–2.5 cm long; Colombia, Ecuador *C. bonariensis*
- 5b. Stem base tuberous especially in older plants; fruit 0.7–0.8 mm wide; cauline leaves simple, oblanceolate; petiole <1 cm long; Argentina, Chile *C. nana*
- 6a. Cauline leaves trifoliolate 7
- 6b. Cauline leaves pinnately compound 8
- 7a. Leaflets long-acuminate to subcaudate *C. aschersoniana*
- 7b. Leaflets acute *C. fulcrata*
- 8a. Rhizomes fleshy, thickened, usually tuberous, scaly; basal and lowermost cauline leaves 13–23-foliolate *C. lojanensis*
- 8b. Rhizomes not fleshy, slender, not scaly; basal and lowermost cauline leaves (3–)5–11(–13)-foliolate, very rarely simple 9

KEY TO THE NATIVE SOUTH AMERICAN SPECIES CONT.

- 9a. Petals 2–4 mm long; fruit (0.7–)1.5–2.2(–2.8) cm long 10
 9b. Petals (5–)6–22 mm long; fruit (2.5–)3.5–5.5(–7.0) cm long 11
 10a. Replum glabrous; ovules 20–40 per ovary; rachis straight *C. bonariensis*
 10b. Replum pilose; ovules 18–22 per ovary; rachis flexuous *C. kruessellii*
 11a. Lower and middle cauline leaves (3–)5(–7)-foliolate; petals white or rarely pale lavender, 5–7 mm long *C. ovata*
 11b. Lower and middle cauline leaves 7–11(–13)-foliolate; petals dark purple, violet or rarely pale lavender, (8–)10–22 mm long 12
 12a. Lowermost fruiting pedicels 1–2(–3) cm long; style 3–8(–10) mm long; racemes bracteate only basally; petals (8–)10–14 mm long
 *C. jamesonii*
 12b. Lowermost fruiting pedicels (2.0–)2.5–4.2(–5.0) cm long; style (6–)8–16(–20) mm long; racemes bracteate throughout; petals 1.5–2.0 cm long
 *C. picta*
 13a. Cauline leaves simple, rarely lowermost with 1 or 2 minute lateral leaflets 14
 13b. Cauline leaves compound, 3-, 5- or 7-foliolate 17
 14a. Plants with numerous tubers *C. tuberosa*
 14b. Plants not tuberous 15
 15a. Cauline leaves lanceolate to ovate *C. variabilis*
 15b. Cauline leaves cordate or flabellate 16
 16a. Stems 6–25 cm tall; leaves 3–5-toothed; sepals 3.5–4.0(–4.5) mm long *C. cordata*
 16b. Stems 20–60 cm tall; leaves undulate-crenate; sepals 1–2 mm long *C. rostrata*
 17a. Plants tuberous 18
 17b. Plants not tuberous 21
 18a. Rhizomal and lowermost cauline leaves 3-foliolate; rhizomes and stolons tuberous at apex; stem and rachis angular-flexuous *C. hispidula*
 18b. All leaves 5- or 7-foliolate; only stem base tuberous; stem and rachis straight or (in *C. marginata*) flexuous but not angular 19
 19a. Style stout, almost as wide as fruit apex *C. glacialis*
 19b. Style slender, distinctly narrower than fruit apex 20
 20a. Petals 2.5–3.2 × 0.7–1.0 mm; rachis of raceme flexuous; ovules 6–10 per ovary; fruit 1.0–1.7 cm × 1.8–2.5 mm *C. marginata*
 20b. Petals (5–)6–9 × 2.0–3.5 mm; rachis of raceme straight; ovules 20–34 per ovary; fruit 2–4 cm × 1.0–1.5 mm *C. vulgaris*
 21a. Leaflets strongly lobed or compound 22
 21b. Leaflets entire, dentate, crenate, or serrate 23
 22a. Lateral leaflets with sessile lobes; petals broadly obovate, (0.8–)10.0–15.0 × 4–8 mm; Patagonian Argentina and Chile *C. geraniifolia*
 22b. Lateral leaflets 3-foliolate; petals oblong-oblongate, 8–12 × 3–4 mm; Peru *C. peruviana*
 23a. Petals purple, 4.0–6.5 mm wide; Bolivia *C. speciosa*
 23b. Petals white, 1.5–4.0(–6.0) mm wide, central Chile and Patagonian Chile and Argentina 24
 24a. Leaflets of basal and lower cauline leaves orbicular to reniform or broadly ovate, those of upper leaves filiform, linear, or narrowly oblong
 25
 24b. Leaflets of basal leaves similar morphologically to cauline but larger 26
 25a. Rhizomes slender; sepals (3.2–)3.5–4.5 mm long; petals (6–)7–12 mm long; terminal lobe of lower cauline leaves broadly ovate, 3-toothed
 *C. tenuirostris*
 25b. Rhizomes robust; sepals 2.2–3.0 mm long; petals 5.0–6.5 mm long; terminal lobe of lower cauline leaves orbicular to reniform, crenate to
 subentire *C. vulgaris*
 26a. Terminal leaflet distinctly longer than lateral ones 27
 26a. Terminal leaflet about as long as lateral ones 28
 27a. At least some leaves simple; leaflets obovate to flabellate *C. cordata*
 27b. All leaves pinnately compound; leaflets ovate to oblong *C. variabilis*
 28a. Rhizomes thickened apically; petals 1.5–3.0 mm wide; style stout, almost as thick as fruit apex *C. glacialis*
 28b. Rhizomes slender apically; petals 2.5–4.0(–5.0) mm wide; style slender, distinctly narrower than fruit apex *C. volckmannii*

MEXICAN AND CENTRAL AMERICAN CARDAMINE

Rollins (1993) recognized 15 native species of *Cardamine* in Mexico and Central America excluding the Caribbean Islands. Of those, *C. ramosa* Rollins, *C. flaccida* Cham. & Schltdl., and *C. innovans* O.E. Schulz are minor variants of *C. longipedicellata* Rollins, *C. bonariensis*, and *C. africana*, respectively. By contrast, a recent floristic account of Central America and southern Mexico (Al-Shehbaz & Fuentes Soriano, 2015) recognized only eight species. Finally, Sjöstedt (1975) recognized only five species in all of Central and South America and drastically reduced the vast

majority of 97 names to their synonymy. Such a very broad species concept was not followed by subsequent workers.

With the addition of *Cardamine guatemalensis* Al-Shehbaz and *C. karol-marholdii* Al-Shehbaz, which are endemic to Guatemala and Mexico, respectively, Central America and Mexico combined have 15 native species, of which Mexico has 11 (three endemic) and Guatemala has eight (three endemic) (Table 2). Belize, El Salvador, and Nicaragua are the only countries in the region without native species. The following species require some notes.

TABLE 2. Country distribution of the native Caribbean, Central American, and Mexican species of *Cardamine*. An asterisk (*) indicates presence, and E means endemic to that country. Country abbreviations are: CRI: Costa Rica; CUB: Cuba; DOM: Dominican Republic; GTM: Guatemala; HND: Honduras; HTI: Haiti; MEX: Mexico; and PAN: Panama.

SPECIES	CRI	CUB	DOM	GTM	HND	HTI	MEX	PAN
<i>Cardamine auriculata</i> S.Watson							E	
<i>Cardamine balnearia</i> Standl. & Steyerl.				E				
<i>Cardamine bonariensis</i> Pers.	*			*			*	
<i>Cardamine californica</i> (Nutt.) Greene							*	
<i>Cardamine eremita</i> Standl. & Steyerl.				E				
<i>Cardamine fulcrata</i> Greene	*			*	*		*	*
<i>Cardamine guatemalensis</i> Al-Shehbaz				E				
<i>Cardamine hintonii</i> Marhod & Al-Shehbaz			*			*	*	
<i>Cardamine jejuna</i> Standl. & Steyerl.	*			*			*	
<i>Cardamine karol-marholdii</i> Al-Shehbaz							E	
<i>Cardamine longipedicellata</i> Rollins				*			*	
<i>Cardamine macrocarpa</i> Brandege							*	
<i>Cardamine mexicana</i> O.E.Schulz							E	
<i>Cardamine ocoana</i> O.E.Schulz			E					
<i>Cardamine oligosperma</i> Nutt.							*	
<i>Cardamine ovata</i> Benth.	*			*				*
<i>Cardamine porphyrophylla</i> Ekman ex Urb.		E						

1. *Cardamine carrii* B.L. Turner

Turner (2012) described this species from South-Central Texas, and he closely compared it with, and annotated it in 1997 as, *Cardamine macrocarpa*, a species distributed in Texas (Brewster, Kinney, Jeff Davis, and Uvalde counties) and Mexico (Chihuahua and Nuevo Leon). Since then, we have studied several additional collections, and it is evident that *C. carrii* is indistinguishable from the former. The holotype has aborted flowers with smaller petals than those of typical *C. macrocarpa*, and the other alleged differences between them in fruit width and pedicel length show continuous variation and are unreliable. In every other aspect, plants of the two are indistinguishable. Therefore, a single species is involved, and its synonyms are listed below.

Cardamine macrocarpa Brandege, Zoe 5: 233. 1906. TYPE: MEXICO. Coahuila, Sierra de Parras, March 1905, *C. A. Purpus 1029* (Holotype: UC [136075]; Isotypes: GH [00018932], NY [00172736]).

Cardamine macrocarpa var. *texana* Rollins, J. Arnold Arbor. 21: 394. 1940. TYPE: UNITED STATES. Brewster Co., Camp Mountain, Chisos Mountains, September 1933, *V. L. Cory 7141* (Holotype: GH [00018914]).

Cardamine carrii B.L. Turner, Phytoneuron 49: 1. 2012, syn. nov. TYPE: UNITED STATES. Texas, Kinney Co.: Kickapoo Cavern State Park, ca. 400 ft NW of BM 1822, ca. 1700 ft SE of windmill at BM 1717, SW ¼ of park, 29°35'48"N, 100°27'25"W, clay loam and duff over rock rubble on slope at shaded base of NW-facing limestone bluff, 1700–1720 ft, 20 April 1990, *W. R. Carr 10,458* (Holotype: TEX [00208722]; Isotype: TEX [00028533]).

2. *Cardamine cebollana* B.L. Turner

This Mexican species was based on a single diffuse plant that was most likely grazed at the tips, became multibranching at the base, and appeared as if it is perennial. It resembles diffuse plants of *Cardamine longipedicellata*, especially in leaf morphology, flower size, second racemes, fruiting pedicels, fruits, and seeds. The examination of many collections of this species from Mexico and Guatemala leaves no doubt that *C. cebollana* is conspecific with *C. longipedicellata*, as indicated below.

Cardamine longipedicellata Rollins, J. Arnold Arbor. 21: 395. 1940: 395. TYPE: MEXICO. [Nuevo León]:

Sierra Madre Oriental, San Francisco Canyon, about 15 miles southwest of Pueblo Galeana, 11 May 1934, 7500–8500 ft [2286–2591 m], *C. H. Mueller & M. T. Mueller 298* (Holotype: GH [00018931]).

Cardamine cebollana B.L. Turner, *Phytologia* 94: 384. 2012, syn. nov. TYPE: MEXICO. Nuevo León: Mpio. Montemorelos, 6 km SE of La Trinidad, in La Sierra Cebolla, just below the summit, 2900 m, 25°11'N, 100°07'W, 5 August 1988, *T. F. Patterson 6150* (Holotype: TEX [00147820]).

3. *Cardamine obliqua* Hochs. ex A. Rich.

Schulz (1903) confused the limits of the African *Cardamine obliqua* Hochs. ex A. Rich., and cited (p. 518) two collections from Africa and a third from Mexico. Rollins (1940, 1993) followed Schulz and recognized that Mexican collection and another as a distinct variety of this species.

The typification of *Cardamine obliqua* is incomplete, and Jonsell (1982) listed the holotype at P but did not annotate any of the duplicates cited below. However, P has three sheets, of which two, as well as duplicates in other herbaria, have printed labels, whereas the one designated below as the lectotype has a handwritten label most likely by Achille Richard. It is unknown if Richard examined the two duplicates at P and both sheets at TUB, where Hochstetter's types are housed (see Stafleu & Cowan, 1979). Furthermore, Jonsell indicated that the type locality is Begemdir [sic], but this name is not listed on any sheet of the type collection or in Richard (1847), who gave the locality Boauhit in (Prov. Semien), a name listed as Bachit on all labels of the type collection. Gillett (1972) indicated that Bachit, or Bauhit, is located at 13°15'N, 38°15'E of Province Semien, which is north of Prov. Begemder.

Cardamine obliqua Hochs. ex A. Rich., *Tent. Fl. Abyss.* 1: 19. 1847. TYPE: AETHIOPIA. "In regione superioris montis Bachit ad rivulos," 24 June 1838, [W. G.] *Schimper 989* (Lectotype, here designated; P [00364836]; Isolectotypes: B [10-0386989], BR [0000008248770], BR [0000008886973], HAL [0081734], K [000230709], K [000230711], KW [001000745], M [0108035], P [00364834], P [00364835], S-G-[8719], STU [000327], TUB [000540], TUB [00541]).

Cardamine obliqua grows in the alpine belt, on lake and stream shores, and in moist mountain forests at 2000–4900 m in its native range in Ethiopia, Kenya, Rwanda, Tanzania, Uganda, and Zaire (Jonsell, 1982). It is not known from any other African country. Its disjunct distribution (as var. *stylosa*) in Mexico is highly dubious, and there is no other Brassicaceae that has such an allegedly disjunct African-American native distribution. A closer examination of numerous collections (including types) from Africa and fewer from Mexico show that there are some settled differences between the two, though there is also a great deal of overlap in morphology, especially in leaf characters.

Unfortunately, there is no molecular phylogenetic study that dealt with samples from both continents, and such study should reveal whether or not those bicontinental populations are somewhat related or not. Moreover, according to the data by Jonsell (1976) from East Africa, this species represents a polyploid complex, comprising hypertetraploids ($2n = 36$), heptaploids ($2n = 56$), (hypo)octoploids ($2n = 62, c.64$) and nonaploids ($2n = 72$). For now, however, the Mexican populations are treated as the following distinct species, and a complete description is given.

Cardamine hintonii Marhold & Al-Shehbaz, *nom. nov.*

Basionym: *Cardamine obliqua* var. *stylosa* Rollins, *J. Arnold Arbor.* 21: 392. 1940; non *C. stylosa* D.C., *Syst. Veg.* 2: 248. 1821. TYPE: MEXICO. [State of Mexico] Las Cruces, Tamascaltepe, 3350 m, 13 June 1934, *G. B. Hinton 6080* (Holotype: GH [0001834]; Isotypes: K [000485041], MICH [1115033], NY [00172737]; US [00100046]).

Perennial herbs; rhizomes non-fleshy, not scaly. *Stems* 30–60 cm tall, erect to ascending, simple or few-branched above, glabrous to occasionally pubescent. Basal and lowermost cauline *leaves* pinnately compound, 5–7-foliolate; *leaflets* subsessile to short petiolulate, ovate to suborbicular, entire or somewhat dentate, glabrous, sparsely ciliate along the margin; terminal leaflets slightly larger than to subequaling laterals; middle and upper leaves similar to basal, not auriculate. *Raceme* several flowered, ebracteate, glabrous, elongated in fruit; fruiting pedicels ascending, straight, lowermost 1.0–2.3 cm long. *Sepals* erect, 2–3 mm long, ovate, green, glabrous; *petals* white, obovate, 4.5–7.0(–8.0) mm long, cuneate to claw-like base; *stamens* white, slender; *anthers* 1.0–1.5 mm long. *Fruit* linear, 2.3–4.0 cm × 1.0–1.8 mm, glabrous; *style* slender, (2–)3–5 mm long.

The species grows in wet areas in mountains, steep gullies, winding gorges, and along creek and stream margins. It is distributed in Hispaniola (see below) and México (Ciudad de México, Durango, Estad. México, Morelos).

Cardamine hintonii generally resembles *C. obliqua* in habit, foliage, and ebracteate racemes that are elongated in fruit. However, the basal and lowermost leaves in *C. hintonii* are 5–7-foliolate (vs. (7–)9–11-foliolate), the petals are always white (vs. violet, pink, or white), the styles are slender (vs. stout), and the fruit is usually subappressed (vs. divaricate). Ranges of the two species are separated by a distance of some 12,000–15,000 air km.

Schulz (1903) cited *Pringle 5327* (GH, as H.C.) as a representative of *Cardamine obliqua* from the New World, and Rollins (1940) cited that collection as a paratype of his Mexican *C. obliqua* var. *stylosa*. A recent search for that specimen in the Harvard University Herbaria failed to locate it despite the fact that one of us (IAS) examined it several years ago, and it is likely misplaced. There are no duplicates of this collection in Pringle's Herbarium (VT) or herbaria in Europe and the United States (e.g., CAS, NY, UC, US).

CARIBBEAN SPECIES

The vast majority of Caribbean Islands have one or more naturalized weedy species of *Cardamine*, including *C. africana*, *C. flexuosa*, *C. hirsuta*, and *C. impatiens* (see Adams, 1972; Al-Shehbaz, 1988; Fournet, 2002; Liogier &

Martorell, 2000; Liogier, 1983). The last author reported *C. pensylvanica* Muhl. ex Willd. from Haiti based on a collection (Sto. Dominigo, *Ventenant s.n.* (G)) that was annotated by Schulz on 26 March 1902 and cited by him

(Schulz, 1903: 521) as *C. flexuosa* subsp. *pensylvanica* (Muhl.) O.E. Schulz. One of us (IAS) examined the specimen in May 2024, and it definitely belongs to *C. hirsuta*. *Cardamine pensylvanica* is restricted to southern Canada and the United States (see Al-Shehbaz et al., 2010). Furthermore, Liogier who reported *C. debilis* Don from the Dominican Republic based on *Turchheim 2949* (G), and based on its examination, it is definitely *C. occulta*, a species shown by Marhold et al. (2016) to be widely naturalized worldwide and often misidentified as *C. flexuosa*.

Schulz (1903) broadly delimited *Cardamine jamesonii* Hook. (Colombia, Ecuador, Venezuela) to include at least three species, and Liogier (1983) listed its occurrence in Hispaniola (Haiti and the Dominican Republic). An examination of several of Ekman's collections from Haiti, all annotated by Schulz as *C. jamesonii*, revealed that these collections clearly do not belong to this species. Instead, they belong to *C. hintonii*, which differs from the latter by having 5–7-foliolate (vs. 7–11(–13)-foliolate) leaves, basally ebracteate (vs. bracteate) racemes, green (vs. dark purple)

sepals, white (vs. purple, violet, or red but rarely lavender) petals 4.5–7.0(–8.0) (vs. (8–)10–14) mm long, fruit 2.3–4.0 (vs. 3–7) cm long, and (2–)3–5 (vs. (3–)5–8(–10) mm long. It is not known if these disjunct Hispaniola populations of *C. hintonii* are remnants of a wider distribution that included Mexico, or were introduced around the turn of the 20th century.

The Caribbean Islands have two native *Cardamine* species, of which *C. porphyrophylla* Ekman ex Urb. is endemic to Cuba and currently known from a number of localities (Rodríguez & Greuter, 2009). The other, *C. ocoana* O.E. Schulz, is known previously only from the type collection in the Dominican Republic, *Ekman 11702* (Holotype: S-R [7298]; Isotype: B [10-0243591]). A second collection that perhaps belongs here is *Hill 23933* (MO [4320943]) from Dominica, a small island of the Lesser Antilles disjunct from the above type locality by some 1000 km, and it is likely a recent introduction. Plants of both collections have procumbent stems that produce several well-spaced rosettes with 5–7-foliolate leaves and terminate in ebracteate racemes.

KEY TO THE CARIBBEAN, CENTRAL AMERICAN, AND MEXICAN *CARDAMINE* SPECIES

In addition to the 17 native species present in the countries and areas above, the key also includes the five weedy species *Cardamine africana*, *C. flexuosa*, *C. hirsuta*, *C. impatiens*, and *C. occulta*. This should help in their separation from each other and the native species. Šlenker et al. (2018) is followed in separating *C. flexuosa* from *C. occulta*.

- 1a. Plants annual 2
- 1b. Plants perennial 11
- 2a. Petiole base of cauline leaves auriculate *C. impatiens*
- 2b. Petiole base of cauline leaves not auriculate 3
- 3a. Bases of at least some leaflet petiolules with stalked or sessile auricles *C. auriculata*
- 3b. Bases of leaflet petiolules without auricles 4
- 4a. Stems and petioles usually densely hirsute with long trichomes; terminal leaflets crenate, suborbicular, usually cordate or oblique at the base *C. mexicana*
- 4b. Stems and petioles glabrous to sparsely pubescent; terminal leaflets entire or dentate, variously shaped but rarely cordate 5
- 5a. Basal leaves forming well-developed rosettes with ciliate petioles 6
- 5b. Basal leaves not rosulate, or forming loose rosettes usually with glabrous petioles 8
- 6a. Racemes 3–5-flowered; cauline leaves few, reduced, or absent; alpine endemic of Guatemala *C. jejuna*
- 6b. Racemes many flowered; cauline leaves several, well developed 7
- 7a. Stamens 4, rarely 5 or 6; seeds narrowly margined; fruit usually appressed to rachis; valves glabrous; widespread weed. *C. hirsuta*
- 7b. Stamens 6; seeds not margined; fruit not appressed to rachis; valves glabrous or pubescent; native to Baja California. *C. oligosperma*
- 8a. Racemes secund; lowermost fruiting pedicels (0.8–)1.0–2.5 cm long *C. longipedicellata*
- 8b. Racemes not secund; lowermost fruiting pedicels rarely to 1 cm long 9
- 9a. Racemes strongly flexuous to geniculate; fruit (2.5–)3.0–4.6 cm × 1.7–2.0 mm; petals 6–8 mm long *C. macrocarpa*
- 9b. Racemes not or hardly flexuous at base; fruit 1.0–2.5(–3.2) cm × 1.0–1.5 mm; petals 2–4(–5) mm long 10
- 10a. Basal rosette absent; upper surfaces of middle cauline leaves and upper stems usually glabrous; petals more than two times wider than sepals; terminal leaflet of middle cauline leaves with (1–)3–5(–7) sinuses *C. occulta*
- 10b. Basal rosette present; upper surfaces of middle cauline leaves and upper stems usually pubescent; petals less than two times wider than sepals; terminal leaflet of middle cauline leaves with 1–7(–9) sinuses. *C. flexuosa*
- 11a. Plants woody at base; stem and raceme rachis strongly flexuous, geniculate; leaves pinnatisect *C. karol-marholdii*
- 11b. Plants herbaceous throughout; stem and raceme rachis straight, not geniculate; leaves pinnately compound or trifoliolate, rarely simple . 12
- 12a. Basal leaves simple, reniform to orbicular, palmately veined, rarely with minute 1 or 2 lateral lobes; cauline leaves absent or 1 *C. guatemalensis*
- 12b. Basal leaves compound, trifoliolate or pinnate; cauline leaves usually several 13
- 13a. Rhizomes bulbous; plants of Baja California *C. californica*
- 13b. Rhizomes not bulbous; plants from elsewhere 14
- 14a. Rhizomes thickened, simple; leaves 9–13-foliolate *C. balnearia*
- 14b. Rhizomes slender, often branched; leaves 3–7(–9)-foliolate 15
- 15a. Racemes bracteate at least basally 16
- 15b. Racemes ebracteate 19
- 16a. Fruit (0.7–)1.5–2.2(–3.0) cm long; petals to 5 mm long; terminal leaflet 0.3–2.5 cm long 17
- 16b. Fruit (2.8–)3.5–5.5(–6.5) cm long; petals 4.5–9.0 mm long; terminal leaflet (2–)3–9 cm long 18

KEY TO THE CARIBBEAN, CENTRAL AMERICAN, AND MEXICAN *CARDAMINE* SPECIES CONT.

- 17a. Terminal leaflet orbicular, reniform, or rarely ovate; raceme not secund in fruit *C. bonariensis*
 17b. Terminal leaflet linear-oblongate to oblongate; raceme secund in fruit *C. eremita*
 18a. Middle cauline leaves trifoliolate *C. fulcrata*
 18b. Middle cauline leaves 5–9-foliolate *C. ovata*
 19a. Leaves trifoliolate throughout 20
 19b. Leaves pinnate, 5–7-foliolate 21
 20a. Terminal leaflet lanceolate to ovate, acute at apex, on petiolule 2–5 cm long; fruit (2.5–)3.5–5.0(–6.0) cm long; sepals 1.5–4.0 mm long; petals 3.5–9.0 mm long; widespread naturalized weed *C. africana*
 20b. Terminal leaflet suborbicular, rounded at apex, on petiolule 1.0–1.5 cm long; fruit 2.5–3.0 cm long; sepals to 2 mm long; petals to 5 mm long; endemic to Cuba *C. porphyrophylla*
 21a. Plants erect to ascending; fruit 2.3–4.0 cm long; petals 4.5–7.0(–8.0) mm long; style (2–)3–5 mm long *C. hintonii*
 21b. Plants prostrate or procumbent; fruit 1.5–2.5 cm long; petals 3–4 mm long; style 0.5–1.0(–1.5) mm long *C. ocoana*

LITERATURE CITED

- ADAMS, C. D. 1972. Flowering plants of Jamaica. University of the West Indies. Mona.
 AL-SHEHBAZ, I. A. 1988. Cruciferae. Pages 276–292 in R. A. HOWARD, ED., *Flora of the Lesser Antilles Leeward and Windward Islands*, vol. 4 (part 1). Arnold Arboretum, Jamaica Plain.
 ———. 2024. Brassicaceae. Pages 37–155 in C. PERSSON, R. ERIKSSON, K. ROMOLEROUX, AND B. STÄHL, EDS., *Flora of Ecuador*, No. 98. Elanders Sverige AB, Mölnlycke, Sweden.
 AL-SHEHBAZ, I. A., AND S. FUENTES SORIANO. 2015. Brassicaceae. Pages 267–289 in G. DAVIDSE, M. SOUSA, S. KNAPP, F. CHIANG, C. ULLOA, AND F. R. BARRIE, EDS., *Flora Mesoamericana*. Vol. 2, part 3. Universidad Nacional Autónoma de México, Missouri Botanical Garden, and The Natural History Museum (London).
 AL-SHEHBAZ, I. A., AND K. MARHOLD. 2023. *Cardamine peruviana* (Cardamineae; Brassicaceae), a new species from Peru. *Phytotaxa* 594: 237–240.
 AL-SHEHBAZ, I. A., AND D. L. SALARIATO. 2012. Brassicaceae. In A. M. ANTON AND F. O. ZULOAGA, EDS., *Flora of Argentina*, Vol. 8. Oboda, Imbiv, Conicet, Buenos Aires.
 AL-SHEHBAZ, I. A., K. MARHOLD, AND J. LIHOVÁ. 2010. *Cardamine*. Pages 464–484 in *FLORA OF NORTH AMERICA EDITORIAL COMMITTEE*, *Flora of North America North of Mexico*, volume 7. Oxford University Press, New York and Oxford.
 AL-SHEHBAZ, I. A., M. MUÑOZ-SCHICK, AND V. MORALES. 2011. The present status of Brassicaceae taxa described by Rodolfo and Federico Philippi. *Harvard Pap. Bot.* 16: 279–291.
 BOELCKE, O., AND M. C. ROMANCZUK. 1984. Cruciferae. Pages 373–544 in M. N. CORREA, ED., *Flora Patagónica*, vol. 8(4a). Col. Ci. INTA, Buenos Aires.
 CANDOLLE, A. P. DE. 1821. *Regni vegetabilis systema naturale, sive ordines, genera et species plantarum secundum methodi naturalis normis digestarum et descriptorum*. Vol. 2. Treuttel and Würtz, Paris.
 DÍAZ ROMERO, B. 1920. *Flora pacensis*, descripción de las plantas indígenas y exóticas que existen en la hoya de La Paz. *Bol. Direcc. Nac. Estad. y Estud. Geogr.*, La Paz, Segunda Epoca 3(nos. 25–27): 40–87.
 FOURNET, J. 2002. *Flore illustrée de phanérogames de Guadeloupe et de Martinique*, vol. 1. Gondwana Editions, Montpellier, France.
 GILLET, J. B. 1972. Schimper's botanical collecting localities in Ethiopia. *Kew Bull.* 27: 115–128.
 HEENAN, P. B. 2017. A taxonomic revision of *Cardamine* L. (Brassicaceae) in New Zealand. *Phytotaxa* 330: 1–155.
 HEENAN, P. B., AND P. J. DE LANGE. 2018. *Cardamine pantaoha* (Brassicaceae), a new, threatened, alpine species from New Zealand. *Phytotaxa* 379: 255–260.
 JONSELL, B. 1976. Some tropical African Cruciferae. Chromosome numbers and taxonomic comments. *Bot. Notiser* 129: 123–130.
 JONSELL, B. 1982. Cruciferae. In R. M. POLHILL, ED., *Flora of tropical East Africa*. A. A. Balkema, Rotterdam.
 LIOGIER, H. A. 1983. *La Flora de la Española*. II, vol. 44. Universidad Central del Este, San Pedro de Macorís, Santo Domingo.
 LIOGIER, H. A., AND L. F. MARTORELL. 2000. *Flora of Puerto Rico and adjacent islands*. A systematic synopsis, ed. 2. Editorial de la Universidad de Puerto Rico, San Juan.
 MARHOLD, K., M. ŠLENKER, H. KUDOH, AND J. ZOZOMOVÁ-LIHOVÁ. 2016. *Cardamine occulta*, the correct species name for invasive Asian plants previously classified as *C. flexuosa*, and its occurrence in Europe. *PhytoKeys* 62: 57–72.
 MARHOLD, K., M. KEMPA, J. KUČERA, K. SKOKANOVÁ, J. SMATANOVÁ, B. ŠINGLIAROVÁ, M. ŠLENKER, AND J. ZOZOMOVÁ-LIHOVÁ. 2022. Database of names, chromosome numbers, ploidy levels and genome sizes of the tribe Cardamineae. <https://cardamine.sav.sk>
 RICHARD, A. 1847. *Tentamen florae abyssinicae seu enumeratio plantarum hucusque in plerisque Abyssiniae provinciis detectarum et praecipue beatis doctoribus Richardo Quartino Dillon et Antonio Petit (Annis 1838–1843) lectarum*, vol. 1. Apud Arthus Bertrand, Paris.
 RODRÍGUEZ, R. R., AND W. GREUTER. 2009. Brassicaceae. *Flora de la República de Cuba* 15: 1–51. A. R. Gantner Verlag, Ruggel.
 ROLLINS, R. C. 1940. Notes on some crucifers of Texas, Mexico, and South America. *J. Arnold Arbor.* 21: 392–396.
 ROLLINS, R. C. 1993. *The Cruciferae of Continental North America*. Stanford University Press, Stanford.
 SCHULZ, O. E. 1903. *Monographie der Gattung Cardamine*. *Bot. Jahrb. Syst.* 32: 280–623.
 SJÖSTEDT, B. 1975. Revision of the genus *Cardamine* L. (Cruciferae) in South and Central America. *Bot. Notiser* 128: 9–19.
 ŠLENKER, M., J. ZOZOMOVÁ-LIHOVÁ, T. MANDÁKOVA, H. KUDOH, Y. ZHAO, A. SOEJIMA, T. YAHARA, K. SKOKANOVÁ, S. ŠPANIEL, AND K. MARHOLD. 2018. Morphology and genome size of the widespread weed *Cardamine occulta*: how it differs from cleistogamic *C. kokaiensis* and other closely related taxa in Europe and Asia. *Bot. J. Linn. Soc.* 187: 456–482.
 ŠLENKER, M., M. PERNÝ, J. ZOZOMOVÁ-LIHOVÁ, AND K. MARHOLD. 2021. Taxonomic position and circumscription of *Cardamine barbaraeoides* (Brassicaceae), a systematically challenging taxon from the Balkan Peninsula. *Phytotaxa* 502: 111–132.
 STAFLEU, F. A., AND R. S. COWAN. 1976. *Taxonomic Literature*, vol. 1 (A–G). Bohn, Scheltema & Holkema, Utrecht.
 ———. 1979. *Taxonomic Literature*, vol. 2 (H–L). Bohn, Scheltema & Holkema, Utrecht.
 TURNER, B. L. 2012. A new species of *Cardamine* (Brassicaceae) from South-Central Texas. *Phytoneuron* 49: 1–5.