

NOMENCLATURE ARTICLE

Notes on the genus *Exostema* (Rubiaceae), its limits and sectional subdivisionWerner Greuter¹  & Rosa Rankin-Rodríguez² ¹ Botanischer Garten & Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Str. 6–8, Berlin, 14195, Germany² Jardín Botánico Nacional, Universidad de la Habana, C.P. 19230 Calabazar, Boyeros, Cuba

Addresses for correspondence: Werner Greuter; w.greuter@bgbm.org; Rosa Rankin-Rodríguez; r.rankin@bgbm.org

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Abstract Based on recent molecular work by Paudyal & al., the generic limits of the Neotropical woody genus *Exostema* are reassessed with a view of making them more compatible with traditional, morphology-based generic concepts. A wide circumscription is favoured, congruent with Paudyal & al.'s "clade B" (the *Exostema-Solenandra-Coutarea-Hintonia* group). Thus defined, *Exostema* is a genus with 40 species and five natural sections and incorporates three generic splits that were proposed by Paudyal & al. To minimise nomenclatural disruption, a proposal to conserve the name *Exostema* Rich. against *Coutarea* Aubl. has been presented separately. Two new combinations at sectional rank are proposed.

Keywords *Adolphoduckea*; circumscription; *Coutarea*; *Coutareopsis*; *Exostema*; *Hintonia*; *Motleyothamnus*; nomenclature; phytogeography; pollination ecology; *Solenandra*; typification

■ INTRODUCTION

While updating the information in our Checklist (Inventario) of the vascular plants of Cuba (Greuter & Rankin-Rodríguez, 2017) with the view of preparing its third consolidated edition, we encountered some incongruences between our current edition and the concepts upheld in the new revision of Cuban Rubiaceae (Borhidi & al., 2017, 2018). In particular, we were faced with the alternative of merging or distinguishing the genera *Exostema* (Pers.) Bonpl. and *Solenandra* Hook.f. The scope of the present paper is to discuss that issue and justify our current choice of names. Our conclusions make it desirable to propose conservation of the generic name *Exostema*, to which effect a proposal has been published separately (Greuter & Rankin-Rodríguez, 2021).

Exostema in the traditional sense is a genus of 30 species, many previously described ones being now considered synonyms or belonging to other genera. Of these 30 species, according to our sources (Liogier, 1962, 1995; Adams, 1972; Axelrod, 2011; McDowell, 2012; Greuter & Rankin-Rodríguez, 2017; IPNI, 2021; PoWo, 2021), 26 occur in the Greater Antilles and no less than 25 are confined to them: 20 (14 endemic) are found in Cuba, 10 (4 endemic) in Hispaniola, 3 (2 endemic) in Jamaica, and 2 (none endemic) in Puerto Rico. The single widespread Antillean species is *E. caribaeum* (Jacq.) Schult., found throughout the Caribbean islands and extending to the American mainland (Florida, Mexico to Colombia). *Exostema sanctae-luciae* is endemic to the Lesser Antilles. The three

species restricted to the mainland of America (PoWo, 2021) are *E. mexicanum* A.Gray (Mexico to Panama), *E. corymbosum* (Ruiz & Pav.) Spreng. (Peru), and *E. maynense* Poepp. (Colombia to Peru and N Brazil).

By and large, the genus *Exostema* has been accepted in the above circumscription by most authors of the 20th and 21st century. A major exception was the description of a separate genus *Solenandra* by Hooker (in Bentham & Hooker, 1873), based on Cuban material brought to France by Sagra and subsequently named *S. ixoroides* Hook.f.; the genus *Solenandra* has been revived recently by Borhidi (2002; see below).

McDowell (1996), in a cladistic analysis based on both morphological and molecular (ITS) data, recognized three morphologically defined sections in the genus: *E. sect. Exostema*, characterised by long flowers in axillary, 1–3-flowered inflorescences; *E. sect. Brachyanthum* DC. (as '*Brachyantha*'), with numerous shorter flowers in terminal inflorescences; and *E. sect. Pitonia* DC., again with terminal inflorescences with fewer and still longer flowers. McDowell & Bremer (1998), combining morphological and molecular data, confirmed these sections as monophyletic groups as did further, more broadly based molecular analyses, in particular that of Paudyal & al. (2018). McDowell & Bremer (1998) removed the two S American species from within their section (*E. maynense* from *E. sect. Pitonia*, *E. corymbosum* from *E. sect. Brachyanthum*), moving them to a basal position within the genus.

Borhidi (2002) championed the revival of *Solenandra* as a distinct genus, in the circumscription of *E. sect. Brachyanthum*

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(bar *E. corymbosum*), but subsequently was surprisingly fickle in the matter. In his comprehensive work on Cuban Rubiaceae (Borhidi & al., 2017) he reverted to his former, broad concept of *Exostema*, including *Solenandra*; but then he changed his mind again and kept the two separate (Borhidi & al., 2018). In the latter reappraisal he was influenced by the work of Paudyal & al. (2018).

A molecular-based biogeographical analysis of the *Exostema* complex (except *Hintonia*) was performed by McDowell & al. (2003). The three clades that these authors recognized in the complex, each corresponding to one of the afore-mentioned sections, were thought to have at their root one (or a few) Antillean colonization events from S America (or Mexico), followed by insular radiation. One may note that *E. maynense*, which in McDowell & al.'s (2003) tree is the basal species of their clade B (*E. sect. Pitonia*), was shifted to a position within clade B3 (our *E. sect. Brachyanthum*) in Paudyal & al.'s (2018) analysis.

Paudyal & al. (2018) performed a molecular sequence analysis of both plastid and nuclear DNA for a large number of species of the tribe Chiococceae Benth. & Hook.f., including 17 of *Exostema* s.l., representing all sections. In order to obtain monophyletic genera, they split the traditional *Exostema* into no less than four genera, two of them unispecific and newly described. We remain unconvinced of the soundness of that approach because, based on the same data and analysis, there is at least one morphologically and biogeographically more convincing while less disruptive alternative solution that fulfils the monophyly criterion. We opt for widening the circumscription of *Exostema*, adding to it two clades (each as an independent section), one corresponding to the genus *Hintonia* Bullock, the second to *Coutarea* Aubl. plus its recent segregate *Coutareopsis* Paudyal & Delprete plus the two S American *Exostema* species that correspond to the newly described genera *Motleyothamnus* Paudyal & Delprete and *Adolphoduckea* Paudyal & Delprete.

As traditionally circumscribed, *Exostema* is characterised by a capsular fruit and flattened, winged seeds; and by a salver-shaped (hypocrateriform), 4–5-merous corolla with a narrow tubular basis, long, linear, ± recurved lobes, and widely exerted stamens with linear, basifix anthers. In terms of reproductive biology, this indicates adaptation to bee or moth pollination, and wind dispersal. It is to be expected that a shift in reproductive strategies (to pollination by hummingbirds or bats rather than moths; or to water rather than wind dispersal) may entail quantum changes in correlated morphological characters; such shifts are bound to make the genus less uniform and more difficult to define. This is what we assume has happened in *Exostema*: A pollinator shift has likely occurred at the basis of *E. sect. Hintonia*, and two independent such shifts appear to have happened within *E. sect. Brachyanthum*. McDowell & Bremer (1998) suggest similar pollinator shifts within the “core sections” of *Exostema*, between a bee pollination syndrome (flowers short, diurnal scented, white eventually turning pale yellow to maroon) and a moth or hawkmoth pollination syndrome (flowers long, dusk or nocturnal scented, white turning pink or purplish).

It may be tempting to honour by the recognition of separate taxa morphologically spectacular changes driven by evolutionary

pressure related with fundamentally trivial shifts such as changes of pollination agents. But we believe that such changes in formal taxonomy are neither necessary nor helpful for the recognition of the phylogenetic context of these evolutionary changes. The strongly supported “subclade B3” recovered in Paudyal & al.'s (2018) molecular sequence analyses is indeed uncomfortably polymorphic with respect to floral morphology. It comprises nine species, seven previously placed in *Coutarea* Aubl. (including its nomenclatural type) plus the two mainland S American representatives of *Exostema*. Paudyal & al. (2018) split this small but natural group into no less than four genera: *Adolphoduckea* based on *Exostema maynense*; *Motleyothamnus* to accommodate *E. corymbosum*; *Coutareopsis*, with three species formerly placed in *Coutarea* Aubl.; and with only four species subsisting in *Coutarea* proper, *C. hexandra* (Jacq.) K.Schum., *C. diervilloides* Planch. & Linden, *C. mollis* Cham., and *C. alba* Griseb.

Our own generic circumscription and sectional classification of *Exostema* is detailed below; whereas the necessary eight species transfers and new combinations are not formalised here, pending the fate of our conservation proposal; they are left to the care of specialists of the flora of tropical continental America who are better acquainted with these plants than we are. As Aublet's name *Coutarea* has priority over *Exostema*, we have presented a separate conservation proposal to permit maintenance of the latter (Greuter & Rankin-Rodríguez, 2021).

■ MATERIALS AND METHODS

The *Exostema* material present in the herbaria at Berlin (B) and Palermo (PAL-Gr) has been used for comparison with the published taxonomic treatments and keys. Original literature, including all relevant protologues, has been consulted and interpreted in the light of the provisions of the current international nomenclatural *Code* (Turland & al., 2018). The distributions given for individual taxa are based on the data in PoWo (2021), of which the accuracy has not been critically reassessed in detail.

■ A NEW SECTIONAL CLASSIFICATION OF EXOSTEMA

The genus *Exostema* as circumscribed traditionally on the basis of its characteristic corolla (see above) has long posed problems as to its appropriate position within the Rubiaceae family. In a cladistic analysis based on morphological characters (Andersson & Persson, 1991) *Coutarea* and *Exostema* were found to form a clade of their own in some but not all of the trees, and were transferred from Cinchoneae DC. to Condamineae Benth. & Hook.f. That joint placement is consistent with the results of early molecular analyses using cpDNA restriction site data, by Bremer & Jansen (1991), which associate these two genera with *Chiococca* P.Browne and *Erithalis* P.Browne

in the tribe Chiococceae, where they remain to date, as confirmed by Paudyal & al. (2014), in an analysis that also included *Hintonia*.

The genus *Exostema* was described by Richard (1807) in the botanical part of Humboldt & Bonpland's travel account, but was not then a new genus, as Persoon (1805: 196) had used its name as the epithet for a subgenus (see Persoon, 1805: ix) of *Cinchona* L. Sectional nomenclature has been impaired by the fact that early authors, following Urban (1897), were unaware of Richard's genus being based on Persoon's subgenus and, by consequence, considered the single species described by Richard, *E. parviflorum* Rich., to provide the generic type. Indeed Urban (1897), when sinking *Solenandra* into the synonymy of *Exostema*, explicitly stated *E. parviflorum* to be the type of *Exostema*. However, *E. parviflorum* is not among the original elements of *Cinchona* subg. *Exostema* Pers., and is not eligible as type. Urban's error was flagged by Rogers (1987), who chose *E. caribaeum* instead, and that type designation must stand. For details, see the discussion by McDowell (1996: 282–283).

The appropriate authorship of the name *Exostema* may also be questioned. It is agreed that Aimée Bonpland authored the text of the book (Humboldt & Bonpland's *Plantae aequinoctiales*), in which the name *Exostema* was validly published. But part of the correlated account, including the generic description, was credited by Bonpland to Richard (Louis Claude Richard, not his son Achille, well known to Cuban botanists). The tricky question is whether Bonpland also ascribed to Richard the name *Exostema* itself, in addition to the generic description. In Richard's (1807) text there is the sentence "The genus *Exostema* is close to *Cinchona*" [p. 132; translated from Latin], which suggests that it is Richard himself, not Bonpland, who created and first used the name *Exostema*; but three pages further on, in a text portion written by Bonpland, the following statement appears: "Le mot d'*Exostema*, sous lequel je désigne ce nouveau genre, a déjà été employé par M. Persoon comme nom de section" [The word *Exostema*, by which I designate this new genus, has already been used by Mr Persoon as a section name]. Being written in the first person ["I designate"], this statement suggests that Bonpland claims authorship of the name *Exostema* for himself; and as this is the only place in which indirect reference is made to Persoon's basionym, we accept Bonpland's authorship claim, by application of Art. 46.2 and Ex. 3 of the nomenclatural *Code* (Turland & al., 2018).

***Exostema* (Pers.) Bonpl.** in Humboldt & Bonpland, *Pl. Aequinoct.* 1: 135. 1807, nom. cons. prop. (Greuter & Rankin-Rodríguez in *Taxon* 70: 906. 2021) ≡ *Cinchona* subg. *Exostema* Pers., *Syn. Pl.* 1: 196. 1805 – Type (designated by Rogers in *J. Arnold Arbor.* 68: 165. 1987): *Cinchona caribaea* Jacq., *Enum. Syst. Pl.*: 16. 1760 (≡ *Exostema caribaeum* (Jacq.) Roem. & Schult., *Syst. Veg.* 5: 18. 1819).

This genus coincides with clade B, the "*Exostema-Solenandra-Coutarea-Hintonia* group", of Paudyal & al. (2018, clade B). As defined by those authors, it is said to comprise all capsular-fruited, wing-seeded genera of their Chiococceae

tribe (note, however, the exception of *Morierina* Vieill., which is not included in the *Exostema* group). Clade B, of which an impressive number of species has been sequenced, is moderately well supported by the cladistic analysis; which analysis "clearly establishes the monophyly of *Hintonia* and its close relationship with *Exostema* and *Coutarea*". The three species of *E.* sect. *Hintonia* and seven of the nine species of the *Coutarea* clade (*E.* sect. *Brachyanthum*) deviate from the general *Exostema* corolla type described above, as detailed below.

1. ***Exostema* (Pers.) Bonpl. sect. *Exostema***

– "*Exostema* sect. *Oligantha* Borhidi" in *Acta Bot. Hung.* 35: 301. 1991, not validly published (Art. 22.2).

As defined, at generic level, by Paudyal & al. (2018; clade B1), this section consists of eight species: one (*Exostema caribaeum*) widespread, being found throughout the Caribbean islands and extending to the American continent (Florida, Mexico to Colombia), one (*E. spinosum*) restricted to Cuba and Hispaniola, one (*E. acuminatum*) endemic to Hispaniola, and five Cuban endemics. The section is characterised by bearing flowers solitary or up to three together in the leaf axils, not in terminal inflorescences; salver-shaped (hypocrateriform), actinomorphic corollas of medium length (2–10 cm), with a narrowly tubular base and 4–5 narrow, recurved lobes, white turning yellow or lavender, fragrant, moth-pollinated.

2. ***Exostema* sect. *Brachyanthum* DC.** in *Biblioth. Universelle Sci. Belles-Lettres Arts, Sci. Arts* 41: 157. 1829 ('*Exostemma*') – Type (McDowell in *Opera Bot. Belg.* 7: 292 [but not: 288!]. 1996): *Exostema corymbosum* (Ruiz & Pav.) Spreng. (≡ *Portlandia corymbosa* Ruiz & Pav.), ≡ *Motleyothamnus* Paudyal & Delprete in *Bot. J. Linn. Soc.* 187: 386. 2018 – Type: *Motleyothamnus corymbosus* (Ruiz & Pav.) Paudyal & Delprete.

= *Coutarea* Aubl., *Hist. Pl. Guiane*: 314. 1775, nom. rej. prop. (Greuter & Rankin-Rodríguez in *Taxon* 70: 906. 2021) – Type: *C. speciosa* Aubl., nom. illeg. (= *Portlandia hexandra* Jacq., *Coutarea hexandra* (Jacq.) K. Schum.).

= *Adolphoduckea* Paudyal & Delprete in *Bot. J. Linn. Soc.* 187: 384. 2018 – Type: *Adolphoduckea maynensis* (Poepp.) Paudyal & Delprete (≡ *Exostema maynense* Poepp.).

= *Coutareopsis* Paudyal & Delprete in *Bot. J. Linn. Soc.* 187: 385. 2018 – Type: *Coutareopsis andrei* (Standl.) Paudyal & Delprete (≡ *Coutarea andrei* Standl.).

Exostema sect. *Brachyanthum* (*Coutarea* in Paudyal & al., 2018, clade B3) is the most polymorphic *Exostema* clade, consisting of nine species that Paudyal & al. (2018) place in four different genera. The section is not, however, quite as heterogeneous as that treatment might suggest. Taylor & Lorence (2010) had already noted the marked resemblance between the *Coutarea* species studied by them (later placed in *Coutareopsis*) and, in particular, *E. corymbosum*, here included in the same section. For their *Coutarea*, which included *Coutareopsis* but neither *Adolphoduckea* nor *Motleyothamnus*, they postulated a recent evolutionary radiation corresponding with the Andean

uplift. All nine species of our *E.* sect. *Brachyanthum* inhabit mainland South America, but one of them, *Coutarea hexandra*, extends northward through Central America to S Mexico and to Venezuela's offshore islands. All share the flattened, winged seeds characteristic of our redefined *Exostema*, but they show pronounced diversity in flower characters, presumably linked with pollinator shifts. The inflorescence is few-flowered, terminal, and of axillary flowers. The corolla is 5–7(–9)-merous (4–5-merous in other sections, except *E.* sect. *Hintonia*); the characteristically shaped corolla of *Exostema* (straight and actinomorphic; narrowly tubular with long, narrow divisions) has, in *Coutarea* and *Coutareopsis*, evolved into a 5–7-merous, funnel-shaped corolla with broadly triangular divisions, and in *Coutarea* proper, further into a curved and zygomorphic one; and the stamens, normally exerted as the generic name suggests, have become partly or totally included in *Coutareopsis*. Whereas *Exostema*, as a general rule, shows an apian or lepidopteran pollination syndrome, most species of this section are likely hummingbird-pollinated (Taylor & Lorence, 2010) and some at least, bat-pollinated (Dwyer, 1980: 136).

3. *Exostema* sect. *Hintonia* (Bullock) Greuter & R.Rankin, **comb. & stat. nov.** ≡ *Hintonia* Bullock in Hooker's Icon. Pl. 33: ad t. 3295. 1935 – Type: *Hintonia latiflora* (Sessé & Moç. ex DC.) Bullock (≡ *Coutarea latifolia* Sessé & Moç. ex DC.).

Exostema sect. *Hintonia* (Paudyal & al., 2018, clade B2) is coextensive with the former genus *Hintonia* (Bullock, 1935), generally considered to be close to *Coutarea* phylogenetically (e.g., by Bremer, 1992). It is a genus of three species, ranging from Mexico to Central America (Ochoterena, 2012a,b). It was split off from *Portlandia* P.Browne principally on the basis of its flattened, winged seeds (Bullock, 1935). It was contrasted with *Coutarea* by corolla features: straight, actinomorphic, widely funnel-shaped, with broadly triangular lobes; and flower colour: white with greenish shades, suggesting bat pollination. The flowers are 6- or 8–9-merous, axillary, with stamens included in or only partly exerted from the corolla.

4. *Exostema* sect. *Pitonia* DC. in Biblioth. Universelle Sci. Belles-Lettres Arts, Sci. Arts 41: 157. 1829 ('*Exostemma*') ≡ *Solenandra* sect. *Pitonia* (DC.) Paudyal & Delprete in Bot. J. Linn. Soc. 187: 387. 2018 – Type (McDowell in Opera Bot. Belg. 7: 288, 293. 1996): *Exostema sanctae-luciae* (Kentish) Britten (≡ *Cinchona sanctae-luciae* Kentish, *Solenandra sanctae-luciae* (Kentish) Paudyal & Delprete), ≡ *Exostema* sect. *Floribunda* Borhidi in Acta Bot. Hung. 35: 301. 1991 ('*Floribundae*') ≡ *Solenandra* sect. *Floribundae* (Borhidi) Borhidi & al. in Acta Bot. Hung. 60: 303. 2018 – Type: *Exostema sanctae-luciae* (Kentish) Britten (*Cinchona sanctae-luciae* Kentish). [Note that Borhidi's sectional name, having been published prior to the type designation for *Exostema* sect. *Pitonia*, is legitimate.]

= *Exostema* sect. *Longiflora* Borhidi in Acta Bot. Hung. 35: 300. 1991 ('*Longiflorae*') – Type: *Exostema longiflorum*

(Lamb.) Roem. & Schult. (≡ *Cinchona longiflora* Lamb., *Solenandra longiflora* (Lamb.) Paudyal & Delprete).

= *Exostema* sect. *Polyphylla* Borhidi in Acta Bot. Hung. 35: 301. 1991 ('*Polyphyllae*') – Type: *Exostema polyphyllum* Urb. & Ekman (≡ *Solenandra polyphylla* (Urb. & Ekman) Paudyal & Delprete).

This and the next following section (Paudyal & al., 2018: clade B4a and B4b, respectively), of 10 species each, are very close, both morphologically and by DNA nucleotide sequence criteria. They share the typical *Exostema* corolla, with a tubular base and narrow, ligulate or linear lobes, white turning yellowish or purplish after anthesis; the flowers are said to be nocturnal and sweetly scented, suggesting moth pollination (McDowell & Bremer, 1998); they are arranged in terminal corymbs or are single, terminal. In the present section, *Exostema* sect. *Pitonia*, the flowers are axillary, single or few together, with large or medium-sized, at least 5 cm long corolla. In some species, the tubular flowers can reach a length of 20 cm, suggesting pollination by hawkmoths. This section is limited to the islands of the Caribbean: two species are endemic to Cuba, three to Hispaniola, two to Jamaica, one grows on Cuba and Hispaniola, one (*E. ellipticum* Griseb.) ranges from Cuba to Puerto Rico, and one, *E. sanctae-luciae*, grows on the Lesser Antilles. Two or three riparian species (*E. longiflorum* (Lamb.) Roem. & Schult. and *E. stenophyllum* Britton, and variably so, *E. polyphyllum*) differ from the generic pattern by having wingless seeds, a trait associated with rheochorous dispersal (McDowell & Bremer, 1998).

5. *Exostema* sect. *Solenandra* (Hook.f.) Greuter & R.Rankin, **comb. nov.** ≡ *Solenandra* Hook.f. in Bentham & Hooker, Gen. Pl. 2(1): 12, 43. 1873 [non *Cryptandra* subg. *Solenandra* Reissek in Lehmann, Pl. Preiss. 2: 288. 1848 ≡ *Solenandra* (Reissek) Kuntze, Revis. Gen. Pl. 1: 120. 1891 ≡ *Studelago* Kuntze, Revis. Gen. Pl. 1: 298. 1891] ≡ *Solenandra* Hook.f. sect. *Solenandra* per Paudyal & Delprete in Bot. J. Linn. Soc. 187: 387. 2018 – Type: *Solenandra ixoroides* Hook.f. (≡ *Exostema ixoroides* (Hook.f.) T.McDowell).

– "*Exostema* sect. *Exostema*" sensu Borhidi in Acta Bot. Hung. 35: 300. 1991.

– "*Exostema* sect. *Brachyanthum*" sensu McDowell in Opera Bot. Belg. 7: 288. 1996 ('*Brachyantha*'), as to type.

– "*Exostema* subg. *Solenandra* Borhidi & al.", Rubiaceae Cuba: 103. 2017, not validly published.

Last, *Exostema* sect. *Solenandra* (Paudyal & al., 2018, clade B4b) differs from the closely similar previous section mainly in having smaller, up to 2(–3) cm long, and more numerous, diurnal, bee-pollinated flowers (Borhidi & Fernández-Zequeira, 1991; McDowell & Bremer, 1998; Paudyal & al., 2018). One of its 10 species, aptly named *E. mexicanum* A.Gray, ranges from Mexico to Central America, seven of the others are Cuban endemics and two, *E. scabrum* Borhidi & M.Fernández and *E. parviflorum*, are found in Cuba and Hispaniola. For reasons of priority, Candolle's (1829) sectional name, *Exostema* sect. *Brachyanthum*, cannot be maintained

for this section, even though it has, in the past, been used mainly for it. McDowell (1996) had even once typified it in that sense (by *E. parviflorum*) but, perhaps realising that this element was not originally included by Candolle, he corrected himself in the same paper. Usage of the name *Exostema* sect. *Brachyanthum* in a sense excluding its type has not been either wide or persistent, so that the *Code* (Turland & al., 2018: Art. 57) cannot be invoked for its rejection.

■ CONCLUSIONS

A natural and at the same time practical classification of the *Exostema-Solenandra-Coutarea-Hintonia* group defined by Paudyal & al.'s (2018) molecular studies is best achieved by including *Coutarea*, *Hintonia*, *Solenandra*, and three recently described generic splits in an expanded genus *Exostema*. That genus, the name of which is being proposed for conservation against the older name *Coutarea*, consists of 40 species, here grouped into five natural sections. Three of these sections are endemic to the Greater Antilles, or nearly so, the remaining two are restricted to tropical mainland America, from Mexico southward to the Andes of Peru and to Amazonia. Diversification within the genus is believed to have been triggered by and to be concomitant with switches in pollinators, from bees or moths to hummingbirds and bats.

■ AUTHOR CONTRIBUTIONS

Both authors contributed by equal shares to all aspects of this paper. — WG, <https://orcid.org/0000-0002-8677-7544>; RRR, <https://orcid.org/0000-0002-7328-0395>

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