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REDEFINITION OF THE NEOTROPICAL GENERA *CODONANTHE* (MART.) HANST. AND *CODONANTHOPSIS* MANSF. (GESNERIACEAE)

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ABSTRACT. Recent phylogenetic studies based on molecular data have indicated that the epiphytic genus *Codonanthe* is not monophyletic, but segregated in two unrelated clades. This result completed with a close examination of biogeographical and morphological features that characterize these lineages led to the redefinition of monophyletic genera *Codonanthe* and *Codonanthopsis*. A key to the genera and a taxonomic treatment including revised generic descriptions, a list of the currently accepted species with their complete synonymies and distribution data are provided. *Codonanthe* is now reduced to eight species that are endemic to the Brazilian Atlantic forest. *Codonanthopsis* has been enlarged from two to 13 species distributed in Central America, the Caribbean, northwestern South-America, and the Amazonian basin. This expanded circumscription of *Codonanthopsis* requires the transfer of ten taxa traditionally recognized as *Codonanthe* and one originally described in *Paradrymonia*. This publication includes 11 new combinations and 9 lectotypifications.

Key words: Episcieae, taxonomy, *Paradrymonia*, Brazilian Atlantic forest, epiphytic plants, ant gardens, myrmecophily

INTRODUCTION

Recent studies of phylogenetic relationships in the tribe Episcieae have revealed for the first time the non monophyly of the genus *Codonanthe* and the need to revise the generic boundaries for members of the related genera *Codonanthopsis* and *Nematanthus* Schrad. (Clark et al. 2006, Clark et al. 2012). Subsequent phylogenetic study based on a near complete taxonomic sampling in *Codonanthe*, *Codonanthopsis* and *Nematanthus* have confirmed that *Codonanthe* is not monophyletic, but divided in two unrelated clades (FIGURE 1; Perret et al. 2013). The first clade comprises the *Codonanthe* species endemic to the Brazilan Atlantic forest, including *Codonanthe gracilis*, the type species of the genus. This clade, that we recognize as the *Codonanthe s.s.*, is found sister to the genus *Nematanthus*, forming a larger lineage restricted to the Atlantic forest biome (Perret et al. 2013). The remaining *Codonanthe* species are clustered in a second clade together with the two species of *Codonanthopsis* and *Paradrymonia anisophylla* (Clark et al. 2006, Perret et al. 2013). This clade is sister to the Brazilian endemic lineage and distributed over a vast area comprising Central America, the Caribbean, the Guianas, northern South America and the Amazon basin.

Despite a general similarity among *Codonanthe* species (e.g., epiphytic habit, white funnel-shaped corollas), the *Codonanthe s.s.* can be distinguished from the other *Codonanthe* species by several diagnostic features. In respect to flower morphology, the taxa from northern South American and Central America present corollas that are narrowly funnel-shaped with a spur at base, whereas corollas are tubular-campanulate and often ventricose in all Brazilian endemic *Codonanthe s.s.* except *C. mattos-silvae* (FIGURE 2). The presence of a spurred corolla (along with a two-lobed calyx) had led Smith (1933) to propose section *Spathuliformae* L. B. Sm. within genus *Codonanthe* for his *C. bipartita*, but this section has not been recognized in subsequent taxonomic revision (Moore 1973). Wiehler (1983) observed the anther connectives and pointed to a unique structure in Neotropical Gesneriaceae he considered a trademark for the genus *Codonanthe*. He observed that they were very broad causing a spatial separation of the pairs of thecae. Based on a closer examination of this feature, we found that the relative size of the connective in relation to the size of the thecae is a diagnostic character that distinguishes two lineages of *Codonanthe*. In the Brazilian endemic *Codonanthe s.s.* species, the thecae are mostly or totally covered on their back by a wide, inflated, translucent connective, whereas in the other *Codonanthe* and *Codonanthopsis*, the thecae may appear separated, but the connective is narrow, not inflated and covers only a small portion of the anther thecae dorsal side (FIGURES 3, 4).

Regarding fruits, species of *Codonanthe* s.s. can be identified by their orange indehiscent berries, whereas fruits in the other *Codonanthe* and *Codonanthopsis* are either tardily dehiscent capsules or fleshy display capsules that are fully reflexed at maturity (FIGURE 5). Comparative

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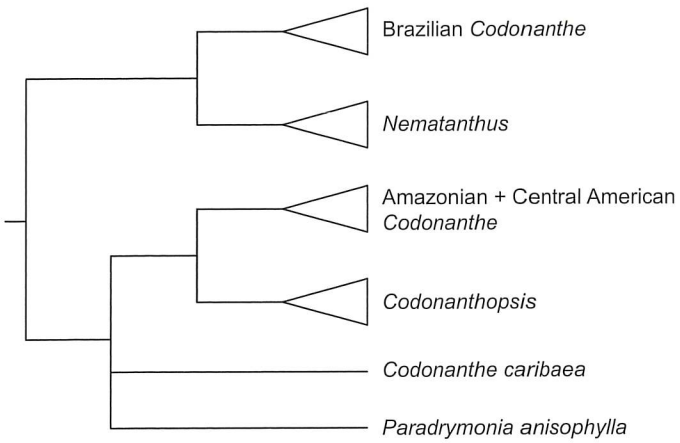

FIGURE 1. Diagrammatic representation of the phylogenetic hypothesis for the relationships among species of *Codonanthe, Codonanthopsis, Nematanthus* and *Paradrymonia anisophylla* following the results of Perret et al. 2013 and Clark et al. 2006. Triangles representing terminal taxa indicate a sample size of two or more species.

studies on the morphology of the leaf epidermis have also indicated that the *Codonanthe* species occurring outside the Atlantic forest can be characterized vegetatively based on epidermal characters like presence of glandular trichomes and extrafloral nectaries that are absent in the Brazilian endemic species (Yuen and Dehgan 1982, Belin-Depoux and Sarthou 1988).

FIGURE 2. Lateral view of flowers showing the presence of a corolla spur in *Codonanthopsis* (A-C) and its absence in *Codonanthe* (D-F). **A.** *Codonanthopsis elegans* (AC-2511). **B.** *C. uleana* (AC-1308). **C.** *C. corniculata* (AC-2607). **D.** *Codonanthe devosiana* (AC-1126). **E.** *C. serrulata* (AC-1307). **F.** *C. venosa* (AC-1701). Photographic images from plants cultivated at the Botanical Garden of Geneva. Accession numbers of living collections are indicated in brackets.

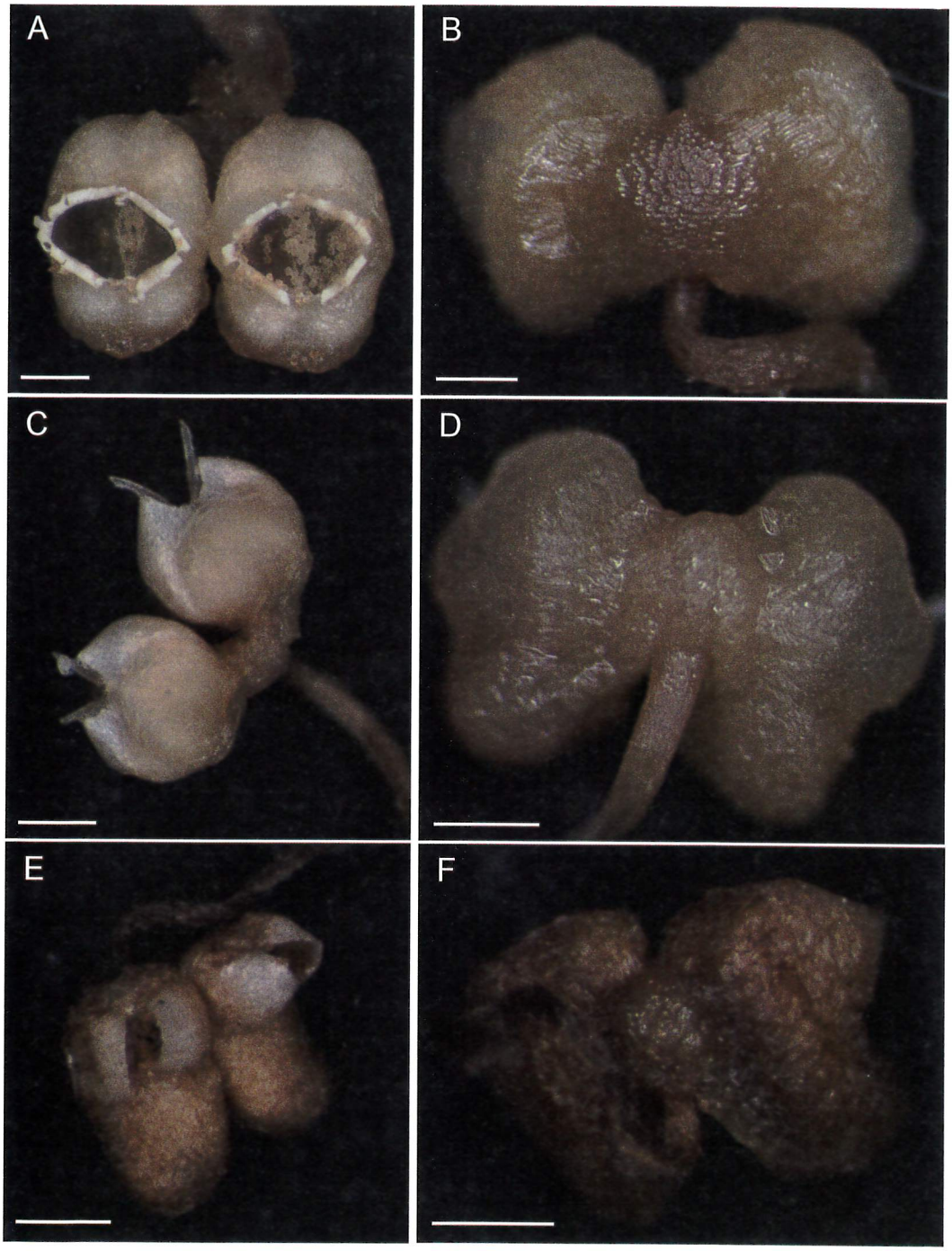

FIGURE 3. Ventral and dorsal view of the anther pairs in *Codonanthopsis*. Dorsal views show the connective covering only a small portion of the dorsal surface of anther thecae. **A–B.** *C. chiricana* (M. Perret & A. Chautems 20). **C–D.** *C. uleana* (AC-1182). **E–F.** *C. ulei* (AC-2801). Photographic images from field collection or from plants cultivated at the Botanical Garden of Geneva. Voucher specimens at G or accession numbers of living collections are indicated in brackets. Scale bars indicate 500 μm.

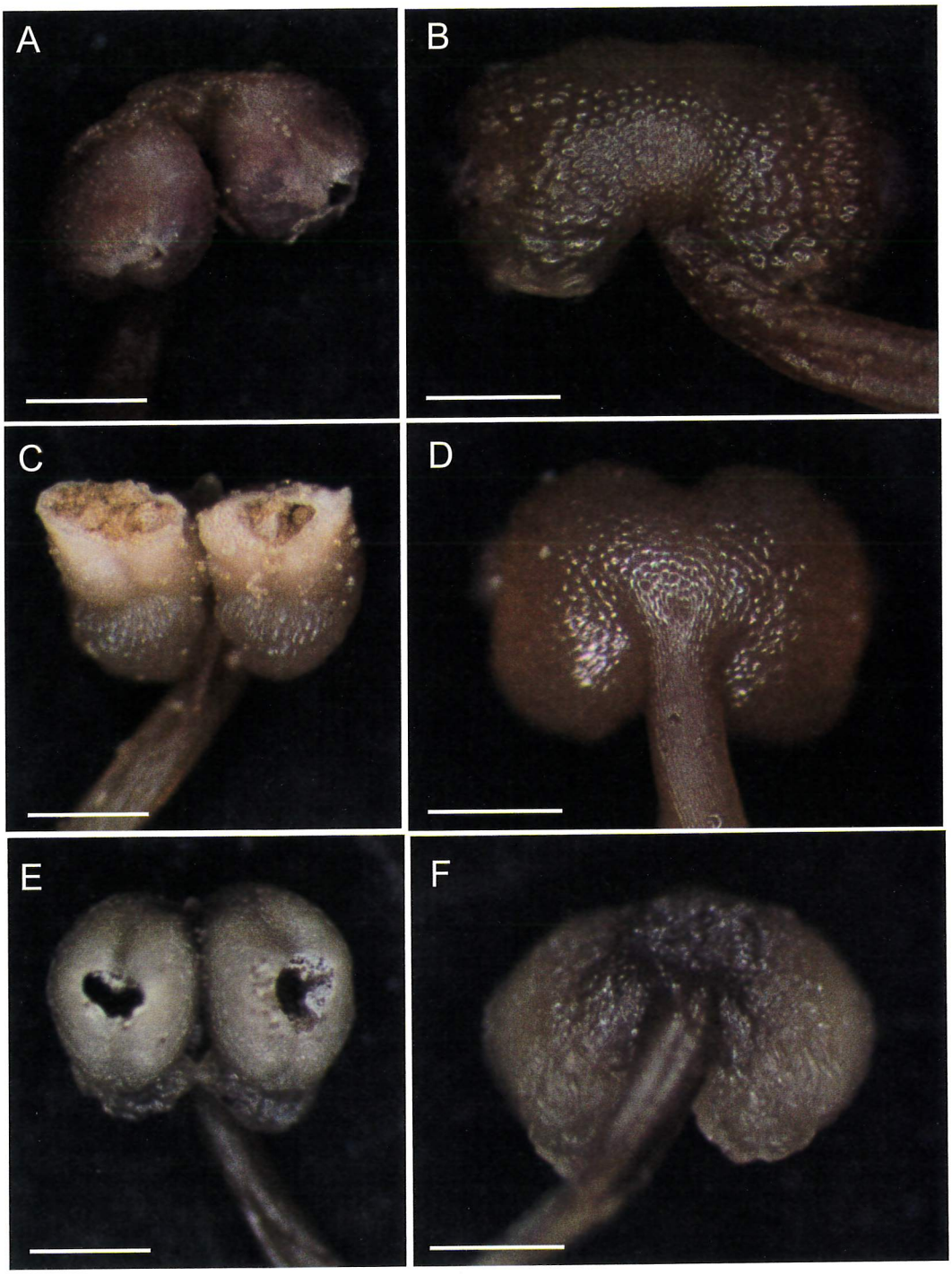

FIGURE 4. Ventral and dorsal view of the anther pairs in *Codonanthe*. Dorsal views show the connective covering entirely the dorsal surface of anther thecae. **A–B.** *C. devosiana* (AC-1019). **C–D.** *C. gracilis* (AC-1115). **E–F.** *C. serrulara* (AC-1307). Photographic images from plants cultivated at the Botanical Garden of Geneva. Accession numbers of living collection are indicated in brackets. Scale bars indicate 500 µm.

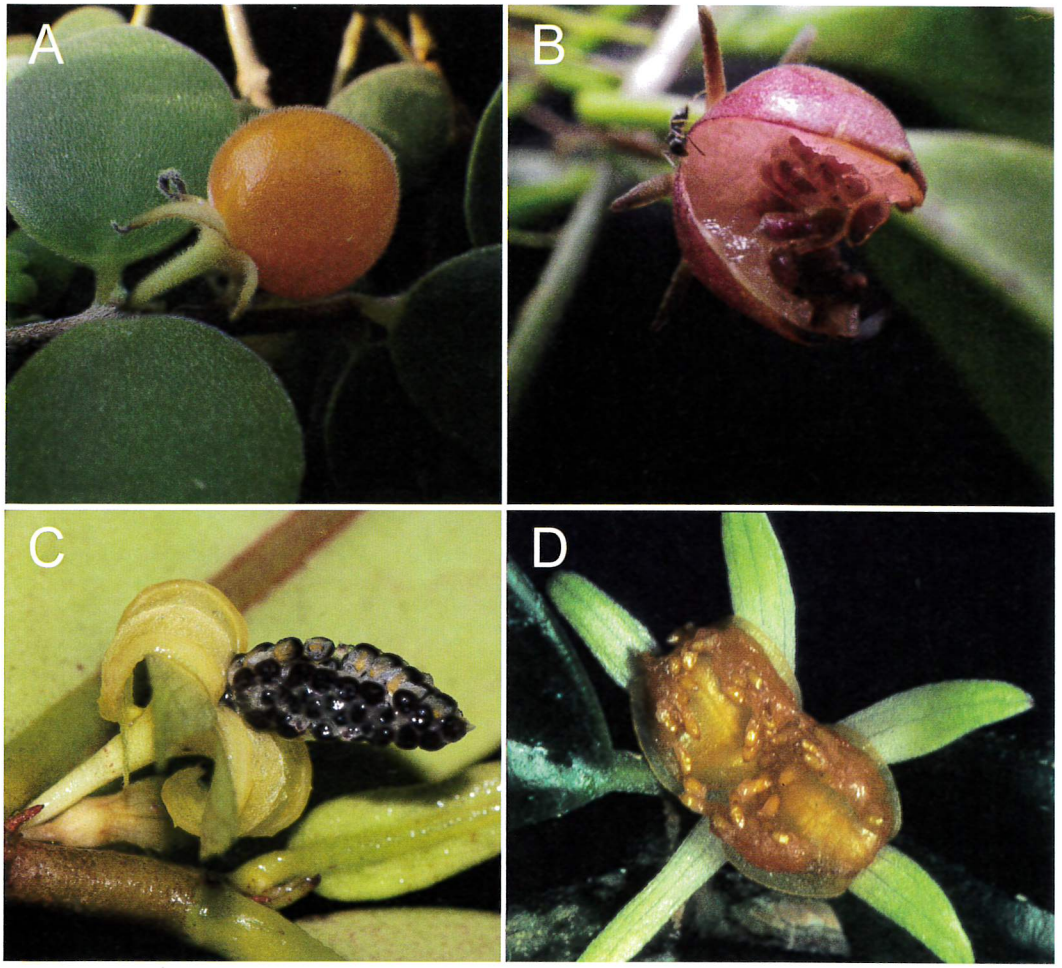

FIGURE 5. Variation in fruit morphologies in *Codonanthe* and *Codonanthopsis*. **A.** Berry in *Codonanthe devosiana* (AC-1120). **B.** tardily berrylike capsule in *Codonanthopsis crassifolia* (AC-3504). **C.** fleshy bivalve capsule with a cone-shaped mass of seeds in *C. dissimulata* (J. L. Clark 9548). **D.** fleshy capsule with seeds attached to the septum of reflexed valves (J. L. Clark 04). Accession numbers of living collections or voucher specimens at U.S. are indicated in brackets. Photos: A-B by Mathieu Perret, C by John L. Clark, D by Laurence E. Skog).

Finally, species of *Codonanthe* occurring in Central America, the Caribbean, northwestern South-America and the Amazonian basin as well as species of *Codonanthopsis* constitute an important element of the specialized flora of ''ant-gardens'' that result from their mutualistic association with arboreal tropical ants as reported for *Codonanthe calcarata, C. crassifolia, C. uleana and Codonanthopsis ulei* (Wheeler 1921, Kleinfeldt 1978, Madison 1979, Marini 1999). In this relationship, the ants are the agent of seed dispersal, carrying seeds to their arboreal carton nests, where they germinate. The plants fibrous roots reinforce the nests, providing structural support, and food for the ants is available in the form of floral and extra-floral nectar, fruit pulp and seed arils. This specialized association with ants has not been reported in the literature for *Codonanthe s.s* and was never observed during our many years of exploration in Brazil. In one case, during field work in Bahia, we observed *C. uleana* growing in an ant nest reaching the size of a grapefruit, but in other field observations this species was thriving alone. Furthermore, the presence of ants is much less frequently mentioned on herbarium labels of coastal Brazil specimens than on Amazonian specimens of this taxon. We may conclude then that the association is less obligate in coastal Brazil forests for *C. uleana* than in Amazonian forests.

These phylogenetic, morphological and ecological data clearly indicate that the *Codonanthe*

TABLE 1. Distinguishing characters between *Codonanthe* and *Codonanthopsis*.

	Codonanthe	*Codonanthopsis*
Distribution	Atlantic forest in Brazil	Central America, Caribbean, northwestern South-America, Amazonian basin, (*C. uleana* disjunct also in eastern Brazil Atlantic forest)
Ecology	Epiphytic (sometimes lithophytic), never growing in ant-gardens	Epiphytic, often growing in ant-gardens
Leaf pairs	Mostly isophyllous (except moderately anisophyllous in *C. mattos-silvae* and *C. venosa*)	Isophyllous or moderately anisophyllous or strongly anisophyllous with smaller leaf stipule-like or deciduous, i.e., phyllotaxy appearing alternate
Foliar nectaries	Absent	Present on abaxial lamina surface in some species
Leaf trichomes (Yuen 1982)	Multicellular-uniseriate non glandular and glandular trichomes with a four-celled head and a short body	Unicellular non glandular (multicellular only in *C. caribaea*) and glandular trichomes with a two-celled head
Inflorescence	Solitary (except *C. venosa* always cymose, *C. mattos-silvae* solitary or cymose)	Cymose (1–4(–12)) flowered
Corolla tube	Funnel-shaped, often ventricose, erect in calyx (narrowly funnel-shaped and oblique in calyx in *C. mattos-silvae*)	Narrowly funnel-shaped, oblique in calyx
Corolla spur	Absent, (except *C. mattos-silvae*)	Present at base
Anther connective	Wide, inflated, covering most or all the of the dorsal surface of anther thecae	Narrow, not inflated, covering only a small portion of the dorsal surface of anther thecae
Anther thecae	Never horned	Horned in some species
Pollen exine ornamentation (Yuen and Dehgan 1982); (Yuen 1982); (Gasparino 2008); (Fourny et al. 2010)	Reticulate or microreticulate lacking spinules	Reticulate with supratectate spinules in most species or rugulate (*C. uleana*) or reticulate-secondarily foveolate (*C. caribaea*)
Fruits	Yellow-orange to dark orange berries	Red, pink, purple berrylike capsules, tardily dehiscent or greenish, yellowish or reddish fleshy capsules dehiscing by 2 recurving valves
Seed length	1–1.2 mm	2–3 mm
Chromosome numbers (n)	8, 16	8, 9, 16

species occurring outside the Atlantic forest should be segregated from the Brazilian endemic *Codonanthe s.s.* In this paper, we propose to include them in an expanded definition of *Codonanthopsis* along with *Paradrymonia anisophylla* Feuillet & L.E. Skog, a recently described species from Guyana (Feuillet & Skog 2002). These taxa constitute a monophyletic group and most of them share morphological characters like the spurred corolla, the anthers connective covering only a small portion of the back-side of the anther thecae, the dehiscent fleshy capsule and the association with ants for seed dispersal. Many of these features still need to be evaluated for *Paradrymonia anisophylla* but according to the phylogenetic results by Clark et al. (2006) this species is best included as a member of *Codonanthopsis*. This expanded circumscription of *Codonanthopsis* now comprises 13 species and requires 11 new combinations. As a consequence, the genus *Codonanthe s.s.*, is reduced to eight species all endemic to the Brazilian Atlantic forest (Chautems 1997, Rossini and Chautems 2007). The following key allows for the distinction between the redefined *Codonanthe* and *Codonanthopsis* and TABLE 1 summarizes the discriminating characters.

KEY TO THE GENERA

1. Plants occurring exclusively in the Brazilian Atlantic forest, never growing on ant-nests, extra-floral nectaries absent, corolla erect in calyx, funnel-shaped or ventricose, lacking basal spur (except in *C. mattos-silvae*), anther connective wide, inflated, covering most or all the dorsal side of the anther thecae, fruit an orange berry ..... *Codonanthe*

1. Plants occurring in Central America, the Caribbean, northwestern South-America and the Amazonian basin, (nevertheless *C. uleana* occurs in the whole area, except the Caribbean, and presents also a disjunct distribution in the north-eastern part of the Brazilian Atlantic forest), often growing on ant-nests, extrafloral nectaries often present on the abaxial lamina surface, corolla oblique in calyx, tube narrowly funnel-shaped with a basal spur, anther connective covering only a small portion of the dorsal side of the anther thecae, fruit either a red, pink, purple tardily dehiscent fleshy capsule or a greenish, yellowish, reddish fleshy capsule dehiscing by 2 recurving valves ..... *Codonanthopsis*

Taxonomic Treatment

Codonanthe (Mart.) Hanst. (1858), based on *Hypocyrta gracilis* Mart. 1829. *Codonanthe* (Mart.) Hanst., Linnaea 26: 209 "1853"[April 1854], nom. cons. *Hypocyrta* sect. *Codonanthe* Mart. 1829. TYPE SPECIES: *Codonanthe gracilis* (Mart.) Hanst. (non *Codonanthus* G. Don, Gen. Hist. 4: 164, 166. 1837 (*nom. rej.*). now = *Calycobolus* in the family Convolvulaceae based on *C. africanus* G. Don ('*africana*') nom. rej. vs. *Codonanthe* (Mart.) Hanst. 1854 (*nom. cons.*). *Coccanthera* C. Koch & Hanst. (1855). Type: *Coccanthera devosiana* (Lem.) C. Koch & Hanst., Ind. Sem. Hort. Bot. Berol.: App. 17. 1855. = *Codonanthe devosiana* Lem.

Epiphytic subshrub, occasionally rupiculous, never growing in ant gardens, stems pendent or creeping or ascending, sparsely branched, often producing adventitious roots. Leaves opposite, isophyllous or moderately anisophyllous, lamina fleshy, entire, sometimes serrulate, glabrous or often pubescent or pilose, foliar nectaries absent, petiole short or nearly lacking. Inflorescences 1-few flowers in the upper leaf axils, rarely cymose with peduncles well developed, pedicels up to 1 cm. Flowers with sub-campanulate calyx, 5 lobes subequal, erect, linear, elliptic, oblong or ovate, margin entire, green, sometimes reddish; corolla erect in calyx, funnel-shaped or ventricose, lacking basal spur (except in *C. mattos-silvae* spurred basally and oblique in calyx), white, pinkish, sometimes dotted with maroon and yellow within throat and maroon outside, limb formed of 5 spreading lobes, rounded; stamens 4, included, filaments briefly adnate to the base of the corolla tube, recoiled after anthesis, anthers coherent in pairs with the 2 thecae united by a wide connective, covering most or all the dorsal surface of the anther thecae, dehiscent by a central pore, pollen exine ornamentation reticulate or microreticulate lacking spinules, bilobed nectary gland in dorsal position; ovary superior, style included, stigma bilobed to stomatomorphic. Fruit yellow-orange to dark orange berry; seeds fusiform, 1–1.2 mm long, striate, carried by fleshy funicles but not enclosed by them.

Chromosome counts. Five counts of $N = 8$ were reported for different accessions of the species currently accepted as *C. devosiana* (Wiehler 1975, Oliver and Skog 1981); and one counts of $N = 16$ were reported for an accession of a species currently accepted as *C. gracilis* (Wiehler 1975).

Codonanthe carnosa (Gardner) Hanst. in Mart., Fl. Brasil. 8(1): 418. 1864. *Hypocyrta carnosa* Gardner, London J. Bot. 1: 178. 1842. Type: Brazil, Rio de Janeiro, Corcovado, September 1836, *Gardner 73* (Holotype: K!; Isotypes: BM! E! G! P! W!).

Orobanche carnosa Vell., Fl. Flumin.: 255. 1829. Type: Brazil, Rio de Janeiro (lectotype designated here: Fl. Flumin. Atlas 6: pl. 61. 1831). *Codonanthe carnosa* (Vell.) Hoehne, non (Gardner) Hanst.

Codonanthe florida Pamp., Nuovo Giorn. Bot. Ital. (n.s.) 14: 597. 1907. Type: Culta in Horto Botanico Florentino (no specimen found in FI).

Codonanthe hookeri Lem., Ill. Hort. 2: sub pl. 56. 1855. *Hypocyrta gracilis* Hook., non Mart., Bot. Mag. 76: pl. 4531. 1850. Type: Cultivated, Hort. Backhouse (Holotype: K!).

Coccanthera hookeriana C. Koch & Hanst., nom. illeg., Ind. Sem. Hort. Berol. 1855, App. 17.1855.

Columnea scandens-hirsuta Schott ex Hanst. in Mart. Fl. Bras. 8: 417. 1864, nom. nud. pro syn.

Codonanthe hookeri f. *oblongifolia* Hoehne, Sellowia 9: 52. 1958. Type: Brazil, Rio de Janeiro, Pilar, 30 September 1931, *Brade 11152* (Holotype: R).

Distribution: Brazil (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo).

No type material for *C. florida* could be localized by the curators at the FI herbarium who did check their collection of dried and alcohol preserved specimens (C. Neri, pers. comm.). As already discussed by Pampanini in the protologue, the species is morphologically closely related to *C. carnosa* or could even be a variety of the latter. We follow also the decision of (Moore 1973) who put the two species in synonymy. Pampanini diagnose's gives a size of 20 mm for the corolla tube. This character allow to distinguish *C. carnosa* (corolla 2–2.5 cm) from *C. devosiana*

(corolla 1.2–1.8 cm) as established in the key to the *Codonanthe* species from coastal Brazil (Chautems 1997). The only doubtful indication in Pampanini's protologue is his information about the origin of the cultivated plant that is said to come from the neighborhood of Bahia. This is an imprecise information that could mean either the city of Salvador de Bahia, in Bahia state or the "bahia de Guanabara" (Guanabara bay) around the city of Rio de Janeiro, in Rio de Janeiro state. *C. carnosa* is known to occur in the vicinity of Rio de Janeiro city, but has never been registered in the state of Bahia.

Codonanthe cordifolia Chautems, Candollea 52: 159. 1997. TYPE: Rio de Janeiro, Estrada Cunha-Parati, 26 km do trevo da saida de Cunha, 2 January 1991, *Chautems & Peixoto 392* (Holotype: SP!; Isotypes: G! U.S.!).

DISTRIBUTION: Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Santa Catarina).

Codonanthe devosiana Lem. Ill. Hort. 2: pl. 56. 1855. TYPE: Cultivated, Hort. Verschaffelt (lectotype designated here: Ill. Hort. 2: pl. 56. 1855). *Codonanthe ciliosa* Lem., Ill. Hort. ii. 1855 sub t. 56. *Coccanthera devosiana* (Lem.) C. Koch & Hanst., Ind. Sem. Hort. Bot. Berol.: App. 17 1855.

Aeschynanthus albus Hort. ex Hanst. in Mart., ("*Aeschinanthus*") nom. nud. pro syn.

Aeschynanthus gracilis Hort. ex Hanst. in Mart., ("*Aeschinanthus*") nom. nud. pro syn.

Aeschynanthus pulchellus Hort. ex Hanst. in Mart., ("*Aeschinanthus*") nom. nud. pro syn.

Codonanthe digna Wiehler, Selbyana 5: 214. 1979. TYPE: Probably from southeastern Brazil, raised by D. Allen, 1970 and distributed by F. Batcheller, cultivated at greenhouses of University of Miami and at Selby Botanical Gardens under acc. no. W-1139, 6 September 1973, *Wiehler, H. 7330* (Holotype: SEL!; Isotypes: F! HB INPA K! MO! NY! R! RB SP! U.S.!).

Codonanthe paula Wiehler, Selbyana 5: 215. 1979. TYPE: Brazil, nursery outside São Paulo, obtained by Jean Hurlburt of Miami in 1976, thought to be native to vicinity of Sao Paulo, cultivated at Selby Botanical Gardens, Sarasota, FL, 8 August 1979, *Wiehler 79360* (Holotype: SEL!; Isotype: U.S.!).

DISTRIBUTION: Brazil (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul).

Codonanthe gibbosa Rossini & Chautems, Candollea 62: 216. 2007. TYPE: Brazil, Espírito Santo, Mun. Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, trilha da tronqueira, 8 October 2002, *Vervloet et al. 1171* (Holotype: MBML!; Isotype: G!).

DISTRIBUTION: Brazil (Espírito Santo).

Codonanthe gracilis (Mart.) Hanst., Linnea 26: 209. 1854. *Hypocyrta gracilis* Mart., Nov. Gen. Sp. Pl. 3: 50. 1829. TYPE: Brazil, Rio de Janeiro, *Martius* [lectotype designated by Moore (1973): M!]. *Columnea gracilis* (Mart.) Kuntze, Rev. Gen. Pl. 2: 472. 1891.

Orobanche crenata Vell., Fl. Flumin.: 254. 1829. TYPE: Brazil, Rio de Janeiro (lectotype designated here: Fl. Flumin. Atlas 6: pl. 60. 1831).

Orobanche ventricosa Vell., Fl. Flumin.: 259. 1829. TYPE: Brazil, Rio de Janeiro (lectotype designated here: Fl. Flumin. Atlas 6: pl. 74. 1831). *Codonanthe ventricosa* (Vell.) Hoehne, Sellowia 9: 53. 1958.

Codonanthe picta Lem., Ill. Hort. 4: pl. 144. 1857. TYPE: Cultivated, Hort. Verschaffelt (lectotype designated here: Ill. Hort. 4: pl. 144. 1857).

DISTRIBUTION: Brazil (Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul).

Codonanthe mattos-silvae Chautems, Revista Brasil. Bot. 14: 52. 1991. TYPE: Brazil, Bahia, Mun. Ubaíra, km 6 da rod. BR-420, trecho Ubaíra-Mutuípe, Faz. Palmeira, 13 October 1977, *Santos 3145* (Holotype: CEPEC!; Isotype: R!).

DISTRIBUTION: Brazil (Alagoas, Bahia, Sergipe).

Codonanthe serrulata Chautems, Revista Brasil. Bot. 14: 54. 1991. TYPE: Brazil, Bahia, Mun. Camacã, Estrada que liga a rodovia BR-101 a Santa Luzia-Una (altura da ponte sobre o Córrego de Ouro), ca. 10 km da entrada, depois da sede da fazenda Santa Cruz, 19 February 1987, *Chautems & Edwards 217* (Holotype: CEPEC!; Isotype: G!).

DISTRIBUTION: Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

Codonanthe venosa Chautems, Candollea 52: 162. 1997. TYPE: Brazil, São Paulo, Picinguaba, trilha do lado esquerdo do Rio Picinguaba, 10 October 1988, *Cunha et al. 215* (Holotype: HRCB!; Isotypes: MO! SP! SPF!).

DISTRIBUTION: Brazil (Rio de Janeiro, São Paulo).

Codonanthopsis Mansf., Repert. Spec. Nov. Regni Veg. 36: 120. 1934. TYPE SPECIES:***Codonanthopsis ulei*** Mansf. Synonyms: *Codonanthopsis* sect. *Homorphosepala* Hoehne.,

Sellowia 9: 48. 1958. *Codonanthe* sect. *Spathuliformae* L. B. Sm., Bull. Torrey Bot. Club 60: 657. 1933. *Codonanthe* sect. *Codonanthopsis* (Mansf.) H. E. Moore, Baileya 19: 25. 1973.

Epiphytic subshrub, often growing on ant gardens, stems pendent, creeping or rarely erect, sparsely branched, 0.3–1(–2) m long, occasionally producing adventitious roots. Leaves opposite, isophyllous or moderately anisophyllous or strongly anisophyllous with the smaller leaf stipule-like or deciduous, lamina fleshy to coriaceous, entire, sometimes serrulate towards the apex, reddish extrafoliar nectaries often present on abaxial surface, petioles short. Inflorescences 1–4(–12) flowers in the upper leaf axils, peduncles rarely well developed, pedicels short. Flowers with 5-lobed calyx or rarely bilabiate, lobes usually linear or narrowly lanceolate, rarely narrowly triangular, dorsal lobe often reduced in size and recurved around the spurred base; corolla oblique in calyx, mostly white, sometimes yellowish or pinkish or wine-red spotted, reddish lines or spots on the spur, tube narrowly funnel-shaped, sometimes dorsally arcuate, throat often with yellow blotch or reddish marks, limb formed of 5 spreading lobes, rounded; stamens 4, included, filaments briefly adnate to the base of the corolla tube, recoiled after anthesis, anthers coherent in pairs, the two thecae of each anther separated by narrow connective that covers only a small portion of the dorsal surface of anther thecae, dehiscent by a central or upper pore or entirely dehiscent (in *C. dissimulata*), often surrounded by 2 horns; pollen exine ornamentation variously spinulose or rugulate or reticulate-secondarily foveolate; bilobed nectary gland in dorsal position; ovary superior, style included, stigma bilobed to stomatomorphic. Fruit a fleshy berrylike capsule, globose, ovoid or somewhat compressed, yellowish, red, pink or purple, usually tardily dehiscent, in some case a fleshy capsule dehiscing by 2 recurving valves; seeds fusiform, 2–3 mm long, obliquely striate, partly or mostly enclosed by fleshy funicles.

Chromosome counts. A chromosome number of $N = 9$ has been reported for *Codonanthopsis dissimulata* (Wiehler 1978). This unique number within Episcieae was suggested by Wiehler (1983) to be a diagnostic feature for *Codonanthopsis* as previously defined. This was later revealed untrue by Oliver and Skog (1985), who counted $2n = 16$ in *C. ulei,* the second species originally described in *Codonanthopsis*. All other species originally placed in *Codonanthe* are mainly characterized by a chromosome count of $N = 16$ or $2n = 32$ (Möller et al. 2002 onwards). The number $N = 8$ has been registered only in *C. caribaea* and in one accession of *C. luteola* (Lee 1966, Wiehler 1975). It is worth noting that for this latter species two other counts made on different accessions gave $N = 16$ (Wiehler 1975, Oliver and Skog 1981).

Codonanthopsis anisophylla (Feuillet & L.E. Skog) Chautems & Mat. Perret, **comb. nov.,** *Paradrymonia anisophylla* Feuillet & L.E. Skog, Brittonia 54: 354. 2003. TYPE: Guyana, Cuyuni-Mazaruni region, Partang River, wet forest on top of Merume Mountain, 1 July 1960, *Tillet, Tillet & Boyan 43948* (Holotype: U.S.!; Isotype: NY).

DISTRIBUTION: Guyana.

Codonanthopsis calcarata (Miq.) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe calcarata* (Miq.) Hanst., Linnaea 34: 416. 1865. *Nematanthus calcaratus* Miq., Linnaea 22: 472 (1849). TYPE: Suriname, *Focke 941* (Holotype: U).

Codonanthe bipartita L.B. Sm., Bull. Torrey Bot. Club 60: 657, figs. 1–6. 1933, type for section Spathuliformae. TYPE: Guyana, Kartabo region, July–August 1920, *I. W. Bailey 181* (Holotype: GH!; Isotype: NY!).

DISTRIBUTION: Bolivia (Beni, Cochabamba, La Paz, Santa Cruz), Brazil (Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima), Colombia (Amazonas), French Guiana, Guyana, Suriname, Venezuela (Amazonas, Anzoátegui, Apure, Barinas, Bolívar, Delta Amacuro, Monagas).

Codonanthopsis caribaea (Urb.) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe caribaea* Urb., Symb. Antill. 2: 365. 1901. TYPE: Guadeloupe, Bord de la Rivière Noire, 1896, *Duss 3376* (Holotype destroyed in B; lectotype designated here NY0011422; isolectotypes: F! MO! NY! U.S.!).

Codonanthe eggersii Urb., Symb. Antill. 2: 366. 1901. TYPE: Trinidad & Tobago,Tobago, Great Dog River, November 1889, *Eggers 5848* (Holotype destroyed in B, lectotype designated here: K000644106! isolectotypes: P! U.S.!).

Codonanthe triplinervia Britton, Bull. Torrey Bot. Club 48: 339. 1922. Trinidad & Tobago, Trinidad, Oratoire River, Guayaguayare Road, 25 March 1921, *Britton et al. 2543* (Holotype: NY00312585!; Isotypes: GH! U.S.!).

Codonanthe triplinervia var. *latifolia* C.V. Morton, Fl. Trinidad and Tobago 2(5): 309. 1955. TYPE: Trinidad & Tobago, Trinidad, summit of El Tucuche, 2 January 1948, *Simmonds 241* (isotype: fragment U.S.!).

Codonanthe triplinervia var. *purpurea* C.V. Morton, Fl. Trinidad and Tobago 2(5):309. 1955. TYPE: Trinidad & Tobago, Trinidad, 11th ml.

of Arima – Blanchisseuse Road, 17 August 1977, *Simmonds 147* (isotype: fragment U.S.!).

DISTRIBUTION: Guadeloupe, Trinidad and Tobago (Tobago, Trinidad), Venezuela (Aragua, Carabobo, Falcón, Sucre).

Codonanthopsis chiricana (Wiehler) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe chiricana* Wiehler, Selbyana 2: 95. 1977. TYPE: Panama, Chiriqui, near Valle Hornito and Cerro Hornito, Fortuna Dam site, 1 July 1977, *Wiehler 77110* (Holotype: SEL001571!; Isotype: K! MO! PMA! U.S.!).

DISTRIBUTION: Panama.

Codonanthopsis corniculata (Wiehler) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe corniculata* Wiehler, Selbyana 2: 95. 1977. TYPE: Peru, Loreto, near Iquitos, cultivated at Selby Botanical Gardens, 1 July 1977, *Wiehler 77111* (Holotype: SEL001570!; Isotypes: F! K! MO! NY! U.S.!).

DISTRIBUTION: Peru (Loreto, San Martín).

Codonanthopsis crassifolia (H. Focke) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe crassifolia* (H. Focke) C.V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1159. 1938. *Hypocyrta crassifolia* H. Focke, Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 5: 199. 1852. TYPE: Suriname, *Focke s.n.* colored drawing (L photo U.S.).

Centrosolenia glabra sensu Hook., non Benth., Icon. Pl. 9: pl. 873. 1852. *Episcia hookeri* Hanst., Linnaea 34: 350. 1865. TYPE: Trinidad & Tobago, Trinidad, *Purdie s.n.* (lectotype designated by Leeuwenberg (1958): Hooker's Ic. Pl. 9: pl. 873).

Codonanthe confusa Sandw., Bull. Misc. Inform. Kew 1931: 492. 1931. TYPE: French Guiana, Karouany, 1854, *Sagot 426* (Holotype: K000450095!; Isotypes: BM! BR! G! MPU! P, U, W!).

Codonanthe stenantha Hoehne, Sellowia 9: 51. 1958. TYPE: Brazil, Mato Grosso, Cerrado do Rio Juina, October 1911, *Hoehne-Comissão Rondon 5541* (Holotype: R 96946!).

After examination of the type collection in R, we add here *Codonanthe stenantha* Hoehne as a new synonym of *C. crassifolia*. The decisive character is the size of the corolla (about 2 cm long) and its narrow tube that is reflected by the specific epithet «stenantha» that means narrow flowers. *C. crassifolia* is characterized by corolla tubes that are narrow (2–4 mm for most of their length) and flowers usually measuring 1.5–2.5 cm, whereas most other species in the genus possess flowers that are 2–4 cm long with a wider corolla tube. Hoehne (1958) commented that his species may have some affinity with the latter species, but that the calyx lobes are more "ovo-triangular" shaped (vs. linear lanceolate). This calyx character and the other observations of Hoehne on the small leaf size of reddish color are not sufficient for recognizing a different species considering that *C. crassifolia* has the greatest range and the most variable morphology of any species in the genus, as already noted by Moore (1973).

PHYSIOLOGY: Crassulacean Acid Metabolism (CAM) has been documented for *Codonanthopsis crassifolia* (Guralnick et al. 1986).

DISTRIBUTION: Belize, Bolivia (La Paz, Pando, Santa Cruz), Brazil (Amapá, Amazonas, Mato Grosso, Pará, Roraima), Colombia (Amazonas, Antioquia, Caquetá, Chocó, Meta, Nariño, Risaralda, Santander, Valle del Cauca, Vaupés), Costa Rica, Ecuador (Esmeraldas, Guayas, Los Ríos, Manabí, Morona-Santiago, Napo, Pastaza, Pichincha, Sucumbios), French Guiana, Guatemala, Guyana, Honduras, México (Chiapas, Tabasco), Nicaragua, Panama, Peru (Amazonas, Cuzco, Huánuco, Junín, Loreto, San Martín), Suriname, Trinidad and Tobago (Trinidad), Venezuela (Amazonas, Apure, Bolívar, Delta Amacuro, Portuguesa, Táchira, Zulia).

Codonanthopsis dissimulata (H. E. Moore) Wiehler, Selbyana 5: 61. 1978. *Codonanthe dissimulata* H. E. Moore, Baileya 19: 25. 1973. TYPE: originally collected in Peru, Iquitos, cultivated at Bailey Hortorium, Ithaca, NY, 14 September 1971, *Stone 1143* (Holotype: BH).

Codonanthopsis peruviana Wiehler, Selbyana 7: 346. 1984. TYPE: originally collected in Peru, Huanuco, Panguana, cultivated at Selby Botanical Gardens, Sarasota, FL, 29 July 1983, *Wiehler 8302* (Holotype: USM; Isotypes: CUZ GH K! MO! NY SEL! U.S. W!).

DISTRIBUTION: Brazil (Acre, Amazonas, Roraima), Colombia (Amazonas), Ecuador (Esmeraldas, Morona-Santiago, Napo, Sucumbios, Zamora-Chinchipe), French Guiana, Guyana, Peru (Amazonas, Huánuco, Loreto, Madre de Dios, Pasco, San Martín), Venezuela (Amazonas).

Codonanthopsis elegans (Wiehler) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe elegans* Wiehler, Selbyana 7: 344. 1984. TYPE: originally collected in Belize, Toledo, Abraham Camp, between San José and Edwards Central, cultivated at Selby Botanical Gardens, Sarasota, FL, 29 July 1983, *Wiehler 8301* (Holotype: SEL001573!).

DISTRIBUTION: Belize.

Codonanthopsis erubescens (Wiehler) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe*

erubescens Wiehler, Phytologia 73(3): 221. 1992. TYPE: Ecuador, Morona-Santiago, 22 April 1988, *Wiehler & GRF Expedition 88152* (neotype designated by (Clark et al. 2003): Gesneriana 1: 32, fig. 2, 1995).

DISTRIBUTION: Ecuador (Morona-Santiago, Zamora-Chinchipe).

Codonanthopsis luteola (Wiehler) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe luteola* Wiehler, Selbyana 1(2): 159. 1975. TYPE: Panama, Cerro Jefe, ca. 20 km N of Tocumen airport; near road to orchidarium, 11 August 1971, *Wiehler & Dressler 71184* (Holotype: US00126532!; Isotypes: B! F! GH! K! MO! NY! S! P! PMA! SEL!).

DISTRIBUTION: Panama.

Codonanthopsis macradenia (Donn. Sm.) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe macradenia* Donn. Sm., Bot. Gaz. 25: 154. 1898. TYPE: Costa Rica, Boruca, March 1892, *Tonduz 6769* (lectotype US00126533! designated by Moore (1973) isolectotypes: BM! BR! P! U!).

DISTRIBUTION: Belize, Colombia (Chocó, La Guajira, Santander), Costa Rica, Guatemala, Honduras, Mexico (Oaxaca), Panama.

Codonanthopsis uleana (Fritsch) Chautems & Mat. Perret, **comb. nov.,** *Codonanthe uleana* Fritsch, Bot. Jahrb. Syst. 37: 492. 1906. TYPE: Brazil, ["Amazonas"] Acre, Juruá Miry, Rio Juruá sup., *Ule 5617* (Holotype B, destroyed; lectotype designated by Wiehler (1975) HBG517532! isolectotype MG!).

Codonanthe uleana var. *integrifolia* Fritsch, Bot. Jahrb. Syst. 37: 492. 1906. TYPE: Brazil, ["Amazonas"] Acre, Juruá Miry, Rio Juruá super., *Ule 21b* (B, destroyed, isotypes not found).

Codonanthe formicarum Fritsch, Bot. Jahrb. Syst. 37: 491. 1906. TYPE: Brazil, Rio Jurua sup., *Ule 5776* (Holotype: B, destroyed; lectotype designated here HBG517533!).

Codonanthe decurrens I. M. Johnst., Sargentia 8: 275. 1949 - based on *Columnea calcarata* Donn. Sm, non *Codonanthe calcarata* (Miq.) Hanst. TYPE: Guatemala, Alta Verapaz, Cubilquitz, *von Tuerckheim 7645* (Holotype US00126460!; Isotypes: GH, K! U.S.!).

DISTRIBUTION: Belize, Bolivia (La Paz, Beni), Brazil (Amazonas, Acre, Alagoas, Bahia, Espírito Santo, Mato Grosso, Mato Grosso do Sul, Paraíba, Pernambuco, Rondônia, Roraima), Colombia (Amazonas, Antioquia, Caquetá, Chocó, Cundinamarca, Meta, Putumayo, Santander, Valle del Cauca, Vaupés), Costa Rica, Ecuador (Carchi, Esmeraldas, Los Ríos, Napo, Pastaza, Pichincha, Sucumbios), Guatemala, Honduras, Mexico (Chiapas, Oaxaca, Tabasco), Nicaragua, Panama, Peru (Amazonas, Cuzco, Huánuco, Loreto, Madre de Dios, San Martín, Ucayali), Trinidad and Tobago (Trinidad), Venezuela (Amazonas, Apure, Barinas, Bolívar, Carabobo, Mérida, Táchira, Zulia).

Codonanthopsis ulei Mansf., Repert. Spec. Nov. Regni Veg. 36: 120. 1934. TYPE: Brazil, Amazonas, Rio Negro, Manaus, Cachoeira Grande, March 1912, *Ule 8962* (Holotype B, destroyed; lectotype designated here: US00126517! isolectotypes G! K! NY!).

Codonanthopsis huebneri Mansf., Repert. Spec. Nov. Regni Veg. 36: 120. 1934. TYPE: Brazil, Baixo-Amazonas, April 1928, *Hübner 13* (Holotype B, destroyed, isotypes not found).

Codonanthopsis mansfeldiana Hoehne, Sellowia 9: 48. 1958. TYPE: Brazil, Amazonas, Manaus, 19 December 1945, *Murça Pires & Black 1015* (Holotype: IAN!).

DISTRIBUTION: Brazil (Amazonas, Acre, Pará), Colombia (Amazonas), Ecuador (Napo, Pastaza), Peru (Amazonas, Huánuco, Junín, Loreto), and Venezuela (Amazonas).

The examination of several herbarium sheets as well as different accessions of live material in cultivation, including material originally collected in the surroundings of the city of Manaus, allowed us to observe a continuous variation in the size of the flowers. Leaves vary also in length between 5 and 30 cm. Separating the examined material in various taxonomic entities does not seem possible, therefore we consider that only a single and rather variable species must be recognized. As the corolla length described by Mansfeld for his *C. ulei* is in the middle of the range of variation, we decide to retain this name and place in synonymy *C. huebneri* whose descriptions gives corollas length of up to 1.2 cm whereas *C. mansfeldiana* has corollas described as measuring some 2.5 cm. Nevertheless, no type material for *C. huebneri* could be found, the type material designated by Mansfeld and another Huebner collection cited in the protologue were very likely destroyed during World War II bombing of the Berlin herbarium. Our decision is then based only on the rather detailed decriptions given by Mansfeld.

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APPENDIX 1. Index of names for *Codonanthe* and *Codonanthopsis* (accepted names in bold).

Taxa	Accepted names
Aeschynanthus albus Hort. ex Hanst.	***Codonanthe devosiana***
Aeschynanthus gracilis Hort. ex Hanst.	***Codonanthe devosiana***
Aeschynanthus pulchellus Hort. ex Hanst.	***Codonanthe devosiana***
Centrosolenia glabra sensu Hook., non Benth	***Codonanthopsis crassifolia***
Coccanthera devosiana Lem.	***Codonanthe devosiana***
Coccanthera hookeriana C. Koch & Hanst.	***Codonanthe carnosa***
Codonanthe bipartita L.B. Sm.	***Codonanthopsis calcarata***
Codonanthe calcarata (Miq.) Hanst.	***Codonanthopsis calcarata***
Codonanthe calcarata sensu Hanst.	***Codonanthopsis crassifolia***
Codonanthe caribaea Urb.	***Codonanthopsis caribaea***
***Codonanthe carnosa* (Gardner) Hanst.**	
Codonanthe carnosa (Vell.) Hoehne, non (Gardner) Hanst	***Codonanthe carnosa***
Codonanthe chiricana Wiehler	***Codonanthopsis chiricana***
Codonanthe ciliosa Lem.	***Codonanthe devosiana***
Codonanthe confusa Sandw.	***Codonanthopsis crassifolia***
***Codonanthe cordifolia* Chautems**	
Codonanthe corniculata Wiehler	***Codonanthopsis corniculata***
Codonanthe crassifolia (H. Focke) C.V. Morton	***Codonanthopsis crassifolia***
Codonanthe decurrens I. M. Johnst.	***Codonanthopsis uleana***
***Codonanthe* devosiana Lem.**	
Codonanthe digna Wiehler	***Codonanthe devosiana***
Codonanthe dissimulata H. E. Moore	***Codonanthopsis dissimulata***
Codonanthe eggersii Urb.	***Codonanthopsis caribaea***
Codonanthe elegans Wiehler	***Codonanthopsis elegans***
Codonanthe erubescens Wiehler	***Codonanthopsis erubescens***
Codonanthe florida Pamp.	***Codonanthe carnosa***
Codonanthe formicarum Fritsch	***Codonanthopsis uleana***
***Codonanthe gibbosa* Rossini & Chautems**	
***Codonanthe gracilis* (Mart.) Hanst.**	
Codonanthe hookeri Lem.	***Codonanthe carnosa***
Codonanthe hookeri f. *oblongifolia* Hoehne	***Codonanthe carnosa***
Codonanthe luteola Wiehler	***Codonanthopsis luteola***
Codonanthe macradenia Donn. Sm.	***Codonanthopsis macradenia***
***Codonanthe mattos-silvae* Chautems**	
Codonanthe paula Wiehler	***Codonanthe devosiana***
Codonanthe picta Lem.	***Codonanthe gracilis***
***Codonanthe serrulata* Chautems**	
Codonanthe triplinervia Britton	***Codonanthopsis caribaea***
Codonanthe triplinervia var. *latifolia* C. V. Morton	***Codonanthopsis caribaea***
Codonanthe triplinervia var. *purpurea* C. V. Morton	***Codonanthopsis caribaea***
Codonanthe uleana Urb.	***Codonanthopsis uleana***
Codonanthe uleana var. *integrifolia* Fritsch	***Codonanthopsis uleana***
***Codonanthe venosa* Chautems**	
***Codonanthopsis calcarata* (Miq.) Chautems & Mat. Perret**	
***Codonanthopsis caribaea* (Urb.) Chautems & Mat. Perret**	
***Codonanthopsis chiricana* (Wiehler) Chautems & Mat. Perret**	
***Codonanthopsis corniculata* (Wiehler) Chautems & Mat. Perret**	
***Codonanthopsis crassifolia* (H. Focke) Chautems & Mat. Perret**	
***Codonanthopsis dissimulata* (H. E. Moore) Wiehler**	
***Codonanthopsis elegans* (Wiehler) Chautems & Mat. Perret**	
***Codonanthopsis erubescens* (Wiehler) Chautems & Mat. Perret**	
Codonanthopsis huebneri Mansf.	***Codonanthopsis ulei***
***Codonanthopsis luteola* (Wiehler) Chautems & Mat. Perret**	
***Codonanthopsis macradenia* (Donn. Sm.) Chautems & Mat. Perret**	
Codonanthopsis mansfeldiana Hoehne	***Codonanthopsis ulei***
Codonanthopsis peruviana Wiehler	***Codonanthopsis dissimulata***
***Codonanthopsis uleana* (Urb.) Chautems & Mat. Perret**	
***Codonanthopsis ulei* Mansf.**	
Columnea gracilis (Mart.) Kuntze	***Codonanthe gracilis***
Columnea scandens-hirsuta Schott ex Hanst.	***Codonanthe carnosa***
Episcia hookeri Hanst.	***Codonanthopsis crassifolia***
Hypocyrta carnosa Gardner	***Codonanthe carnosa***

APPENDIX 1. Continued.

Taxa	Accepted names
Hypocyrta crassifolia H. Focke	***Codonanthopsis crassifolia***
Hypocyrta gracilis Mart.	***Codonanthe gracilis***
Hypocyrta gracilis Hook., non Mart.	***Codonanthe carnosa***
Nematanthus calcaratus Miq.	***Codonanthopsis calcarata***
Orobanche carnosa Vell.	***Codonanthe carnosa***
Orobanche ventricosa Vell.	***Codonanthe gracilis***
Paradrymonia anisophylla Feuillet & L. E. Skog	***Codonanthopsis anisophylla***