REVISION AND MORPHOLOGICAL PHYLOGENY OF *EPHEDRANTHUS*, A NEOTROPICAL GENUS OF ANNONACEAE[1]

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ABSTRACT

Ephedranthus S. Moore is a Neotropical genus of Annonaceae distributed from Colombia and the Guianas to Bolivia and southeastern Brazil, comprised of seven species: *E. amazonicus* R. E. Fr., *E. boliviensis* Chatrou & Pirie, *E. colombianus* Maas & Setten, *E. dimerus* J. C. Lopes, Chatrou & Mello-Silva, *E. guianensis* R. E. Fr., *E. parviflorus* S. Moore, and *E. pisocarpus* R. E. Fr. The genus is recognized by the combination of leaves with impressed adaxial veins, short pedicels, two to five bracts, androdioecy (i.e., some plants with only staminate flowers, other plants with only bisexual flowers), and 1-seeded monocarps. This revision updates the knowledge about the genus, providing a morphological phylogenetic analysis of *Ephedranthus* species, with a key, descriptions, distribution maps, and illustrations of the diagnostic characters of the species. The phylogenetic analysis shows *Ephedranthus* defined by having staminate flowers and basal placentation, and the seven species related as ((*E. colombianus*, *E. boliviensis*) ((*E. guianensis*, *E. amazonicus*) (*E. dimerus* (*E. parviflorus*, *E. pisocarpus*)))); based on this, the current subdivision of *Ephedranthus* is not monophyletic, and the sections are here synonymized.

Key words: Androdioecy, Annonaceae, *Ephedranthus*, Malmeeae, Neotropics.

Ephedranthus S. Moore (Annonaceae) is a Neotropical genus distributed from Colombia and the Guianas to Bolivia and southeastern Brazil. Its species occur in almost all forested regions of South America, in the Amazon Forest, in the caatinga, cerrado, and Atlantic Forest in Brazil, in the chiquitanos forest in Bolivia, and in the Andean forests of Colombia. There are seven known species, three endemic to Brazil (*E. dimerus* J. C. Lopes, Chatrou & Mello-Silva, *E. parviflorus* S. Moore, and *E. pisocarpus* R. E. Fr.), one each endemic to Colombia (*E. colombianus* Maas & Setten) and to the Guianas (*E. guianensis* R. E. Fr.), and two more widely distributed in the Amazon region (*E. amazonicus* R. E. Fr. and *E. boliviensis* Chatrou & Pirie).

The genus is recognized by the combination of leaves with impressed adaxial veins, flowering pedicels 0–10 mm long, two to five bracts, androdioecy (with individual plants having either staminate or bisexual flowers), and 1-seeded stipitate monocarps. Other morphologically related genera with numerous bracts are *Oxandra* A. Rich and *Pseudoxandra* R. E. Fr. (Maas & Westra, 2003; Junikka et al., 2016). These genera are distinguished from *Ephedranthus* by having leaves with adaxial secondary veins consistently flat, only bisexual flowers (with few exceptions in both genera), and narrow stamens with tonguelike connective extension versus peltate stamen with truncate connective in *Ephedranthus*.

Moore (1895) described *Ephedranthus*, with one species, *E. parviflorus*. Fries (1931) described *E. guianensis* with two varieties, *E. guianensis* var. *oligantha* R. E. Fr. and variety *guianensis*, and later described *E. amazonicus* and divided the genus in two sections, *Ephedranthus* sect. *Ephedranthus* ("*Eu-Ephedranthus*"), which included *E. guianensis* and *E. parviflorus*, and *Ephedranthus* sect. *Sphaeranthema* R. E. Fr., including solely *E. amazonicus* (Fries, 1934). Section *Ephedranthus* was characterized by having long hairs on the pedicels, oblong, erect-patent petals, and ovoid ovary with long stigma, and section *Sphaeranthema* by having short hairs on the pedicels, orbicular-concave petals, and prismatic ovary with truncate stigma (Fries, 1934). Fries (1941) described one more species, *E. pisocarpus*, and included it in section *Ephedranthus*. More than 40 years later, Maas et al. (1988) described *E. colombianus*, and 11 years after that, Oliveira and Sales (1999) published the first taxonomic revision of *Ephedranthus*. More recently, two new species were

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described, *E. boliviensis* (Chatrou & Pirie, 2003), and *E. dimerus* (Lopes et al., 2014).

Multiple molecular phylogenetic analyses support *Ephedranthus* as a monophyletic assemblage (Pirie et al., 2006; Chatrou et al., 2012; Guo et al., 2017; Lopes et al., 2018). However, the phylogenetic relationships among its species have not been recovered yet. Pirie et al. (2006) and Guo et al. (2017) each sampled three species of *Ephedranthus* using eight molecular markers in their phylogenetic analyses, and Chatrou et al. (2012) and Lopes et al. (2018) each sampled only two species, using nine and 66 molecular markers, respectively. *Ephedranthus* belongs to tribe Malmeeae (subfamily Malmeoideae), a monophyletic clade of 13 genera (Pirie et al., 2006; Chatrou et al., 2012; Guo et al., 2017; Lopes et al., 2018), but the position of *Ephedranthus* within the tribe remains unclear. It was recovered as sister to the monophyletic *Ruizodendron* R. E. Fr. by Pirie et al. (2006) and Chatrou et al. (2012), but in Lopes et al. (2018) *Ephedranthus* emerged in a polytomy within a polyphyletic *Oxandra*.

Here we present the taxonomic revision of *Ephedranthus*, as part of the phylogenetic studies in tribe Malmeeae (Lopes et al., 2018), and a phylogenetic analysis of its species based on morphological data.

Materials and Methods

A total of 500 *Ephedranthus* specimens from BM, BR, CEN, EAFM, IAN, IBGE, INPA, K, MG, NY, P, RB, S, SPF, U, UB, US, and WAG herbaria were analyzed (acronyms according to Thiers, 2018), together with material from Reflora (2019). A barcode and exclamation point indicate that the material was analyzed. Measurements of vegetative and reproductive structures were taken, and morphological variation was observed using a stereomicroscope. Nomenclature of shapes and leaf structure follows Hickey (1979).

Maps were prepared using Quantum Gis (QGIS Development Team, 2009). Shape files with South American and Brazilian political divisions were downloaded from <http://www.forest-gis.com/download-de-shapefiles/>. Illustrations were prepared by Laura Montserrat and were based on photos and herbarium material.

Cladistic analysis

The cladistic analysis was undertaken using all seven species of *Ephedranthus* and four species as outgroup, three from tribe Malmeeae, *Bocageopsis pleiosperma* Maas, *Pseudoxandra obscurinervis* Maas, and *Ruizodendron ovale* (Ruiz & Pav.) R. E. Fr., plus *Anaxagorea phaeocarpa* Mart. (Farris, 1972; Nixon & Carpenter, 1993). A total of 25 morphological characters were measured (Tables 1, 2). Although the morphological data are more limited than molecular data in terms of number of informative characters and of the environmental influence on the phenotype (Hillis, 1987), this analysis attempts to include characters from all parts of the plant, including leaf, flower, pollen, fruit, and seeds, using the outgroup criterion of homology (Watrous & Wheeler, 1981; Farris, 1982; Maddison et al., 1984). Some characters were taken from Doyle and Le Thomas (1996), mainly the leaf, floral, and pollen characters. Character states of leaf anatomy, pollen, and seeds were taken from van Setten and Koek-Noorman (1986, 1992) and Walker (1971). Maas and Westra (1984, 1985, 2003), Maas et al. (2007), and Erkens et al. (2017) were consulted for outgroup character states. Voucher specimens are cited in the taxonomic treatment. Brief descriptions of each character and its states are below.

Characters 1–6. Leaf

Simple hairs on the leaves is an important character in the distinction of the *Ephedranthus* species (Moore, 1895; Fries, 1931, 1934, 1941; Maas et al., 1988; Oliveira & Sales, 1999; Chatrou & Pirie, 2003; Lopes et al., 2014). Papillae are unspecialized epidermal cells and are found in some genera of Malmeeae and few species of *Annona* L. (van Setten & Koek-Noorman, 1986). Oil cells have been reported to occur in the lamina of Annonaceae species. These cells occur mostly in the sponge parenchyma, or in the intermediate zone between the palisade and sponge parenchyma. However, oil cells also occur in the palisade parenchyma and less often immediately below the epidermis (van Setten & Koek-Noorman, 1986). The relative position of primary and tertiary veins is an informative character in Annonaceae (Doyle & Le Thomas, 1996). The outline of primary veins is also an important feature in the recognition of genera in tribe Malmeeae (Maas & Westra, 2003; Maas et al., 2007).

Characters 7–15. Flower

Flowers are either always solitary or rarely in pairs, or borne in determinate inflorescences that vary within a given species from one to many, normally with many flowers (Doyle & Le Thomas, 1996). Length of the flower pedicel is an important feature in the recognition of species in *Ephedranthus* (Fries, 1941). Petal aestivation in Annonaceae is valvate, reduplicate-valvate, imbricate, transversely folded, and apert (or open, with margins not touching) (van Heusden, 1992). Within tribe Malmeeae (Koek-Noorman et al., 1990), petal aestivation varies from imbricate in *Cremastosperma* R. E. Fr., *Ephedranthus*, *Klarobelia* Chatrou, *Malmea* R. E. Fr., *Mosannona* Chatrou, *Oxandra*,

Table 1. Characters analyzed and coding for cladistic analysis of *Ephedranthus*.

1. Hairs on the abaxial side of lamina: absent (0); present (1)
2. Papillae (van Setten & Koek-Noorman, 1986, 1992): absent (0); present (1)
3. Oil cell in palisade parenchyma (van Setten & Koek-Noorman, 1986, 1992): absent (0); present (1)
4. Idioblasts with silica bodies (van Setten & Koek-Noorman, 1986, 1992): absent (0); present (1)
5. Midrib (Doyle & Le Thomas, 1996): concave or flat (0); convex (1)
6. Tertiary veins on the abaxial side of lamina: immersed to slightly raised (0); distinctly raised-reticulate (1)
7. Flower number: always one (or two) (0); one to many (1)
8. Length of flower pedicel: more than 3 mm (0); 0–2 mm (1)
9. Petal aestivation (Doyle & Le Thomas, 1996): valvate (0); imbricate (1)
10. Petal texture: coriaceous (0); chartaceous (1)
11. Outer petal shape: narrowly obovate to oblanceolate to elliptic (0); ovate, orbiculate to suborbiculate (1); narrowly oblong to oblong (2)
12. Male flower: absent (0); present (1)
13. Stamen shape (Doyle & Le Thomas, 1996): laminar (0); narrow with tonguelike connective (1); peltate-truncate (2)
14. Stigma shape (Doyle & Le Thomas, 1996): lobed (0); capitate (1); cylindrical (2)
15. Ovule number: one (0); two (1); two to five (2)
16. Infratectal structure (Walker, 1971): granular (0); columellar (1)
17. Hairs on fruit pedicel: absent (0); present (1)
18. Veins on monocarp wall: absent (0); present (1)
19. Texture of monocarp wall: smooth (0); verrucose (1)
20. Monocarp shape (Doyle & Le Thomas, 1996): club-shaped (0); ellipsoid (1); globose to ovoid (2); cylindrical (3)
21. Monocarp apex: rounded (0); apiculate (1); umbonate (2)
22. Stipe length: 0–11 mm (0); 12–19 mm (1); 20–40 mm (2)
23. Placentation (van Setten & Koek-Noorman, 1986, 1992): basal (0); lateral (1)
24. Raphe (van Setten & Koek-Noorman, 1986, 1992): indistinct (0); ribbed (1); grooved (2)
25. Rumination (van Setten & Koek-Noorman, 1986, 1992): ribbon-shaped (0); spiniform (1); lamellate (2)

Pseudephedranthus Aristeg., *Pseudomalmea* Chatrou, *Pseudoxandra*, and *Ruizodendron* to valvate in *Bocageopsis* R. E. Fr., *Onychopetalum* R. E. Fr., and *Unonopsis* R. E. Fr. (Lopes et al., 2018). Petals in Annonaceae are usually fleshy (van Heusden, 1992), becoming coriaceous in dried material. Chartaceous petals are less common. Petal shape is variable, usually also between inner and outer petals, the inner ones being narrower (van Heusden, 1992). Petal shape was one of the features used in the sectional classification of *Ephedranthus* (Fries, 1934). In general, flowers in Annonaceae are bisexual, but staminate and pistillate flowers occur in monoecious, dioecious, or androdioecious species (van Heusden, 1992; Saunders, 2010). Some members of tribe Malmeeae have androdioecious species, characterized by individuals with bisexual flowers and others with staminate ones (Lopes et al., 2018). The stamens of Annonaceae are mainly narrowly oblong to oblanceoloid, with a very short filament, two linear thecae and a connective with shieldlike prolongation (van Heusden, 1992). Stigma shape varies from lobed to capitate, those with a distinct basal constriction, and to cylindrical (Doyle & Le Thomas, 1996). Number of ovules in Annonaceae varies from one to numerous; *Anaxagorea* A. St.-Hil. has generally two ovules per carpel (Maas & Westra, 1984; Chatrou et al., 2012). In the rest of the taxa analyzed, there are groups either with a single ovule, or with two to five ovules.

Character 16. Pollen

The pollen wall is formed by two layers. The outer layer, the exine, is also divided in inner and outer layers. The exine outer layer, the sexine, is usually sculptured. The tectum is either granular or columellar (Walker, 1971; Punt et al., 2007). Columellar pollen grain is a characteristic of tribe Malmeeae (Walker, 1971). Walker (1971) was the first to place *Bocageopsis*, *Onychopetalum*, and *Unonopsis* (Unoneae, Unonopsis group, Fries, 1959; Xylopiineae, Hutchinson, 1964) together with *Cremastosperma*, *Ephedranthus*, *Malmea* s.l., *Oxandra*, *Pseudoxandra*, and *Ruizodendron* (Uvarieae, Fries, 1959; Hutchinson, 1964; Cremastosperma group, van Heusden, 1992) and species of *Enantia* Oliv. (van Setten & Maas, 1990), now assigned to the African genus *Annickia* Setten & Maas (previously in a tribe called Malmea). His classification was based on pollen features in all these genera, having columellar monosulcate pollen grains. Except for *Annickia*, this is the current delimitation of tribe Malmeeae (Chatrou et al., 2012).

Characters 17–22. Fruit

All fruit characters are important for recognizing species of *Ephedranthus* and have been used in

Table 2. Morphological matrix. Characters and their states follow Table 1. Missing data are indicated with a question mark (?) and inapplicable data with a dash (–).

	1111111111222222
	12345678901234567890123 45
Anaxagorea phaeocarpa	10100010001000100?00--000
Bocageopsis pleiosperma	11011110001012211001001 11
Pseudoxandra obscurinervis	00111011101021010002101 21
Ruizodendron ovale	10000100110021010001111 22
Ephedranthus amazonicus	00010000101121010001120 22
Ephedranthus boliviensis	00010100101121010111000 22
Ephedranthus colombianus	0101010010?121010011100 22
Ephedranthus dimerus	10010000101121011003200 22
Ephedranthus guianensis	11010000101121010101220 22
Ephedranthus parviflorus	10010001112121011003100 22
Ephedranthus pisocarpus	10010001112121011002100 22

taxonomic treatments. The monocarp is usually ellipsoid, but in few species it ranges from globose to ovoid or cylindrical; club-shaped monocarps are exclusively found in *Anaxagorea* (Maas & Westra, 1984). The monocarp apex is either rounded or apiculate or umbonate. The stipe, connecting the monocarp to the receptacle, varies from 5 to 40 mm long in *Ephedranthus*. This character has been used to distinguish *E. guianensis*, *E. parviflorus*, and *E. pisocarpus* (Fries, 1941), also in *Ephedranthus* species keys (Oliveira & Sales, 1999; Lopes et al., 2014), and to distinguish *E. boliviensis* from *E. amazonicus* (Chatrou & Pirie, 2003). Despite the arbitrary division of states of this character, most species of *Ephedranthus* have stipes that are 0–11 mm long (*E. boliviensis* 7–11 mm; *E. colombianus* 6–7 mm; *E. dimerus* 6.5–11 mm; *E. parviflorus*, 5–8 mm; *E. pisocarpus*, 5–7 mm), and two species have stipes varying from 20 to 40 mm long (*E. amazonicus* 20–30 mm; *E. guianensis* 30–40 mm). A third state was necessary to include the intermediate stipe length of *Ruizodendron ovale* (12–19 mm long).

Characters 23–25. Seeds

Apocarpous fruits have usually marginal seeds; those with one seed show mainly basal placentation (van Setten & Koek-Noorman, 1992). Rumination in seeds, a synapomorphy of Annonaceae, is due to the infolding of dark inner layer of the seed coat into the lighter-colored endosperm (van Setten & Koek-Noorman, 1992). The ruminations are categorized in two main cross section divisions, spiniform and lamellate, ribbon-shaped rumination being found only in *Anaxagorea*.

An exhaustive search using parsimony was conducted in PAUP 4.0a150 (Swofford, 2002). Character-state optimization used accelerated transformation (ACCTRAN). Standard bootstrap analysis was conducted with 1000 replications.

Results

Phylogenetic relationships in *Ephedranthus*

There are 20 parsimony-informative characters and five parsimony-uninformative ones. One most parsimonious tree, with 51 steps, was recovered with 0.6863 consistency index (CI) and 0.5429 retention index (RI) (Fig. 1, 20 changes, Table 3, 31 changes). Bootstrap values were 63% for the clade *Ephedranthus dimerus*, *E. parviflorus*, and *E. pisocarpus*, 90% for *E. pisocarpus* sister to *E. parviflorus*, and 69% for *E. colombianus* sister to *E. boliviensis*. Bootstrap values for all the other nodes were below 50% (Fig. 1).

Ephedranthus is monophyletic with three main clades (Table 3). One non-homoplastic character, male flowers (character 12: 1), and a homoplastic one, basal placentation (character 23: 0) support the genus. Within *Ephedranthus*, *E. colombianus* and *E. boliviensis* are sister to the rest of the genus. The sister relationship of *E. colombianus* and *E. boliviensis* is supported by glabrous leaves on the adaxial surface (character 1: 0) and verrucose monocarp wall (character 19: 1). The monophyly of the clade comprising *E. guianensis*, *E. amazonicus*, *E. dimerus*, *E. parviflorus*, and *E. pisocarpus* is supported by leaves with immersed to slightly raised tertiary veins (character 6: 0). Within this group, *E. guianensis* and *E. amazonicus* are sister to the group formed by *E. dimerus*, *E. parviflorus*, and *E. pisocarpus*. *Ephedranthus guianensis* and *E. amazonicus* are supported by stipes 20–40 mm long (character 22: 2). The group *E. dimerus*, *E. parviflorus*, and *E. pisocarpus* is supported by cylindrical monocarps (character 20: 3) and fruit pedicel covered by yellowish hairs (character 17: 1). The sister relationship of *E. parviflorus* and *E. pisocarpus* is supported by narrowly oblong to oblong petals (character 11: 2), chartaceous petals (character 10: 1), and pedicel 0–2 mm long (character 8: 1) (Fig. 1).

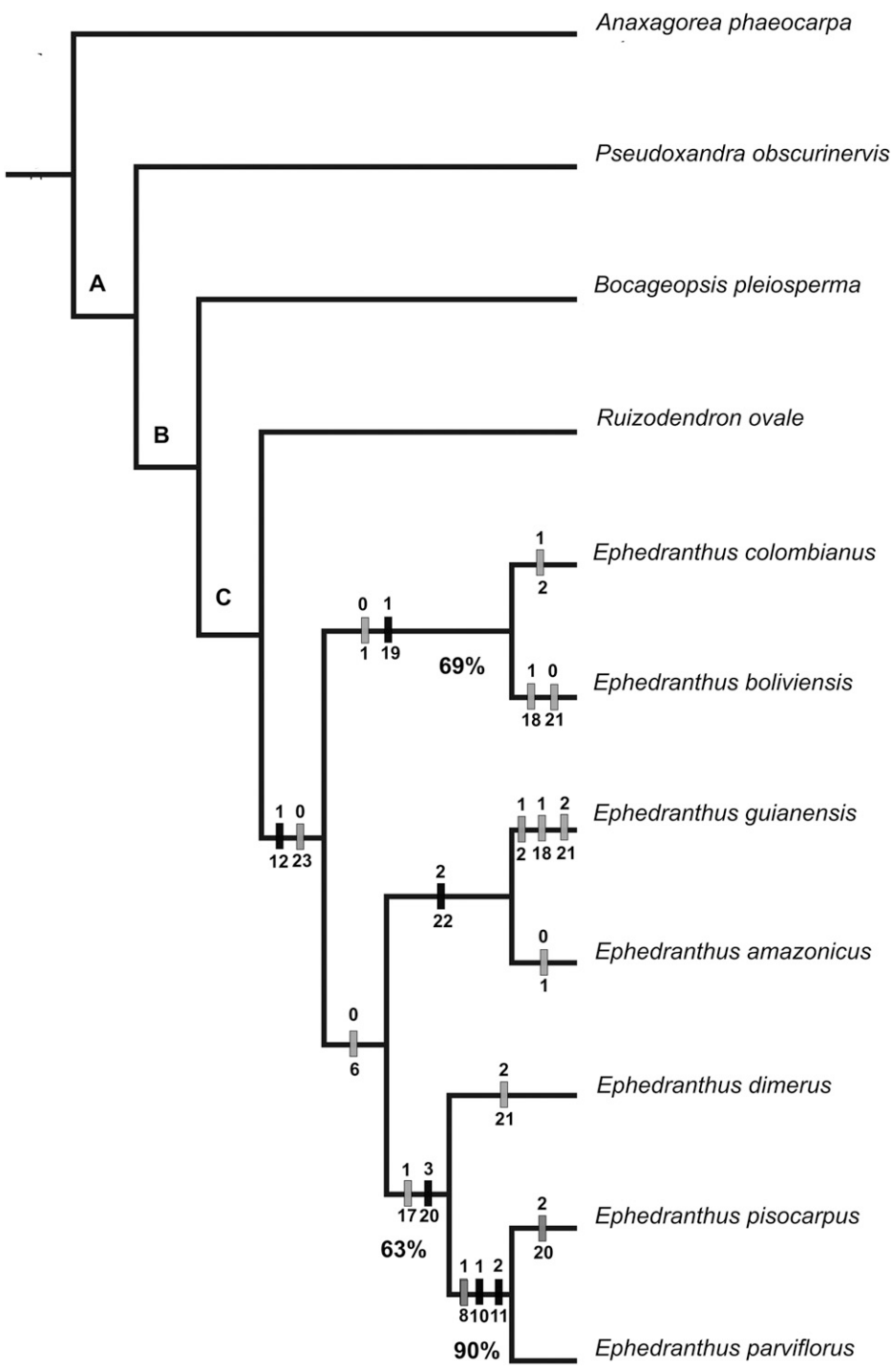

Figure 1. Most parsimonious tree. Bars represent character state changes: black = unique; gray = homoplasy. Numbers below bars are character numbers, and those above are character states (see Table 1). Character state changes in outgroups are only those cited in the text. Percentage in the nodes are bootstrap values; nodes without any indication have bootstrap values below 50%.

Table 3. Changes per clade from the cladistic analysis of *Ephedranthus*, not shown in the cladogram (Fig. 1). <=>, ambiguous direction of transformation; ==>, direction of transformation.

Branch	Character	Change
Node A <=> *Anaxagorea*	4. idioblasts	1 <=> 0
	5. midrib	1 <=> 0
	9. petal aestivation	1 <=> 0
	13. stamen shape	2 <=> 0
	14. stigma shape	1 <=> 0
	15. ovule number	0 <=> 1
	16. infratectal structure	1 <=> 0
	20. monocarp shape	1 <=> 0
	23. placentation	1 <=> 0
	24. raphe	2 <=> 0
	25. rumination	1 <=> 0
Node A ==> Node B	3. oil cell	1 ==> 0
	6. tertiary veins	0 ==> 1
Node B ==> *Bocageopsis*	2. papillae	0 ==> 1
	9. petal aestivation	1 ==> 0
	13. stamen shape	2 ==> 1
	14 stigma shape	1 ==> 2
	15. ovule number	0 ==> 2
	17. hairs on fruit pedicel	0 ==> 1
	21. monocarp apex	1 ==> 0
	24. raphe	2 ==> 1
Node B ==> Node C	5. midrib	1 ==> 0
	7. flower number	1 ==> 0
	25. rumination	1 ==> 2
Node C ==> *Ruizodendron*	4. idioblasts	1 ==> 0
	10. petal texture	0 ==> 1
	11. outer petal shape	1 ==> 0
	22. stipe length	0 ==> 1
Node A ==> *Pseudoxandra*	1. hairs on lamina	1 ==> 0
	8. length of flower pedicel	0 ==> 1
	20. monocarp shape	1 ==> 2

Taxonomic Treatment

Ephedranthus S. Moore, Trans. Linn. Soc. London, Bot. 4: 296, pl. 21, 38. 1895. TYPE: *Ephedranthus parviflorus* S. Moore.

Ephedranthus sect. *Sphaeranthema* R. E. Fr., Acta Horti Berg. 12(1): 201. 1934, syn. nov. TYPE: *Ephedranthus amazonicus* R. E. Fr., Acta Horti Berg. 12(1): 200. 1934.

Trees or shrubs 5–30 m. *Leaves* distichous, venation brochidodromous, primary veins impressed to flat adaxially, raised abaxially, secondary veins mostly distinct, impressed to flat adaxially, raised abaxially. Inflorescence axillary, on older branches in the leafless zone, 1- or 2-flowered; bracts 2 to 5, 1.5–5 × 4 mm, ovate to broadly ovate. Flowering pedicel 0–10 mm, fruiting pedicel 6–40 mm. *Flower* actinomorphic, bisexual or staminate; sepals and petals similar in size and shape in both sexes; plant androdioecious; perianth 1 whorl of sepals and 2 whorls of petals; sepals (2 to)3, imbricate, free, smaller than the petals; petals (4 to)6, imbricate, free; bisexual flower with 20 to 30 stamens, extrorse, connective shield truncate; 9 to 75 carpels, ovary with 1 basal ovule, stigma capitate; male flower 50 to 190 stamens; androecium and gynoecium arranged in irregular whorls. *Fruit* apocarpous, 2 to 80 stipitate monocarps; monocarps ellipsoid, ovoid, globose to cylindrical, wall papyraceous to woody. *Seeds* 1 per monocarp, transversally ellipsoid, transversely striate, ruminations lamellate, divided in 4 equal parts in cross section.

Key to the Species of *Ephedranthus*

1a. Leaves glabrous on abaxial surface.
  2a. Leaves with tertiary veins impressed abaxially; fruit stipe 20–30 mm (Amazonian region) . . . *E. amazonicus* R. E. Fr.
  2b. Leaves with tertiary veins distinctly raised abaxially; fruit stipe 6–10 mm (Colombian Andes, Bolivia, and Brazil [Acre]).

3a. Petals narrowly obovate to narrowly elliptic; fruiting pedicel 12–20 mm; monocarps ca. 28 mm (Colombian Andes) ..... *E. colombianus* Maas & Setten
3b. Petals ovate; fruiting pedicel 7–8 mm; monocarps ca. 18 mm (Bolivia and Brazil [Acre]) ..... *E. boliviensis* Chatrou & Pirie

1b. Leaves sparsely to densely pubescent on abaxial surface.
4a. Fruiting pedicel glabrous; monocarps 30 to 80; stipe 30–40 mm (Guianas) ..... *E. guianensis* R. E. Fr.
4b. Fruiting pedicel covered by yellowish hairs; monocarps 2 to 20; stipe 5–10 mm (Brazil).
5a. Flowering pedicel 5–10 mm; perianth with 2 sepals and 4 petals; petals coriaceous (eastern Brazil [Bahia, Espírito Santo, Minas Gerais]) ..... *E. dimerus* J. C. Lopes, Chatrou & Mello-Silva
5b. Flowering pedicel 0–2 mm; perianth with 3 sepals and 6 petals; petals chartaceous.
6a. Mature monocarp cylindrical, 15–20 mm (central Brazil [Goiás, Mato Grosso, Mato Grosso do Sul, Tocantins]) ..... *E. parviflorus* S. Moore
6b. Mature monocarp globose, ovoid, or ellipsoid, 11–13 mm (northeastern Brazil [Ceará, Maranhão, Piauí]) ..... *E. pisocarpus* R. E. Fr.

1. Ephedranthus amazonicus R. E. Fr., Acta Horti Berg. 12(1): 200. 1934. TYPE: Brazil. Amazonas: Manaus, capoeirão na Estrada da Raiz, 9 Apr. 1932 (fl., fr.), *W. A. Ducke s.n.* (holotype, S S-R-1918!; isotypes, B [barcode] B 10 0243195!; HB not seen, RB-23891 [2 sheets] [bc] 00534179 and 00534095!, K [bc] K000487281!; US [bc] US00104269!). Figures 2A, B, 3.

Tree 5–30 m tall, DBH 5–30 cm; branchlets, petioles, and buds densely covered by appressed, straight, yellowish hairs to glabrescent. Petiole 5–8 mm; lamina 7–32 × 3–11 cm, narrowly elliptic to elliptic, oblanceolate, or narrowly oblong; apex acute to acuminate, base acute, obtuse to slightly asymmetric, coriaceous to chartaceous, glabrous adaxially, glabrous to glabrescent, rarely densely covered by appressed, straight hairs abaxially; primary vein impressed, forming a sulcus near base adaxially, prominent abaxially, secondary veins flat to impressed adaxially, raised abaxially, 9 to 16 pairs of secondary veins, tertiary veins impressed and nonreticulate on both sides, angles between primary and secondary veins 55°–70°. Inflorescence 1-flowered; bracts 3 or 4. Flower pedicel 4–5 mm, fruiting pedicel 8–15 mm, glabrous; flower buds globose-flattened; sepals 3, 2–4 × 3–6 mm, widely ovate, densely covered by appressed, crisped, yellowish hairs; petals 6, in 2 whorls of 3 petals each, coriaceous, sparsely to densely covered by appressed, crisped, yellowish hairs; outer petals 9–25 × 10–16 mm, ovate to suborbiculate; inner petals 10–15 × 10 mm, orbiculate to elliptic with obtuse apex; bisexual flower: stamens not seen, carpels ca. 75, ovary cylindrical prismatic, densely covered by appressed, straight, goldish hairs; male flower with 120 to 150 stamens, 2 mm. Fruit with ca. 23 monocarps, 15–40 × 8–20 mm, ellipsoid, rarely globose, apex shortly apiculate, immature yellow, mature red, stipe 20–30 mm; fruit wall smooth. Seed 18 × 10, ellipsoid.

Habitat and distribution. *Ephedranthus amazonicus* is widely distributed in the Amazon region of Brazil, Colombia, and Peru, with a single known collection from Venezuela. It occurs in non-inundated forests on lateritic soil, at elevations from 50 to 200 m. It flowers from April to June, rarely in October, and fruits throughout the year, mainly from April to August.

Vernacular names. Cargero (Spanish, Colombia), envira, envira-preta (Portuguese, Brazil), pari (Yurí, Colombia).

Notes. The fruits with 23 monocarps, with smooth wall, distinguish *Ephedranthus amazonicus* from its sister species, *E. guianensis*. Their close relationship is supported by stipes 20 to 40 mm long (Fig. 1, character 22). Leaves of *E. amazonicus* are in general very long, up to 32 cm long. *Ephedranthus colombianus*, a non-related species, also has large leaves, but they are instead reticulate abaxially, and the fruit stipes are smaller, from 6 to 7 mm long.

The collection *Aldana 271*, from Boyacá, Colombia, is peculiar because of its leaves densely covered with brownish hairs abaxially, and its geographical occurrence, in the Andean region, typical of *Ephedranthus colombianus*. Nonetheless, it shows the long stipes typical of *E. amazonicus* and is maintained here under this species until more collections become available for analyses.

Additional specimens examined. BRAZIL. **Acre:** BR-317, Km. 68 (NY); Xapuri, Rio Acre, 3 hrs. by boat downstream from Xapuri & 1 hr. walking inland from left bank, *Daly et al. 7164* (INPA, NY, U, UFACPZ); cut-off to Esperança on Brasiléia-Assis Brasil rd., ca. 6 km from Brasiléia, *Lowrie et al. 722* (INPA, K, MG, NY, U, UFACPZ); Estrada Rio Branco-Porto Acre, Km. 33, *Nelson 687* (NY); Seringal Boa Água, *Pires 13745* (IAN). **Amazonas:** Atalaia do Norte, rio Javari, localidade Estirão do Equador, a 3 km da estrada do campo de pouso, *Cid Ferreira et al. 9893* (CEN, NY), *9896* (CEN, NY); Borba, BR 320, estrada Transamazônica, 3 km E of Sucundri, *Henderson 321* (NY, U, UB); Itacoatiara, *Kinupp 1370* (INPA); Manaus, along rd. to Aleixo, *Krukoff 7981* (BR, K, NY, P, U); campus da Universidade do Amazonas, próximo ao viveiro do Departamento de Botânica, *Oliveira & Silva 146* (NY), *147* (NY); *Maas et al. 6955* (NY); margem do igarapé Bindá, *Chagas s.n.* (INPA 1310); Manaus, Itacoatiara rd. Km. 146, roadside forest, *Bisby et al. P18068* (INPA, MG, NY); Estrada Manaus–Itacoatiara Km. 64, *Rodrigues & Coelho 5303* (NY); Reserva Florestal Walter Egler, rd. Manaus–Itacoatiara, Km. 64, *Prance et al. 9048* (INPA, NY, U); Estrada do Aleixo, grounds of Companhia das Plantações, *Prance et al. 18787* (INPA, K, MG, NY, U); Reserva Florestal Ducke, Manaus–Itacoatiara, Km. 26, *Coêlho D13* (HFSL, INPA, K, L, MG, U, ULM); *Assunção & Pereira 203* (INPA K, L, MG, U, UB, ULM); *Costa & Silva 318* (HAMAB, INPA, K, L, U,

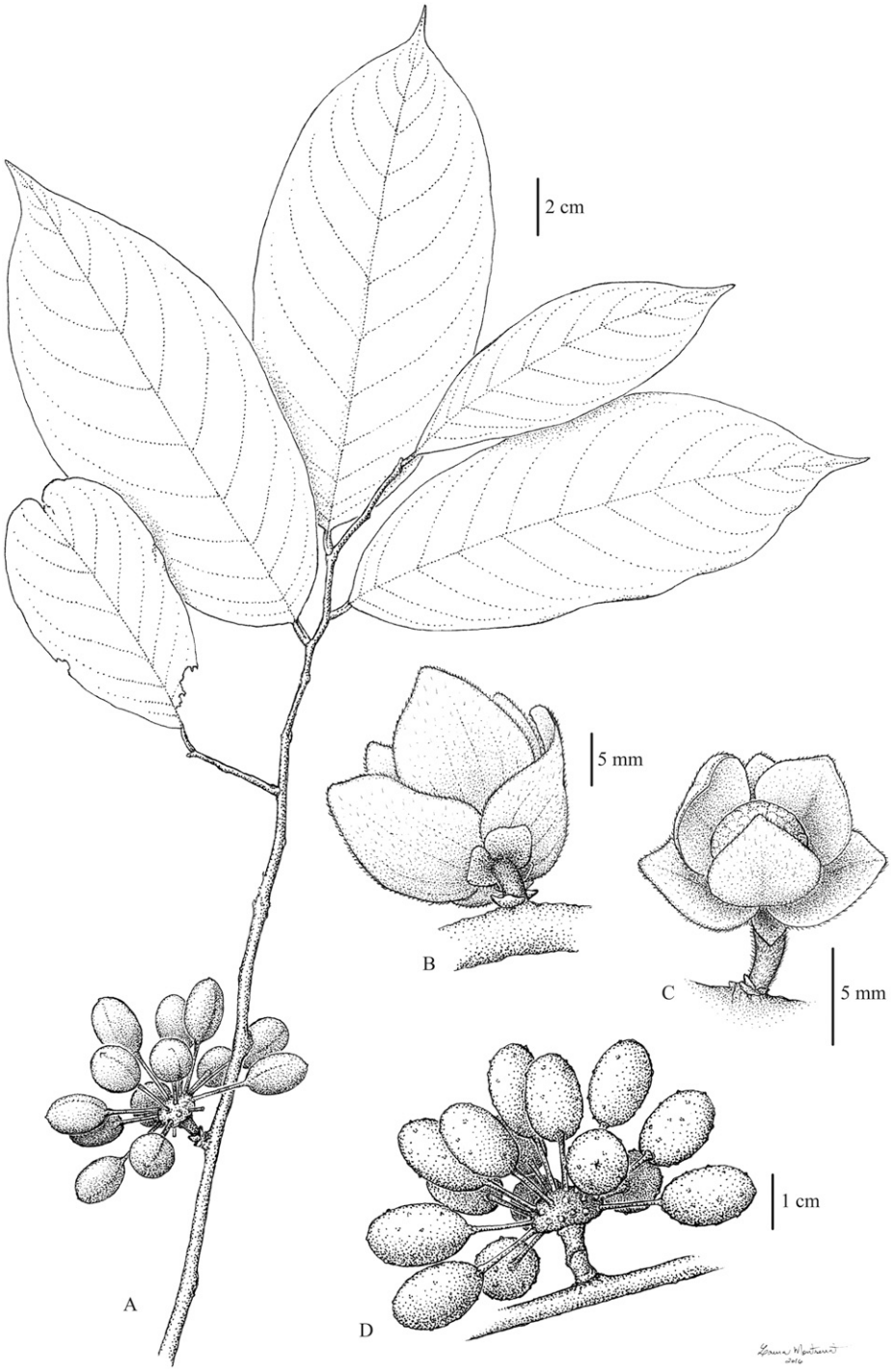

Figure 2. A, B. *Ephedranthus amazonicus* R. E. Fr. —A. Twig with fruit. —B. Flower. C, D. *Ephedranthus boliviensis* Chatrou & Pirie. —C. Flower. —D. Fruit. A, *Vicentini et al. 991* (U); B, *Van Dulmen 270* (U); C, *Solomon 6484* (U); D, *Jardim 251* (U).

UFACPZ); *Hopkins et al. 1434* (INPA, K, L, MG, MO, U, UFMT, ULM); *Prance et al. 4692* (INPA, K, MG, NY, P, U); *Prance et al. 2165* (NY); *Ribeiro et al. 1617* (BM, INPA, K, L, MG, R, RB, U, UB, ULM, US, VEN); *Ribeiro et al. 1671* (INPA, L, U); *Ribeiro & Silva 1383* (INPA, K, L, U); em frente à meteorologia, *Assunção et al. 223* (IAN, INPA, U); *Vicentini et al. 991* (COL, F, INPA, K, L, MG, R, U, UB, ULM, VEN); igarapé Ipiranga, *Ribeiro et al. 938* (INPA, L, U); Igarapé da

Figure 3. Northern region of South America showing distribution of *Ephedranthus amazonicus* R. E. Fr. (●), *E. colombianus* Maas & Setten (■), and *E. guianensis* R. E. Fr. (▲).

Bolívia, sentido bairro Sabiá, *Ribeiro et al. 856* (INPA, K, L, U); trilha à esquerda do Km. 0.35, estrada alojamento-torre, *Vicentini et al. 467* (INPA, K, L, MG, U, ULM); Estrada do Acará, *Coelho & Lima D26* (INPA, K, L, MG, U, ULM); Distr. Agropecuário, Reserva 1501, Km. 41 da Smithsonian/INPA, *Freitas et al. 22* (NY, U); *Freitas et al. 856* (U); *Mori et al. 19527* (NY, U), *21371* (NY, U); *Mori et al. 20598* (NY); rio Cuieiras, igarapé Lobisomem, *Mori & Gracie 21811* (INPA, NY, U); upstream, farm of sr. Nemério, *Campbell P21815* (INPA, NY); rio Negro, próximo ao rio Arara, *Loureiro s.n.* (INPA 37883, MG); rio Tarumã, mata alta central, *Froés 24940* (IAN); rio Urubu, betw. cachoeira Iracema & Natal, at Manaus–Caracaraí rd., *Prance et al. 4987* (INPA, NY, U); Novo Airão, área indígena Waimiri Atroari, rio Camanaú, vic. of aldeia Maré, *Miller 356* (INPA), *590* (INPA); Presidente Figueiredo, estrada do Pau Rosa, cerca de 5 km da margem da estrada, *Silva et al. 797* (INPA); rio Abacaxis, Terra Preta, *Todzia et al. 2321* (NY). **Mato Grosso:** Aripuanã, margem da baía, ao lado das picadas da encanação de água, *Gomes 458* (INPA); Serra do Cachimbo, *Nascimento 463* (MG). **Pará:** Alto Tapajós, Vila Nova, perto da Cachoeira do Cachorrão, *Pires 4028* (IAN); Conceição do Araguaia, fazenda São José, *Lobato et al. 2823* (MG); Entre Estreito e Marabá, *Pires 13636* (IAN); Oriximiná, rio Trombetas, mineração Santa Patrícia, estrada para Porto Trombetas, Serra da Onça, *Martinelli 7299* (INPA, MG, U); Tucuruí, *Silva et al. 424* (MG). **Rondônia:** Buritis, fazenda do sr. José Vespal, *Carlos et al. 1226A* (MG); Forte Príncipe da Beira, *Rodrigues et al. 4279* (NY, INPA); Porto Velho, usina hidrelétrica de Jirau, *Pereira-Silva 13596* (INPA); Machadinho d'Oeste, near Tabajara, upper Machado River region, *Krukoff 1358* (K, NY, P, U), *1597* (K, NY, P, U); Serra dos Parecis, a 27 km de Alta Floresta d'Oeste, na linha 65 da Topografia BASE VI, *Lisboa et al. 2512* (MG).

COLOMBIA. **Amazonas:** Casaquiare, río Casaquiare, Capihuara, *Colella & Guayamare 1740* (U); río Caquetá, frente a Villa Azul, terraza baja, *van Andel et al. 495* (U); al S de la desembocadura de la quebrada Bocaduche y el rio Caquetá, frente a la isla Sumaeta, *Van Dulmen 209* (COAH, U); *Van Dulmen 270* (U); *Van Dulmen 345* (L, U); rio Igara-Parana (affl. rio Putumayo), corr. La Chorrera territoire des Witoto aimeniuñoniani, famille Diaillare, *Gasché-Desplasts 1007* (P). **Boyacá:** Cmto de Pto. Pinzón, Reserva Natural de Avel El Paujil, *Aldana et al. 271* (ANDES). **Caquetá:** trocha al Yarí, *Murillo & Román 590* (U); *Murillo & Román 606* (U).

PERU. **Loreto:** Maynas, acampamento Explorama Lodge, zona Bushmaster, *Díaz et al. 1182* (U); Explornapa Camp, on Río Sucurasi affluent of Río Napo, 75 km of Iquitos, *Chatrou et al. 173* (U); Yanomono, Explorama Tourist Camp, Río Amazonas, halfway betw. Indiana & mouth of Río Napo, *Gentry & Vasquez 42408* (MO, U); *Gentry et al. 29075* (MO, U); above mouth of Río Napo on Río Amazonas, *Gentry et al. 27769* (MO, U); Quebrada Sucursari, Río Napo, *Gentry et al. 42687* (MO, U).

VENEZUELA. **Amazonas**, Casiquiare, rio Casiquiare, Capihuana, *Collela 1740* (U).

2. Ephedranthus boliviensis Chatrou & Pirie, Revista Soc. Boliv. Bot. 4(1): 25, f. 1, 2. 2003. TYPE: Bolivia. Beni: Vaca Diez, Cachuela Esperanza, along Río Beni, 10°32′S 65°38′W, ca. 200 m, 9 Nov. 2001 (fl.), *L. W. Chatrou et al. 420* (holotype, LPB [bc] LPB0000441!; isotypes, AAU not seen, K [bc] K000380822!, MO [bc] 1281801!, U [bc] U0088277!, USZ not seen, WU not seen). Figures 2C, D, 4.

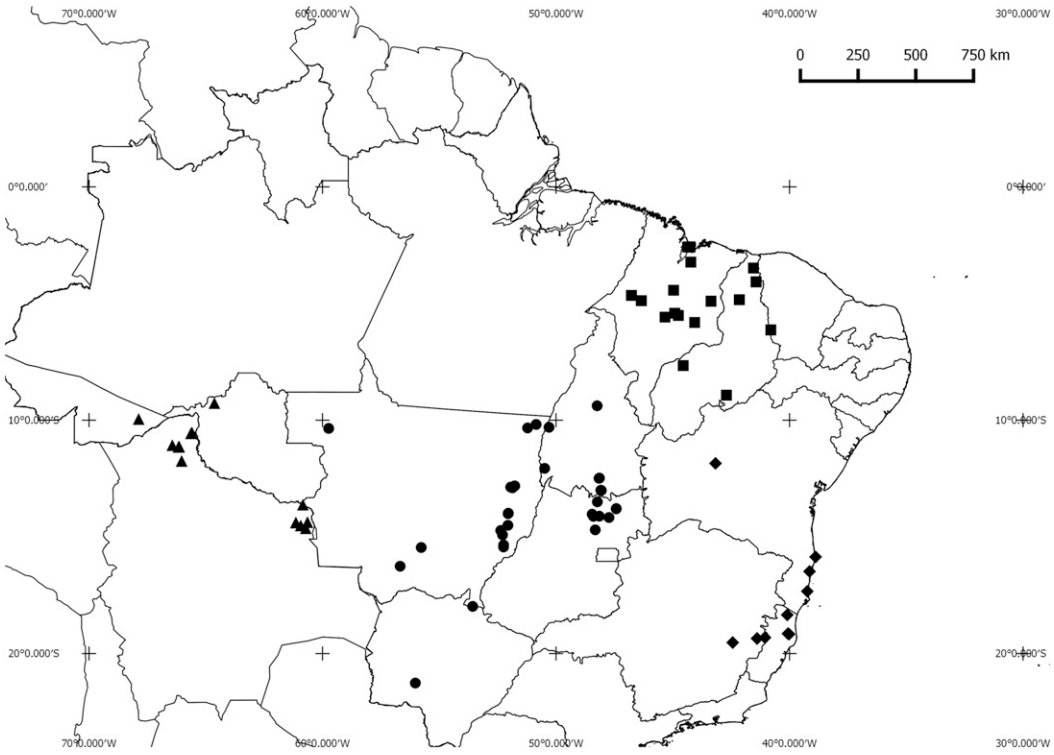

Figure 4. Central portion of South America showing distribution of *Ephedranthus boliviensis* Chatrou & Pirie (▲), *E. dimerus* J. C. Lopes, Chatrou & Mello-Silva (♦), *E. parviflorus* S. Moore (●), and *E. pisocarpus* R. E. Fr. (■).

Tree 3–19 m tall, DBH 15–24 cm; branchlets, petioles, and buds sparsely to densely covered by appressed, straight to crisped, yellowish to ferruginous hairs to glabrescent. Petiole 3–6 mm; lamina 6–17 × 2.5–7 cm, narrowly elliptic to elliptic, elliptic-obovate, oblong, or ovate; apex acute to acuminate, base obtuse, acute to slightly asymmetric, chartaceous, glabrous with appressed, crisped, yellowish hairs along the primary vein adaxially, glabrescent abaxially; primary vein flat, sometimes with a sulcus near the base adaxially, prominent abaxially, secondary veins flat to impressed adaxially, raised abaxially, 8 to 14 pairs of secondary veins, tertiary veins indistinct adaxially, distinctly raised-reticulate abaxially, angles between primary and secondary veins 50°–70°. Inflorescence 1-flowered; bracts 4. Flowering pedicel ca. 3 mm, fruiting pedicel 7–8 mm, glabrous; flower buds flattened-globose; sepals 3, 1.5–3 × 2–3 mm, widely ovate to triangular, densely covered by appressed, crisped, yellowish hairs; petals 6, in 2 whorls of 3 petals each, coriaceous, sparsely to densely covered by appressed, crisped, yellowish hairs; outer petals 5–10 × 5–9 mm, ovate; inner petals 6–10 × 5–6 mm, ovate; bisexual flower not seen; male flower with 50 stamens, 1.5 mm. Fruit with 10 to 30 monocarps, 18 × 7–11 mm, ellipsoid, apex rounded, yellow in vivo, stipe 10 mm; fruit wall verrucose. Seed 14 × 8 mm, ellipsoid.

Habitat and distribution. *Ephedranthus boliviensis* occurs in Bolivia and Brazil, in dry chiquitanos forest, and disturbed forests, at elevations from 125 to 300 m. It flowers from September to November and fruits in November.

Vernacular names. Joisi (Chácobo, Bolivia), peraquina (Spanish, Bolivia).

Notes. *Ephedranthus boliviensis* is distinguished from *E. parviflorus* by the 3-mm-long pedicels (vs. sessile flowers in *E. parviflorus*), widely ovate to triangular sepals 1.5–3 mm long (vs. ovate sepals 3–5 mm long), and ellipsoid and verrucose monocarps (vs. cylindrical and smooth monocarps). Collections of *E. boliviensis* occurring close to the border between Bolivia and Brazil have been included in *E. parviflorus* by Oliveira and Sales (1999), as *E. boliviensis* had not been described at that time.

Additional specimens examined. BOLIVIA. **Beni:** Cachuela Esperanza, Río Yuta, *Meyer s.n. U14968* (U); *Meyer 112* (INPA, U); Vaca Diez, vic. of the Chácobo village, Alto Ivon, *Boom 4396* (U); *Boom 4460* (INPA, U); Tumi Chucua, 30 km S of Riberalta, *Solomon 6484* (U). **Pando:** Madre de Dios, along Río Madre de Dios, at Puerto Candelaria, *Nee 31829* (U). **Santa Cruz:** Velasco,

Parque Nacional Noel Kempff Mercado, *Jardim 222* (U), *251* (U), *3079* (U); *Chatrou et al. 301* (U), *336* (U).

BRAZIL. **Acre:** Rio Branco, Parque Zoobotânico, trail behind herbarium HPZ, *Maas et al. 9254* (HPZ, NY, U).

3. Ephedranthus colombianus Maas & Setten, Proc. Kon. Ned. Akad. Wetensch., C 91(3): 248, f. 5–7. 1988. TYPE: Colombia. Antioquia: San Luís, Canõn del Río Claro, NW sector, left bank, 375–600 m, 9 Mar. 1984 (fl.), *A. Cogollo 1448* (holotype, JAUM [bc] JAUM0000126!; isotypes, NY not seen, US not seen). Figures 3, 5A–D.

Tree 5–20 m tall, DBH 4–40 cm; branchlets, petioles, and buds densely covered by appressed, straight, ferruginous hairs or covered by papillae. Petiole 3–8 mm; lamina 9.5–24 × 3–9 cm, narrowly oblong to oblong or narrowly elliptic; apex acute to acuminate, base obtuse, chartaceous to coriaceous, glabrous with appressed, crisped, yellowish hairs along the primary vein adaxially, glabrous abaxially; primary vein impressed adaxially, prominent abaxially, secondary veins impressed adaxially, raised abaxially, 8 to 14 pairs of secondary veins, tertiary veins indistinct adaxially, distinctly raised-reticulate abaxially, angles between primary and secondary veins 60°–80°. Inflorescence 1- or 2-flowered; bracts 2. Flower pedicel 6–10 mm, fruiting pedicel 12–20 mm, glabrous to covered by papillae; flower buds not seen; sepals 3, ca. 7 × 4 mm, lanceolate, densely covered by crisped, yellowish hairs; petals 6, in 2 whorls of 3 petals each, coriaceous, densely covered by appressed, crisped, brownish hairs; outer and inner petals 15 × 4–5 mm, narrowly obovate to narrowly elliptic; bisexual flower: stamens not seen, carpels ca. 15, ovary densely covered by appressed, straight, brownish hairs; male flower not seen. Fruit with ca. 6 monocarps, 28 × 11 mm, ellipsoid, apex apiculate, immature green, mature purple to dark purple, stipe 6–7 mm; fruit wall verrucose, with apparent veins. Seed 15–19 × 7–8 mm, ellipsoid to ovoid.

Habitat and distribution. *Ephedranthus colombianus* occurs in the Colombian departments of Antioquia, Santander, and Sucre. It is present mainly in forests from the Andean region, at elevations from 30 to 410 m, reaching up to 2300 m in La Ceja, Antioquia. In Sucre it occurs also in limestone formations. It flowers in April and fruits from June to September.

Notes. *Ephedranthus colombianus* differs from the other *Ephedranthus* species by the leaves with tertiary veins distinctly raised-reticulate abaxially and the verrucose monocarps, with apparent veins. Verrucose monocarps (character 19: 1) and glabrous leaves abaxially (character 1: 0, homoplastic) support its sister relationship with *E. boliviensis* (Fig. 1). Collections bearing flowers are less common than fruiting collections, and in general, flowering herbarium sheets bear old flowers, from which stamens had already fallen, so that male flowers have not been seen in the available specimens.

Additional specimens examined. COLOMBIA. **Antioquia:** La Ceja, vereda El Tabor, *Alzate & Sierra 875* (HUA, U); Puerto Berrío, vereda Alicante, finca El Rebaño, en la via San Juan de Bedout–La Cabaña, *Callejas 9333* (NY, U); San Luis, cañon del Río Claro, sector Sur, *Sanchéz 1058* (U); Turbo, Corregimiento Lomas Aisladas, Finca las Aisladas, *Alzate & Cardona 1259* (HUA, U), *Alzate & Cardona 1262* (HUA, K); Caldas, La Dourada, *Espintal 268* (COL), *1196* (COL). **Santander:** Cimitarra, Corregimiento de Puerto Olaya, hacienda El Bosque, *Alzate 1266* (HUA, U); vic. to Cimitarra, rd. N from airport betw. Río Guasdualito & 5 km beyond the bridge, *Gentry & Forero 15471* (COL, MO, U); Río Segovia, *Rentería 2364* (COL); San Luís, cañon del Río Claro, *Cogollo 503* (COL), *631* (COL), *1262* (COL); alrededores de la vereda Chorro de Oro, *Cogollo 4594* (COL); Turbo, carretera Panamericana, Tapón del Darién, sector Río León, lomas Aisladas, *Brand 1146* (COL). **Sucre:** Colosó, Estación de Primatos, *Gentry & Cuadros 68213* (MO, U).

4. Ephedranthus dimerus J. C. Lopes, Chatrou & Mello-Silva, Brittonia 66 (online): 71, f. 1, 2. 9 July 2013. TYPE: Brazil. Espírito Santo: Linhares, Reserva Florestal da Companhia Vale do Rio Doce, aceiro Lasa, G. Santos, Km. 0.658, lado direito, 23 Nov. 1982 (fl.), *D. A. Folli 414* (holotype, SPF!; isotypes, CVRD!, K [bc] K000959856!, MO not seen, NY [bc] NY01842936!, U [bc] U0064072!). Figure 4 (see also figure in Lopes et al. [2014]).

Tree 2–30 m tall, DBH up to 25 cm; branchlets, petioles, and buds covered with simple, straight to crisped, erect hairs, sometimes glabrescent, branches glabrous. Petiole 3.5–5.5 mm; lamina 7–14.5 × 3–6.5 cm, oblanceolate to obovate or elliptic; apex acute, rarely obtuse or emarginate, base cuneate to acute, chartaceous, glabrous or sparsely covered with erect, straight hairs on primary vein adaxially, sparsely to densely covered with straight to crisped, erect hairs abaxially; primary vein impressed adaxially and raised abaxially, secondary vein impressed adaxially and raised abaxially, 9 to 14 pairs of secondary veins, tertiary veins impressed and non-reticulate on both sides, angles between primary and secondary veins 50°–60°. Inflorescence 1-flowered; bracts 4 or 5. Flowering pedicel 5–10 mm, fruiting pedicel 1–2 cm, glabrous to densely covered by yellowish hairs; flower buds globose; sepals 2, 3–4.5 × 5–5.5 mm, widely ovate, densely covered with appressed, straight, goldish hairs; petals 4, in 2 whorls of 2 petals each, coriaceous, densely covered with appressed, crisped hairs abaxially, almost glabrous adaxially; outer and inner petals 7–10 × 5–9.5 mm, the outer ones orbiculate, the inner ones oblanceolate; bisexual flowers with ca. 20 stamens, carpels ca. 40, ovary glabrescent; male flowers with ca. 80 stamens, 1.5 mm. Fruit with 2 to 20 monocarps,

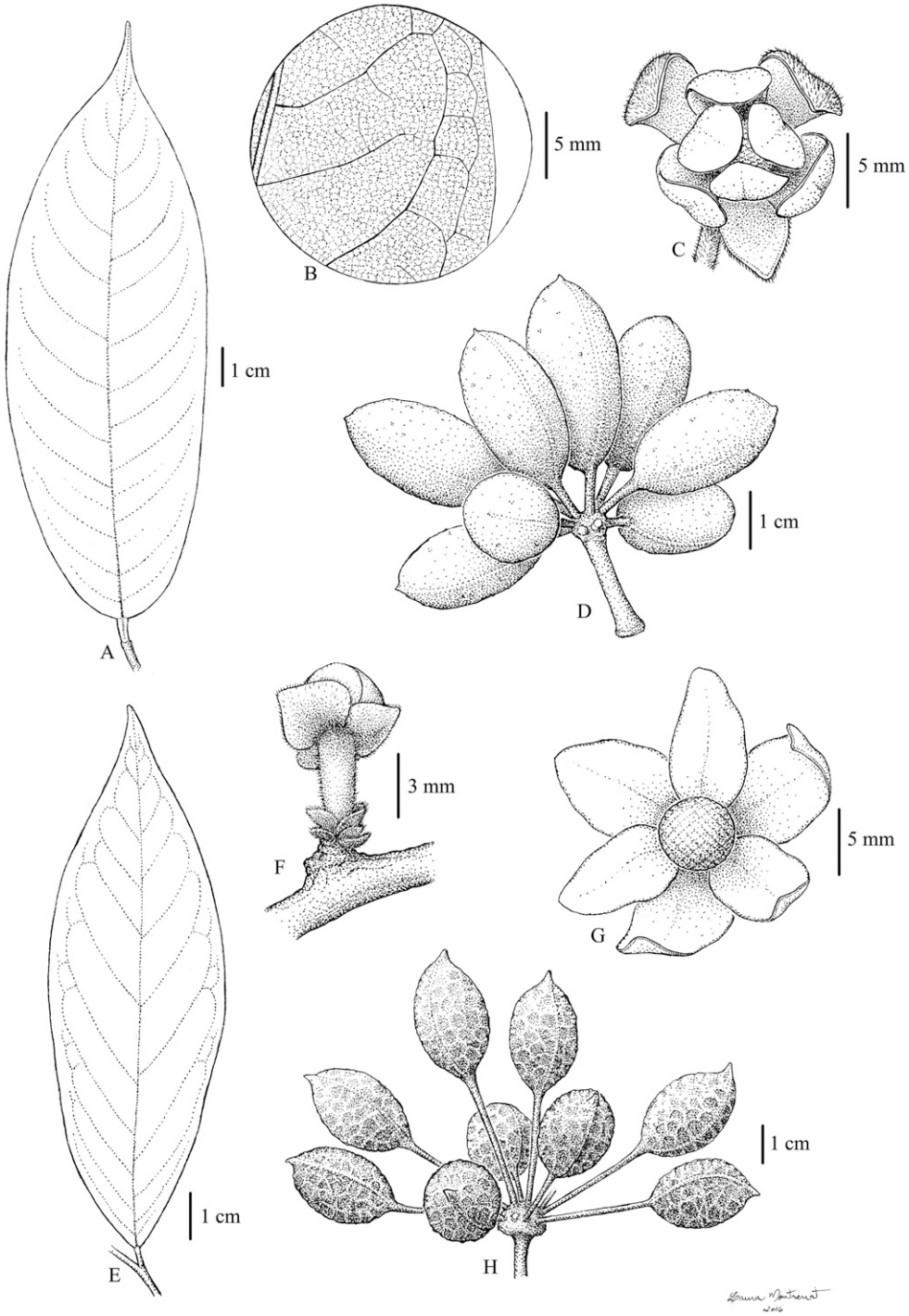

Figure 5. A–D. *Ephedranthus colombianus* Maas & Setten. —A. Leaf. —B. Detail of the leaf reticulation. —C. Flower. —D. Fruit. E–H. *Ephedranthus guianensis* R. E. Fr. —E. Leaf. —F. Flowering pedicel with bracts. —G. Flower. —H. Fruit. A, B, *Gentry & Forero 15471* (U); C, based on photo by Andrés Link; D, *Sánchez 1058* (U); E, F, *Irwin 55720* (U); G, *Schulz 8568* (U); H, *Sabatier & Prévost 3389* (U).

15–25 × 10–15 mm, ellipsoid to cylindrical, apex rounded to umbonate, immature green, mature orange to dark red, stipe 6.5–11 mm; fruit wall smooth. Seeds 15 × 10 mm, ellipsoid.

Habitat and distribution. *Ephedranthus dimerus* occurs in the Atlantic Forest of Brazil, along the Doce River basin, in Minas Gerais and Espírito Santo, and in Bahia, near the coast with a single inland collection in the municipality of Barra. It flowers from October to November and fruits from February to June.

Vernacular names. Pindaíba-preta (Portuguese, Brazil).

Notes. *Ephedranthus dimerus* is the only species in the genus with flowers showing two whorls of two petals each and one whorl with two sepals. It is also the only *Ephedranthus* from the Brazilian Atlantic Forest. Moreover, it has the longest flowering pedicel among the species of the genus, up to 1 cm long. *Ephedranthus dimerus* is sister to (*E. parviflorus* and *E. pisocarpus*), and the group is supported by yellowish hairs covering the fruiting pedicel and cylindrical monocarps (Fig. 1, character 17: 1 and character 20: 3).

Additional specimens examined. BRAZIL. **Bahia:** Barra, brejos Olhos d'Água, Buracão, *Costa & Nascimento Júnior 679* (ASE); Belmonte, Estação Experimental de Belmonte, CEPLAC, *Santos 1105* (CEPEC, NY, U); Prado, Reserva Florestal da Brasil de Holanda Indústrias S.A., entrance at Km. 18 E of Itamaraju on rd. to Prado, 8 km from entrance, *Thomas et al. 10132* (K, NY, RB, U); Santa Cruz Cabrália, área da Estação Ecológica do Pau-Brasil (ESPAB), cerca de 16 km a W de Porto Seguro, BR 367 (Porto Seguro–Eunápolis), *Santos 732* (CEPEC, U); *Santos 904* (U). **Espírito Santo:** ao N Serra do Cristalino, *Duarte 3990* (NY); Linhares, Reserva Florestal da Companhia Vale do Rio Doce, estrada Macanaíba-Pele-de-Sapo, próximo à estrada Baba-de-Boi, *Folli 2278* (CVRD, RB, SPF); Estrada Cinco-Folhas, atrás do laboratório, próximo ao Lago do Jacaré, *Folli 465* (CVRD, NY, RB); *Lopes et al. 322* (CVRD, NY, SPF); Estrada Flamengo, ca. de 900 m da BR 101, na borda da mata, *Lopes et al. 145* (CVRD, SPF); Estrada Cinco-Folhas, próximo à Lagoa do Jacaré, atrás do Laboratório de Sementes, *Lopes et al. 149* (CVRD, SPF); próximo ao lago indo para o galpão de máquinas, *Siqueira 677* (CVRD, SPF); Estrada Mantegueira, 1.4 km, próximo ao pomar, *Lopes et al. 154* (CVRD, SPF); *Lopes et al. 323* (CVRD, NY, SPF); Estrada Mantegueira, 1.5 km from Flamengo, near orchard, *Maas et al. 8826* (CVRD, K, NY, U); Estrada Cinco–Folhas, 200 m, *Folli 5998* (CVRD); Estrada Flamengo, 1450 m, *Folli 5463* (CVRD); Pinheiros, Reserva Biológica Córrego do Veado, interior da floresta, *Leoni 5840* (RB, SPF). **Minas Gerais:** Caratinga, fazenda Montes Claros, Trilha do Jequitibá, *Andrade & Lopes 155* (BHCB, SPF); Estação Biológica de Caratinga, Mata do Jaó, *Gomes 5* (BHCB, SPF); *Couto 181* (BHCB, SPF); *Andrade & Lopes 371* (BHCB, SPF); *Pereira 1022* (BHCB); *Strier 696* (NY). Itueta, Usina Hidrelétrica de Aimorés, fazenda Adolfo Schumaker, *Tameirão Neto 2446* (BHCB, SPF). Santa Rita do Itueto, Quatituba à Cachoeira do Peão, *Luz 275* (CVRD).

5. Ephedranthus guianensis R. E. Fr., Acta Horti Berg. 10(2): 176. 1931. TYPE: Surinam. Coppename, Raleighvallen, 17 Aug. 1923 (fl.), *G. Stahel & J. W. Gonggrijp BW6312* (holotype, U [bc] U0000269!; isotypes AAU not seen, BR!, S S-R-1920 fragment!, U [bc] U0064108!). Figures 3, 5E–H.

Ephedranthus guianensis var. *oligantha* R. E. Fr., Acta Horti Berg. 10(2): 177. 1931. TYPE: French Guiana. S. Jean, 26 Apr. 1914 (fl.), *R. Benoist 1159* (holotype, P [bc] P00751066!; isotypes P [bc] P00751067!, S [bc] S-R-7053 fragment!).

Tree to shrub 1.5–18 m tall, DBH 3–20 cm; branchlets, petioles, and buds densely covered by erect, straight, yellowish hairs to glabrescent. Petiole 4–8 mm; lamina 6.5–19 × 2.5–6 cm, narrowly elliptic to elliptic, narrowly oblong to oblanceolate; apex acuminate to attenuate, acute, base acute to obtuse or slightly asymmetric, chartaceous, glabrous, with erect, straight, yellowish hairs along the primary vein adaxially to glabrescent, sparsely to densely covered by appressed, straight, whitish hairs and papillae abaxially; primary vein impressed adaxially, prominent abaxially, secondary veins flat to impressed adaxially, raised abaxially, 5 to 11 pairs of secondary veins, tertiary veins impressed and non-reticulate on both sides, angles between primary and secondary veins 55°–70°. Inflorescence 1-flowered; bracts 3 to 5. Flowering pedicel 5–8 mm, fruiting pedicel 1.5–4 cm, glabrous; flower buds ovoid; sepals 3, 2–4 × 3–6 mm, triangular, densely covered by appressed, crisped to straight, brownish hairs; petals 6, in 2 whorls of 3 petals each, coriaceous, densely covered by appressed to erect, crisped, brownish hairs; outer petals 9–20 × 6–14 mm, widely ovate to oblong-ovate; inner petals 9–18 × 5–10 mm, elliptic, oblanceolate to narrowly obovate; bisexual flower with ca. 30 stamens, carpels ca. 100, ovary cylindrical, densely covered by appressed, straight hairs; male flower with 75 to 190 stamens, 1.5–3 mm. Fruit with (6 to)30 to 80 monocarps, 17–30 × 12–20 mm, ellipsoid, apex apiculate to umbonate, immature green, mature red-purple to red-orange, stipe 30–40 mm; fruit wall fleshy, smooth, with apparent veins, transversal raised line around the monocarp and longitudinal intrusions apparent on dried monocarps. Seed 18–22 × 10–12 mm, ellipsoid.

Habitat and distribution. *Ephedranthus guianensis* occurs in Guyana, Surinam, and French Guiana, in forest on lateritic soil, at elevations from 200 to 900 m. It flowers from January to February and from August to October, and fruits from June to September, rarely in April.

Vernacular names. Karishiri (Creole, Guyana), man-pika-pika (Sranan, Surinam), mamayawé (Creole, French Guiana), mouamba (Paramaka, French Guiana).

Notes. *Ephedranthus guianensis* is recognizable by the medium-sized, 6.5–19 × 2.5–6 cm, usually

oblanceolate leaves, fruits with very long stipes 30–40 mm long, and up to 80 monocarps with apparent veins on the wall. *Ephedranthus guianensis* var. *oligantha* has been distinguished from the typical variety by its smaller flowers, with sepals 1.5–2 mm (vs. 2–2.5 mm in the typical variety), and outer petals 6 × 4 mm (vs. 10–13 × 7–8 mm) (Fries, 1931). Nevertheless, it was based on a single collection with atypical flowers, and Oliveira and Sales (1999) considered this name a synonym of *E. guianensis*.

Additional specimens examined. FRENCH GUIANA. **Saint-Laurent-du-Maroni:** *BAFOG (Service Forestier) 7478* (P, U); Entre Citron et le Mont Décou Décou, *Cremers 8235* (CAY, P, U); Banafokondre, *Sauvain 134* (CAY, P, U); Rivière Grand Inini, basin du Maroni, *Sabatier & Prévost 3389* (CAY, NY, P, U); Montagnes de la Trinité, Inselberg Nord Ouest, *Granville et al. 6112* (BR, CAY, G, K, MG, P, U); Piste de Saint-Elie, interfluve Sinnamary-Counamama, *Prévost & Sabatier 4130* (CAY, U); Km. 25, bord de zone defrichés, *Riéra 466* (U); Station des Nouragues, basin de l'Arataye, *Sabatier & Prevost 2782* (K, MO); Godebert, *Wachenheim 274* (P).

GUYANA. **Upper Demerara-Berbice:** Mabura Hill, near Ecological Reserve guest house, *Maas et al. 7135* (K, MO, U); 180 km SSE of Georgetown, near Reserve house, *ter Steege et al. 280* (U). **West Demerara:** Hill area, Tropenbos reserve, *Scharf 64* (BRG, LZ, U); Takutu Ck. Puruni R., Mazaruni Rivier, *Fanshawe 2052* (U); *Forest Department of British Guiana 4788* (K).

SURINAME. **Nickerie:** area of Kabalebo Dam project, *Lindeman 333* (K, U); *Lindeman 753* (BBS, U); Zuid Rivier, 2 km above confluence with Lucie Rivier, *Irwin 55720* (U); Jodensavanne-Mapane kreek area, *Schulz 8568* (U); *Schulz 7518* (U); *LBB 9888* (U); *Lindeman 6749* (U); Boven-Suriname Rivier bij Goddo, *Stahel 44* (U); Juliana top, 14 km N of Lucie Rivier, *Irwin 54720* (MO, U); Paris Jacob-kreek, *Maas et al. LBB11029* (U); Raleighvallen, Voltzberg Natuurreservaat, *De Jong LBB15778* (U); Coppename River Raleigh Falls, *Stahel BW6269* (IAN, K, U); *Boom 1126* (U); Sipaliwini, Central Suriname Nature Reserve, ca. 2 km SE of E & of Kayserberg Airstrip, *Rosário et al. 1793* (K, MG, MO); vic. of camp on W bank of Zuid River, *Rosário et al. 2064* (MG, MO, P).

6. Ephedranthus parviflorus S. Moore, Trans. Linn. Soc. London, Bot. 4: 296, pl. 21, 38. 1895. TYPE: Brazil. Mato Grosso: Barra do Bugres (Santa Cruz), in sylvulis juxta Santa Cruz, Sep. 1891 (fl.), *S. Moore 310* (holotype, BM [bc] 000522448!; isotype, NY [bc] NY00622078!). Figures 4, 6A, B.

Tree to shrub 3–18 m tall, DBH 12–30 cm; branchlets, petioles, and buds densely covered by appressed to erect, crisped, yellowish hairs. Petiole 3–8 mm; lamina 5.5–16 × 2.5–7 cm, narrowly elliptic, elliptic to widely elliptic, narrowly obovate to oblanceolate, suborbiculate; apex acute, rarely obtuse to attenuate, base acute, obtuse to slightly asymmetric, rarely slightly cordate, chartaceous, glabrous with erect, straight hairs along the primary vein adaxially, sparsely covered by erect, straight hairs abaxially; primary vein impressed, forming a sulcus near the base adaxially, raised abaxially, secondary veins impressed adaxially, raised abaxially, 7 to 13 pairs of secondary veins, tertiary veins impressed adaxially and slightly raised abaxially and non-reticulate on both sides, angles between primary and secondary veins 50°–70°. Inflorescence 1-flowered; bracts ca. 5. Flowering pedicel sessile, fruiting pedicel 6–20 mm, densely covered by yellowish hairs; flower buds globose; sepals 3, 3–5 × 4 mm, ovate, densely covered by appressed, straight, goldish hairs; petals 6, in 2 whorls of 3 petals each, chartaceous, densely covered by appressed, straight, goldish hairs; outer petals 6–8 × 3–5 mm, ovate to narrowly oblong with acute to rounded apex; inner petals 8.5–9 × 3–4 mm, oblong to narrowly oblong with acute to rounded apex; bisexual flower with 27 to 30 stamens, carpels 9 to 16, ovary ovoid, densely covered by appressed, straight hairs; male flower with ca. 100 stamens, 1.5–2 mm. Fruit with 4 to 14 monocarps, 15–20 × 8–10 mm, immature ellipsoid to globose, mature cylindrical, apex shortly apiculate, immature green, mature yellowish to red, stipe 5–8 mm; fruit wall smooth. Seed 16–19 × 7–8 mm, ellipsoid.

Habitat and distribution. *Ephedranthus parviflorus* occurs in central-western Brazil, in the states of Goiás, Mato Grosso, Mato Grosso do Sul, Pará, and Tocantins, and in Paraguay, in riparian forests of the cerrado domain, on clay to sandy soils, at elevations from 350 to 750 m. It flowers from June to August and fruits from October to December.

Vernacular names. Adzo waihi (Aquém, Brazil), conduru, meju-do-porco (Portuguese, Brazil).

Notes. *Ephedranthus parviflorus* shares with *E. boliviensis*, *E. dimerus*, and *E. pisocarpus* the medium-sized leaves, 5.5–17 × 2.5–7 cm, with apparent secondary veins on the upper side. It is distinguished from *E. boliviensis* and *E. pisocarpus* by the monocarps, ellipsoid or globose in *E. boliviensis* and *E. pisocarpus* and cylindrical in *E. parviflorus*, and from *E. dimerus* by its dimerous flowers with 1-cm-long pedicel (vs. 2 whorls of 3 petals and sessile pedicel in *E. parviflorus*). *Ephedranthus parviflorus* and *E. pisocarpus* are sister species supported by sessile flowers and oblong to narrowly oblong, chartaceous petals (Fig. 1, character 8: 1, character 11: 2, and character 10: 1). *Ephedranthus parviflorus* is usually confused with *Oxandra saxicola* Maas & Junikka. Both species occur in Goiás and have similar leaves, with brownish-yellow veins on the upper side. However, *O. saxicola* shows reticulate venation, and one or two globose, glaucous monocarps, with very short stipes.

Additional specimens examined. BRAZIL. **Goiás:** Alto Paraíso de Goiás, fazenda Antônio Sertão, a 20 km de Alto Paraíso, *Nóbrega 871* (HEPE, SPF); Anápolis, entre Araguaína e Colina, *Silva 57769* (K, NY); Cavalcante, Rio do Carmo (rio

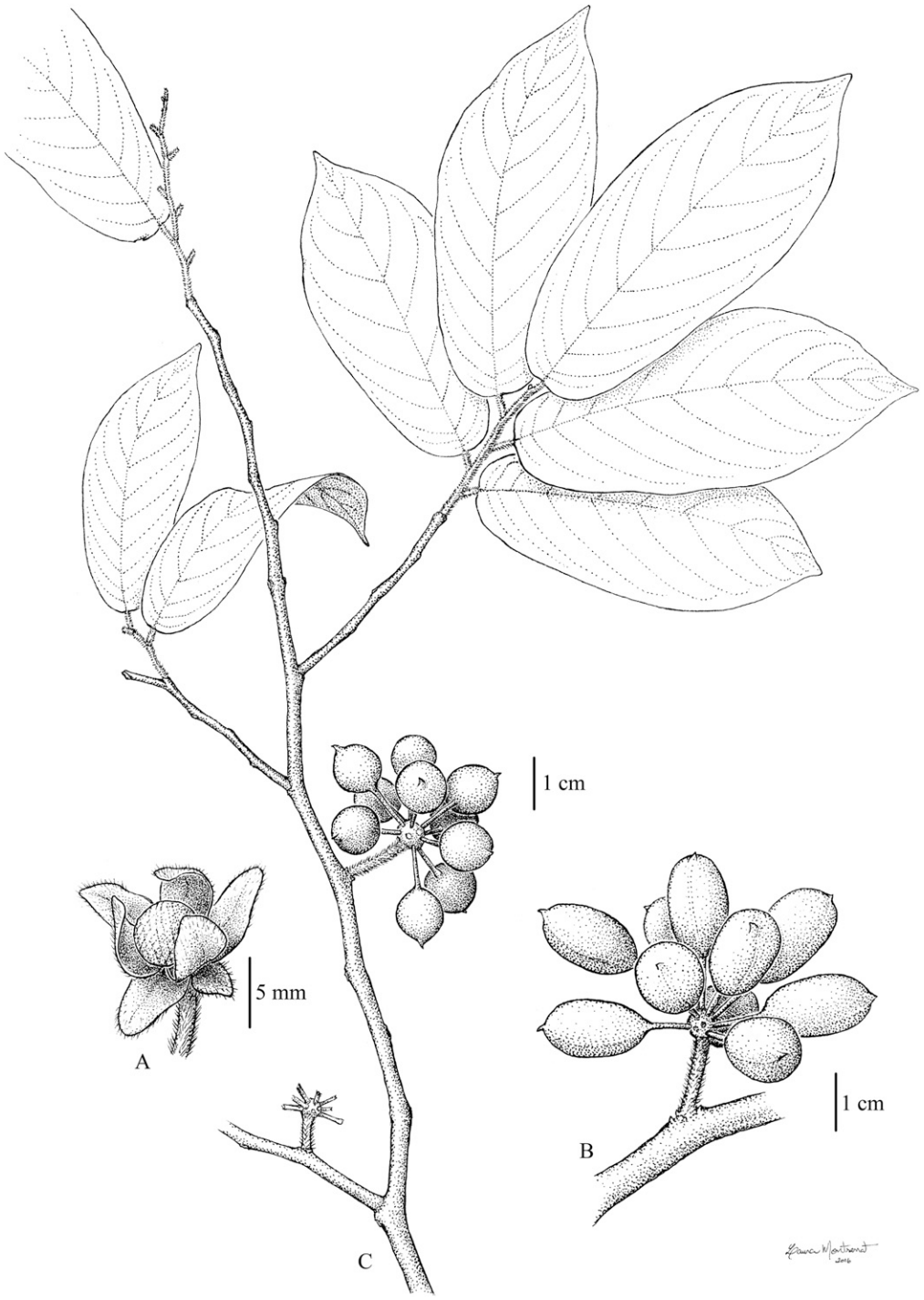

Figure 6. A, B. *Ephedranthus parviflorus* S. Moore. —A. Flower. —B. Fruit. C. *Ephedranthus pisocarpus* R. E. Fr., twig with fruit. A, *Solórzano et al. 93* (UB); B, *Pereira-Silva 5776* (SPF); C, *Daly et al. 500* (U).

Tocantins) Km. 4, *Pereira-Silva et al. 5741* (CEN, SPF); balsa do rio Tocantins (Serra Branca), rio Macacão, cerca de 800 m do rio Tocantins, *Pereira-Silva 5776* (CEN, SPF); Colinas do Sul, bacia da inundação da usina hidrelétrica Serra da Mesa, rio Tocantinzinho, *Santos et al. 38* (CEN, SPF); Estrada Colinas do Sul–Minaçu, à esquerda, 5 km após Vila Borba, *Santos 573*

(CEN); Jussara, fazenda Santa Rita do Araguaia, *Silva 114* (IBGE); Minaçu, futuro reservatório do aproveitamento hidrelétrico Serra da Mesa, *Walter et al. 3571* (CEN, SPF); Niquelândia, Serra Negra, estrada paralela ao rio Bagagem, *Walter et al. 2491* (CEN, SPF); Planaltina, Córrego Rico to Sapé (Smith & Smith, 1967), *Burchell 8080* (P); Fazenda Serra Negra, bacia da inundação da usina hidrelétrica Serra da Mesa, ao lado da linha de transmissão elétrica, *Walter et al. 1635* (CEN, SPF); bacia da inundação da usina hidrelétrica Serra da Mesa, na Serra Negra, *Santos et al. 58* (CEN, SPF); a montante da balsa entre Niquelândia e Campinaçu, pelo rio a cerca de 5 km da balsa, mata ciliar do rio Maranhão (Tocantins), margem direita, *Walter 2837* (CEN, SPF); Santa Isabel, Ilha do Bananal, Parque Nacional do Araguaia, *Silva 369* (UB). **Mato Grosso:** Água Boa, Reserva Indígena Areões, 8 km da aldeia Mutum, *Marimon 147* (SPF); *Marimon 79* (UB); Barra do Garça, Vale dos Sonhos, ca. 10 km N of Aragarças on the Aragarças–Xavantina rd., *Ratter et al. 406* (K, NY, P, UB); *Ratter et al. 2199* (UB); Chapada dos Guimarães, base aérea do SINDACTA, *Hatschbach 63697* (MBM, SPF); vic. of Buriti, *Prance 19246* (INPA, K, NY, U); drainage of upper rio Araguaia, 25 km S of Xavantina, *Irwin 17100* (IAN, NY, U); *Irwin 16794* (IAN, NY); Nova Xavantina, Reserva Biológica Mário Viana, mata de galeria do córrego Bacaba, *Marimon 169* (SPF, UB); Novo Santo Antônio, Parque Estadual do Araguaia, *Solórzano et al. 93* (UB); near the base camp of the expedition, ca. 270 km N of Xavantina, *Ramos et al. 140* (K, NY, P, U); expedition base camp, *Harley & Souza 10082* (IAN, K, NY, P, UB); *Harley et al. 11010* (K, P, NY, UB); *Onishi et al. 473/1252* (K); *Philcox et al. 3082* (IAN, K, NY, P, UB); *Castro 10553* (NY, P, UB); Cabeceira do Guariba a 3 km SE do acampamento da expedição inglesa, *Sidney & Onishi 1252* (UB); Santa Terezinha, hillside forest along rd. to Santa Terezinha (MT 413), 7 km E of jct. with BR 158, *Thomas et al. 4368* (MG, NY, SPF, U); BR 158, rodovia para Vila Rica, a 21 km S da cidade de Santa Terezinha, Serra da Cobrinha, *Cid Ferreira et al. 6433* (K, MG, NY, SPF, U); São Félix do Araguaia, área da fazenda Jamaica, 28 km S do cruzamento da estrada BR 158 e MT 242, *Cid Ferreira et al. 6486* (INPA, K, MG, NY, SPF, U); Poconé, *Maciel 117* (INPA). **Mato Grosso do Sul:** Guia Lopes da Laguna, fazenda Trincheira, 9 km N of Guia Lopes da Laguna on the rd. to Nioaque (BR419), *Ratter et al. R7575V* (UB). **Pará:** Alto dos Montes, região do Araguaia, campos gerais, *Froés 29889* (NY). **Tocantins:** Ilha do Bananal, Parque Nacional do Araguaia, ca 2 km of Macaúba, *Ratter et al. 4402* (K, NY, UB); Novo Acordo, Usina Hidrelétrica Novo Acordo, Rio do Sono, *Haidar & Santos 1144* (IBGE); Paranã, entroncamento balsa do Coronel Valente–Rio Custódio, Km. 5, *Pereira-Silva & Moreira 11053* (CEN); balsa do Coronel–vila Rosário, Km. 1, ribeirão Funil, *Pereira-Silva et al. 11984* (CEN); cerca de 500 m a E da sede da fazenda do Coronel Valente, ribeirão Funil, *Pereira-Silva et al. 12328* (CEN); São Salvador do Tocantins, córrego Obá, estrada para o córrego Mutum, *Pereira-Silva et al. 10701* (CEN); canteiro de obras da Usina Hidrelétrica São Salvador, margem esquerda do rio Tocantins, *Pereira-Silva et al. 10625* (CEN); fazenda Serrinha, *Pereira-Silva et al. 12351* (CEN); Tocantínia, 16 km from Lajeado on the rd. to Tocantínia, Xerente Reserve, *Ratter et al. 7860* (K, UB).

PARAGUAY. *Balansa 2299a* (P).

7. **Ephedranthus pisocarpus** R. E. Fr., Acta Horti Berg. 13(3): 108, f. 1a, b. 1941. TYPE: Brazil. Maranhão, São Luís, island of São Luiz, Feb.–Mar. 1939 (fr.), *R. Froés 11592* (holotype, S S-R-1921!; isotype A [bc] A00039312!, CAS [bc] CAS0003085!, F [bc] F0047787F!, K [bc] K000487280!, LIL [bc] LIL000481!, MICH [bc] MICH1115396!, NY [bc] NY00622080!, SP [bc] SP000292!, US [bc] US00104271!, WIS [bc] WIS00000293MAD!). Figures 4, 6C.

Tree to shrub 4.5–22 m tall, DBH 7.5–10 cm; branchlets, petioles, and buds densely covered by appressed to erect, crisped, yellowish hairs. Petiole 2–5 mm; lamina 5–11 × 2.5–5 cm, narrowly oblong to oblong, elliptic, or narrowly obovate to obovate; apex acute to acuminate, rarely obtuse, base obtuse to slightly cordate, rarely acute, papyraceous to chartaceous, glabrous with erect hairs along the primary vein adaxially, densely covered by erect, crisped hairs abaxially; primary vein impressed, forming a sulcus near the base adaxially, raised abaxially, secondary veins impressed adaxially, raised abaxially, 8 to 10 pairs of secondary veins, tertiary veins impressed adaxially and slightly raised abaxially and non-reticulate on both sides, angles between primary and secondary veins 50°–75°. Inflorescence 1- or 2-flowered; bracts ca. 5. Flowering pedicel sessile, fruiting pedicel 7–10 mm, densely covered by yellowish hairs; flower buds not seen; sepals 3, 4–6 × 4–7 mm, ovate, densely covered by appressed, straight hairs; petals 6, in 2 whorls of 3 petals each, chartaceous, densely covered by appressed, straight hairs; outer and inner petals 15–20 × 6–10 mm, oblong; bisexual flower: stamens not seen, carpels ca. 20; male flower with ca. 100 stamens, ca. 1 mm. Fruit with 2 to 13 monocarps, 11–13 × 7–10 mm, ovoid, globose to ellipsoid, apex shortly apiculate, mature yellowish to dark red, stipe 5–7 mm; fruit wall smooth, with longitudinal intrusions apparent on dried monocarps. Seed 10 × 7 mm, ellipsoid.

Habitat and distribution. *Ephedranthus pisocarpus* occurs in the northeastern Brazilian states of Ceará, Maranhão, and Piauí, in forests from cerrado and caatinga. It flowers in August and fruits from January to March.

Vernacular names. Conduru, cunduru-brabo, cunduru-amarelo, envira-de-cocho (Portuguese, Brazil).

Notes. The mature monocarps of *Ephedranthus pisocarpus*, small and ellipsoid to globose, are similar to the unripe ones of *E. parviflorus*. *Ephedranthus pisocarpus* and *E. parviflorus* are distinguishable by the leaf and fruit pedicel size, usually smaller in *E. pisocarpus*. Another species generally confused with *E. pisocarpus* is *Oxandra sessiliflora* R. E. Fr. Both are sympatric and share the small leaves with brown primary vein on the upper side. Nevertheless, *O. sessiliflora* has narrowly elliptic leaves and almost sessile monocarps, whereas *E. pisocarpus* has oblong to obovate leaves and stipitate monocarps.

Additional specimens examined. BRAZIL. **Ceará:** Novo Oriente, Ibiapaba, Estrondo, *Araújo 135* (EAC); São Benedito, Serra de Ibiapaba, mata à margem de uma vereda, *Bezerra 409* (U). **Maranhão:** Buriticupu, Reserva Florestal da Companhia Vale do Rio Doce, *Oliveira et al. 143* (MG, U); *Oliveira et al. 144* (NY); Barra do Corda, Canela Indian Village & vic., ca. 50 km SW of Barra do Corda, *Eiten 461* (UB); Carema, Cantagalo, *Froés 25693* (IAN); Caxias, *Ducke 792* (MG); Fortuna & Buriti-Bravo along the rio Itapecuru, the border betw. the two municipalities, 15 km SE of Fortuna, *Schatz et al. 732* (K, MG, NY); Santa Luzia, localidade de Bom Jesus, penetração à margem direita da BR 222 em frente ao Km. 100, a 12 km da rodovia, fazenda CODOMINAS, às margens do Rio dos Sonhos, *Silva 1034* (IAN, INPA, MG, NY, U); cerrado near dirt rd., approx. 40 km E of Barra do Corda toward Presidente Dutra, *Daly et al. 557* (IAN, INPA, MG, NY, U); São Luís, Island of São Luis, *Krukoff 11592* (U); Ilha de São Luís, *Gottsberger 12-12283* (U); São Luiz, Reserva Florestal do Sacavem, *Muniz 2* (INPA); Fazenda Bacaba, Doctor Haroldo, 5 km S of MA 119 from entrance 3 km NW of Lago do Junco, *Daly et al. 500* (IAN, INPA, K, MG, NY, U); Tuntum, Palmeirinhas, 46 km W of Presidente Dutra on the rd. to Barra do Corda, then 20 km S to Angelim, then 20 km E, *Schatz 776* (MG, NY). **Piauí:** Brasileira, baixa do Tinguizeiro, Parque Nacional de Sete Cidades, *Alencar 468* (SPF, TEPB); Campo Maior, Alto do Comandante, *Lopes et al. 52* (SPF, TEPB); Cocal, *Chaves et al. 216* (SPF, TEPB); Piracuruca, *Haidar et al. 43* (UB); São Raimundo Nonato, Boqueirão Grande, *Emperaire 2311* (U); *Emperaire 2547* (P); Parque Nacional Serra da Capivara, *Moura 275* (JPB, NY); Uruçuí, fazenda Boa Vista, *Miranda 4833* (INPA).

Discussion and Conclusions

Ruizodendron ovale is sister to *Ephedranthus* (Fig. 1, Table 3), in the same relationship recovered by Chatrou et al. (2012) and Pirie et al. (2006). However, in the phylogenetic analysis of Lopes et al. (2018), *Ephedranthus* emerges in a polytomy together with *Klarobelia*, *Oxandra*, *Pseudomalmea*, *Pseudephedranthus fragrans* (R. E. Fr.) Aristeg., and *R. ovale*.

Some of the synapomorphies within the *Ephedranthus* clade have already been used for taxonomic purposes, establishing the same relationships of the *Ephedranthus* species in previous, non-phylogenetic treatments (Fig. 1). Leaf with immersed to slightly raised tertiary veins (character 6: 0), which supports the clade *E. guianensis*, *E. amazonicus*, *E. dimerus*, *E. parviflorus*, and *E. pisocarpus*, was used in the key to species (Lopes et al., 2014). Pedicels 0–2 mm long (character 8: 1) and narrowly oblong to oblong, chartaceous petals (character 10: 1 and character 11: 2), which support *E. parviflorus* plus *E. pisocarpus*, were used to differentiate these species (Fries, 1941; Oliveira & Sales, 1999; Lopes et al., 2014). Fruit pedicel covered by yellowish hairs (character 17: 1), which supports the clade *E. dimerus*, *E. parviflorus*, and *E. pisocarpus*, was one of the characteristics used to distinguish the sections in *Ephedranthus* (Fries, 1934). Finally, stipe 20–40 mm long (character 22: 2), which is the synapomorphy of *E. guianensis* and *E. amazonicus*, was used to differentiate *E. pisocarpus* from *E. amazonicus* and *E. parviflorus* (Fries, 1941) and in the key to species of *Ephedranthus* (Oliveira & Sales, 1999; Lopes et al., 2014). Thus, the morphological analysis has clarified the putative evolutionary meaning of the characters involved and the potential for using them in taxonomy.

The current subdivision of *Ephedranthus* as established by Fries (1934), *Ephedranthus* sect. *Ephedranthus*, including *E. guianensis*, *E. parviflorus*, and *E. pisocarpus*, and *Ephedranthus* sect. *Sphaeranthema*, including *E. amazonicus*, is not monophyletic, and its sections may not be recognized. One of the characters used to delimit these two sections is the petals shape. Oblong petals characterized *Ephedranthus* sect. *Ephedranthus*, and orbicular-concave petals characterized *Ephedranthus* sect. *Sphaeranthema* (Fries, 1934). Oblong petal is a synapomorphy of *E. parviflorus* and *E. pisocarpus*. However, petal shape in *E. guianensis* is variable, ranging from widely ovate to oblong-ovate, and better characterized as ovate, orbiculate to suborbiculate petals (character 11: 1). In addition, *E. guianensis* is sister to *E. amazonicus*, sharing stipes 20–40 mm long (character 22: 2). Thus, section *Sphaeranthema* is nested in section *Ephedranthus* (Fig. 1), rendering this last section non-monophyletic and legitimatizing (Backlund & Bremer, 1998) their synonymization under *Ephedranthus*.

Excluded Name

Ephedranthus fragrans R. E. Fr., Mem. New York Bot. Gard. 9: 327. 1957. *Pseudephedranthus fragrans* (R. E. Fr.) Aristeg., Mem. New York Bot. Gard. 18: 43. 1969. TYPE: *Maguire & Wurdack 34954* (holotype, S!).

Literature Cited

Backlund, A. & K. Bremer. 1998. To be or not to be—Principles of classification and monotypic plant families. Taxon 47: 391–400.

Chatrou, L. W. & M. D. Pirie. 2003. Two new species of Annonaceae from Bolivia. Revista Soc. Boliv. Bot. 4: 25–30.

Chatrou, L. W., M. D. Pirie, R. H. J. Erkens, T. L. P. Couvreur, K. M. Neubig, J. R. Abbott, J. B. Mols, et al. 2012. A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. Bot. J. Linn. Soc. 169: 5–40.

Doyle, J. A. & A. Le Thomas. 1996. Phylogenetic analysis and character evolution in Annonaceae. Bull. Mus. Natl. Hist. Nat., B, Adansonia 18: 279–334.

Erkens, R. H. L., J. Oosterhof, L. Y. T. Westra & P. J. M. Maas. 2017. Revisions of *Ruizodendron* and *Pseudephedranthus* (Annonaceae) including a new species and an overview of most up-to-date revisions of Neotropical Annonaceae genera. Phytokeys 86: 75–96.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. Amer. Naturalist 106: 645–668.

Farris, J. S. 1982. Outgroup and parsimony. Syst. Zool. 31: 328–334.

Fries, R. E. 1931. Revision der Arten einiger Annonaceen-Gattungen II. Acta Horti Berg. 10: 129–341.

Fries, R. E. 1934. Revision der Arten einiger Annonaceen-Gattungen III. Acta Horti Berg. 12: 135–154.

Fries, R. E. 1941. Nueu Amerikanische Annonaceen. Acta Horti Berg. 13: 108–116.

Fries, R. E. 1959. Annonaceae. Pp. 1–171 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Band 17a, II. Duncker und Humblot, Berlin.

Guo, X., C. C. Tang, D. C. Thomas, T. L. P. Couvreur & R. M. K. Saunders. 2017. A mega-phylogeny of the Annonaceae: Taxonomic placement of five enigmatic genera and support for a new tribe, Phoenicantheae. Sci. Rep. 7: 7323.

Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 *in* C. R. Metcalfe & L. Chalk (editors), Anatomy of the Dicotyledons, Vol. I. Systematic Anatomy of Leaf and Stem, with a Brief History of the Subject. 2nd ed. Clarendon Press, Oxford.

Hillis, D. 1987. Molecular versus morphological approaches to systematics. Annu. Rev. Ecol. Evol. Syst. 18: 23–42.

Hutchinson, J. 1964. The Genera of Flowering Plants, Angiospermae. Clarendon Press, Oxford.

Junikka, L., P. J. M. Maas, H. Maas-van de Kamer & L. Y. Th. Westra. 2016. Revision of *Oxandra* (Annonaceae). Blumea 61: 215–266.

Koek-Noorman, J., L. Y. T. Westra & P. J. M. Maas. 1990. Studies in Annonaceae. XIII. The role of morphological characters in subsequent classifications of Annonaceae: A comparative survey. Taxon 39: 16–32.

Lopes, J. C., L. W. Chatrou & R. Mello-Silva. 2014. *Ephedranthus dimerus* (Annonaceae), a new species from the Atlantic Forest of Brazil, with a key to the species of *Ephedranthus*. Brittonia 66: 70–74.

Lopes, J. C., L. W. Chatrou, R. Mello-Silva, P. L. Rudall & M. G. Sajo. 2018. Phylogenomics and evolution of floral traits in the Neotropical tribe Malmeeae (Annonaceae). Molec. Phylogen. Evol. 118: 379–391.

Maas, P. J. M. & L. Y. T. Westra. 1984. Studies in Annonaceae. II A monograph of the genus *Anaxagorea* A.St.-Hil. Bot. Jahrb. Syst. 105: 73–134.

Maas, P. J. M. & L. Y. T. Westra. 1985. Studies in Annonaceae. II A monograph of the genus *Anaxagorea* A.St.-Hil. Part 2. Bot. Jahrb. Syst. 105: 145–204.

Maas, P. J. M. & L. Y. T. Westra. 2003. Revision of the Neotropical genus *Pseudoxandra*. Blumea 48: 201–259.

Maas, P. J. M., E. C. H. van Heusden, J. Koek-Noorman, A. K. van Setten & L. Y. T. Westra. 1988. Studies in Annonaceae. IX. New species from the Neotropics and miscellaneous notes. Proc. Kon. Ned. Akad. Wetensch., C 91: 243–282.

Maas, P. J. M., L. Y. T. Westra & M. Vermeer. 2007. Revision of the Neotropical genera *Bocageopsis*, *Onychopetalum*, and *Unonopsis* (Annonaceae). Blumea 52: 413–554.

Maddison, W. P., M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

Moore, S. M. 1895. The phanerogamic botany of the Matto Grosso Expedition, 1891–92. Trans. Linn. Soc. London, Bot. 4 (1894–1986): 265–516.

Nixon, K. C. & J. M. Carpenter. 1993. On outgroups. Cladistics 9: 413–426.

Oliveira, J. & M. F. Sales. 1999. Estudos taxonômicos dos gêneros *Ephedranthus* e *Pseudephedranthus* Aristeg.: Annonaceae. Bol. Mus. Paraense Emilio Goeldi, N.S. Bot. 15: 117–166.

Pirie, M. D., L. W. Chatrou, J. B. Mols, R. H. J. Erkens & J. Oosterhof. 2006. 'Andean-centred' genera in the short-branch clade of Annonaceae: Testing biogeographical hypotheses using phylogeny reconstruction and molecular dating. J. Biogeogr. 33: 31–46.

Punt, W., P. P. Hoen, S. Blackmore, S. Nilsson & A. Le Thomas. 2007. Glossary of pollen and spore terminology. Rev. Palaeobot. Palynol. 143: 1–81.

QGIS Development Team. 2009. QGIS Geographic Information System. Open Source Geospatial Foundation. <http://qgis.osgeo.org>, accessed 28 May 2019.

Reflora. 2019. Reflora Virtual Herbarium. <http://reflora.jbrj.gov.br/reflora/herbarioVirtual>, accessed 17 January 2019.

Saunders, R. M. K. 2010. Floral evolution in the Annonaceae: Hypotheses of homeotic mutations and functional convergence. Biol. Rev. Cambridge Philos. Soc. 85: 571–591.

Smith, L. B. & R. C. Smith. 1967. Itinerary of William John Burchell in Brazil, 1825–1830. Phytologia 14: 492–506.

Swofford, D. L. 2002. PAUP: Phylogenetic Analysis Using Parsimony (and Other Methods), Vers. 4. Sinauer Associates, Sunderland, Massachusetts.

Thiers, B. 2018 [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih>, accessed 28 May 2019.

van Heusden, E. C. H. 1992. Flowers of Annonaceae: Morphology, classification, and evolution. Blumea 7(Suppl.): 1–218.

van Setten, A. K. & J. Koek-Noorman. 1986. Studies in Annonaceae. VI. A leaf anatomical survey of genera of Annonaceae in the Neotropics. Bot. Jahrb. Syst. 108: 17–50.

van Setten, A. K. & P. J. M. Maas. 1990. Studies in Annonaceae. XIV. Index to generic names of Annonaceae. Taxon 39: 675–690.

van Setten, A. K. & J. Koek-Noorman. 1992. Studies in Annonaceae. XVII. Fruits and seeds of Annonaceae: Morphology and its significance for classification and identification. Biblioth. Bot. 142: 1–101.

Walker, J. W. 1971. Pollen morphology, phytogeography, and phylogeny of the Annonaceae. Contr. Gray Herb. 202: 1–132.

Watrous, L. E. & Q. D. Wheeler. 1981. The outgroup method of character analysis. Syst. Zool. 30: 1–11.