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Morphology and distribution support *Pseudaraeococcus* (Bromeliaceae, Bromelioideae) as a new genus from the Atlantic forest of Northeastern Brazil

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Abstract

After a revision of the genus *Araeococcus* Brong. two distinct morpho-biogeographical groups, also supported by anatomical characters, became evident and contradictory. Thus, here we elevate a subgenus to the generic level and propose the new *Pseudareococcus* to accommodate species bearing a unique combination of vegetative, reproductive and biogeographical features. *Pseudaraeococcus* differs from *Araeococcus* by the utriculate rosette with a developed tank (vs. fasciculate rosette and tank inconspicuous or absent), leaves nearly entire (vs. serrate), petals patent or reflexed (vs. petals erect), filaments cylindrical (vs. complanate), anther apex apiculate (vs. caudate), stigma conduplicate-spiral (vs. convolute-obconic, convolute blade I or simple-erect), seed coat with alveolar cells (vs. with cells with linear shapes), and by the Atlantic forest (vs. Amazonian/Central America) distribution. Six new combinations were made to accommodate species, and an identification key, a distributional map, and photographs of plants and structures are provided.

Keywords: Atlantic forest, Bahia, bromeliad, epiphyte, taxonomy, new genus, Poales, Rainforest.

1. Introduction

Bromeliaceae is almost exclusively Neotropical, except for a single species – *Pitcairnia feliciana* (Harms) Mildbraed – that occurs in Guinea in western Africa (Smith & Downs, 1974). The family comprises 3630 species in 77 genera (Gouda & al. 2020). Bromelioideae is the most genera rich subfamily represented in Brazil by at least 21 genera, several of them endemic to the Atlantic Forest of eastern Brazil, which is the center of diversity for this subfamily (Smith, 1955; Smith & Downs, 1979).

Araeococcus is a rare genus of the core Bromelioideae

(Schulte & al. 2009), which currently has 10 species (Gouda & al. 2020). It was described as monotypic, in 1841, to accommodate a single species of *Aechmea* lacking petal appendages. During the 20th century the genus remained somehow stable, with four species and few additions for a long time (Broadway & Smith 1933; Mez 1934; Smith 1955; Smith & Downs 1979; Leme 1999).

Regarding the infrageneric classification, Mez (1934) divided the genus into two subgenera. The subgenus *Eu-Araeococcus* (with two species: *A. micranthus* and *A. pectinatus*) was characterized by its sessile flowers and spiny leaves, and both species were from Central America and the Caribbean. While *Pseud-Araeococcus* was characterized by the pedicellate flowers and entire leaves, and included two species: *A. flagellifolius* from Amazonia, and *A. parviflorus*, from Northeastern Brazil (Mez 1934).

Additionally, the subgenus *Eu-Araeococcus* was characterized by Mez (1934) as having spiny leaves arranged in close bundles or clusters (fasciculate), inflorescence composed by spikes, sepals never mucronate and symmetric, and only two ovules in each locule. As this is the typical subgenus, Smith & Downs (1979) used the name *Araeococcus* subg. *Araeococcus*, removing the prefix *Eu-*, since this is an autonym.

The second subgenus was also described by Mez (1934) in the same monograph and was called *Pseud-Araeococcus*, at that time, written with a hyphen, what was later changed to *Pseudaraecoccus* by Smith & Downs (1979), but still with the same species.

As proposed by Mez (1934), the subgenus *Pseudaraeococcus* was characterized by having rosulate leaves forming a tank (*utriculatim*), inflorescence composed by racemose branches, mucronate and strongly asymmetric sepals, and up to 10 ovules in each locule. Considering the biogeography, specimens cited by Mez (1934) from the typical subgenus are confined to Central (Costa Rica) and northern South America (Guyana and Brazilian Amazonia) and the Caribbean (Trinidad, Tobago) (Fig. 1). *Pseudaraecoccus* included both a single Amazonian species (*A. flagellifolius* from northern Brazil) and one from Northeastern Brazil (*A. parviflorus* from Bahia state). Later, Smith (1955) described *A. goeldianus* L.B. Sm., which was also placed in the subgenus *Araeoccocus*, totaling three species, while subg. *Pseudoaraeococcus* totaled two species (Smith & Downs, 1979). Further additions to the genus were species from the Northeastern Brazil, placed in the subgenus *Pseudaraeococcus*, described by Leme (1999, *Araeococcus montanus* Leme) and, more recently, by Leme & Siqueira-Filho (2006, *Araeococcus chlorocarpus* (Wawra) Leme &

J.A. Siqueira, *Araeococcus nigropurpureus* Leme & J.A.Siqueira, and *Araeococcus sessiliflorus* Leme & J.A. Siqueira) and Pontes & al. (2019, *Araeococcus lageniformis* R.A. Pontes & Versieux).

Some inconsistencies in the subgenus *Pseudoaraeococcus* as described by Mez (1934) may have hindered the uniqueness of Northeastern Brazil species. First, Mez mentions in the identification key (Mez, 1934: 75) that the leaf is spineless, but then refers to a spinulose leaf above the sheath for the Amazonian *A. flagellifolius,* treated as belonging to subgenus *Pseudaraeococcus*. Further on there were also inconsistencies based on the number of ovules per locule, a key character that he used to delimit both subgenera. Apparently, he included *A. flagellifolius* (Amazonian) and *A. parviflorus* (from Northeastern Brazil) in the same subgenus based on the presence of flowers' pedicels alone, because according to the number of ovules, both species differed markedly. *Araeococcus flagellifolius* has only two ovules per locule, as found in other species of the typical subgenus. While *A. parviflorus* has up to 10 ovules per locule. Unfortunately, Mez did not have access to specimens or details of the number of ovules for this Amazonian species. Later, Leme and Siqueira-Filho (2006) made substantial contributions to our understanding of the subgenus *Pseudaraeococcus*. In addition to considering it endemic to Northeastern Brazil, they described two new species and resurrected one taxon.

Since the work of Terry & al. (1997) that based on *ndh*F suggested a sister relationship of the genus *Araeococcus* to *Quesnelia*, different placements and different sampling for *Araeococcus* have been used in phylogenetic reconstructions. Sampling only Amazonian taxa (*Araeococcus flagellifolius* and *A. goeldianus*) and using nuclear and plastid markers, Schulte & al. (2009) recovered both these *Araeococcus* as sister species, but nested in a clade with other Amazonian species of *Aechmea* (*A. mertensii, A. filicaulis*) within the core Eu-Bromelioideae. Definitive evidence of the polyphyletic nature of *Araeococcus* s.l. was provided by the molecular data based phylogeny of Sass & Specht (2010) where the Amazonian species plus *Aechmea jungurudoensis* Luther & K.F. Norton form a well-supported clade, while the Atlantic forest species *Araeococcus parviflorus*, the oldest species of the subgenus *Pseudaraeococcus* of Mez appeared in a distinct clade, isolated, sister to a clade containing species of *Hohenbergia*.

During the taxonomic revision of *Araeococcus*, a deep morphological analysis was conducted, and new evidence reinforced the unique morphological traits of Atlantic forest species of *Araeococcus* (Pontes, 2019). After investigating the combination of features presented by these taxa, we concluded
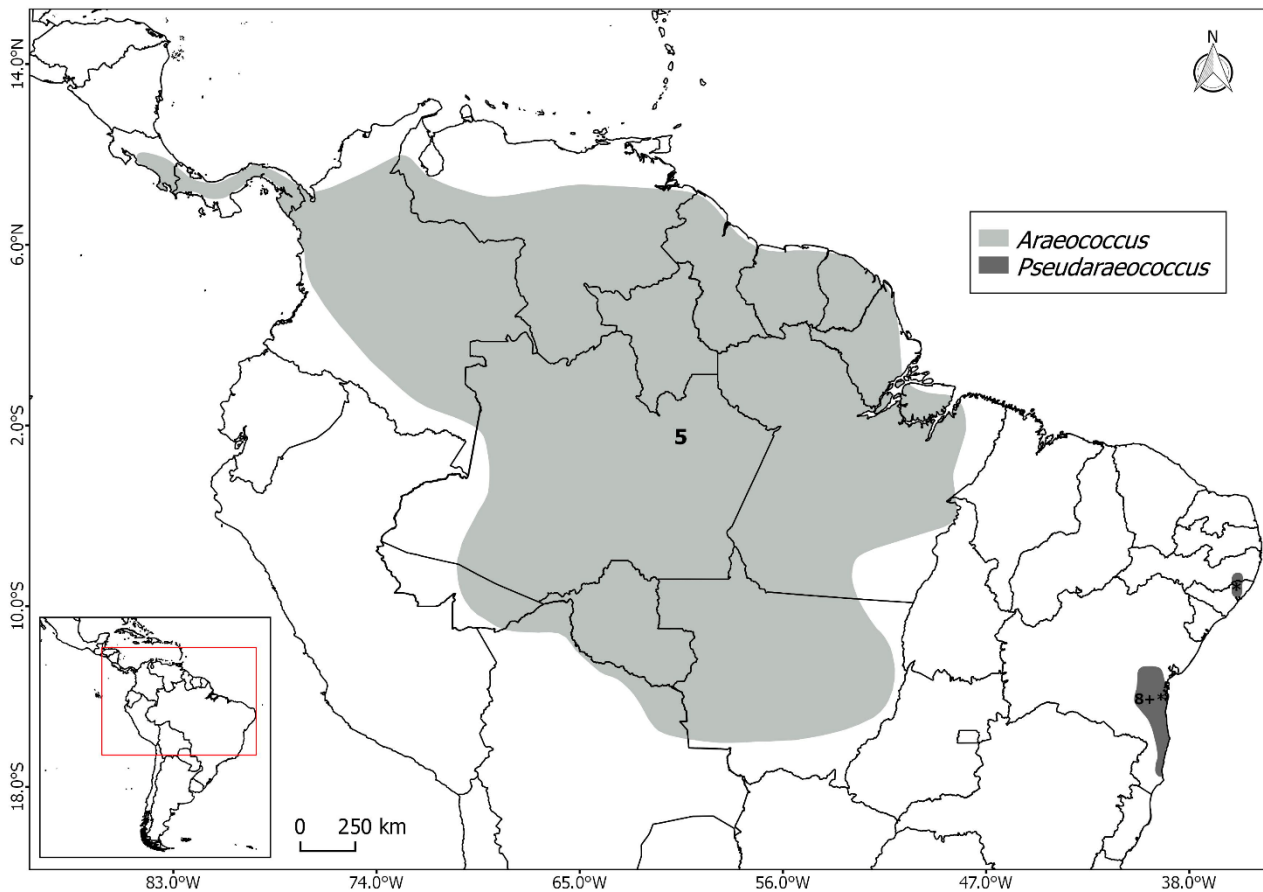
FIGURE 1. Map of geographic distribution of the genera *Araeococcus* and *Pseudaraeococcus* with the respective numbers of species, with a marked disjunction by Central Brazil.

that *Araeococcus* subg. *Pseudaraeococcus* would be better accommodated under a new status, at the generic rank.
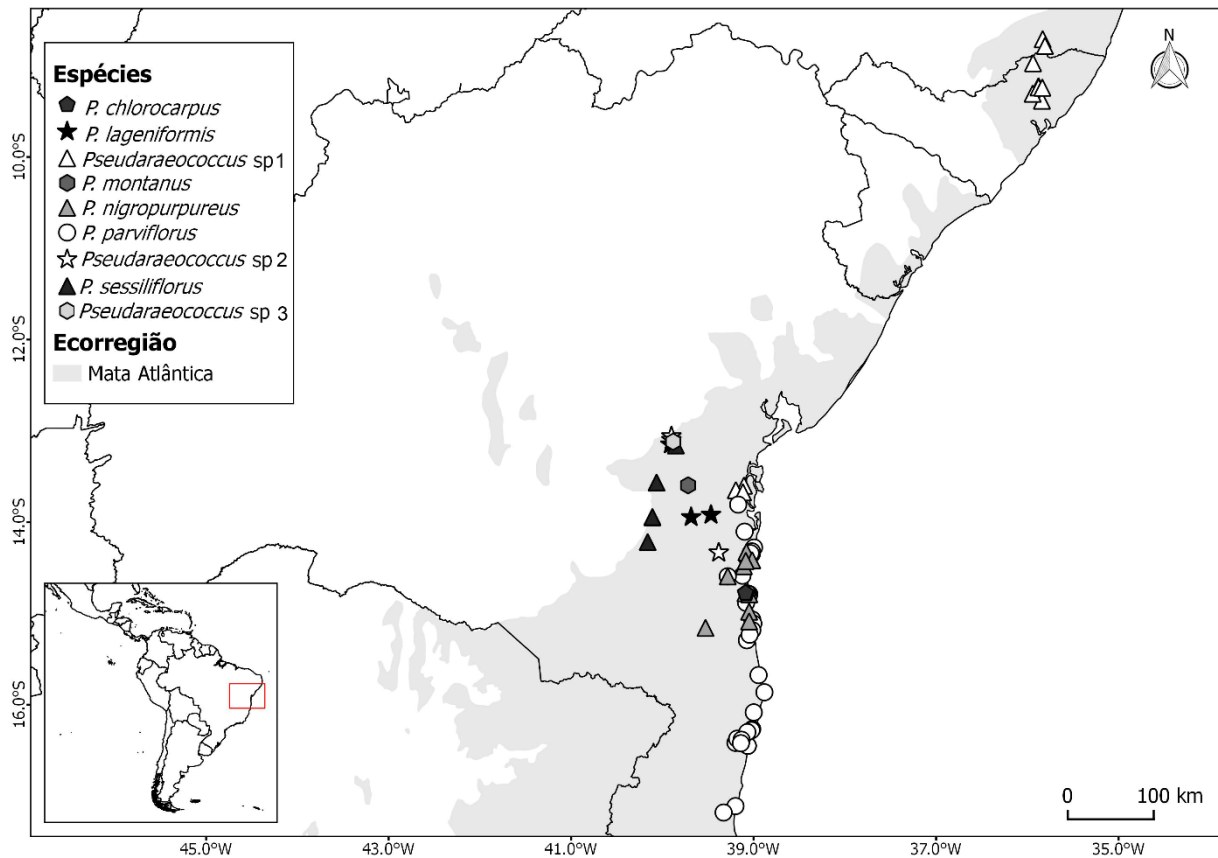
The new genus *Pseudaraeococcus* is restricted to the Atlantic Forest of Northeastern Brazil and its center of diversity is the mega diverse and humid Atlantic forest of Bahia state (Figs.1, 2). Our taxonomic decision to segregate these taxa was supported not only by the molecular phylogeny of Bromelioideae (Sass & Specht, 2010), but also by the ecological, biogeographical and morphological data described below.

Pseudaraeococcus, as a genus, has a morphological affinity with the genus *Lymania* Read, however, it differs because of a series of consistent morphological characters such as the absence of lateral folds flanking the filaments in the petals (which are present in *Lymania*), free antipetalous stamens (vs. adnate to the petals), ovary and fruit smooth or discretely corrugated at base (vs. ovary and fruit deeply furrowed or winged) (Smith & Downs, 1979; Sousa & Wendt 2008).

2. New genus: description and relationship

Pseudaraeococcus (Mez) R.A.Pontes & Versieux, **stat. nov.** ≡ *Pseudaraeococcus* Mez, Pflanzenr. IV. 32: 76. 1934, as "*Pseud-Araeococcus*" – TYPE: *Pseudaraeococcus parviflorus* (Mart. ex Schult. f.) R.A.Pontes & Versieux (≡ *Billbergia parviflora* Mart. ex Schult. f. ≡ *Araeococcus parviflorus* (Mart. ex Schult. f.) Lindm. Figs. 1, 2, 3.

Epiphytic, eventually terrestrial or saxicolous, propagating by thin stolons, usually long, and involving the phorophytes. Rosette lageniform or infundibuliform, tank conspicuous. Leaves of 3 to 10, concolor or discolor, chartaceous; lanceolate blade, which may present the upper portion wider than the base, entire or rarely inconspicuously spinescent margins, green to wine-red, presence of a longitudinal central canal along the blade; sheath elliptic to oval, subchartaceous, brownish to green-wine-red. Peduncle erect, shorter than the leaves; bracts of peduncle lanceolate, subchartaceous, pale green to pale pink, persistent in anthesis, lepidote. Bracts of the peduncle becoming straw-like. Inflorescence paniculate or spiculous, laxly branched, exceeding or not the height of the

FIGURE 2. Geographic distribution of the species of the genus *Pseudaraeococcus* in the Atlantic Forest of the Northeast Brazil, where most species are endemic to Bahia state. The Atlantic forest domain is represented in light grey

leaves. Floral bracts ovate to linear-lanceolate, broad-lanceolate or broad-oval, at the base of the pedicel or ovary, pale green. Flowers sessile or pedicellate, erect, laxly distributed on the branches, bisexual, rarely perfumed; sepals long-oval, asymmetric to subsymmetric, apiculate, discreetly winged, free, ecarinate, with 1 or 3 marked nerves, membranous; petals spatulate, free, patent or reflexed, usually white, or rarely blue, petal appendages absent, lateral folds on the adaxial face of the petals absent. Stamens free, exposed in the anthesis; filaments white, cylindrical; anthers dorsifixed near the base, apex apiculate, shorter than the pistil, yellow; stigma conduplicate-spiral, white or yellowish; ovary ovate or elliptical, smooth or discretely corrugated at base, green, pale green, bluish or dark purple; ovules 2-6 per locule. Fruit bacaceous, spherical, smooth, bluish or blackish when ripe; seed 1.1-1.6 mm long, reddish-brown, ellipsoid, almost straight to curved, alveolar cells.

Etymology — We kept the name already used by Mez (1934), since we believe the prefix Pseud- meaning false is a clue about how different plants were between Amazonian and Atlantic forest biomes. Although Mez (1934) kept these two groups within the same genus, he emphasized some key differences between both, including the shoot vegetative organization, rosette shape, inflorescence type and number of ovules per locule. In addition, the use of the suffix -*araeococcus*, refers to the memory of the species already known, facilitating the use of the name by biologists, ecologists and conservationists.

IDENTIFICATION KEY FOR *PSEUDARAEOCOCCUS* AND ALLIED GENERA

1. Rosette fasciculate, tank inconspicuous or absent, plants from the Amazonian or Central America and the Caribbean regions .... ***Araeococcus*** Brongn.
1. Rosette infundibuliform, lageniform, tank conspicuous, plants from the Atlantic forest of Northeastern Brazil **2**
2. Floral bracts absent or rarely inconspicuous; flowers always sessile; lateral folds on the adaxial face of the petal present; stamens with antipetalous filaments adnate to the petals; ovary and fruit deeply furrowed or winged.................***Lymania*** Read
2. Floral bracts always present; flowers sessile or pedi-cellate; lateral folds on the adaxial face of the petals absent; antipetalous stamens free; ovary and fruit smooth or discretely corrugated at base ....***Pseudaraeococcus***

1. ***Pseudaraeococcus parviflorus*** (Mart. ex. Schult. f.) R.A. Pontes & Versieux, **comb. nov.** ≡ *Billbergia parviflora* Mart. ex Schult. f. in Syst. Veg. 7(2): 1270. 1830. ≡ *Araeococcus parviflorus* (Mart. ex. Schult. f.) Lindm. in Kongl. Svenska Vetensk.-Akad. Handl., sér. 3, 24(8): 12. 1891 – Holotype: Brazil. Bahia. Ilheús, near Almada, 10 Nov - 11 Dec 1818, *Martius 2048* (M barcode M0111405, image!).

2. ***Pseudaraeococcus chlorocarpus*** (Wawra) R.A.Pontes & Versieux, **comb. nov.** ≡ *Lamprococcus chlorocarpus* Wawra. in Bot. Ergebn. 162, t. 28. 1866 ≡ *Araeococcus chlorocarpus* (Wawra) Leme & J.A.Siqueira, Fragm. Atlantic Forest N. E. Brazil: 251. 2007 – Holotype: Brazil. Bahia. Ilheús, nec non Rio de Janeiro prope Esperança, 1860, *Wawra & Maly 232* (W [destroyed]; isotype: LE barcode LE00006238, image!).

3. ***Pseudaraeococcus nigropurpureus*** (Leme & J.A.Siqueira) R.A.Pontes & Versieux, **comb. nov.** ≡ *Araeococcus nigropurpureus* Leme & J.A.Siqueira, Fragm. Atlantic Forest N. E. Brazil: 399. 2007 – Holotype: Brazil. Bahia. Uruçuca (Água Preta), estrada Uruçuca-Serra Grande, estrada secundária para a fazenda São José, 14°31'19.3"S e 39°09'23.7"O, 130 m elev., 22 Set 2005, Leme & Paixão 6732 (HB barcode HB93219!; isotype: CEPEC [not found]).

4. ***Pseudaraeococcus sessiliflorus*** (Leme & J.A.Siqueira) R.A.Pontes & Versieux, **comb. nov.** ≡ *Araeococcus sessiliflorus* Leme & J.A.Siqueira Filho, Fragm. Atlantic Forest N. E. Brazil 395. 2007 – Holotype: Brazil. Bahia. Jequié, 10.5 km ao sul de Mandacaru (entroncamento entre a estrada do estádio e a estrada para Jequié) na estrada para a Serra dos Brejos, 13°56'37"S e 40°06'40"O, 575-650 m. 5 Fev 2004, *Thomas et al. 13.853* (CEPEC barcode CEPEC00102955!; isotype: NY [not found]).

5. ***Pseudaraeococcus montanus*** (Leme) R.A.Pontes & Versieux, **comb. nov.** ≡ *Araeococcus montanus* Leme in Harvard Pap. Bot. 4(1): 142–144, f. 6. 1999 – Holotype: Brazil. Bahia, Wenceslau Guimarães. Estação Ecológica Nova Esperança, 25 Jul 1998, cult. Dez 1998, *Leme & Alves 4371* (HB barcode HB030000373!).

6. ***Pseudaraeococcus lageniformis*** (R.A.Pontes & Versieux) R.A.Pontes & Versieux, **comb. nov.** ≡ *Araeococcus lageniformis* R.A.Pontes & Versieux in Syst. Bot. 44(4): 790–797. 2019 – Holotype: Brazil. Bahia. Apuarema. Concessão da Rio Tinto, 13°56'43"S, 39°41'10"W, 20 Nov 2013 (fl.; fr.), *Aona et al. 3279* (HURB barcode HURB7446!; isotype: UFRN [not found, erroneously cited in the original description]).

3. Discussion

The subfamily Bromelioideae is historically complex in relation to generic delimitation and correct circumscription of species, and modifications were made by several authors (Smith & Downs, 1979; Sousa & al., 2007; Sousa & Wendt, 2008; Aguirre-Santoro, 2017). According to Louzada & Versieux (2010), the observation of morphological characters of fresh material that are difficult to be examined in herbarium specimens can result in nomenclatural changes. Thus, the collection of fresh material and the return to the typical localities revealed other characters not yet analyzed to segregate these two subgenera, especially related to the reproductive and anatomical structures (Table 1).

We believe that a closer observation and comparative analysis of morphological characters with a comprehensive sampling prevented earlier authors to segregate the two disjunct groups: the Atlantic forest species are quite easily separated from the Central America/Amazonian species, either by the position of the petals, number of ovules per locule or the distinct growth and architecture of the rosettes and spines on the leaf margins. Regarding the Amazonian group, still more work is needed since there are variable characters such as the stigma morphology and the polyphyly of the genus was also indicated by a strong dataset presented by Sass & Specht (2010). Nevertheless, the Atlantic forest group is well delimited and consistent regarding its morphology.

The use of scanning electron microscopy (SEM) techniques also contributed to reveal important features such as the morphology of the seed coat (testa) and the distribution of peltate trichomes and stomata on the surface of the leaf blade in both groups. The use of this technique is confirmed by Khan & al. (2017) as an important research tool and in the identification of species and delimitation of supra-specific groups. In *Pseudaraeococcus*, seeds have a surface pattern with evidently hexagonal cells (Fig. 3), a type of ornamentation called by Whiffin & Tomb (1972) as *microlicioides-type*, which differentiates this new genus from the Amazonian group. This pattern was observed for *P. nigropurpureus* and *P. lageniformis* by Pontes & Versieux (Pontes et al., 2019). The leaves surfaces have stomata and peltate trichomes distributed randomly throughout the surface, the latter having regular borders and rarely overlapping (Table 1). Anatomical and micromorphological characters were discussed in more detail by Pontes & al. (2019).

According to Benzing (2000), *Araeococcus* s.l. would fit into two ecological types, I and III, referring to the shoot architecture, forming (in Northeastern Brazil species) or not

TABLE 1. Diagnostic characters between *Pseudaraeococcus* and *Araeococcus s.s.*

Character	Pseudaraeococcus	Araeococcus
Plant Architecture/Tank	Lageniform or infundibuliform /Present	Fasciculate/Inconspicuous or absent
Vegetative reproduction	Stolon	Basal offset
Spinescence	Inconspicuous/Absent	Conspicuous
Position of the petals	Patent or reflex	Erect
Filaments	Cylindrical	Complanate
Anthers apex	Apiculate	Caudate
Stigma*	Conduplicate-spiral	Convolute-obconic, convolute-blade I or simple-erect
Testa of the seeds	With alveolar cells	With longitudinal lines or wrinkly
Number of ovules per locule	2–6	≥ 10
Distribution of fiber bundles	Never dispersing in mesophyll	Dispersing in mesophyll
Arrangement of trichomes and stomata	Aleatory	In longitudinal rows
Edge of the peltate trichomes	Regular edge	Irregular edge
Geographic distribution	Atlantic Forest	Amazon Forest

*Types according to Barfuss & al. (2016).

(in the Amazonian species) a phytotelma, as well as other differences regarding photosynthetic syndrome, root system and foliar trichomes. Aoyama & Sajo (2003) compared the anatomy of four species of *Araeococcus* and found substomatic chambers filled by cells in one Amazonian species while in the Northeastern Brazil species cells did not fill this area of the leaf. When looking at the distribution of fibers strands, these authors could completely segregate the Amazonian species from the Atlantic forest ones by the existence of isolated subepidermic fiber strands only in the later. Such observations were also confirmed by Pontes (2019) with a broadened sampling.

Several authors have used reproductive traits of flowers in Bromeliaceae to solve taxonomic problems, such as the stigma morphology and presence/absence of petal appendages. For example, these structures may provide variation and utility for classification of Bromelioideae (Brown & Gilmartin, 1984;

Brown & Terry, 1992) and Tillandsioideae (Barfuss & al., 2016) taxa and are also useful for *Pseudaraeococcus* and *Araeococcus*. Leme & Siqueira-Filho (2006) described the morphology of the stigmas of Atlantic Forest species known at that time, while Pontes & Versieux (2018) show in SEM the morphology of the Amazonian species *A. goeldianus*, at that time poorly known. Pontes (2019) provided the detail of the micromorphology of almost all the stigmas of *Pseudaraeococcus* and *Araeococcus*. The morphology of the stigmas are evidence of the existence of two distinct groups, one with stigma conduplicate-spiral (6 spp. plus two potentially new species) (Fig. 3) comprising the species of the Atlantic Forest and the other with three stigmas types, convolute-obconic (1 sp.), convolute-blade (1 sp.) (Fig. 3G) and simple-erect (1 sp.) (Fig. 3O), only *A. pectinatus* and *Araeococcus* sp. nov. were not observed.

Petal appendages were not observed in species of both
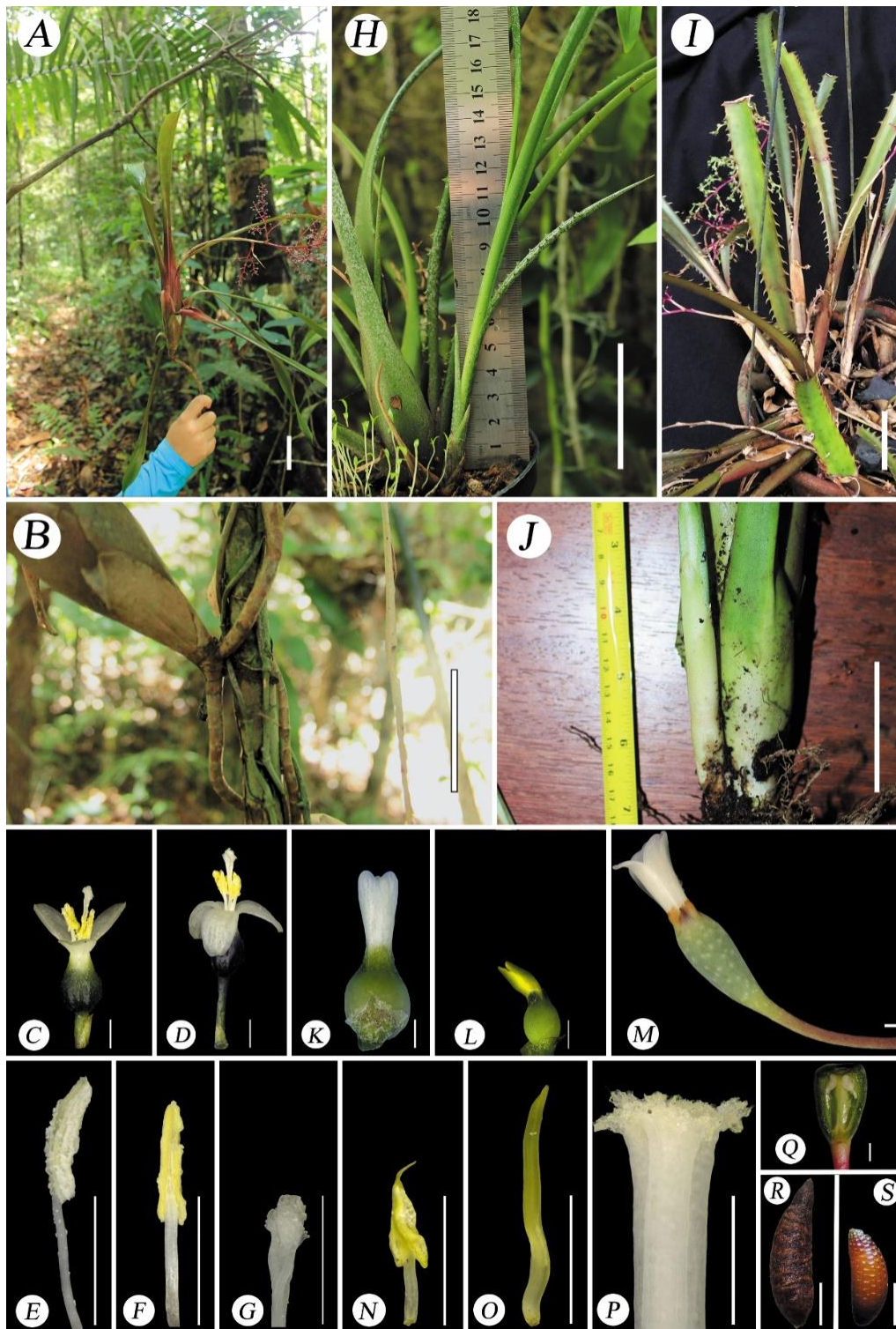
Figure 3. Comparative morphology of species of *Pseudaraeococcus* (A–G, S) and *Araeococcus* (H–R). A. *P. nigropurpureus*. B. Reproduction by slender stolons. C. Flower of *P. parviflorus*. D. Flower of *P. nigropurpureus.* E. Stamen of *P. lageniformis.* F–G. Stamen and stigma of *P. chlorocarpus*. H. *A. flagellifolius* fasciculate rosette with spiny leaves. I. *A. micranthus* fasciculate rosette with spiny leaves. J. Reproduction by basal offset. K. Flower of *A. goeldianus*. L. Flower of *A. micranthus*. M. Flower of *A. flagellifolius*. N-O. Stamen and pistil of *A. micranthus*. P–Q. Stigma and longitudinal section of the ovary of *A. flagellifolius.* R. Seed of *A.* sp. nov. S. Seed of *P. lageniformis* (Scale bars: A, B, H, I, J = 5 cm; C, D, E, F, G, K, L, M, N, O, P, Q, R = 1 mm; S = 0.5 mm).

genera; only *A. flagellifolius* presents lateral folds at the base of the petal flanking the antipetalous stamens, already observed by Brown & Terry (1992). The absence and presence of the lateral folds at the base of the petal can be used to separate *Pseudaraeococcus* and *Lymania* that share the same geographic distribution area (Fig. 2).

4. Conclusion

The description of the new genus is based on an in-depth analysis of morphological characters and a taxonomic review of all species of *Araeococcus* Brong. conducted by the first author and studies of the populations in the field carried out in the entire geographic distribution area. Only after examining living plants some contrasting features become evident, as the position of the petals in the anthesis, vegetative characters, and delicate and weakly preserved structures, but of great importance, such as the stigma morphology. So, based on morphological, anatomical and biogeographic evidence, and by earlier molecular phylogenetic works, it became clearer now the need to accommodate the species of the eastern Brazil Atlantic forest in a new genus. Conservation actions are necessary since all species grow in the Atlantic forest of Northeastern Brazil, which is severely threatened by secular occupation, deforestation and growth of human settlements, despite the rich Bromeliaceae flora there (see Leme & Siqueira-Filho, 2006).

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Phylogenetic Relationships of *Pilosocereus* (Cactaceae) and Taxonomic Implications

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Abstract

The aim of this paper was to investigate the phylogenetic relationships within *Pilosocereus* (Cactaceae, Cactoideae), one of the most emblematic genera of cacti of the Neotropical dry woodlands. The genus includes 42 species and eight subspecies placed in two subgenera: *Pilosocereus* subg. *Pilosocereus* and *Pilosocereus* subg. *Gounellea*. We used an expanded sampling and a broad coverage of genomic regions (*psb*D-*trn*T, *trn*L-*trn*T, *pet*L-*psb*E, *trn*S-*trn*G, *ycf*1 and *Phy*C) resulting in an aligned concatenated matrix of 4563 bp length. Maximum parsimony and Bayesian analyses recovered a non-monophyletic *Pilosocereus* as well as four consistently non-monophyletic species. We propose taxonomic changes to accommodate para- or polyphyletic taxa including the resurrection of three species, three new synonyms, two new names and a new circumscription for *Pilosocereus* with 42 species and four subspecies. *Xiquexique* is proposed as a new genus characterized by molecular and morphological characters, composed of three species formerly positioned in *P*. subg. *Gounellea*.

Keywords: Cacti, dry woodland, molecular phylogenetics, xerophytes, *Xiquexique*.

1. Introduction

Monophyly, the direct relationship of an ancestor and all its descendent lineages forming a clade, has been considered a key point in delimiting groups in contemporary systematics. Although initially questioned by some authors, that considered necessary to stretch the monophyletic requirement in order to retain the natural and useful grouping of organisms in the last century (see Cronquist 1968), many current taxonomical rearrangements are proposed following such rule (e.g. Clark et al. 2000; Bartish et al. 2002; Hardy and Faden 2004; Baker et al. 2006; Metzgar et al. 2008; Su et al. 2010; Middleton and Livshultz 2012; Xue et al. 2014; Ortiz-Rodriguez et al. 2016). As more phylogenetic hypotheses emerge at the generic level using broad species sampling, particularly in speciose taxa from high diversity tropical areas, many species traditionally accepted may appear as para- or polyphyletic. Such results may be a consequence of biological processes (e.g. hybridization, incomplete lineage sorting) or mere artifacts of the earlier interpretation and taxonomy of the species. In the present work we use the genus *Pilosocereus* Byles & Rowley (Cactaceae), with high species density across the Neotropical region, to test for species delimitation using six molecular regions.

Cactaceae is one of the most representative families in the Neotropics, with 130 genera and 1850 species (Nyffeler and

Eggli 2010). Striking features of the group include: the presence of succulent photosynthetic stems; CAM metabolism; specialized root system (with high water absorption capacity) (Edwards and Diaz 2006); reduced or absent leaves; areoles (axillary meristematic regions where distinct structures, like branches, flowers and fruit arise) commonly displaying a great amount of spines, hairs and bristles (Gibson and Nobel 1986; Nyffeler 2002), as well as a great diversity of growth forms and habits (Hernández-Hernández et al. 2011). The group is highly variable and with many conspicuous, dominant and relevant taxa in arid and deserted areas in the Americas (Nyffeler 2002; Hernández-Hernández et al. 2011; Hernández-Hernández et al. 2014).

Among the four subfamilies (Cactoideae, Opuntioideae, Pereskioideae and Maihuenioideae), Cactoideae is the largest with six tribes and about 1,530 species (Nyffeler and Eggli 2010), which make up about 83% of the total family species richness. Cereeae is the largest of Cactoideae tribes, with 41 genera and 589 species (subdivided into the subtribes Rebutiinae, Cereinae and Trichocereinae), presenting a great variety of growth forms (Nyffeler and Eggli 2010). Except for *Harrisia* Britton, *Melocactus* Link & Otto and *Pilosocereus*, Cereeae could be recognized as an exclusively South American tribe (Nyffeler and Eggli 2010). In phylogenetic studies encompassing the whole family or for large groups (such as subfamilies and tribes) Cereeae (sensu Nyffeler and Eggli 2010, corresponding to the BCT clade) is nested within the RNBCT clade (core Rhipsalideae, core Notocacteae, plus BCT) (Nyffeler 2002; Bárcenas et al. 2011).

Pilosocereus is one of the largest genera of the tribe Cereeae and subtribe Cereinae, in number of species and range of distribution (Hunt et al. 2006). It currently includes 42 species and 8 subspecies distributed from the U.S.A. to the east of Brazil (Hunt et al. 2006; Zappi and Taylor 2011). It comprises columnar cacti with long or short areolar hairs (reproductive or non-reproductive); absent cephalium or with a pseudocephalium in some species (such as *P. densiareolatus* and *P. chrysostele*) (Zappi 1994). The flowers are usually nocturnal, and fruit are dehiscent by transversal slits, depressed-globose, with persistent floral remnants (erect or pendent) and with white or colored funicular pulp (Zappi 1994). *Pilosocereus* species may be shrubs or tree-like, densely branched above or at the base level (or unbranched), and with a wide variation in number and color of spines and number of ribs (Zappi 1994).

A single taxonomic revision published for the genus (Zappi 1994) proposed the division of *Pilosocereus* into two subgenera: *Pilosocereus* subg. *Pilososcereus* and *Pilosocereus* subg. *Gounellea*. *Pilosocereus* subg. *Gounellea* is recognized by the candelabriform branching pattern; sinuate ribs sinuses with conspicuous podaria beneath the areoles; and erect to pendent (not immersed at the apex of the fruit) floral remnants. It includes *P. gounellei*, *P. tuberculatus* and, more recently, *P. frewenii* Zappi & Taylor (Zappi and Taylor 2011). *Pilosocereus* subg. *Pilosocereus* includes all the remaining species of the genus (39 species) and is characterized by the erect branching pattern, straight rib sinuses and pendent floral remnants (immersed in the apex of

the fruit, see Fig. 1). In addition, Zappi (1994) proposed the delimitation of five informal groups within *P.* subg. *Pilosocereus* based on floral morphology, spine and habit of the species.

Some studies have been developed for groups of species within the genus, especially for the group *P. aurisetus* (sensu Zappi 1994), which is composed of a complex of species with great morphological variety, overlapping diagnostic characters and taxonomic uncertainty (Jesus 2010; Moraes et al. 2012; Bonatelli et al. 2013, 2014, 2015; Menezes et al. 2016; Perez et al. 2016). However, the great majority of the studies involving *Pilosocereus* focused on isolated species and on various aspects such as morphology (e. g. Godofredo 2009; Menezes and Loiola 2015; Franck et al. 2019), reproductive biology (e. g. Locatelli et al. 1997; Rivera-Marchand and Ackerman 2006; Lucena 2007; Rocha et al. 2007a,b; Meiado et al. 2008; Munguía-Rosas et al. 2010 Abud et al. 2010; Martins et al. 2012, Rocha et al. 2019), and population genetics (e. g. Nassar et al. 2003; Moraes et al. 2005; Figueredo-Urbina et al. 2010; Khattab et al. 2014; Monteiro et al. 2015, Barbosa et al. 2020).

Calvente et al. (2017) published the more comprehensive molecular phylogeny focused in *Pilosocereus* to date and demonstrated the non-monophyly of the genus. Despite presenting well-resolved trees, Calvente et al. (2017) suggested that additional studies (encompassing more species and different markers) are still necessary for a better resolution of relationships within and outside the genus. Lavor et al. (2018) published the reconstructed spatio-temporal evolution for the genus, with a more complete data set, finding a very recent diversification for *Pilosocereus*. Despite the well-supported phylogeny presented by Lavor et al. (2018), *Pilosocereus* was recovered as polyphyletic and its relationships in the most inclusive branches remained uncertain. Lavor et al. (2020) also published a paper addressing the conservation, distribution, and endemism for the genus.

Hunt et al. (2006) mentioned that the "great battle" of delimitation in Cactaceae occurs at the generic level, since it is in this rank that the greatest uncertainties and taxonomic instabilities occur. Many cacti genera harbor many species with morphological similarity that can be only the result of convergent evolution, a process thought to be common in the family (Hernández-Hernández et al. 2011). Consequently, hindered by their superficial similarities, many studies of molecular phylogenetics have been recovering non-monophyletic taxa, requiring further investigation with increased taxa sampling and various genomic regions and the reevaluation of the traditional circumscriptions (Bárcenas et al. 2011).

Thus, to improve the knowledge of relationships within *Pilosocereus* and among lineages of the genus with other groups of the subtribe Cereinae, we added new taxa, samples and molecular data for *Pilosocereus* and outgroups to the data set used by Calvente et al. (2017) and present a broader and more robust phylogeny in this paper. We use this phylogenetic backbone to evaluate the monophyly of taxa and to propose taxonomic changes.

2. Material and methods

2.1 Taxon Sampling

In order to better define and confirm relationships of lineages of *Pilosocereus* in subtribal and tribal levels we used an outgroup sampling with ten taxa from two distinct subfamilies and from main clades in Cactoideae (according to the phylogenetic hypothesis presented in Hernández-Hernández et al. 2014): *Pereskia grandifolia* (subfamily Pereskioideae); *Copiapoa cinerea*, *Rhipsalis baccifera*, *Browningia microsperma*, *Cleistocactus* sp., *Oreocereus hempelianus, Arrojadoa rhodantha, Cereus jamacaru, Melocactus zehntneri* and *Stephanocereus leucostele* (subfamily Cactoideae) (Table 1). For *Pilosocereus*, we include 43 ingroup taxa reaching nearly 85 % of the species of the group (35 species and eight subspecies out of 41 species and nine subspecies according to Hunt et al. (2006) classification). Appendix 1 includes voucher information and GenBank accession numbers.

2.2 DNA Extraction, Amplification and Sequencing

Genomic DNA was either extracted from silica dried stems or roots, or from herbarium specimens, using the NucleoSpin plant II kit (Macherey-Nagel, Düren, Germany) or the Qiagen DNeasy plant mini kit (Qiagen, Hilden, Germany) in accordance to manufacturers' protocols. Amplification reactions conditions and primers for six regions, four non-coding intergenic spacers of chloroplast DNA (cpDNA): *trn*S-*trn*G, *psb*D-*trn*T, *trn*L-*trn*T, *pet*L-*psb*E, one nuclear low-copy gene, Phytochrome C (*Phy*C), followed protocols described in Calvente et al. (2017). Furthermore, we added sequences for one plastid gene, *ycf*1, in this work (Appendix 2). Amplifications for *ycf*1 were conducted in a 20 µl reaction containing the following reagents (adding water to complete the final volume) and conditions: 4 µl of 5X GoTaq Buffer, 2.4 µl of 3 mM MgCl2, 1.6 µl of each primer (120 ng), 0.2 µl of GoTaq, 0.5 µl of 250 µM dNTPs, 1 µl of template DNA; 94 °C for 3 min, followed by 40 cycles of 94 °C for 45 sec, 45 °C for 45 sec, 72 °C for 2 min and 30 sec and finishing at 72°C for 5 min. Compared to Calvente et al. (2017), the present work expanded coverage of taxa and genomic regions including: the addition of 50 taxa for *ycf*1; 32 taxa for *psb*D-*trn*T; 29 taxa for *pet*L-*psb*E; 27 taxa for *Phy*C; 24 taxa for *trn*S-*trn*G and 24 taxa for *trn*L-*trn*T (added taxa are listed in Appendix 1). For all cases, we coded absent data as missing characters (-). The amplification products were purified using the NucleoSpin Gel or PCR clean-up kit (Macherey-Nagel, Düren, Germany) and QIAquick PCR purification kit (QIAGEN, Crawley, UK), following the manufacturer's protocol. Automated sequencing was performed by Macrogen Inc. Korea and Netherlands.

2.3 Alignment and Phylogenetic Analyses

Complementary sequences were assembled in Sequencher 4.1.4 (Gene Codes, Ann Arbor, Michigan) and aligned manually in Mesquite v. 3.04 (Maddison and Maddison 2015). Indels were coded using the simple indel coding method (Simmons and Ochoterena 2000) and included in phylogenetic analyses as presence/absence data. *Pereskia grandifolia* was used as outgroup to root the trees in all analyses based on previous knowledge of phylogenetic relationships in Cactaceae and on its position near the primary node of divergence within subfamily, Pereskioideae (Arakaki et al. 2011; Hernández-Hernández et al. 2014).

We performed maximum parsimony (MP) analyses for all regions individually, but as the analyzes for the individual regions present low resolution (see Fig. S1a-f, supplementary information: DOI 10.6084/m9.figshare.12895133), we built a concatenated matrix with two partitions (all plastid markers and *Phy*C) for a total evidence approach. All analyses were performed using heuristic searches with 1000 replicates of random taxon addition (retaining 20 trees at each replicate), tree bisection reconnection (TBR) branch swapping and equal weighting of all characters in PAUP* v4.0a147 (Swofford 2002). Support was assessed with non-parametric bootstrap analysis (BS) using 1000 replicates of random-taxon addition and TBR branch swapping. Clades with bootstrap percentages of 50–74 % are described as weakly supported, 75–89 % as moderately supported and 90–100 % as strongly supported.

We also inferred phylogenetic relationships using Bayesian inference (BI) in MrBayes 3.2.2 (Ronquist et al. 2011), hosted on the CIPRES Science Gateway (Miller et al. 2010). Choice of substitution models used the Akaike information criterion implemented in MrModelTest 2.2 (Nylander 2004) and run in PAUP* v4.0a147 (Swofford 2002). Bayesian analyses performed on individual genes used molecular substitution models selected for each marker: GTR for *psb*D-*trn*T, GTR + I for *pet*L- *psb*E, GTR + G for *ycf*1, GTR + I + G for *trn*S-*trn*G, F81 + I for *trn*L-*trn*T and HKY + G for *Phy*C. As the analyzes for the individual regions present low resolution (see Fig. S2a-f, supplementary information), we built a concatenated matrix with two partitions (all plastid/*Phy*C), using GTR + I + G and HKY + G as the best-fit model for each partition, respectively, and the overall substitution rate unlinked between partitions. MrBayes was set to build two independent runs of four chains each, for 10 million generations, sampling every 1000th generation. We assessed convergence between runs by monitoring the standard deviation of split frequencies (< 0.01) and using the potential scale reduction factor (PSRF). After discarding the first 25% samples as burn-in, we pooled the remaining trees to construct a 50% majority rule consensus tree. We describe clades as weakly supported when the posterior probability (PP) < 0.8; as moderately supported when PP ranged from 0.8 to 0.95, and as strongly supported when PP > 0.95.

TABLE 1. Species sampled in this study and their classification following Nyffeler and Eggli (2010) (outgroups are printed in bold). Type species of *Pilosocereus* subgenera are underlined (Zappi 1994).

Subfamily	Tribe	Subtribe	Species and subspecies
Pereskioideae			1. **Pereskia grandifolia** Haw.
			2. **Copiapoa cinerea** (Phil.) Britton & Rose
	Rhipsalideae		3. **Rhipsalis baccifera** (J. S. Mueller) Stearn.
		Rebutiinae	4. **Browningia microsperma** (Werderm. & Backeb.) W. T. Marshall.
		Trichocereinae	5. **Cleistocactus** sp. Lem.
			6. **Oreocereus hempelianus** (Gurke) D. R. Hunt
			7. **Arrojadoa rhodantha** Britton & Rose
			8. **Cereus jamacaru** D. C.
			9. **Melocactus zehntneri** (Britton & Rose) Luetzelb.
			10. **Stephanocereus leucostele** (Gurke) A.
			Pilosocereus subg. *Pilosocereus*:
			11. *Pilosocereus albisummus* P. J. Braun & Esteves
			12. *Pilosocereus alensis* (F. A. C. Weber) Byles & G. D. Rowley
			13. <u>*Pilosocereus arrabidae*</u> (Lem.) Byles & G. D. Rowley
			14. *Pilosocereus aureispinus* (Buining & Brederoo) F. Ritter
			15. *Pilosocereus aurisetus* (Werderm.) Byles & G. D. Rowley subsp. *aurisetus*
			16. *Pilosocereus aurisetus* subsp. *aurilanatus* (F. Ritter) Zappi
			17. *Pilosocereus azulensis* (F. A. C. Weber ex Rol. Goss) Byles & G. D. Rowley
			18. *Pilosocereus bohlei* Hofacker
			19. *Pilosocereus brasiliensis* (Britton & Rose) Backeb subsp. *brasiliensis*
			20. *Pilosocereus brasiliensis* subsp. *ruschianus* (Buining & Brederoo) Zappi
			21. *Pilosocereus catingicola* (Gurke) Byles & G. D. Rowley subsp. *catingicola*
			22. *Pilosocereus catingicola* subsp. *salvadorensis* (Werderm.) Zappi
Cactoideae	Cereeae	Cereinae	23. *Pilosocereus chrysacanthus* (F. A. C. Weber) Byles & G. D. Rowley
			24. *Pilosocereus chrysostele* subsp. *cearensis* P. J. Braun & Esteves
			25. *Pilosocereus flavipulvinatus* (Buining & Brederoo) F. Ritter
			26. *Pilosocereus floccosus* subsp. *quadricostatus* (F. Ritter) Zappi
			27. *Pilosocereus fulvilanatus* (Buining & Brederoo) F. Ritter subsp. *fulvilanatus*

Table 1 (continue)

Subfamily	Tribe	Subtribe	Species and subspecies
Cactoideae	Cereeae	Cereinae	28. *Pilosocereus fulvilanatus* subsp. *rosae* (P. J. Braun) Zappi
			29. *Pilosocereus glaucochrous* (Werderm.) Blyles & G. D. Rowley
			30. *Pilosocereus jauruensis* (Buining & Brederoo) P. J. Braun
			31. *Pilosocereus leucocephalus* (Poselg.) Byles & G. D. Rowley
			32. *Pilosocereus machrisii* (E. Y. Dawson) Backeb
			33. *Pilosocereus magnificus* (Buining & Brederoo) F. Ritter
			34. *Pilosocereus multicostatus* F. Ritter
			35. *Pilosocereus oligolepis* (Vaupel) Byles & G. D. Rowley
			36. *Pilosocereus pachycladus* F. Ritter subsp. *pachycladus*
			37. *Pilosocereus pachycladus* subsp. *pernambucoensis* (F. Ritter) Zappi
			38. *Pilosocereus parvus* (Diers & Esteves) P. J. Braun
			39. *Pilosocereus pentaedrophorus* (Labour.) Byles & G. D. Rowley subsp. *pentaedrophorus*
			40. *Pilosocereus pentaedrophorus* subsp. *robustus* Zappi
			41. *Pilosocereus piauhyensis* (Gurke) Byles & G. D. Rowley
			42. *Pilosocereus polygonus* (Lam.) Byles & G. D. Rowley
			43. *Pilosocereus purpusii* (Britton & Rose) Byles & G. D. Rowley
			44. *Pilosocereus pusillibaccatus* P. J. Braun & Esteves
			45. *Pilosocereus quadricentralis* (E. Y. Dawson) Backeb
			46. *Pilosocereus royenii* (L.) Byles & G. D. Rowley
			47. *Pilosocereus splendidus* F. Ritter
			48. *Pilosocereus ulei* (K. Schum.) Byles & G. D. Rowley
			49. *Pilosocereus vilaboensis* (Diers & Esteves) P. J. Braun
			Pilosocereus subg. *Gounellea*:
			50. *Pilosocereus gounellei* (F. A. C. Weber ex K. Schum.) Byles & G. D. Rowley
			51. *Pilosocereus tuberculatus* (Werderm.) Byles & G. D. Rowley

3. Results

In this work, we assess phylogenetic relationships for *Pilosocereus* based on 220 new sequences produced here and added to the data set used by Calvente et al. (2017). In total, we used 447 sequences for 46 species and eight subspecies (total 75 specimens) from six markers (Appendix 1). Statistics for each genomic region studied are summarized in Table 2. There were no significant differences in the topological analysis with and without indels. The results of the MP and BI analyzes for the individual regions present low resolution but confirm the paraphyly of *Pilosocereus* sensu lato (s.l.). Already for concatenated matrix, the phylogenetic relationships recovered with MP (Fig. 2) and BI (Fig. 3) analyses were generally similar with majority of nodes receiving moderate (BS of 75-89 % and PP > 0.8) to strong support values (BS of 90-100 % and PP > 0.95) (described below).

The tribe Cereeae emerges strongly supported as monophyletic (BS = 100, PP = 1) sister of *Rhipsalis baccifera* (BS = 98, PP = 1). The position of *Browningia microsperma* (subtribe Rebutiinae) and the clade representing subtribe Trichocereinae (*Cleistocactus* sp., and *Oreocereus hempelianus*) is controversial; *Browningia microsperma* appears more closely related to Cereinae in the MP topology (BS = 80), whereas the clade (*Cleistocactus* sp., *Oreocereus hempelianus*) is more closely related to Cereinae in the BI topology (PP = 0.81). Subtribe Cereinae is monophyletic in a strongly supported clade in both analyses (BS = 100, PP = 1).

The genus *Pilosocereus* as circumscribed in Hunt et al. (2006) (*Pilosocereus* sensu lato, Fig. 1) was recovered as paraphyletic in both MP and BI analyses as the clade (*M. zehntneri* (*A. rhodantha*, *C. jamacaru*)) is nested inside the genus. *Pilosocereus* species are distributed in three strongly supported main clades: (I) containing *P. gounellei* and *P. tuberculatus* (*P.* subg. *Gounellea* clade; BS = 100, PP = 1); (II) *P. bohlei* isolated (BS = 100, PP = 1); and (III) the remaining of *Pilosocereus* species (*Pilosocereus* sensu stricto

(s.s.); BS = 100, PP = 1). A closer relationship of the (*M. zehntneri* (*A. rhodantha*, *C. jamacaru*)) clade with the *Pilosocereus* s.s. clade is recovered in both MP and BI results although not strongly supported (BS = 57, PP = 0.86).

In *Pilosocereus* s.s. species are clustered in three main clades: (1) *Pilosocereus aureispinus* isolated; (2) a clade (BS = 80, PP = 1) including all non-Brazilian species clustered (BS = 100, PP = 1) (the relationships are better resolved in the BI topology, although poorly supported) and a clade of the Brazilian species *P. glaucochrous*, *P. pachycladus* subsp. *pernambucoensis*, *P. pentaedrophorus* subsp. *pentaedrophorus* and *P. piauhyensis* (BS = 99, PP = 1); (3) a major strongly supported clade (BS = 94, PP = 1) clustering all remaining Brazilian species, but with poor resolution in more inclusive nodes. In the MP topology (Fig. 2) *P. aureispinus* is the first diverging lineage inside *Pilosocereus* s.s. (BS = 100), however in the BI topology the relationships between clades 1, 2 and 3 are uncertain (Fig. 3).

The relationships within clade 3 are not fully resolved, however six weakly to strongly supported multispecies clades are recovered both in MP and BI analyses: (A) *Pilosocereus ulei*, *P. arrabidae*, *P. catingicola* subsp. *catingicola* and *P. catingicola* subsp. *salvadorensis* (BS = 98, PP = 1); (B) *Pilosocereus oligolepis, P. chrysostele* subsp. *cearensis* and *P. flavipulvinatus* (BS = 95, PP = 1); (C) *Pilosocereus brasiliensis* subsp. *brasiliensis*, *P. brasiliensis* subsp. *ruschianus*, *P. magnificus* and *P. multicostatus* (BS = 85, PP = 0.80); (D) *Pilosocereus fulvilanatus* subsp. *fulvilanatus* and *P. pentaedrophorus* subsp. *robustus* (BS = 79; PP = 0.99); (E) *Pilosocereus azulensis* and *P. floccosus* subsp. *quadricostatus* (BS = 100; PP = 1); (F) *Pilosocereus fulvilanatus* subsp. *rosae* and *P. aurisetus* subsp. *aurilanatus* (BS = 96, PP = 1); (G) *Pilosocereus densiareolatus*, *P. parvus*, *P. pusillibaccatus*, *P. splendidus*, *P. pachycladus* subsp. *pachycladus* e *P. albisummus* (BS = 96, PP = 1); and (H) *Pilosocereus pachycladus* subsp. *pachycladus* and *P. albisummus* (BS = 92;

TABLE 2. Summary statistics from the maximum parsimony analyses of *Pilosocereus* (ingroup and outgroup) for plastid and nuclear regions used in this study (CI = consistency index; RI = retention index).

	*trn*L-*trn*T	*psb*D-*trn*T^GGU	*pet*L-*psb*E	*trn*S-*trn*G	*ycf1*	*Phy*C	Combined dataset
Size of aligned matrix	308	616	555	1327	751	1006	4563
Informative sites (bp)	22	41	42	139	163	48	454
Length of best tree	48	76	103	473	534	136	1418
Number of most parsimonious trees	3974	386	2	120	8732	210	19,338
CI	0.79	0.94	0.87	0.78	0.71	0.88	0.75
RI	0.85	0.96	0.93	0.79	0.83	0.90	0.82
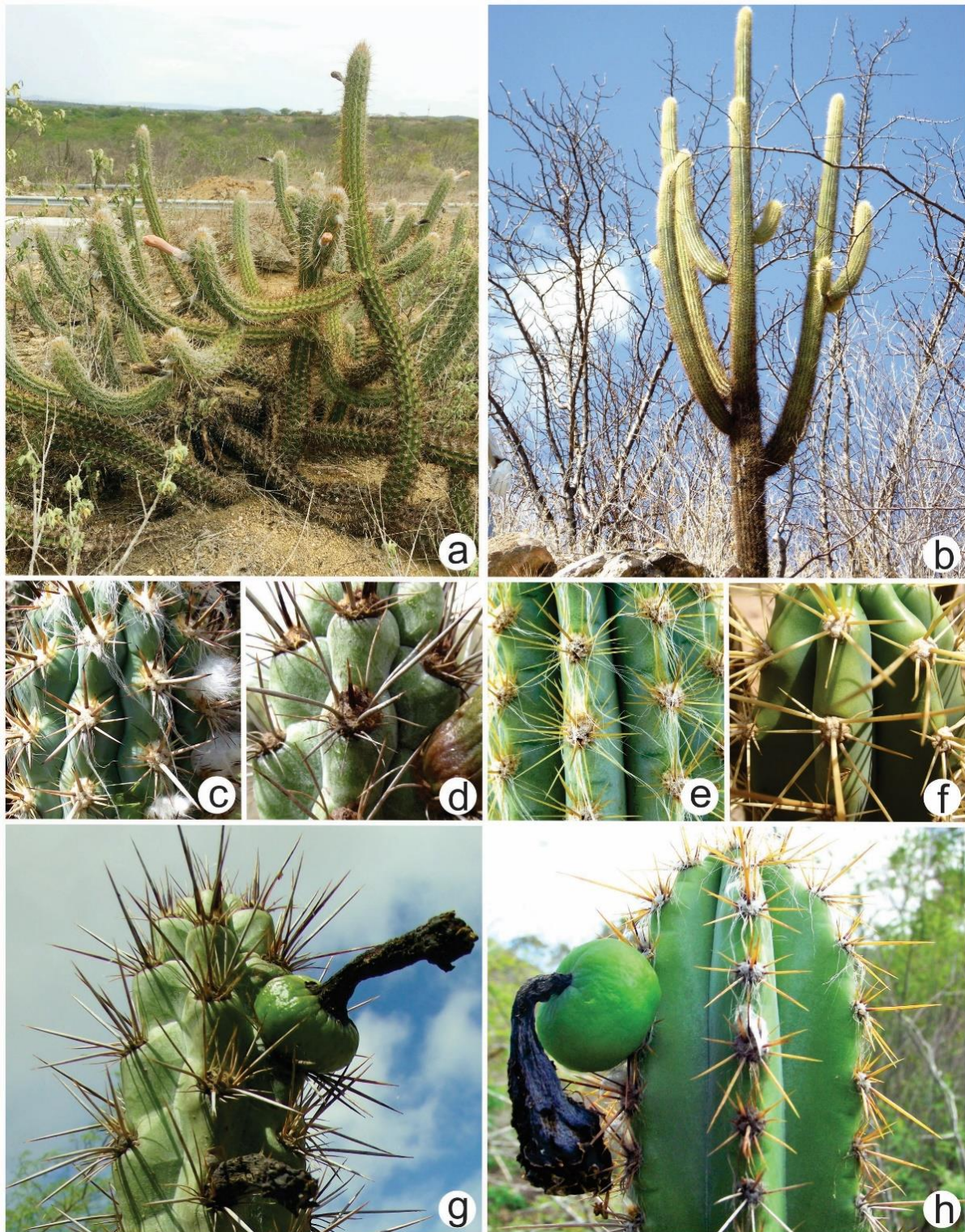
FIGURE 1. Main differences between *Pilosocereus* subgenus *Gounellea* (photos on the left) and *Pilosocereus* subgenus *Pilosocereus* (photos on the right), relative to the branching (**a** – candelabriform pattern; **b** – erect pattern); ribs (**c**, **d** – sinuses sinuate with conspicuous podaria beneath the areoles; **e**, **f** – sinuses straight) and fruit (**g** – floral remnant erect or pendent, not sunken into the apex of the pericarp, circular at point of attachment; **h** – floral remnant pendent, sunken into the apex of the pericarp, forming a linear insertion point) (Species: **a**, **c** – *P. gounellei* subsp. *gounellei*; **b**, **e** – *P. pachycladus* subsp. *pernambucoensis*; **d**, **g** – *P. tuberculatus*; **f** – *P. flavipulvinatus*; **h** – *P. oligolepis*).

PP = 1). In the BI topology (Fig. 2) clade A is the first diverging lineage inside *Pilosocereus* s.s. (BS = 100) while B and C are sister clades, however in the MP topology the relationships between clades A, B and C are uncertain (Fig. 3).

Inside *Pilosocereus* s.s., four species are consistently non-monophyletic in their current delimitation in both MP and BI topologies since their respective subspecies are clustered separately in distinct strongly supported clades: *Pilosocereus pachycladus*, *P. pentaedrophorus*, *P. fulvilanatus* and *P. aurisetus*. *Pilosocereus aurisetus* subsp. *aurilanatus* is closer related to *P. fulvilanatus* subsp. *rosae* than to *P. aurisetus* subsp. *aurisetus*. *Pilosocereus fulvilanatus* subsp. *fulvilanatus* is closer to *P. pentaedrophorus* subsp. *robustus* than to
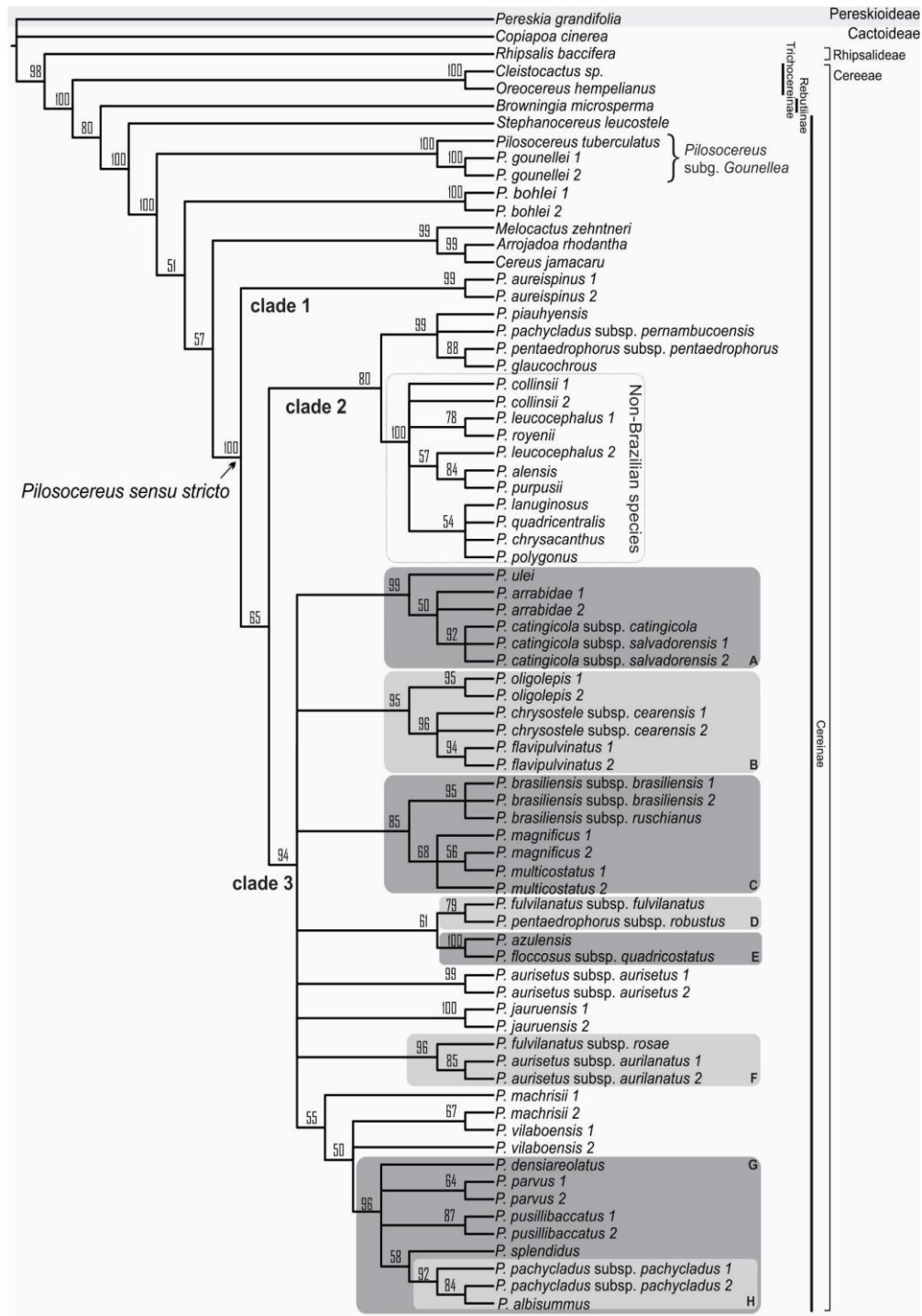
FIGURE 2. Strict consensus tree from maximum parsimony analyses of the combined dataset of (*trn*S-*trn*G, *psb*D-*trn*T, *trn*L-*trn*T, *pet*L-*psb*E, *Phy*C and *ycf*1) produced for *Pilosocereus* and outgroups. Bootstrap values are shown above branches.
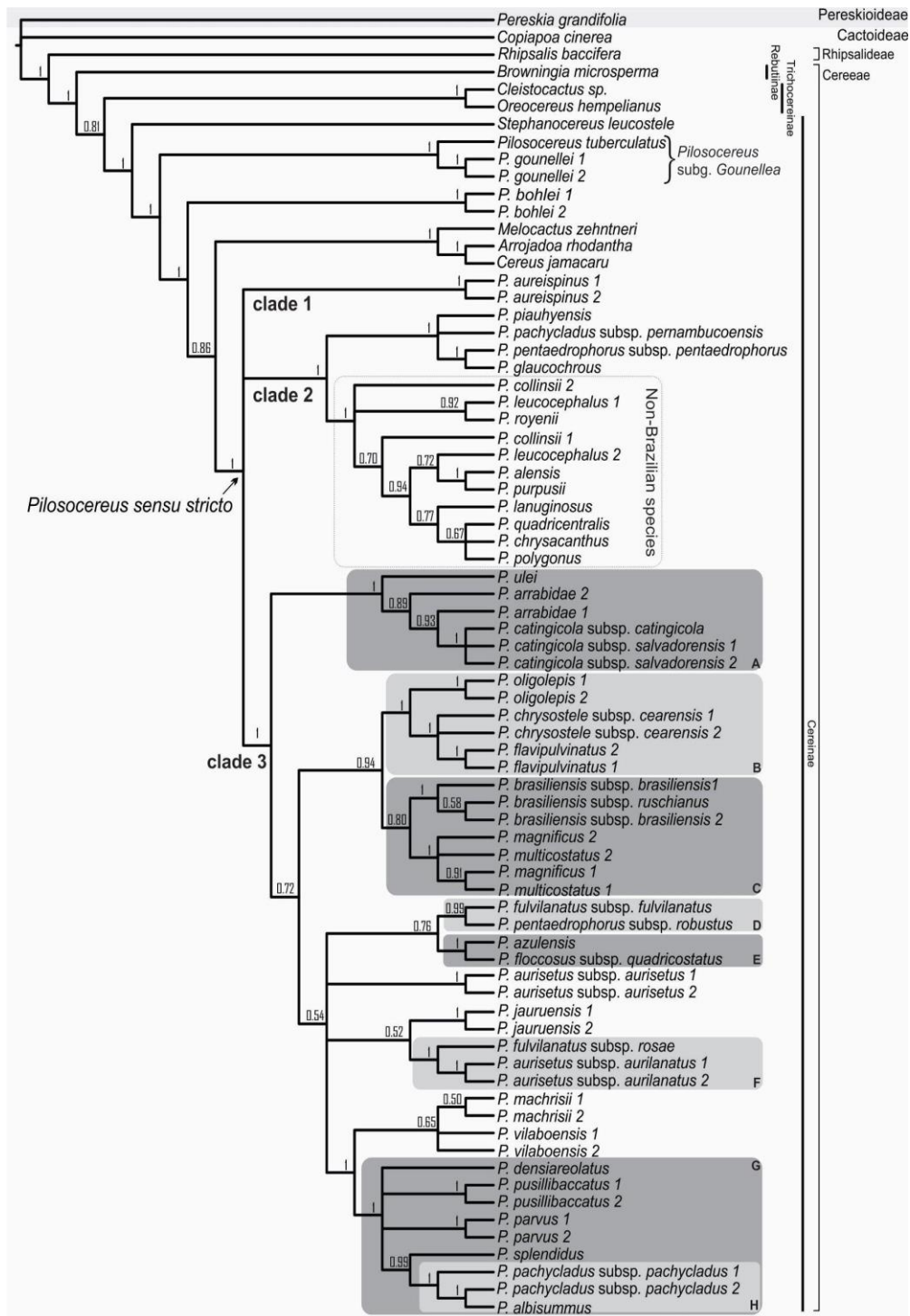
FIGURE 3. Majority rule consensus tree derived from Bayesian analyses of the combined dataset (from *trn*S-*trn*G, *psb*D-*trn*T, *trn*L-*trn*T, *pet*L-*psb*E, *ycf*1 and *Phy*C) produced for *Pilosocereus* and outgroups. Posterior probability values are shown above branches.

P. fulvilanatus subsp. *rosae*. *Pilosocereus pentaedrophorus* subsp. *pentaedrophorus* and *P. pachycladus* subsp. *pernambucoensis* are nested in clade 2 while *P. pentaedrophorus* subsp. *robustus* and *P. pachycladus* subsp. *pachycladus* are nested in clade D and H, respectively. The BI results also indicate the non-monophyly of *P. leucocephalus*, *P. collinsii*, *P. arrabidae*, *P. magnificus* and *P. multicostatus* under moderate to low PP support. However, among those, only *P. leucocephalus*, P. *magnificus* and *P. multicostatus* are non-monophyletic under moderate to low BS support on the MP topology.

4. Discussion

4.1 Relationships within Cactoideae

The results from this work corroborate some relationships found in previous works treating the whole family (Arakaki et al. 2011; Hernández-Hernández et al. 2011, 2014). Despite the controversial positioning of *Browningia microsperma*, the relationships of subtribes within Cereeae (sensu Nyffeler and Eggli 2010) agree with previous results. We found differences in relationships within subfamily Cactoideae, mainly due to the inclusion of *Pilosocereus* subg. *Gounellea* and *P. bohlei*, which had not yet been sampled in any previous major Cactaceae or Cactoideae molecular phylogenetic hypothesis published so far, although similar results were found by Lavor et al. (2018).

Our results show that *Arrojadoa rhodantha* and *Stephanocereus leucostele* do not group together in the same clade, supporting their positioning in separate genera. Due to conspicuous morphological similarities, such as the presence of an apical cephalium when young, supplanted by continuous vegetative growth, then forming cephalium rings, their segregation into two genera have always raised questions on whether these genera would or not form a single group, despite their different pollination mechanisms and floral morphology (Taylor and Zappi 1989). Hunt et al. (2006) even claimed that based on the circumscription they adopt for *Arrojadoa*, and on preliminary molecular evidence, they considered including *Stephanocereus leucostele* within *Arrojadoa*. Our results refute such hypothesis.

We recovered a paraphyletic *Pilosocereus* s.l. corroborating the results found in Calvente et al. (2017) and Lavor et al. (2018) as other genera of tribe Cereinae emerged clustered within the group. We found a clade with *Melocactus*, *Arrojadoa* and *Cereus* species more closely related to *Pilosocereus* s.s. than to *P. bohlei*, *P. gounellei* and *P. tuberculatus* (the two latter belong to *P.* subg. *Gounellea*). Although this relationship is not strongly supported in neither MP nor BI topologies (BS = 57, PP = 0.86), the clade corresponding to *P.* subgenus *Gounellea* is strongly supported as a distinct lineage from a clade including all the other *Pilosocereus* in the BI results (PP = 1, BS = 51).

Pilosocereus subg. *Gounellea* differs morphologically from *Pilosocereus* s.s. due to its candelabriform branching, sinuate ribs, and fruits with floral remnant frequently erect, not sunken into the apex of the pericarp (Zappi 1994, Fig. 1). *Pilosocereus frewenii* (not sampled in our study) more recently described and included in *P.* subg. *Gounellea*, has the same morphological features common to *P. gounellei* and *P. tuberculatus*, however it has smaller habit and seeds and has flowers with different coloration (Zappi and Taylor 2011). Zappi (1994) states that the remarkable features of the subgenus *Gounellea* segregating it from *P.* subg. *Pilosocereus* would be plesiomorphic within the genus. Such hypothesis was raised by the presence of features such as ribs with marked hexagonal podaria, which are also found in some species of the subtribe Trichocereinae (e.g. *Rauhocereus*

Backeb., *Weberbauerocereus* Backeb. and *Haageocereus* Backeb.) (Zappi 1994). Based on our results we believe that morphological characters shared by both subgenera are possibly homoplasious and developed independently in both groups.

According to Taylor and Zappi (2004), *P. bohlei* shares similarities with *P. gounellei* (such as the narrower apical part of the fertile stem) but has fruits with floral remnants inserted in the pericarp (which is a diagnostic character of *P.* subg. *Pilosocereus*). However, the flowers in *P. bohlei* are smaller and S-shaped, different from all the species of the genus. We cannot find satisfying evidence in this work to support either the inclusion or the exclusion of *P. bohlei* from *Pilosocereus* and its inclusion in another new genus is still premature. Further studies are needed to elucidate the positioning of *P. bohlei* using additional molecular and morphological data. An investigation using a broader sampling for Cereinae is currently under course and may lighten its positioning. We found support in our results and on overall morphological diagnostic characters to propose a generic status for *Pilosocereus* subg. *Gounellea*. This new genus accommodates *P. gounellei, P. tuberculatus* and *P. frewenii*.

4.2 Relationship in *Pilosocereus* s.s.

Pilosocereus aureispinus appears isolated from the remaining species of *Pilosocereus* s.s. corroborating other studies using molecular data (Bonatelli et al. 2014, Lavor et al. 2018). We cannot find a conspicuous overall morphological differentiation between *P. aureispinus* and the remainder of *Pilosocereus* s.s. species. The only consistent difference is the globose to depressed-globose fruit and the seed coat (Zappi 1994). Also, a biogeographic pattern that differentiates this species from the others in *Pilosocereus s.s.* is not clear, since the species occurs in the same region as most Brazilian species (eastern Brazil), in an area of Cerrado in the state of Bahia (Taylor and Zappi, 2004, Lavor et al. 2020), within the Caatinga Biome (sensu Olson et al. 2001).

In general, the major clades formed within *Pilosocereus* s.s. (clades 1-3; Fig. 2, 3) apparently do not reflect easily perceived diagnostic characters or clear biogeographic structuring of clades. As discussed by Calvente et al. (2017) it is not easy to find diagnostic characters (even through ancestral states reconstruction analyses) in this group or to explain phylogenetic relationships recovered. Relationships apparently reflect a niche conservatism pattern, with diversification constrained to the same geographic area and habitat type of ancestral lineages or, occasionally, driven by migration events (Lavor et al. 2018).

Clade 2 includes a subclade of Brazilian species. Zappi (1994) reports that *P. pentaedrophorus* is a species related to *P. glaucochorous* because of the shared glabrous flowering areoles, curved flowers and stem epidermis striking blue colored, glaucous. Some populations of *P. pachycladus* subsp. *pernambucoensis* also present glaucous epidermis and these three taxa occur in close (but not sympatric) localities in the Brazilian state of Bahia. Because *P. pachycladus* subsp. *pernambucoensis* has a wide distribution in the northeastern

region of Brazil and is found in localities close to *P. piauhyensis*, there is a misleading history of collections in the state of Piauí for *P. pachycladus* subsp. *pernambucoensis*, however the material referred to this taxa there actually belongs under *P. piauhyensis* (Zappi 1994). All these species are found in the northeastern region of Brazil, as well *P. aureispinus* and other species of clade 3.

The second subclade in clade 2 includes non-Brazilian species. *Pilosocereus collinsii* and *P. purpusii* occur in sympatry in Mexico. Zappi (1994) indicated the first as a synonym of the second. However, Hunt et al. (2006) included both as distinct and accepted species. Main morphological differences among them are the number of ribs (7-10 in the first and 12 in the second) and sizes of the flowers (5 and 7 cm, respectively). Our results corroborate Hunt et al (2006) decision, since *P. collinsii* does not emerge as a sister species of *P. purpusii* in our analyses.

Also, in this clade *P. royenii* and *P. polygonus* apparently require further studies at the population level and possibly a delimitation reevaluation. *Pilosocereus royenii* occurs in Mexico and in the Caribbean Islands, but some authors believe that Mexican populations (specifically in the Yucatán peninsula) are morphologically distinct from the Caribbean ones [these usually identified as *P. gaumeri* (Britton & Rose) Backeb., a synonym of *P. royenii* according to Hunt et al. 2006]. However, the Caribbean populations are sympatric with *P. polygonus*, and these two species are differentiated only by the abundant presence of hairs in the areoles in *P. royenii*, which are absent in *P. polygonus* (Zappi 1994). Hunt et al. (2006) argue that perhaps the populations for these two species occurring in the Caribbean could be the same species that present a variation in the amount of hairs in the areoles. Our results do not serve to refute this idea, since our sample of *P. royenii* is from a population that occurs in the Yucatán peninsula (Mexico). The only biogeographic pattern found in this subclade is that all species occur outside Brazil. As expected, none of them emerge grouped with *P. oligolepis*, which occurs in northern Brazil in the state of Roraima and Guyana (Lavor et al. 2016).

The largest clade of Brazilian species (clade 3), includes clade "A" with three taxa of *P. arrabidae* group (sensu Zappi 1994): *P. catingicola* subsp. *catingicola*, *P. catingicola* subsp. *salvadorensis* and *P. arrabidae*. These three taxa present large flowers, fruit and seeds, small numbers of ribs, and are found in forest formations or sand dunes (*restinga*) on the Brazilian coast. The other species belonging to this clade, *P. ulei*, although presenting a completely different morphology from the species mentioned above is also found restricted to areas of *restinga*, where it grows in sympatry with *P. arrabidae* (Zappi 1994).

Clade "B" presents three taxa: *Pilosocereus flavipulvinatus*, *P. oligolepis* and *P. chrysostele* subsp. *cearensis*. Zappi (1994) suggested a close relationship between the first two based on their morphology. This relationship would be an evidence of a past northern-northeastern Brazil phytogeographical linkage (Taylor and Zappi 2004), since *P. flavipulvinatus* is found in ecotonal areas of Caatinga/Cerrado and Carnaubais (i.e. a *Copernicia*

palm dominated vegetation between Amazon and Caatinga in Brazil) in the Brazilian northeast (Menezes et al. 2013), while *P. oligolepis* is found in rock outcrops in savanna areas in the north of Brazil and Guyana (Lavor et al. 2016). Endemic to the state of Ceará *P. chrysostele* subsp. *cearensis* occurs in savanna formations and rock outcrops (Menezes et al. 2013) in localities close to those of *P. flavipulvinatus*. The similar habitat connection seems to be the link between these closely related taxa. *Pilosocereus chrysostele* subsp. *cearensis* is treated by Taylor and Zappi (2004) and Hunt et al. (2006) as a synonym of *P. piauhyensis*, what is refuted by our results.

Clade "C" is composed by *P. brasiliensis*, *P. magnificus* and *P. multicostatus*. Previous studies based on morphology and habitat evidence have not approximated them. *Pilosocereus magnificus* and *P. multicostatus* have sympatric and restricted distribution in the state of Minas Gerais, while P. *brasiliensis* subsp. *ruschianus* has a wider distribution (occurring in Minas Gerais, Bahia and Espírito Santo states) and *P. brasiliensis* subsp. *brasiliensis* occurs only in the states of Espírito Santo and Rio de Janeiro (Zappi 1994). The geographical proximity seems to be the only connection among these species, however further studies focusing on this clade can elucidate more aspects of its complexity.

We assume the same for clades "D" and "E". Species on these clades although not morphologically similar occur close to each other or in sympatric localities. We find *P. fulvilanatus* subsp. *fulvilanatus* in the north of Minas Gerais state and *P. pentaedrophorus* subsp. *robustus* in the middle east and south of Bahia state and northeast of Minas Gerais, Brazil. Also, in Minas Gerais, *P. azulensis* and *P. floccosus* subsp. *quadricostatus* both occur in the municipality of Pedra Azul (northern Minas Gerais), however *P. floccosus* subsp. *quadricostatus* expands to northeastern Minas Gerais, along the drainage basins of the Pardo and Jequitinhonha Rivers (Zappi 1994). The species of clade "F", *P. fulvilanatus* subsp. *rosae* and *P. aurisetus* subsp. *aurilanatus*, are also morphologically distinct but not sympatric. Both are found in rocky outcrops in the center-north of the Minas Gerais State with restricted distributions (Zappi 1994; Taylor and Zappi 2004).

The species *P. parvus* and *P. pusillibaccatus*, which make up the clade "G", belong to the species complex *P. aurisetus* (sensu Zappi 1994), and have already been synonymized (together with *P. jauruensis*) in Zappi (1994) as *P. machrisii*, but they were accepted by Hunt et al. (2006), delimitation corroborated by our results. *Pilosocereus aurisetus* group is composed of *P. aureispinus, P. aurisetus, P. bohlei, P. jauruensis, P. machrisii, P. parvus, P. pusillibaccatus* and *P. vilaboensis* presenting great morphological variation. It is distributed throughout the central region of Brazil and presents a history of controversial classification (Zappi 1994; Taylor and Zappi 2004; Bonatelli et al. 2013). In our results this group did not appear as monophyletic.

Also, in clade G, *P. splendidus* is considered by Zappi (1994) as a synonym of *P. pachycladus* but is accepted by Hunt et al. (2006). It appears as sister to the clade H, composed of *P. pachycladus* subsp. *pachycladus* and *P. albisummus*, corroborating the classification of Hunt et al.

(2006). The species *P. albisummus* is reported by several authors as a poorly known taxon (e.g. Zappi 1994; Taylor and Zappi 2004; Hunt et al. 2006). The close relationship found in our work for *P. pachycladus* subsp. *pachycladus* and *P. albisummus*, may give a hint to the history of this species.

Within clade 3, we observe some biogeographic patterns, related to the major biomes of the central/eastern region of Brazil (Caatinga, Cerrado, and Atlantic Forest). Some subgroups in this clade present many species restricted to some of these biomes (such as Cerrado) while other species are found in different regions too. The historical biogeography of *Pilosocereus* (Lavor et al. 2018) showed that this pattern could be associated with historical factors (such as the Pleistocene climatic fluctuations). In a recent analysis (Lavor et al. 2020) no correlation was found between the current distribution of species and environmental variables such as vegetation, climate and soil, suggesting that historical factors possibly had a more significant role on shaping the current distribution and impacting phylogenetic relationships observed for the group.

4.3 Intraspecific monophyly

We have evidence for the monophyly of *P. catingicola*, *P. brasiliensis*, *P. gounellei*, *P. bohlei*, *P. aureispinus*, *P. oligolepis*, *P. flavipulvinatus*, *P. jauruensis*, *P. pusillibaccatus*, and *P. parvus* (corresponding near to 23 % of the species of *Pilosocereus* included in this study). Among those, we sampled different subspecies for the first two. *Pilosocereus catingicola* subsp. *catingicola* and *P. catingicola* subsp. *salvadorensis* clustered in our phylogeny in clade A. Although both subspecies are distinct morphologically, they are not found in sympatry as the dry vegetation along the valley of the São Francisco river basin (Brazil) is separating both (Zappi 1994). Similar fact occurs with *P. brasiliensis* subsp. *brasiliensis* and *P. brasiliensis* subsp. *ruschianus* (clade C). Few morphological differences may be noted between these two subspecies, which according to Zappi (1994) would reflect their adaptation to distinct habitats (*P. brasiliensis* subsp. *brasiliensis* occurs in rock outcrops inside restinga formations of the Atlantic Forest domain in Brazil, while *P. brasiliensis* subsp. *ruschianus* occurs in areas of dry forest rock outcrops also in Brazil).

Among the four consistently non-monophyletic species highlighted in this study, *P. aurisetus*, *P. fulvilanatus*, *P. pachycladus* and *P. pentaedrophorus* have two subspecies each, one homotypic and the other heterotypic. For the first three species, the heterotypic subspecies arose from synonyms and lowering of the rank of other species of *Pilosocereus* to the subspecies level by Zappi (1994). Only *P. pentaedrophorus* subsp. *robustus* was described initially as a subspecies. Based on this phylogenetic evidence together with consistencies of morphological and geographical characters we propose to elevate the heterotypic subspecies to the species rank. As the specific epithet "*robustus*" is already taken in *Pilosocereus* for a different taxon, we propose a new name. The other three binomials already exist at the species rank.

Each taxonomic change proposed in this work is discussed below.

5. Taxonomic treatment

We propose a new monophyletic genus including species formerly placed in *Pilosocereus* subg. *Gounellea*, and the elevation of four heterotypic subspecies to the species rank. Following these changes *Pilosocereus* is now composed by the species grouped in *Pilosocereus* s.s. clade plus *P. bohlei*, including a total of 42 species and four heterotypic subspecies.

XIQUEXIQUE Lavor, Calvente & Versieux **nom. nov.** *Pilosocereus* subg. *Gounellea* Zappi, Succ. Pl. Res., 3:36 (1994). TYPE: *Pilosocereus gounellei* (F. A. C. Weber) Byles & G. D. Rowley in Cact. Succ. J. Gr. Brit. 19: 67 (1957). (=*Xiquexique gounellei* (F. A. C. Weber) Lavor & Calvente).

Tree-like to shrubby cacti, main stem upright, mature branches arched, running more or less parallel to the ground, apices ascending, new axes arising subapically (branching candelabriform); ribs 4-15, sinuses sinuate with conspicuous podaria beneath the areoles; fruit with floral remnant frequently erect, not sunken into the apex of the pericarp, circular at point of attachment.

Distribution — In the Eastern region of Brazil (along the entire Northeast region and in the central-north portion of Minas Gerais state).

Etymology — Named in reference to the vernacular name of *Pilosocereus gounellei*, the xique-xique, broadly known in Brazil and one of the most emblematic cacti of the Brazilian semi-arid Northeastern region.

Notes — We publish this new name as a replacement name for *Pilosocereus* subg. *Gounellea* to avoid a generic name derived from one of the species of the genus (recommendation 20A1 from the Melbourne code; McNeill et al. 2012a). We kept the generic name in masculine to maintain the gender of *Pilosocereus* (recommendation 62A from the Melbourne code; McNeill et al. 2012b).

Three species and one heterotypic subspecies that were included within *Pilosocereus* subgenus *Gounellea*, are now transferred to *Xiquexique*.

XIQUEXIQUE GOUNELLEI (F. A. C. Weber) Lavor & Calvente, comb. nov. *Pilocereus gounellei* F. A. C. Weber in K. Schum., Gesamtbeschr. Kakt.: 188 (1897). *Pilosocereus gounellei* (F. A. C. Weber) Byles & G. D. Rowley in Cact. Succ. J. Gr. Brit. 19: 67 (1957), syn. nov. TYPE: BRAZIL. Pernambuco, 'Certão', *Gounelle* s.n. (P†). Neotype (Zappi 1994): Brazil, Paraíba, Várzia, São Gonçalo (Várzea de Souza), Jan. 1936, *P. Luetzelburg* 26921 (M!, K [photo], IPA).

XIQUEXIQUE GOUNELLEI subsp. ZEHNTNERI (Britton & Rose) Lavor & Calvente comb. nov. *Cephalocereus zehntneri* Britton & Rose, Cact. 2: 35 (1920). *Pilosocereus*

gounellei subsp. *zehntneri* (Britton & Rose) Zappi in Succ. Pl. Res. 3: 43 (1994), syn. nov. Type: BRAZIL. Bahia, district of Chique-Chique (Xique-Xique), Serra de Tiririca, Nov. 1917, *Zehntner* s. n. (Zappi 1994) (US, K, US [photo], lectoparatype: NY).

XIQUEXIQUE FREWENII (Zappi & Taylor) Lavor & Calvente comb. nov. *Pilosocereus frewenii* Zappi & Taylor in Bradleya 29: 131 – 136 (2011), syn. nov. Type: BRAZIL. Minas Gerais, Mun. Santana de Pirapama, distrito de Coberto, north of Inhame, Bambuí limestone outcrop in dry forest at the western foot of the Serra do Cipó, 777 meters above sea level, 19 July 2009, *Zappi & Taylor* 2208 (holotype: SPF, isotype: RB).

XIQUEXIQUE TUBERCULATUS (Werderm.) Lavor & Calvente comb. nov. *Pilocereus tuberculatus* Werderm., Bras. Säulenkakt.: 101 (1933). *Pilosocereus tuberculatus* (Werderm.) Byles & G. D. Rowley in Cact. Succ. J. Gr. Brit. 19(3): 69 (1957), syn. nov. Type: BRAZIL. Pernambuco, Serra Negra, '900 m', Mar. 1932, Werdermann (B†). (lectotype: Werdermann l. c. infra [photo] p. 21 (Zappi 1994)].

5.1 New Names and Synonyms for Pilosocereus

PILOSOCEREUS AURILANATUS F. Ritter, Kakt. Südamer. 1: 77–78, Abb. 50 (1979). *Pilosocereus aurisetus* subsp. *aurilanatus* (Ritter) Zappi in Succ. Pl. Res. 3: 123 (1994), **syn. nov.** Type: BRAZIL. Minas Gerais, Joaquim Felício, 1964, *Ritter 1325* (holotype: U).

To propose *P. aurisetus* subsp. *aurilanatus*, Zappi (1994) downgraded *P. aurilanatus* Ritter to the category of subspecies under *P. aurisetus*, based on both taxa morphological similarities (as their very distinct fruit that divides in the apex breaking the floral remnants and by the very smooth seed coats). According to Zappi's (1994) understanding they would compose a continuous distribution for *P. aurisetus* as they occur isolated from each other in rocky outcrops in Minas Gerais (Brazil). The subspecies differ in the flower-bearing areoles, with golden hairs in *P. aurisetus* subsp. *aurilanatus* and with white hairs in *P. aurisetus* subsp. *aurisetus*; and stems size 4.0-7.0 cm diam. in *P. aurisetus* subsp. *aurilanatus* and < 6 cm in *P. aurisetus* subsp. *aurisetus* (Ritter 1979; Zappi 1994; Hunt et al. 2006).

PILOSOCEREUS PERNAMBUCOENSIS F. Ritter, Kakt. Südamer. 1: 65 (1979). *Pilosocereus pachycladus* subsp. *pernambucoensis* (F. Ritter) Zappi in Succ. Pl. Res. 3: 109 (1994), **syn. nov.** Type: BRAZIL. Pernambuco, Araripina, 1963, *Ritter* 1219 (holotype: U).

Pilosocereus pachycladus is one of the most widely distributed species in Northeastern Brazil, with great morphological diversity. The many heterotypic synonyms recognized for this species indicate an extensive history of nomenclatural and taxonomic confusion (Zappi 1994). Zappi (1994) proposed *P. pachycladus* subsp. *pernambucoensis*, synonymizing and lowering *Pilosocereus pernambucoensis* Ritter to the subspecies rank, based on the existence of

morphologically intermediate populations in the region of Juazeiro and Sento Sé (Brazil). These intermediate populations occur to the north of the São Francisco river basin presenting 10-15 ribs and relatively fine spination (Zappi 1994; Taylor and Zappi 2004). However, *P. pachycladus* subsp. *pernambucoensis* differs from *P. pachycladus subsp. pachycladus* by a considerable number of features as the greater number of ribs (13–19 in the first and 5-12 in the latter), which are lower and closer to each other; the overall smaller spines (reaching 1,8 cm in the first and 3 cm in the latter); and the flower-bearing areoles (with scarce wool in the first and with abundant wool in the latter) (Ritter 1979; Zappi 1994; Taylor and Zappi 2004).

PILOSOCEREUS ROSAE P. J. Braun in Kakt. and. Sukk. 35(8): 178–181 (1984). *Pilosocereus fulvilanatus* subsp. *rosae* (P. J. Braun) Zappi in Succ. Pl. Res. 3: 100 (1994), **syn. nov.** Type: BRAZIL. Minas Gerais: Mun. Augusto de Lima, near Santa Bárbara, 6 km from road BR 135, west slopes of the Serra do Espinhaço, 800 m, 1983, *Horst & Uebelmann 546* (ZSS, isotype: K!).

Zappi (1994) and Taylor and Zappi (2004) state that the two subspecies of *P. fulvilanatus* are very similar morphologically, differing in the less robust habit of *P. fulvilanatus* subsp. *rosae*, which has branches smaller than 5.5 cm in diameter (8-12 cm in *P. fulvilanatus* subsp. *fulvilanatus*) and more ribs (5-) 6-8 compared to 4-7 in *P. fulvilanatus* subsp. *fulvilanatus*) (Buining and Brederoo 1973; Braun 1984; Hunt et al. 2006). These taxa occur separated on different sides of the Espinhaço mountain Range (Minas Gerais state, Brazil) (Zappi 1994). The proposition of *P. fulvilanatus* subsp. *rosae* by Zappi (1994) is based on the lowering of *Pilosocereus rosae* P. J. Braun to the subspecies rank.

PILOSOCEREUS ZAPPIAE Lavor & Calvente **nom. nov.** *Pilosocereus pentaedrophorus* subsp. *robustus* Zappi in Succ. Pl. Res. 3: 74 (1994), syn. nov. HOLOTYPE: BRAZIL. Bahia, Mun. Livramento do Brumado, 11 km S of town on road to Brumado, 450 m, 13°45'S, 41°49'W, 23 Nov. 1988, *Taylor & Zappi in Harley 25544* (SPF, isotype: CEPEC!, K!).

Etymology — Named in honor of the botanist Daniela Zappi. Her extensive taxonomic work with Brazilian cacti and *Pilosocereus* has pushed the limits of the knowledge of the genus and of the Brazilian Cactaceae, as a whole.

Zappi (1994) described *Pilosocereus pentaedrophorus* subsp. *robustus* based on observed morphological discontinuities among the populations of *P. pentaedrophorus*. *Pilosocereus pentaedrophorus* subsp. *pentaedrophorus* occurs from the northern of Bahia state to Pernambuco (Brazil) and *P. pentaedrophorus* subsp. *robustus* occurs in the center-south of Bahia to the northeast of Minas Gerais (mainly in the drainage basin of the Contas and Pardo rivers). Besides the geographical separation, *P. zappiae* differs from *P. pentaedrophorus* subsp. *pentaedrophorus* by the stouter branches (never leaning) up to 7.5 cm diam. (up to 4.5 cm in

the latter), with (5-) 6-10 acute ribs (4-6 in the latter) (Zappi 1994).

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Appendixes

APPENDIX 1. Vouchers and GenBank accession numbers for species used in the phylogenetic analyses of *Pilosocereus* (new sequences generated in this study are printed in bold).

Species: collector/voucher herbarium/location (country) - accession numbers *trn*S-*trn*G, *psb*D-*trn*T, *trn*L-*trn*T, *pet*L-*psb*E, *Phy*C and *ycf*1 (Abbreviations — BHCB: Herbário Universidade Federal de Minas Gerais, Brazil; CCTS: Herbário da Universidade Federal de São Carlos (Campus Sorocaba), Brazil; CEPEC: Herbário CEPEC, Brazil; HUEFS: Herbário Universidade Federal de Feira de Santana, Brazil; QCNE: Museo Ecuatoriano de Ciencias Naturales del Instituto Nacional de Biodiversidad, Ecuador; SORO: Herbário do Centro de Ciências e Tecnologia para Sustentabilidade, Universidade Federal de São Carlos (Campus Sorocaba), Brazil; UFRN: Herbário Universidade Federal do Rio Grande do Norte, Brazil; MA: Vascular Plant Herbarium, Real Jardín Botánico de Madrid, Espanha; MEXU: Univ. Nacional Autónoma de México).

Arrojadoa rhodantha: *Machado M. 777*/HUEFS107367/Bahia (Brazil) – KX301205, KX30108, KX301167, KX301129, KX301244, **MF614893**; *Browningia microsperma*: *Madsen JE. 7311*/MA752144/Loja (Ecuador) – **KX387798**, **KX387705**, **KX387770**, **KX387739**, **MF614857**, **MF614884**; *Cereus jamacaru*: *Calvente A. 461*/UFRN/Bahia (Brazil) – KX301200, KX301076, KX301162, KX301119, KX301238, **MF614874**; *Cleistocactus* sp: *Aedo C. 14512*/MA759900/Cochabamba (Bolivia) – **KX387795**, **KX387701**, **KX387766**, **KX387735**, **MF614853**, **MF614880**; *Copiapoa cinerea*: *Rodrigues R. 3120*/MA702058-11019/Antofagasta (Chile) – -, **KX387702**, **KX387767**, **KX387736**, **MF614854**, **MF614881**; *Melocactus zehntneri*: *Calvente A. 462*/UFRN/ Rio Grande do Norte (Brazil) – KX301198, KX301074, KX301160, KX301117, KX301236, **MF614872**; *Oreocereus hempelianus*: *Aedo C. 11369*/MA728565/Moquegua (Peru) – **KX387796**, **KX387703**, **KX387768**, **KX387737**, **MF614855**, **MF614882**; *Pereskia grandifolia*: *Damaso P./*UFRN 7796/Rio Grande do Norte (Brazil) – -, **KX387707**, **KX387772**, **KX387741**, **MF614858**, **MF614886**; *Pilosocereus albisummus*: *Moraes E.M. S141*/SORO4530 /Minas Gerais (Brazil) – KX301216, KX301097, KX301178, KX301140, KX301255, **MF614902**; *P. alensis*: *Sanchez-Mejorada H. 4449*/MEXU/Jalisco (Mexico) – KX301188, KX301064, KX301150, KX301107, KX301226, **MF614866**; *P. arrabidae* (1): *Machado MC. S35M1*/SORO4488/Bahia (Brazil) – **KX387801**, **KX387714**, **KX387774**, **KX387747**, **MF614861**, **MF614891**; *P. arrabidae* (2): *Franco FF S79B1*/SORO 2656/ Rio de Janeiro (Brazil) – KX301222, KX301103, KX301184, KX301146, KX301261, **MF962471**; *P. aureispinus* (1): *Moraes EM. S21*/HUFS642/Bahia (Brazil) – KX301201, **KX387712**, JN035609, -, KC779308.1, **MF962458**; *P. aureispinus* (2): *Moraes EM. S21*/HUFS642/Bahia (Brazil) – JN035414/JN035456, KX301080, KX301163, KX301123, KX301240, -; *P. aurisetus* subsp. *aurisetus* (1): *Moraes EM. S11*/HUFS646/ Minas Gerais (Brazil) – JN035403 /JN035437, **KX387709**, JN035585, **KX387743**, KC779292.1, **MF614887**; *P. aurisetus* subsp. *aurisetus* (2): *Moraes EM. S30*/ SORO2651/Minas Gerais (Brazil) – KC779380.1, KX301082, KC779380.1, KX301125, KX301241, **MF962460**; *P. aurisetus* subsp. *aurilanatus* (1): *Moraes EM. S7*/HUFS639/Minas Gerais (Brazil) – KC779423.1, **KX387708**, KC621246.1, **KX387742**, **MF962439**, **MF962454**; *P. aurisetus* subsp. *aurilanatus* (2): *Moraes EM. S7*/HUFS639/Minas Gerais (Brazil) – KC779425.1, KX301077, KC621248.1, KX301120, KC779288, **MF962455**; *P. azulensis*: *Olsthoorn G. 253*/ SORO 4531/ Minas Gerais (Brazil) – KX301214, KX301095, KX301176, KX301138, KX301253, **MF614901**; *P. bohlei* (1): *Moraes EM. S35*/CCTS3000/Bahia (Brazil) – **KX387802**, **KX387715**, **KX387775**, **KX387748**, **MF962441**, **MF962461**; *P. bohlei* (2): *Moraes EM. S51*/CCTS3000/Bahia (Brazil) – KX301211, KX301092, KX301173, KX301135, KX301250, **MF614899**; *P. brasiliensis* subsp. *brasiliensis* (1):

Franco FF. S86/SORO 4568/Espírito Santo (Brazil) – **KX387810**, **KX387723**, **KX387782**, **KX387755**, **MF962446**, **MF962472**; *P. brasiliensis* **subsp.** *brasiliensis* (**2**): *Franco FF. S79E*/SORO2654/Espírito Santo (Brazil) – KX301223, KX301104, KX301185, KX301147, KX301262, **MF614907**; *P. brasiliensis* **subsp.** *ruschianus*: *Olsthoorn G. 188*/SORO 4540/Minas Gerais (Brazil) – **KX387809**, **KX387722**, **KX387781**, -, **MF962445**, **MF962470**; *P. catingicola* **subsp.** *catingicola*: *Olsthoorn G. 1026*/SORO4532/Bahia (Brazil) – KX301217, KX301098, KX301179, KX301141, KX301256, **MF614903**; *P. catingicola* **subsp.** *salvadorensis* (**1**): *Menezes MOT. 378*/EAC57091/Bahia (Brazil) – **KX387803**, **KX387716**, -, **KX387749**, **MF962442**, **MF962462**; *P. catingicola* **subsp.** *salvadorensis* (**2**): *Menezes MOT. 152*/EAC44189/Ceará (Brazil) – KX301218, KX301099, KX301180, KX301142, KX301257, **MF962469**; *P. chrysacanthus*: *Arias S. 858*/ MEXU/Oaxaca (Mexico) – KX301190, KX301066, KX301152, KX301109, KX301228, **MF614868**; *P. chrysostele* **subsp.** *cearenses* (**1**): *Lavor P. 36*/ UFRN17127/Ceará (Brazil) – **KX387789**, **KX387695**, **KX387761**, **KX387729**, -, **MF614875**; *P. chrysostele* **subsp.** *cearenses* (**2**): *Menezes MOT. 161*/ EAC44385/ Ceará (Brazil) – **KX387804**, **KX387717**, **KX387776**, **KX387750**, **MF962443**, **MF962463**; *P. collinsii* (**1**): *Arias S. 1658*/MEXU/Chiapas (Mexico) – **KX387784**, **KX387690**, **KX387756**, **KX387724**, -, **MF614869**; *P. collinsii* (**2**): *Arias S. 1635*/_ – KX301191, KX301067, KX301153, KX301110, KX301229, **MF962448**; *P. densiareolatus*: *Moraes EM. S43*/ SORO2650/Minas Gerais (Brazil) – KX301208, KX301089, KX301170, KX301132, KX301247, **MF614896**; *P. flavipulvinatus* (**1**): *Lavor P. 71*/_/Ceará (Brazil) – **KX387799**, **KX387706**, **KX387771**, **KX387740**, -, **MF614885**; *P. flavipulvinatus* (**2**): *Menezes MOT. 259*/EAC48762/Ceará (Brazil) – KX301224, KX301105, KX301186, KX301148, KX301263, -; *P. floccosus* **subsp.** *quadricostatus*: *Olsthoorn G. 42*/SORO4558/Minas Gerais (Brazil) – KX301220, KX301101, KX301182, KX301144, KX301259, **MF614905**; *P. fulvilanatus* **subsp.** *fulvilanatus*: *Moraes EM. S42*/SORO2655/Minas Gerais (Brazil) – KX301207, KX301088, KX301169, KX301131, KX301246, **MF614895**; *P. fulvilanatus* **subsp.** *rosae*: *Olsthoorn G. 263*/ SORO 4534/Minas Gerais (Brazil) – KX301215, KX301096, KX301177, KX301139, KX301254, **MF962467**; *P. glaucochrous*: *Machado MC. S35M2*/SORO 4536/Bahia (Brazil) – KX301202, KX301083, KX301164, KX301126, -, -; *P. gounellei* (**1**): *Lavor P. 18*/UFRN16223/Piauí (Brazil) – **KX387787**, **KX387693**, **KX387759**, **KX387727**, **MF614848**, **MF614870**; *P. gounellei* (**2**): *Lavor P. 22*/ UFRN16227/Piauí (Brazil) – **KX387788**, **KX387694**, **KX387760**, **KX387728**, **MF962437**, **MF962451**; *P. jauruensis* (**1**): *Moraes EM. S23*/HUFS 638/Mato Grosso do Sul (Brazil) – KC779348.1, KX387713, KC779348.1, **KX387746**, **MF614860**, **MF614890**; *P. jauruensis* (**2**): *Moraes EM. S25*/SORO 2646/Mato Grosso do Sul (Brazil) – KC779358.1, KX301081, KC779358.1, KX301124, KC779302, **MF962459**; *P. lanuginosus*: *Mero 96*/QCNE/_ – KX387791, **KX387697**, **KX387763**, **KX387731**, **MF614850**, **MF614877**; *P. leucocephalus* (**1**): *Arias S. 1621*/_/_ – **KX387785**, **KX387691**, **KX387757**, **KX387725**, **MF962436**, **MF962449**; *P. leucocephalus* (**2**): *Arias S. 1654*/MEXU/Chiapas (Mexico) – KX301193, KX301069, KX301155, KX301112, KX301231, -; *P. machrisii* (**1**): *Moraes EM. S18*/HUFS 648/Goiás (Brazil) – KC779332.1, **KX387710**, KC621149.1, **KX387744**, **MF614859**, **MF614888**; *P. machrisii* (**2**): *Moraes EM. S17*/HUFS 645/Goiás (Brazil) – KC779262.1/JN035400, KX301078, JN035602, KX301121, KX301239, **MF962456**; *P. magnificus* (**1**): *Moraes EM. S37*/SORO4550/Minas Gerais (Brazil) – **KX387805**, **KX387718**, **KX387777**, **KX387751**, **MF614862**, **MF614892**; *P. magnificus* (**2**): *Taylor NP. & Zappi DC. 755*/BHCB20954/ Minas Gerais (Brazil) – KX301204, KX301085, KX301166, KX301128, KX301243, **MF962464**; *P. multicostatus* (**1**): *Moraes EM. S41*/SORO2649/Minas Gerais (Brazil) – **KX387806**, **KX387719**, **KX387778**, **KX387752**, **MF614863**, **MF614894**; *P. multicostatus* (**2**): *Moraes EM. S39*/SORO2653/Minas Gerais (Brazil) – KX301206, KX301087, KX301168, KX301130, KX301245, **MF962465**; *P. oligolepis* (**1**): *Lavor et al. 60*/UFRN 18663/Roraima (Brazil) – **KX387792**, **KX387698**, **KX387764**, **KX387732**, **MF614851**, **MF614878**; *P. oligolepis* (**2**): *Lavor P. & Lavor J. 69*/UFRN18670/ Roraima (Brazil) – **KX387793**, **KX387699**, **KX387765**, **KX387733**, **MF962438**, **MF962453**; *P. pachycladus* **subsp.** *pachycladus* (**1**): *Taylor NP. 1434*/ CEPEC 50888/Bahia (Brazil) – **KX387807**, **KX387720**, **KX387779**, **KX387753**, **MF962444**, **MF962466**; *P. pachycladus* **subsp.** *pachycladus* (**2**): *Moraes EM. S45*/SORO2647/ Minas Gerais (Brazil) – KX301209, KX301090, KX301171, KX301133, KX301248, **MF614897**; *P. pachycladus* **subsp.** *pernambucoensis*: *Lavor P. 23*/UFRN16228/Piauí (Brazil) – KX301197, KX301073, KX301159, KX301116, KX301235, **MF962452**; *P. parvus* (**1**): *Moraes EM. S47*/SORO2648/Goiás (Brazil) – **KX387808**, **KX387721**, **KX387780**, **KX387754**, **MF614864**, **MF614898**; *P. parvus* (**2**): *Moraes EM. S47*/SORO2648/Goiás (Brazil) – KX301210, KX301091, **KX301172**, KX301134, KX301249, -; *P. pentaedrophorus* **subsp.** *pentaedrophorus*: *Calvente A. 409*/UFRN 13193/Bahia (Brazil) – **KX387783**, **KX387689**, -, -, -, **MF962447**; *P. pentaedrophorus* **subsp.** *robustus*: *Olsthoorn G. 172*/SORO4538/Bahia (Brazil) – KX301212, KX301093, KX301174, KX301136, KX301251, **MF962467**; *P. piauhyensis*: *Lavor P. 14*/UFRN16219/Piauí (Brazil) – **KX387786**, **KX387692**, **KX387758**, **KX387726**, **-**, -; *P. polygonus*: *DNA Bank Kew 45353*/_/_ – **KX387794**, **KX387700**, -, **KX387734**,

MF614852, **MF614879**; *P. purpusii*: *Blancas Vazquez JJ. 119*/MEXU/Nayarit (Mexico) – KX301189, KX301065, KX301151, KX301108, KX301227, **MF614867**; *P. pusillibaccatus* (**1**): *Lavor P. 20*/UFRN16225/ Piauí (Brazil) – KX301195, KX301071, KX301072, KX301157, KX301114, KX301233, **MF614871**; *P. pusillibaccatus* (**2**): *Lavor P. 21*/ UFRN 16226/Piauí (Brazil) – KX301196, KX301072, KX301158, KX301115, KX301234, **MF962450**; *P. quadricentralis*: *Arias S. 2180*/MEXU/Oaxaca (Mexico) – KX301187, KX301063, KX301149, KX301106, KX301225, **MF614865**; *P. royenii*: *S Arias 1098*/MEXU/ Yucatán (Mexico) – KX301192, KX301068, KX301154, KX301111, KX301230, -; *P. splendidus*: *Moraes EM. S139*/ SORO4539/Bahia (Brazil) – KX301213, KX301094, KX301175, KX301137, KX301252, **MF614900**; *P. tuberculatus*: *Lavor P. 47*/UFRN18650/Pernambuco (Brazil) – **KX387790**, **KX387696**, **KX387762**, **KX387730**, **MF614849**, **MF614876**; *P. ulei*: *Franco FF. S79*/SORO4557/Rio de Janeiro (Brazil) – KX301221, KX301102, KX301183, KX301145, KX301260, **MF614906**; *P. vilaboensis* (**1**): *Moraes EM. S20*/HUFS 641/Goiás (Brazil) – **KX387800**, **KX387711**, **KX387773**, **KX387745**, **MF962440**, **MF962457**; *P. vilaboensis* (**2**): *Moraes EM. S19*/CCTS3001/Goiás (Brazil) – KC779340.1, KX301079, KC621157.1, KX301122, KC779305.1, **MF614889**; *Rhipsalis baccifera*: *Rodriguez A. 5318*/MA733603/Limón (Costa Rica) – **KX387797**, **KX387704**, **KX387769**, **KX387738**, **MF614856**, **MF614883**; *Stephanocereus leucostele*: *Calvente A. 413*/UFRN 13195/Bahia (Brazil) – KX301199, KX301075, KX301161, KX301118, KX301237, **MF614873**.

APPENDIX 2. Primers of the different genomic regions used in this study.

Region name	Primers	Source
*pet*L-*psb*E	petL: AGTAGAAAACCGAAATAACTAGTT A psbE: TATCGAATACTGGTAATAATATCAGC	Shaw et al. 2007
*psb*D-*trn*T^{GGU}	psbD: CTCCGTARCCAGTCATCCATA trnT(GGU)-R: CCCTTTTAACTCAGTGGTAG	Shaw et al. 2007
*trn*L-*trn*T	5'trnLUAAR(TabB): TCTACCGATTTCGCCATATC trnT^{UGU}F (TabA): CATTACAAATGCGATGCTCT	Taberlet et al. 1991
*trn*S-*trn*G	5'trnG2S: TTTTACCACTAAACTATACCCGC SGFwd2: CACCCATGGTTCCCATTAGA	Shaw et al. 2005
	trnS^{GCU}: AGATAGGGATTCGAACCCTCGGT SGRev2: TCCGCTCATTAGCTCTCCTC	Bonatelli et al. 2013
*Phy*C	PhyF: AGCTGGGGCTTTCAAATCTT PhyR: TCCTCCACTTGACCACCTCT	Helsen et al. 2009
*ycf*1	ycf1-4182F*: AAATAYRRATAGAAAATATTTKGATT ycf1-5248R*: GAATTCTYAATTCTCTACGACG	Franck et al. 2012

Rápida regeneração natural por plantas nativas da canga em áreas recém-mineradas na Serra Sul, Canaã dos Carajás, Pará, Brasil

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Abstract

The typical vegetation of ironstone outcrops (*canga*) in Serra dos Carajás is unique when compared to the entire Amazonian scenario, holding more than 1,000 species of vascular plants, of which 38 are locally endemic. This flora is highly threatened by iron ore exploitation. In this context, it is important to improve the knowledge about the species useful for restoring degraded areas. Here, I provide a list of 20 plant species observed spontaneously growing on degraded areas of iron-rich substrates in a recently opened mine (S11D), after five and ten months of the beginning of mining activities. Among them, three are restricted to the Carajás region: *Monogereion carajensis*, *Mitracarpus carajasensis*, and *Perama carajensis*. Further, *M. carajensis*, *Mimosa acutistipula* var. *ferrea*, and *Mimosa skinneri* var. *carajarum* are threatened taxa. The majority of species were flowering and/or fruiting; some of them were attracting potential pollinators. This rapid regeneration is probably associated to the presence of a rich seed bank and subterranean organs of the original substrate, as well to the surrounding *canga* vegetation, which may act as an important source of propagules.

Key words: Amazon rainforest, ironstone vegetation, rare species, regeneration, restoration

1. Introdução

A Serra dos Carajás é um conjunto de platôs localizados no sudeste do Pará. Em suas partes mais elevadas há a ocorrência de uma carapaça laterítica ferruginosa, denominada "canga", sobre a qual se desenvolve uma vegetação singular no domínio amazônico (Secco & Mesquita 1983, Porto & Silva 1989, Silva 1991, Mota *et al*. 2015, Viana *et al*. 2016, Mota *et al*. 2018, Zappi *et al*. 2019). Este tipo de vegetação aberta está distribuído como um "arquipélago" em meio a um "mar" de selvas, abrigando várias espécies vegetais de ocorrência restrita, incluindo táxons novos e recentemente descritos (Mota *et al*. 2015, Viana *et al*. 2016, Giulietti *et al*. 2019). Nesse contexto, o recente projeto "Flora das cangas da Serra

dos Carajás", publicado em quatro volumes da revista *Rodriguésia*, entre os anos de 2016 e 2018, caracterizou 1.042 espécies de plantas vasculares, das quais 38 são endêmicas, incluindo três gêneros monotípicos (Viana *et al*. 2016, Viana & Giulietti-Harley 2018, Giulietti *et al*. 2019).

Justamente por se constituírem de substrato ferruginoso, as cangas de Carajás sofrem forte pressão das atividades de mineração, o que representa uma ameaça à sua flora (Madeira *et al*. 2015). Diante da expansão das atividades minerárias na região, houve a necessidade de se priorizar tentativas de recuperação de áreas degradadas, incluindo a seleção de espécies vegetais de alto potencial para este fim (Giannini *et al*. 2017, Zappi *et al*. 2018). Esses trabalhos foram baseados em diversos atributos das espécies, a exemplo de persistência em áreas sob processo de recuperação, facilidade de

propagação, importância nas comunidades nativas de canga e potencial atrativo para elementos da fauna (Giannini *et al.* 2017, Zappi *et al.* 2018).

As espécies de plantas capazes de atuar na recuperação passiva, isto é, na regeneração natural de áreas mineradas, ainda são muito pouco conhecidas na região de Carajás (Zappi *et al.* 2018). Por este motivo, aqui são apresentados registros de plantas da canga observadas se regenerando espontaneamente em áreas recém-mineradas na Serra Sul.

2. Material e métodos

As observações de campo foram efetuadas no complexo minerário S11D, Serra Sul (entre 06°24'28"S e 06°24'37"S - 50°20'29"W e 50°19'06"W), município de Canaã dos Carajás, Pará, Brasil. As amostragens ocorreram cerca de cinco meses após o início da abertura da mina (entre 7 e 9 de abril de 2015) e cerca de 10 meses após a abertura da mina (de 29 de setembro a 2 de outubro de 2015).

Foram registradas todas as plantas nascendo em pilhas de fragmentos do substrato ferruginoso recém-minerados, taludes, canteiros abandonados e estradas. Pelo fato de o autor estar trabalhando no monitoramento de aves e por não possuir autorização para a coleta de material botânico na Unidade de Conservação (Floresta Nacional de Carajás), as plantas foram fotografadas e identificadas com base na bibliografia especializada sobre a flora regional (Silveira *et al.* 1995, Cruz *et al.* 2016, Lombardi 2016, Simão-Bianchini *et al.* 2016, Wood & Scotland 2017, Zappi *et al.* 2017, Amorim *et al.* 2018, Coelho 2018, Fernandes *et al.* 2018, Fernandes-Júnior & Cruz 2018, Giacomin & Gomes 2018, Koch *et al.* 2018, Mattos *et al.* 2018, Zappi *et al.* 2018). No caso de Poaceae a identificação ocorreu por consulta ao especialista P. L. Viana (Herbário MG). Sete táxons não identificados por estarem estéreis não foram incluídos na presente listagem.

Anotou-se se o substrato no qual as plantas estavam crescendo era seco ou submetido a alagamento parcial (úmido). Também foram anotadas informações sobre a fenologia das espécies e eventuais visitantes florais.

As espécies de distribuição restrita à região de Carajás e serras adjacentes foram categorizadas com base nas revisões taxonômicas sobre as famílias envolvidas (Cruz *et al.* 2016, Lombardi 2016, Simão-Bianchini *et al.* 2016, Wood & Scotland 2017, Zappi *et al.* 2017, Amorim *et al.* 2018, Coelho 2018, Fernandes *et al.* 2018, Fernandes-Júnior & Cruz 2018, Giacomin & Gomes 2018, Koch *et al.* 2018, Mattos *et al.* 2018; Viana *et al.* 2018) e na mais recente análise de endemismo apresentada por Giulietti *et al.* (2019).

Todas as espécies foram checadas com relação à raridade (Giulietti *et al.* 2009) e eventual presença nas listas vermelhas

do estado do Pará (SECTAM 2006) e do Brasil (Martinelli & Moraes 2013).

3. Resultados e discussão

Foram identificadas 20 espécies (Figuras 1-4), representantes de 12 famílias, crescendo espontaneamente nas áreas recém-mineradas da Serra Sul (Tabela 1). Ressalta-se que esta é apenas uma parcela do total de espécies que estava se regenerando no local, pois pelo menos sete não puderam ser identificadas por se encontrarem no estágio inicial de desenvolvimento (plântulas) ou estéreis, incluindo, neste último caso, dois representantes da família Poaceae.

A maior parte das espécies (90%, *n* = 18) foi registrada em substratos secos, não sujeitos a alagamentos (Figura 1a). As únicas espécies observadas crescendo sobre áreas úmidas foram *Chamaecrista desvauxii* e *Mimosa skinneri* (Figura 1b).

FIGURA 1. Área recém-minerada na Serra Sul (S11D), Serra dos Carajás, Pará, Brasil: **A.** Regeneração natural da vegetação em substrato seco, com dominância de *Mimosa acutistipula*; **B.** Regeneração natural da vegetação em substrato úmido, com a presença de *Chamaecrista desvauxii* e *Mimosa skinneri*, além de gramíneas não identificadas. (Foto: M.F. Vasconcelos).

As seguintes espécies não constam nos estudos de plantas nativas sugeridas para recuperação de áreas degradadas pela mineração em Carajás, conforme Giannini *et al*. (2017) e Zappi *et al*. (2018): *Anthurium bonplandii* (Figura 2b), *Jacquemontia tamnifolia* (Figura 2f), *Chamaecrista desvauxii* (Figura 3a) e *Axonopus longispicus* (Figura 4d).

A maior parte das espécies (85%, *n* = 17) foi registrada regenerando em áreas recém-mineradas logo nos cinco meses após a supressão e revolvimento da canga. As exceções foram representadas por *Anthurium bonplandii* (Figura 2b), *Sobralia liliastrum* (Figura 4b) e *Solanum crinitum* (Figura 4e), registradas apenas durante a amostragem efetuada 10 meses após as atividades de abertura da mina. Tanto *A. bonplandii* quanto *S. liliastrum* são herbáceas de crescimento relativamente lento, se considerada a germinação de sementes. Ambas pertencem a famílias tidas como bioindicadoras (Barthlott *et al*. 2001), com muitos representantes sensíveis à qualidade do habitat. Nesses dois casos, uma possível rebrota a partir de gemas caulinares explicaria esses registros, ainda que mais tardios.

Dentre as 20 espécies identificadas (Figuras 2, 3, 4), três (15%) são restritas à região de Carajás e serras adjacentes: *Monogereion carajensis* (Figura 2c), *Mitracarpus carajasensis* (Figura 4a) e *Perama carajensis* (Figura 4c). Estas espécies representam 8% do total de plantas endêmicas da região (*n* = 38).

Além de *Monogereion carajensis*, que se encontra "criticamente em perigo" no estado do Pará e no Brasil, destacam-se duas leguminosas ameaçadas de extinção: *Mimosa acutistipula*, cuja população de Carajás (*Mimosa acutistipula* var. *ferrea* - Figura 3d) é tratada como "vulnerável" no Pará; e *Mimosa skinneri*, representada por uma variedade regional (*Mimosa skinneri* var. *carajarum* - Figura 3e) considerada "vulnerável" em nível estadual e "criticamente em perigo" em nível nacional. *Ipomoea marabaensis* (Figura 2d) é a única espécie considerada rara no Brasil (Giulietti *et al*. 2009).

Quase todas as espécies observadas estavam floridas cinco meses após a abertura da mina (*n* = 17) e quatro portavam frutos, sugerindo que o processo de polinização já estivesse ocorrendo nestas áreas recém-mineradas. Durante as observações de campo, foi possível registrar barbeiros da família Pyrrhocoridae na parte externa da corola de *Mandevilla scabra* (Figura 2a). Além disso, abelhas nativas (Xylocopini) e exóticas (*Apis mellifera*) foram observadas visitando flores de *Dioclea apurensis* (Figura 3c) e de *Jacquemontia tamnifolia*, respectivamente. Embora vários indivíduos de *Byrsonima chrysophylla* (Figura 3f) tenham sido registrados frutificando, seus frutos estavam verdes durante as amostragens, não sendo observadas aves potencialmente dispersoras. Na região de Carajás, 47 espécies de aves foram registradas consumindo frutos de outra espécie do gênero (*Byrsonima crispa* A. Juss.) em uma área em recuperação (Leite & Barreiros 2014), mostrando a potencial importância deste grupo faunístico para a dispersão de sementes.

4. Conclusões

Mesmo diante da supressão e do revolvimento da camada superficial da canga durante a abertura da mina no S11D, foi notável a rápida regeneração de várias espécies da flora típica da região, incluindo táxons endêmicos e ameaçados de extinção, a exemplo de *Monogereion carajensis*, gênero monotípico (Cruz *et al*. 2016, Giulietti *et al*. 2019).

É importante ressaltar que esta rápida regeneração de plantas da canga observada no presente estudo não deva ser um padrão em áreas já submetidas às atividades de mineração a céu aberto por longos períodos. No caso específico deste estudo, a primeira frente de lavra pode ter revolvido a camada superficial da canga junto com o rico banco de sementes e órgãos subterrâneos de plantas ali presentes. Além disso, as adjacências imediatas da mina ainda são importantes fontes de propágulos, já que a maior parte da Serra Sul ainda não foi minerada. Tanto a estocagem das primeiras camadas de solo ("topsoil") para serem utilizadas em recuperação de áreas mineradas, quanto o planejamento de um mosaico de áreas no entorno das lavras, que possam vir a ser fontes de propágulos, quando da recuperação, são estratégias já empregadas em processos de recuperação (Kneller *et al*., 2018; Zappi *et al*., 2018).

Por fim, sugere-se a incorporação das espécies aqui listadas que não constam nos estudos de plantas nativas sugeridas para recuperação de áreas degradadas pela mineração em Carajás (Giannini *et al*., 2017; Zappi *et al*., 2018) em futuros programas com este objetivo. Também são sugeridos estudos envolvendo observações sobre potenciais espécies da fauna que possam atuar como polinizadores e dispersores de sementes nessas áreas, já que diretamente afetam a reprodução e o estabelecimento dos vegetais.
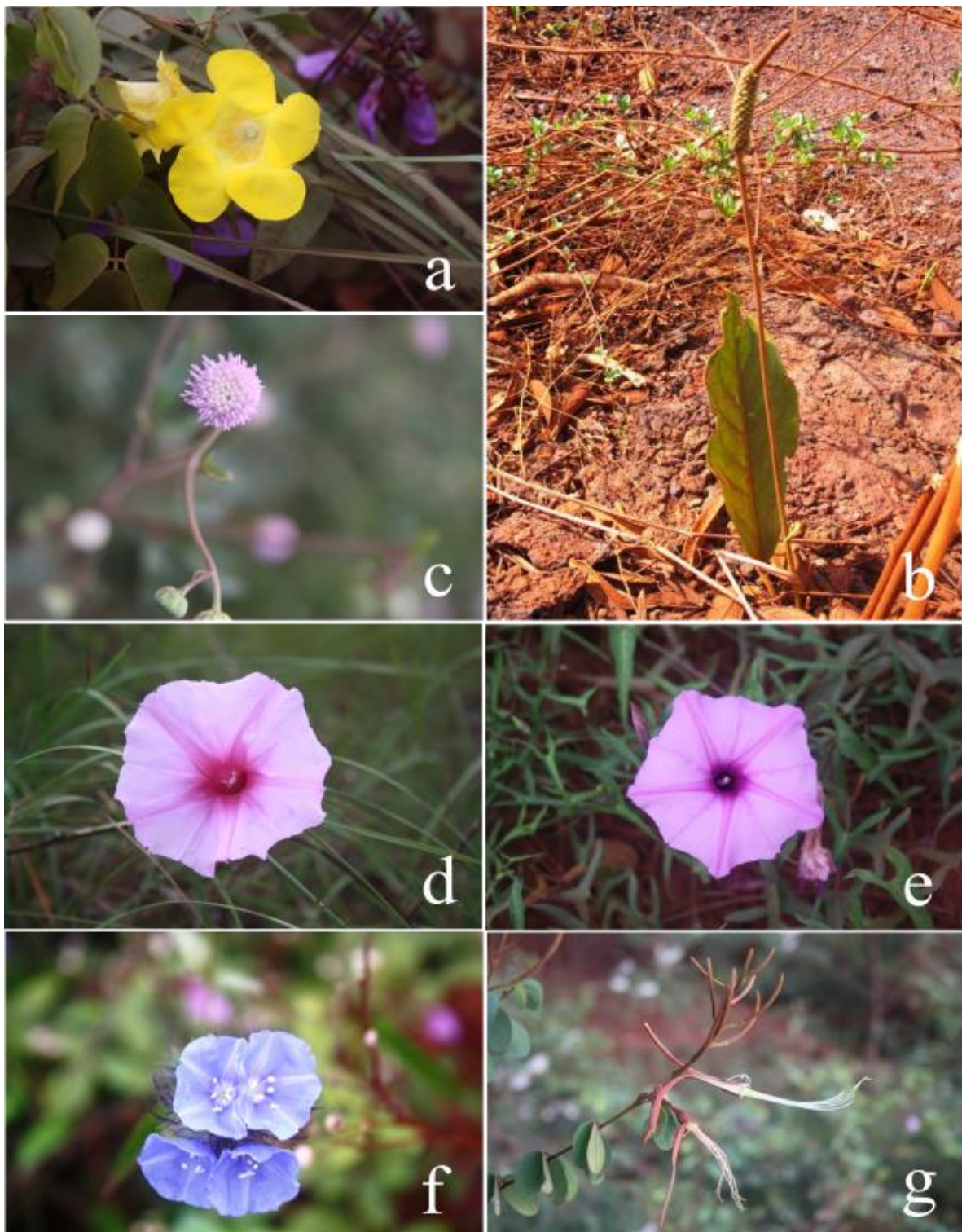
Figura 2. Espécies de plantas regenerando em áreas recém-mineradas na Serra Sul (S11D), Serra dos Carajás, Pará, Brasil: **a.** *Mandevilla scabra*; **b.** *Anthurium bonplandii*; **c.** *Monogereion carajensis*; **d.** *Ipomoea marabaensis*; **e.** *Ipomoea maurandioides*; **f.** *Jacquemontia tamnifolia*; **g.** *Bauhinia pulchella.* (Fotos: M.F. Vasconcelos).
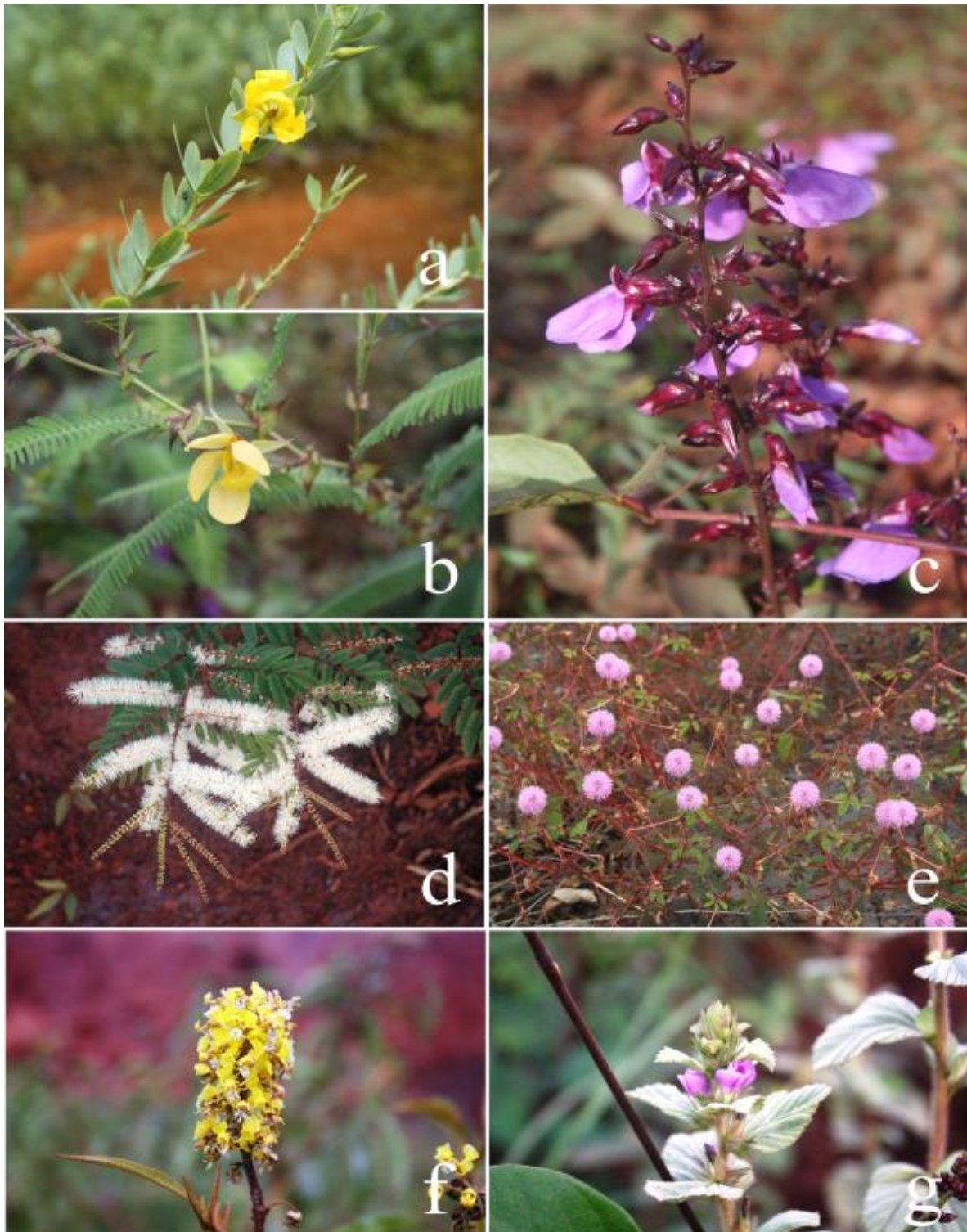
FIGURA 3. Espécies de plantas regenerando em áreas recém-mineradas na Serra Sul (S11D), Serra dos Carajás, Pará, Brasil: **a.** *Chamaecrista desvauxii*; **b.** *Chamaecrista flexuosa*; **c.** *Dioclea apurensis*; **d.** *Mimosa acutistipula*; **e.** *Mimosa skinneri*; **f.** *Byrsonima chrysophylla*; **g.** *Melochia splendens*. (Fotos: M.F. Vasconcelos).
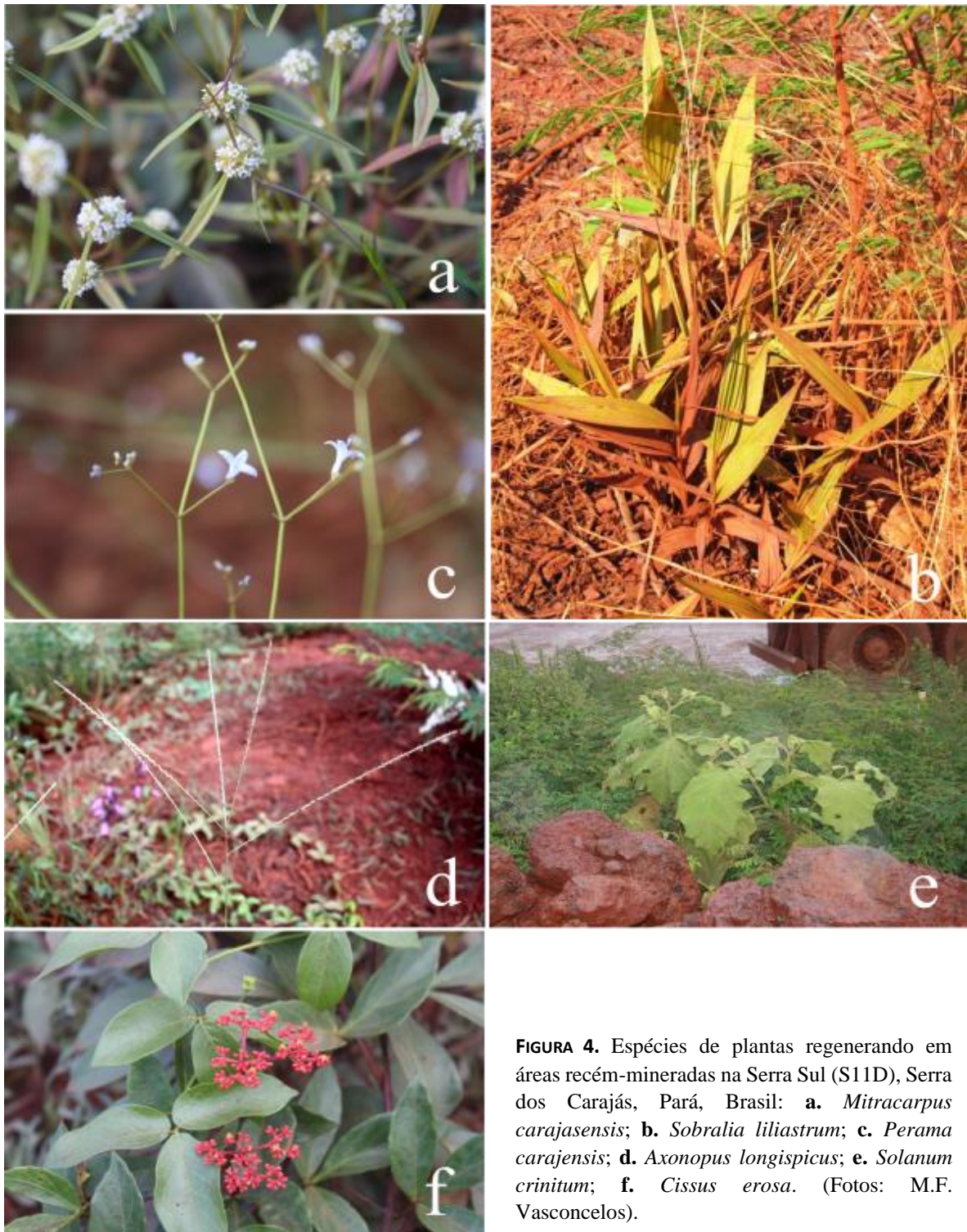
FIGURA 4. Espécies de plantas regenerando em áreas recém-mineradas na Serra Sul (S11D), Serra dos Carajás, Pará, Brasil: **a.** *Mitracarpus carajasensis*; **b.** *Sobralia liliastrum*; **c.** *Perama carajensis*; **d.** *Axonopus longispicus*; **e.** *Solanum crinitum*; **f.** *Cissus erosa*. (Fotos: M.F. Vasconcelos).

TABELA 1. Lista das espécies de plantas observadas regenerando em áreas recém-mineradas na Serra Sul (S11D), Serra dos Carajás, Pará, Brasil.

Família/Espécie	Meses após abertura da mina	Condições do substrato	Endêmica da região de Carajás e serras adjacentes	Lista de plantas nativas sugeridas para recuperação de áreas de mineração em Carajás		Espécie rara	Espécies ameaçadas		Estado fenológico	Visitantes florais
				Giannini *et al.* (2017)	Zappi *et al.* (2018)		PA	BR		
APOCYNACEAE										
Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K. Schum.	5 e 10	Seco		X	X				Vegetativo; flores	Hemiptera: Pyrrhocoridae
ARACEAE										
Anthurium bonplandii Bunting	10	Seco							Vegetativo; flores; frutos	
ASTERACEAE										
Monogereion carajensis G.M. Barroso & R.M. King	5 e 10	Seco	X	X	X		CR	CR	Vegetativo; flores; frutos	
CONVOLVULACEAE										
Ipomoea marabaensis D.F. Austin & Secco	5 e 10	Seco		X	X	X			Vegetativo; flores	
Ipomoea maurandioides Meisn.	5 e 10	Seco		X	X				Vegetativo; flores	
Jacquemontia tamnifolia (L.) Griseb.	5 e 10	Seco							Vegetativo; flores	*Apis mellifera*
FABACEAE										
Bauhinia pulchella Benth.	5 e 10	Seco		X	X				Vegetativo; flores; frutos	
Chamaecrista desvauxii (Collad.) Killip	5 e 10	Úmido							Vegetativo; flores	
Chamaecrista flexuosa (L.) Greene	5 e 10	Seco		X					Vegetativo; flores	
Dioclea apurensis Kunth	5 e 10	Seco		X	X				Vegetativo; flores	Hymenoptera: Xylocopini
Mimosa acutistipula (Mart.) Benth.	5 e 10	Seco		X	X		VU		Vegetativo; flores	
Mimosa skinneri Benth.	5 e 10	Úmido		X	X		VU	CR	Vegetativo; flores	

Continuação... TABELA 1. Lista das espécies de plantas observadas regenerando em áreas recém-mineradas na Serra Sul (S11D), Serra dos Carajás, Pará, Brasil.

Família/Espécie	Meses após abertura da mina	Condições do substrato	Endêmica da região de Carajás e serras adjacentes	Lista de plantas nativas sugeridas para recuperação de áreas de mineração em Carajás		Espécie rara	Espécies ameaçadas		Estado fenológico	Visitantes florais
				Giannini *et al.* (2017)	Zappi *et al.* (2018)		PA	BR		
MALPIGHIACEAE										
Byrsonima chrysophylla Kunth	5 e 10	Seco			X				Vegetativo; flores; frutos	
MALVACEAE										
Melochia splendens A.St.-Hil. & Naudin	5 e 10	Seco			X				Vegetativo; flores	
ORCHIDACEAE										
Sobralia liliastrum Lindl.	10	Seco		X	X				Vegetativo	
POACEAE										
Axonopus longispicus (Döll) Kuhlm.	5 e 10	Seco							Vegetativo; flores	
RUBIACEAE										
Mitracarpus carajasensis E.L. Cabral, Sobrado & E.B. Souza	5 e 10	Seco	X	X					Vegetativo; flores	
Perama carajensis J.H. Kirkbr.	5 e 10	Seco	X	X	X				Vegetativo; flores	
SOLANACEAE										
Solanum crinitum Lam.	10	Seco		X	X				Vegetativo	
VITACEAE										
Cissus erosa Richard	5 e 10	Seco		X	X				Vegetativo; flores; frutos	

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Plant**Now** Gallery

VERA PATURY

Entrevista a Leonardo Versieux

Mostrar as florestas, a natureza rica e ameaçada do Brasil, tem sido a bandeira da artista baiana, arquiteta e ambientalista radicada em Itaipava, Petrópolis, no Rio de Janeiro, Vera Patury (79). Mesclando um conjunto de linguagens, da tapeçaria à cestaria indígena, das pinturas às grandes instalações, Vera busca aproximar e sensibilizar o público quanto às nossas riquezas naturais, ao mesmo tempo em que desperta a curiosidade e o interesse do espectador, frente à uma obra rica, variada, com uma estética diversa. Por meio de seu trabalho, geralmente envolvendo oficinas de criação junto com o público, vem conseguindo conciliar a educação do olhar e a sensibilização ambiental, práticas mais do que necessárias para os tempos nos quais vivemos.

À direita, instalação no Reggio Emilia, de 1999, projeto Mata Atlântica. Abaixo à esquerda "Fogo sob Montanha" acrílico sobre tela com colagens e folha de ouro. À direita

"Relicário Floresta" técnica mista em moldura antiga. Fotos cedidas pela artista.
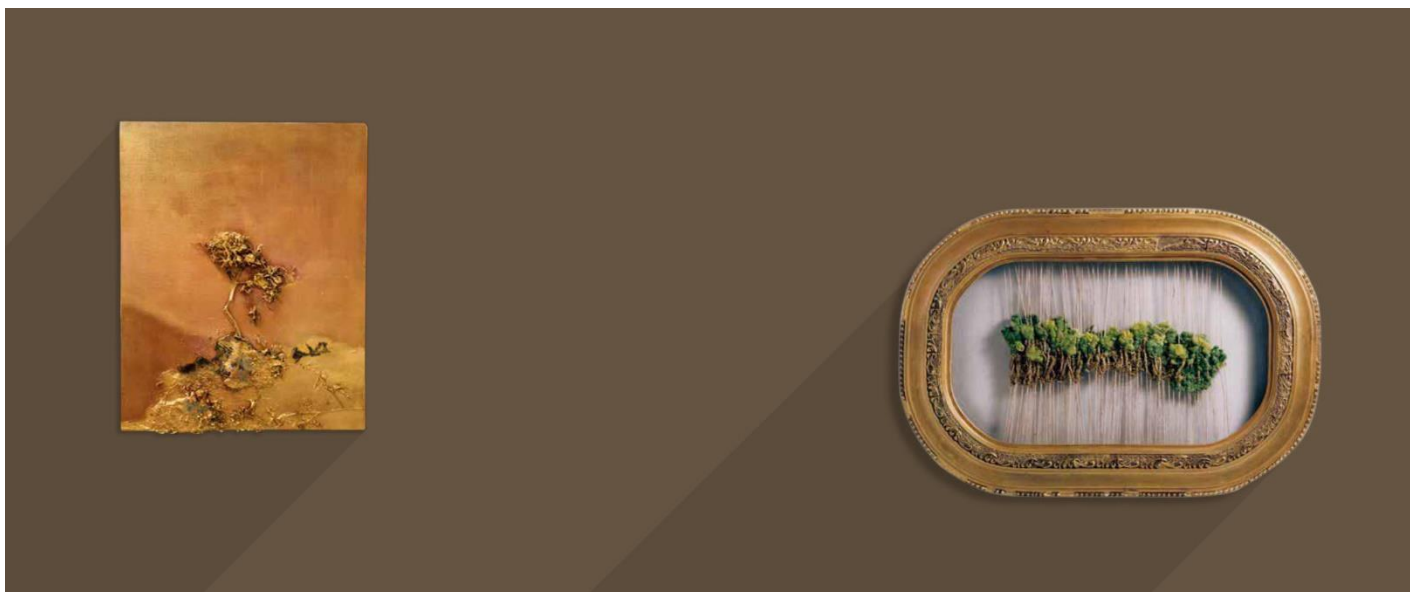
Instalação Mata Atlântica - Tecelagem

Vera, qual é a sua formação?
Estudei arquitetura na UFRJ. Pintura em Paris e no Parque Lage. Escultura em ferro e madeira com Mario Cravo em Salvador e técnicas de cestaria e escultura têxtil e *mixed media* em San Francisco, California. Aprofundei as pesquisas com fibras naturais, visando à realização das instalações.

Você sempre se dedicou a produção artística com ênfase no meio ambiente ou houve uma data/momento em que começou a se dedicar a essa temática?

Quando voltei de Paris, fui morar no sul da Bahia e assisti à destruição da Mata Atlântica naquela área. Impotente para conter o desmatamento, e a violência dos invasores, voltei para o Rio de Janeiro, a seguir fui para a Califórnia, onde fiz pesquisas de materiais e de técnicas com o uso de fibras em San Francisco e Berkeley.

A sua produção é totalmente voltada às questões ambientais ou você se envolve em outras temáticas /poéticas?

Atualmente o meu trabalho é voltado para conscientização sobre a importância e a beleza e a

necessidade de preservação das nossas florestas. Todos eles são *site specific* (específicos para um dado lugar).

Qual linguagem (técnica) tem sido a mais empregada por você em seus trabalhos?

Nas exposições trabalho com pinturas, colagens e tecelagens em molduras recicladas. Nas instalações, grandes esculturas têxteis e cestarias. Nas oficinas, uso teares manuais e os participantes tecem com sisal tingido artesanalmente.

Em que lugar seus trabalhos são mais frequentemente expostos (museus, galerias, na rua, parques públicos etc.)?

Costumo expor em galerias e museus, mas já realizei uma itinerância por 20 cidades de SP armando tendas em cada cidade para realização dos eventos.

Há algum trabalho que você considere mais marcante na abordagem da relação arte e meio ambiente dentro da sua produção?

Considero importante a realização da primeira oficina de arte e meio ambiente, na Itália, em Reggio Emilia, em 1999, sobre a Mata Atlântica e que contou com a participação de toda a população e imigrantes de 30 etnias, ressaltando a importância da aceitação da diversidade. Também está agendada a realização de um evento no Museu do Meio Ambiente, no Jardim Botânico do Rio de Janeiro, com palestras, apresentação da exposição Pindorama, instalações e oficinas de arte, nas quais o público participará de um reflorestamento simbólico. Espero que esse evento venha a ter impacto na conscientização sobre a importância da preservação de nossas riquezas naturais.

Você se preocupa com o impacto ambiental que seu próprio trabalho gera? Tais como a origem e tipo do material empregado, transporte, uso e descarte de forma sustentável...

Meus trabalhos são realizados no meu ateliê em Itaipava, em uma área de floresta preservada. Uso a fibra do sisal, material orgânico, teares rudimentares, com trabalhadores locais e o transporte e a montagem são simples e feitos por esse mesmo pessoal. As instalações são reutilizadas e, algumas, doadas para as escolas participantes.

À esquerda: Instalação Cachoeira, montada no Congresso Water for Peace, 2003. Abaixo: pintura em acrílica sobre telas, à esquerda "Montanhas em ouro", à direita "Florestas em névoa". No pé da página, "Floresta tecida".
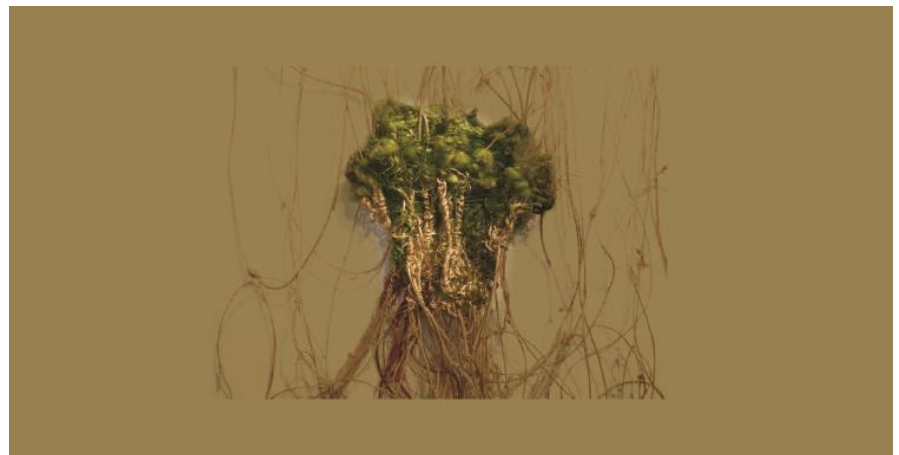
"... Acredito que a arte possa favorecer o desenvolvimento de um olhar mais amoroso em relação à natureza, contribuindo para a mudança do atual paradigma de dominação, e para um pacífico reconhecimento de ser o homem uma espécie entre as espécies."

Vera Patury

PlantNow Recipes

BISCOITOS BOTÂNICOS DE POLVILHO E QUEIJO

Marcela Thadeo

Universidade Estadual de Maringá.

Tempo de preparo: 30 minutos
Tempo no forno: 15 a 30 minutos
Rendimento médio 50 biscoitos pequenos

INGREDIENTES

150 g de polvilho doce (1 xícara e meia)
50 g de queijo parmesão ralado fino (meia xícara)
75 g de queijo prato ralado grosso (meia xícara)
75 g de manteiga sem sal cortada em cubos (meia xícara)
1 colher de chá de sal
2 colheres de sopa de orégano seco
1 ovo levemente batido
Ervas frescas de sua preferência (alecrim, tomilho, salsinha, sálvia e/ou manjericão)
1 ovo levemente batido para pincelar (opcional)

MODO DE FAZER:

Pré-aqueça o forno a 200°C.
Em uma tigela coloque o polvilho e os queijos e misture. Em seguida adicione a manteiga, o ovo, o sal e o orégano e vá misturando com a ponta dos dedos, até que todos os ingredientes estejam integrados e seja possível obter uma bola de massa uniforme.

Dependendo do tamanho do ovo que for usado, talvez seja necessário colocar uma ou duas colheres de água gelada para obter a bola de massa.

Polvilhe um pouco de polvilho na bancada e comece a abrir a massa com um rolo de macarrão. Se preferir coloque a massa sobre dois pedaços de papel manteiga e vá abrindo com o rolo até que fique bem fina e uniforme (isso evita que a massa grude no rolo).

Em seguida, corte a massa usando cortadores de biscoito de sua preferência ou uma faca.

Delicadamente, enfeite os biscoitos com as folhas das ervas de sua preferência, pressionando levemente para que as folhas grudem na superfície da massa. Retire os biscoitos da bancada e os acomode em formas untadas com manteiga ou com spray culinário. Se desejar que fiquem bem corados pincele a superfície dos biscoitos com ovo batido. Não é necessário deixar espaço entre os biscoitos pois eles mantêm seu formato original.

Leve para assar. O tempo de cozimento pode variar de acordo com o tamanho dos biscoitos que forem modelados e do tipo de forno que for utilizado. Biscoitos menores assam em cerca de 15 minutos, mas biscoitos maiores demandam mais tempo ao forno. Teste se estão crocantes e com a superfície corada. Depois de retirar do forno, deixe esfriar e solte os biscoitos da forma. Guarde-os em um vidro bem fechado. Manuseie-os com cuidado para que as folhas decorativas de ervas não se soltem.

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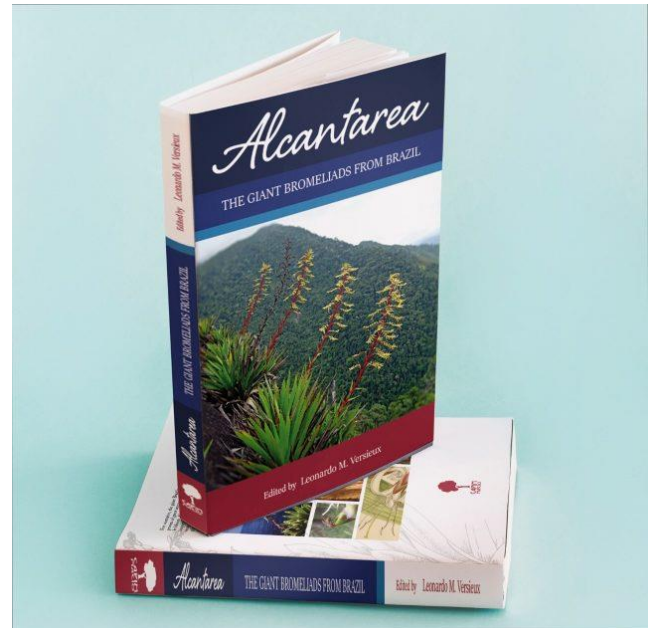
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