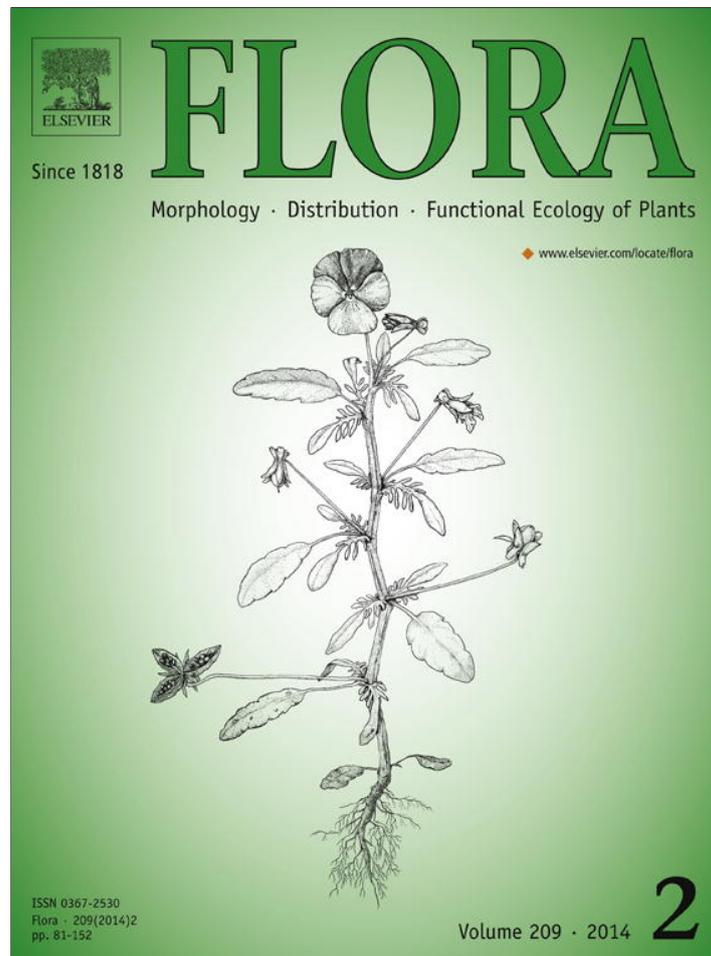


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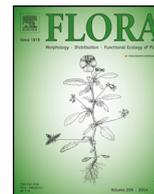
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From open areas to forests? The evolutionary history of *Philodendron* subgenus *Meconostigma* (Araceae) using morphological data



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ABSTRACT

Due to its wide distribution covering three of the largest Neotropical biomes, *Philodendron* subgenus *Meconostigma* is an interesting model to discuss the diversification of Neotropical plants. The aim of this study was to test a previous hypothesis that the Eastern and Southern species of *P. subg. Meconostigma* have plesiomorphic gynoecial structure while in Amazonian species they are apomorphic. To this end, we conducted an analysis of maximum parsimony with generalized frequency coding method using a matrix with 59 morphological characters and 90% of the species of *P. subg. Meconostigma*. The phylogenetic reconstruction suggests that the subgenus is monophyletic and originates from open areas of Cerrado. Four morphological synapomorphies support the monophyly of the subgenus and seven synapomorphies support four minor clades within it. Our results also include characterization of three new gynoecial subtypes (A1, A2 and A3) within the subgenus. Subtype A2 (undeveloped stylar body with long stylar canals, absent central stylar dome, shallow compitum) is basal and represents the ancestral gynoecium in the group. These findings suggest that the balance between pollen uptake and accessibility of the locules were decisive to drive gynoecium evolution in the subgenus *Meconostigma*.

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Introduction

Neotropical plants make up around 37% of the world's total flora and this hyperdiversity has intrigued plant evolutionary biologists (Antonelli and Sanmartín, 2011). Data on evolution of South America plants are fundamental to provide new insights into the patterns of Neotropical plant diversification.

Philodendron Schott is exclusively Neotropical and the second largest genus (ca. 500 species) of Araceae (Boyce and Croat, 2012), an ancient family within monocots (Friis et al., 2004; Cusimano et al., 2011). The infrageneric classification in three subgenera, *Philodendron*, *Pteromischum* and *Meconostigma*, is supported by morphological and anatomical characters (Mayo, 1988), and molecular data (Gauthier et al., 2008). The subgenus *Meconostigma* is an interesting model to understand the diversification of Neotropical plants because of its wide distribution including Amazonia, Atlantic Forest, and Cerrado biomes and the small number of

species – 21 – which facilitates morphological phylogenetic studies. Despite this, no comprehensive phylogenetic study has previously been carried out.

The taxonomy of *P. subgenus Meconostigma* was revised by Mayo (1991) and Gonçalves and Salviani (2002), and a series of anatomical and morphological studies focused on floral traits of *Philodendron* have been published (Mayo, 1988, 1989). Mayo (1988) hypothesized that *P. subg. Meconostigma* was the first of the subgenera to emerge as a distinct clade from ancestral *Philodendron*, that the Eastern and Southern species would present a higher number of plesiomorphic gynoecial characters (low number of locules and simple style), and Amazonian species would have apomorphic characters (high number of locules and elaborated style). However, these hypotheses were based mainly on data from four species and therefore, it remained unclear whether or not they hold true for the whole subgenus.

The aim of the present study was to infer the evolutionary history of *Philodendron subg. Meconostigma* using morphological characters. To this end, we described three new subtypes of gynoecium and analyzed a meristic and polymorphic character matrix using generalized frequency coding (GFC). This is the first phylogenetic study of *Philodendron* using morphological characters and partially confirmed Mayo's evolutionary hypothesis.

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Table 1
List of species used in the study, voucher material and natural distribution in biomes. Herbarium acronyms according to Thiers (constantly updated). JB = Jardim Botânico.

Subgenus	Species	Voucher (Herbarium)	Source – Institution	Biomes Distribution
<i>Meconostigma</i>	<i>H. cochinchinensis</i> Engler	Calazans 36 et al. (RB)	Cultivated – JB Inhotim	Asian Tropical Forest
	<i>P. adamantinum</i> Mart. ex Schott	Bastos 20 et al. (RFA)	Cultivated – JB Plantarum	Campo rupestre
	<i>P. bipinnatifidum</i> Schott ex Endlicher	Calazans 4 (RB)	Cultivated – JB Rio de Janeiro	Caatinga, Cerrado, Atlantic Forest
	<i>P. brasiliense</i> Engler	Bastos 21 et al. (RFA)	Cultivated – JB Plantarum	Cerrado, Atlantic Forest
	<i>P. corcovadense</i> Kunth	Pellegrini 154 (RB)	Field work – Rio de Janeiro	Atlantic Forest
	<i>P. dardanianum</i> Mayo	Calazans 22 et al. (RB)	Cultivated – JB Inhotim	Cerrado
	<i>P. goeldii</i> G.M. Barroso	Calazans 72 et al. (RB)	Field work – Amazonas	Amazonia
	<i>P. lundii</i> Warm.	Calazans 41 et al. (RB)	Cultivated – JB Inhotim	Cerrado
	<i>P. mello-barretoanum</i> Burle-Marx ex G.M. Barroso	Morais 51 (R)	Cultivated – JB Rio de Janeiro	Cerrado
	<i>P. paludicola</i> E.G. Gonç. & Salviani	Calazans 38 et al. (RB)	Cultivated – JB Inhotim	Atlantic Forest
	<i>P. petraeum</i> Chodat & Vischer	Calazans 28 et al. (RB)	Cultivated – JB Inhotim	Cerrado
	<i>P. saxicola</i> K. Krause	Calazans 50 & Morais (RFA)	Field work – Bahia	Campo rupestre
	<i>P. solimoesense</i> A.C. Sm.	Oliveira et al., 57 (INPA)	Field work – Amazonas	Amazonia
	<i>P. speciosum</i> Schott ex Endlicher	Morais 38 (RFA)	Field work – Rio de Janeiro	Atlantic Forest
	<i>P. stenolobum</i> E.G. Gonç.	Bastos 22 et al. (RFA)	Cultivated – JB Plantarum	Atlantic Forest
	<i>P. tweedianum</i> Schott	Calazans 37 et al. (RB)	Cultivated – JB Inhotim	Cerrado
	<i>P. uliginosum</i> Mayo	Calazans 19 et al. (RB)	Cultivated – JB Inhotim	Campo rupestre
	<i>P. undulatum</i> Engler	Calazans 7 (RB)	Cultivated – JB Rio de Janeiro	Atlantic Forest
	<i>P. venezuelense</i> G.S. Bunting	Soares 513 (INPA)	Field work – Amazonas	Amazonia
	<i>Philodendron</i>	<i>P. williamsii</i> J.D. Hooker.	Calazans 54 & Morais (HUEFS)	Field work – Bahia
<i>P. crassinervium</i> Lindl.		Calazans 13 et al. (RFA)	Field work – Rio de Janeiro	Atlantic Forest
<i>P. pedatum</i> (Hook.) Kunth		Morais 47 (RFA)	Field work – Rio de Janeiro	Amazonia, Caatinga, Cerrado, Atlantic Forest
<i>Pteromischum</i>	<i>P. oblongum</i> (Vell.) Kunth	Morais 48 (RFA)	Field work – Rio de Janeiro	Atlantic Forest

Methods

Taxon sampling

The ingroup comprised 19 out of the 21 currently recognized species of subgenus *Meconostigma* (Gonçalves and Salviani, 2002; Croat et al., 2002), two species of subgenus *Philodendron* and one species of subgenus *Pteromischum*. *Philodendron petraeum* Chodat & Vischer, a species currently synonymized in *P. tweedianum* Schott, was included as a distinct species. *Philodendron leal-costae* Mayo & G.M. Barroso and *P. xanadu* Croat, Mayo & J. Boos were not found in flower and therefore were excluded from the analysis. We used *Homalomena cochinchinensis* Engl. as the outgroup, based on the affinities of *Philodendron* and *Homalomena* proposed in the literature (Gauthier et al., 2008; Sakuragui, unpublished data).

The specimens analyzed were obtained from natural populations in the field or from living collections. The inflorescences were preserved in spirit collection (70% ethanol) at the time of collection. Details of the voucher specimens are given in Table 1.

Morphological dataset

We used 59 morphological characters (18 vegetative and 41 reproductive, including anatomical characters – electronic Appendix 1) to construct a matrix (electronic Appendix 2) following the morphological concepts used by Mayo (1989, 1991). For anatomical characters, freehand semi-permanent sections of gynoecium were obtained, cleared in a 50% sodium hypochlorite solution, stained with astra blue and safranin (Kraus and Arduin, 1997), and mounted under a coverslip in 50% glycerin for light microscope viewing.

Except for character 59, all characters were unordered and equally weighted. Character 59 (locule number) is a meristic and polymorphic character and was treated with GFC, following the method of Smith and Gutberlet (2001). In this method, the quantitative character is divided into subcharacters (in the matrix these are represented by characters 59–105) that correspond with each character state and the frequency of specimens for a given

subcharacter is described with frequency bins. The overall effect is that cumulative frequency distributions of character states per taxa are constructed for each character. The frequencies were calculated and codified using CodeThis! software (Gutberlet et al., 2000).

Phylogenetic analysis

The cladistic analysis with maximum parsimony was conducted using PAUP* 4.0b10 (Swofford, 2002) and a heuristic search with 1000 random taxon additions and tree bisection–reconnection (TBR) branch swapping. The consistency (CI) and retention indexes (RI) were calculated. The statistical support for each branch of the cladogram was evaluated by bootstrap (BS) analyses with 500 random addition replication. The characters were optimized on the strict and majority-rule (50% values) consensus trees using Mesquite 2.5 (Maddison and Maddison, 2008).

Results

Gynoecial subtypes in *Philodendron* subg. *Meconostigma*

Six morphological types of gynoecium (A–F) were previously recognized by Mayo (1989). The author found that type A was unique to subgenus *Meconostigma*, presenting as diagnostic characters a well developed compitum and stylar lobes. The analysis of the gynoecium allowed us to recognize three subtypes within type A basic morphology. Subtype A1: stylar body absent and stylar canals short, central stylar dome absent, and compitum deep (*P. adamantinum*, *P. dardanianum*, *P. speciosum*, and *P. williamsii*; Fig. 1a); subtype A2: undeveloped stylar body present with long stylar canals, central stylar dome absent, and compitum shallow (*P. corcovadense*, *P. lundii*, *P. paludicola*, *P. saxicola*, *P. stenolobum*, *P. tweedianum*, and *P. uliginosum*; Fig. 1b); subtype A3: well developed stylar body present with stylar canals long, central stylar dome present and compitum shallow (*P. brasiliense*, *P. bipinnatifidum*, *P. goeldii*, *P. mello-barretoanum*, *P. petraeum*, *P. solimoesense*, *P. undulatum*, and *P. venezuelense*; Fig. 1c).

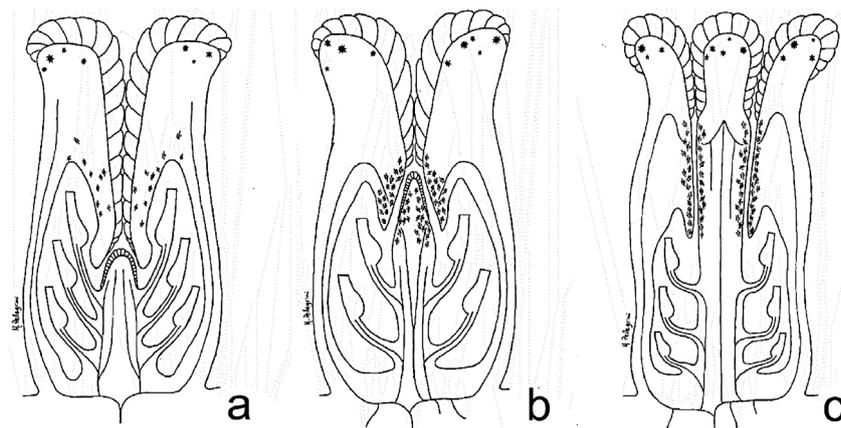


Fig. 1. Gynoecial subtypes in *P.* subgenus *Meconostigma*. (a) Subtype A1; (b) Subtype A2; (c) Subtype A3. Asterisk represents druses, triple stripe represents raphides, hatched lines represent stigma papillae. Raphides are generically represented, may be present or absent depending on the species.

Morphological phylogenetic analysis

A total of 346 trees were recovered as most-parsimonious using the traditional cladistic analyses with a CI of 0.41 and RI of 0.57. After using the GFC method, four trees were recovered as most-parsimonious, with a CI of 0.41 a RI of 0.56. From 105 studied characters, 75 were parsimony-informative. The strict consensus tree and the majority-rule consensus tree (Fig. 2a–b) showed that the monophyly of the subgenus *Meconostigma* was recovered in 100% of the trees. The synapomorphies supporting the clade are: spathe thickened, well developed sterile intermediate zone, presence of stylar lobes, and axial vascular system independent of the funicle supply. In both trees, the Cerrado *s.l.* species *P. brasiliense* and *P. uliginosum* were found in basal position (Figs. 2 and 3). The synapomorphy for the species in Clade A was a constriction in the spathe and for the ones in Clade B the three characters inconspicuous intravaginal squamules, non-entire leaf margin, and resin canals present in the spadix axis aerenchyma (Fig. 2a). The stylar central dome is absent

for all species in Clade C (Fig. 2b). All species in Clade D show absent stylar body and deep compitum (Fig. 2b). The subtype A1 gynoecium is synapomorphic for the species in Clade D. Subtype A2 occurs in the basal position represented by *P. uliginosum* (Fig. 3).

Discussion

The present report fills the gap concerning the evolutionary history of the subgenus *Meconostigma* of *Philodendron*, an interesting study model of the diversification of Neotropical plants. Our phylogenetic reconstruction suggests that this subgenus is monophyletic and originated in open areas of the Cerrado biome *s.l.* We also identified three subtypes within type A of gynoecium originally described by Mayo (1988), a finding that when combined with the phylogenetic reconstruction results allowed us to propose a hypothesis of floral evolution in the group. The findings and the proposed hypothesis are discussed below.

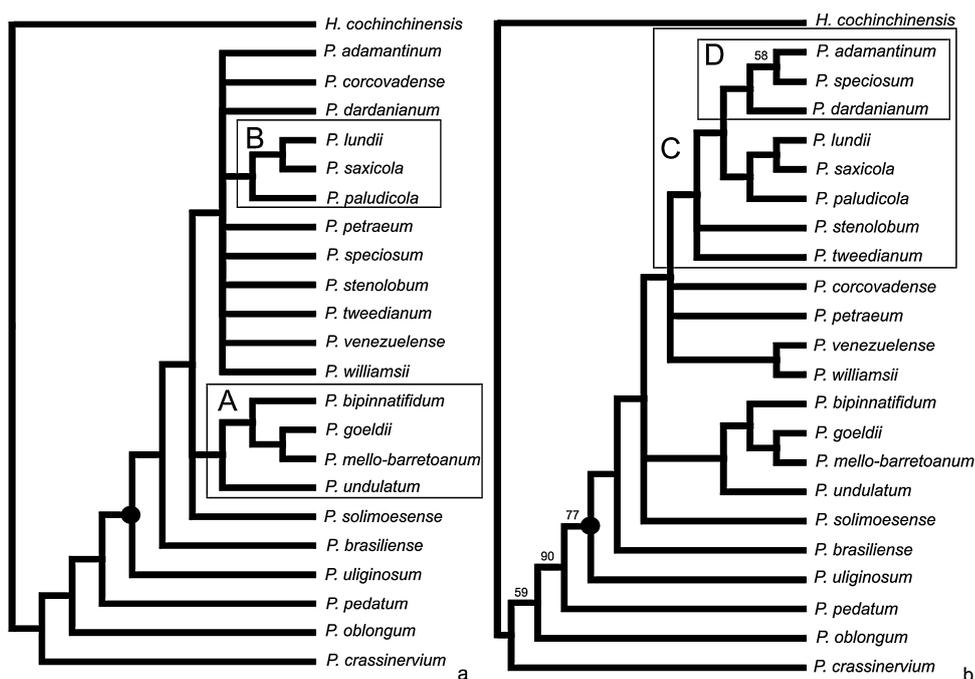


Fig. 2. Consensus of four most-parsimonious trees and the four minor clades within *P.* subgenus *Meconostigma*. (a) Strict consensus tree showing clades A and B; (b) Majority-rule consensus tree showing clades C and D. Dark circle showing *P.* subgenus *Meconostigma* monophyly. Numbers above branches are bootstrap values >50.

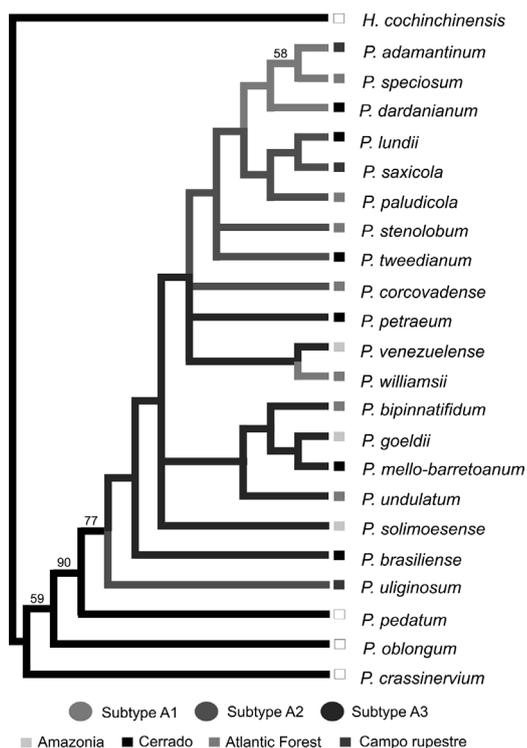


Fig. 3. Gynoecial subtypes and biomes distribution on the majority-rule consensus tree. Numbers above branches are bootstrap values >50.

Since the first taxonomic studies in Araceae, *P.* subg. *Meconostigma* has always been regarded as a well-defined group within the genus. The subgenus has also been proposed as a natural group (Mayo, 1991). Preliminary molecular data of Gauthier et al. (2008) indicated its monophyly, however only six species were sampled. Our phylogenetic analysis establishes the monophyly of the group supported by four morphological synapomorphies, all previously highlighted by Mayo (1991) as diagnostic characters of the subgenus.

The phylogenetic trees recovered show *P. brasiliense* and *P. uliginosum*, respectively from campos rupestres and cerrado, in basal position. These results agree with Mayo's ideas on the origin of *P.* subg. *Meconostigma* in open areas of Eastern Brazil. In addition, the basal position of these species corroborate the suggestion that campos rupestres provided the first open habitats in Eastern Brazil, followed later by the Cerrado (Antonelli et al., 2010). Contradicting Mayo's hypothesis, our morphological analysis suggests that the Amazonian species are not the most derived ones. The three Amazonian species emerged in three different lineages, indicating that the occupation of the Amazon Basin occurred as isolated events during the evolution of subgenus *Meconostigma*.

Although vegetative characters are considered extremely variable and little informative in morphological phylogenies, two of the synapomorphies of Clade B are vegetative: inconspicuous intravaginal squamules and non-entire leaf margin.

Floral characters are believed to be more conservative because their shorter duration reduces exposure to selection pressure (Sivarajan, 1991). The other four synapomorphies of the minor clades are linked to reproductive structures and three of them are gynoecial.

The spathe plays an important role in the reproductive biology of the group, because the lower part can serve as a warm pollination chamber where the pollinators can feed, rest and mate (Gibernau et al., 1999; Gottsberger et al., 2013). The degree of constriction in the spathe could indicate an adaptation as part of a reproductive

strategy, offering a more or less delimited, darker and warmer pollination chamber. Except for *P. brasiliense*, *P. uliginosum* and species of clade A, all the other *P.* subg. *Meconostigma* species have more open spathes, admitting more light, which could be less attractive to pollinating beetles that are usually photophobic (Gibernau et al., 1999).

Except for Clade D, the gynoecium subtypes were not recovered as synapomorphies of the clades. Subtype A2 is basal to subtypes A1 and A3, and could therefore represent the ancestral gynoecium in the subgenus. It is characterized by a deep compitum without central dome, short stilar lobes and long stilar canals. The existence of a compitum is associated with an even distribution of the pollen tubes to the locules, allowing pollen tube growth to select any flower carpels with equal probability (Endress, 1982). Thus, the gynoecium with deep compitum (Subtype A1) presents a large investment in the accessibility of ovules to fertilization. In the subtype A3, the compitum becomes a more limited space with the presence of a central dome. This suggests a reduction in the possibilities of selection and growth of the pollen tubes. However, the central dome represents an extension of the floral apex (Mayo, 1989) and may represent an adaptation to increase pollen uptake. Therefore, a balance between pollen uptake and accessibility of the locules may have been decisive for driving gynoecium evolution in the subgenus *Meconostigma*.

The three new subtypes of gynoecium reported here are a taxonomic tool especially useful in the identification of species with similar vegetative morphology, such as the pair *P. brasiliense* and *P. uliginosum*, and the complex consisting of *P. bipinnatifidum*, *P. lundii*, and *P. mello-barretoanum*. Morphological analysis of gynoecium also provides support for a future reinstatement of *P. petraeum*, because this species shows morphological features which easily differentiate it from *P. tweedianum*, under which it has been subsumed by previous authors (Sakuragui, in prep.).

This study was able to test Mayo's earlier hypothesis of gynoecial evolution in *P.* subgen. *Meconostigma* and to reconstruct the evolutionary history of the subgenus using more complete sampling (90% of species) and more detailed morphological analysis. This widely distributed and relatively small chosen taxon facilitated the collection and observation of almost all species to build a robust morphological matrix within reasonable resource and time limitations. To the best of our knowledge, this is also the first report on morphological phylogeny of plants using the GFC, a method commonly employed in the reptile taxonomy and considered to be an efficient tool for the analysis of polymorphic characters (see Smith and Gutberlet, 2001; Lawing et al., 2008 and references therein to the theoretical basis and advantages of the method). Indeed, our results show that GFC provides significant improvement in the cladistic analysis, with a reduction of ca. 80× in the equally most parsimonious trees universe. This supports the Wiens' statement (1995) that polymorphic characters can contain significant phylogenetic information and should be appropriately treated in morphological phylogenies, and not eliminated from the analysis.

Although large molecular studies of patterns and processes have been conducted with the Neotropical flora (Hughes et al., 2013 and references therein), detailed yet robust morphological studies that can be elucidative to the taxonomy and phylogeny of these plants are lacking. Such studies would be welcome in the construction of a grand scenario of plant occupation in South America and may shed light into the patterns of Neotropical plant diversification.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.flora.2013.12.004>.

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