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RESEARCH

Phylogenetics of Brazilian phyllocladiferous *Phyllanthus* (Phyllanthaceae): a new section exclusive from the Atlantic Rain Forest, with morphological and molecular support

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Abstract

The latest phylogenetic and taxonomic studies emphasizing *Phyllanthus* (Phyllanthaceae) have significantly altered the relationships between its taxa. In this work, we inferred a phylogeny for the Brazilian phyllocladiferous species of *Phyllanthus*, traditionally included within *Phyllanthus* sects. *Choretropsis* and *Xylophylla* from eastern Brazil and Caribbean, respectively. Our analysis demonstrated that Brazilian phyllocladiferous species has no relation to *P*. sect. *Xylophylla* from the Caribbean, but sect. *Choretropsis*, as it currently stands, does not form a monophyletic group. Thus, phylloclades arose in *Phyllanthus* at least in five distinct clades. Most species of sect. *Choretropsis* are recovered among representatives of other groups (sects. *Antipodanthus* and *Phyllanthus* subsect. *Claussenianii*), but no macromorphological feature could be traced for the clades we recovered. One exception is a clade containing *P. dracenoides*, *P. gladiatus* and *P. pedicellatus*, species with dracenoid habit and exclusive to the humid dense forests along Atlantic Forest domain, for which we describe a new section.

Keywords Neotropics · *Phyllanthus* sect. *Choretropsis* · *Phyllanthus* sect. *Xylophylla* · Phylloclades

Introduction

Phyllanthus is one of the most numerous genus of Phyllanthaceae, with species occupying different habitats and with great morphological diversity, notably the phyllanthoid ramification, which is present in several of its species (Webster 1956). Wurdack et al. (2004), Samuel et al. (2005) and Kathriarachchi et al. (2005) recovered *Breynia*, *Glochidion*, *Reverchonia* and *Sauropus* within *Phyllanthus*, indicating the paraphyly of the later. This relationship was also recovered by Bouman et al. (2021), the most recent and comprehensive phylogenetic study proposed for the genus. This framework served as base for a new classification for the tribe Phyllantheae (Bouman et al. 2022) aiming to achieve the monophyly of *Phyllanthus*, splitting it in ten genera, considering basically molecular data. Some of them are very difficult to be morphologically recognized as belonging to different genera.

As it is currently circumscribed, *Phyllanthus* sensu stricto now comprises 213 species restricted to the American continent and the Caribbean (Bouman et al. 2022). Among the *Phyllanthus* s.str., some species are remarkable for the presence of phylloclades and reduced leaves, present only in the early stages of the plant, or completely absent. These species were initially recognized as the distinct genus *Xylophylla* (Linnaeus 1771), which were later recognized as a subgenus or section within *Phyllanthus* (Persoon 1807 and Baillon 1858, respectively). Müller Argoviensis (1863) described *Phyllanthus choretroides* and placed it in a new section, *P.* sect. *Chroretropsis*, distinguished from *P.* sect. *Xyllophylla*, based on the shape of the phylloclades (cylindrical versus flattened, respectively).

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The Brazilian *Phyllanthus gladiatus* and *P. klotzschianus*, which bear flattened phylloclades, were then transferred to *P.* sect. *Choretropsis* by Webster (1958a,b), who proposed significant changes to the delimitation of both phyllocladiferous groups within the genus, restricting *P*. sect. *Xylophylla* to the Caribbean and *P.* sect. *Choretropsis* to Brazil. This new classification was also based on morphology of pollen grains, type of anther opening (reticulate pollen grains and deeply emarginate anthers in *P.* sect. *Choretropsis* versus areolate pollen grains and anthers with more or less horizontal dehiscence in *P.* sect. *Xylophylla*), and branching pattern (pinnatiform in *P.* sect. *Choretropsis* versus bipinnatiform in *P.* sect. *Xylophylla*).

Santiago et al. (2006), organized the species of *P*. sect. *Choretropsis* in two subsections, according to phylloclade morphology: subsect. *Applanata* for the flattened phylloclades species, and subsect *Choretropsis*, for the species with cylindrical/subcylindrical phylloclades. Additionally, three new phyllocladiferous species have been described and placed in the section based solely on morphological characters (Orlandini et al. 2020, 2021, 2022). At the subgeneric level, Bouman et al. (2022) classification points the phyllocladiferous species into subgenus *Phyllanthus* (*P*. sect. *Choretropsis* and the new section here proposed) and subgenus *Xylophylla* (*P*. sect. *Xylophylla*).

In the work by Bouman et al. (2021), *Phyllanthus* sect. *Choretropsis* was recovered within a polytomy comprising the sects. *Antipodanthus*, *Loxopodium* and *Phyllanthus*. However, sect. *Choretropsis* is represented in the phylogenies published so far only by *P*. *klotzschianus*. Therefore, the sampling adopted in these works could not allow either testing the monophyly of *P.* sect. *Choretropsis* or any of the subsections proposed by Santiago et al. (2006). Here we present a phylogenetic framework for *Phyllanthus* sect. *Choretropsis* with a wider sampling effort, aiming to test the monophyly of *P.* sect. *Choretropsis* and the subsections proposed for it by Santiago et al. (2006) and bringing light to the evolution of phyllocladiferous species within *Phyllanthus* s.str. and building foundations for future works involving the evolutionary history of the group.

Material and methods

Taxon sampling

We included ten species from *Phyllanthus* sect. *Choretropsis* for the ingroup, with more than one sample for those with wide distribution range, such as *P. klotzschianus*, following the recommendation by Naciri and Linder (2015). The only species of the group that were not sampled in this study are *P. edmundoi* and *P. goianensis*, which are known only by their types specimens.

To compose the outgroup, we included both representatives of the genera that compose *Phyllanthus* s.lat., with emphasis on *P*. sect. *Xylophylla*, as well as other genera from tribe Phyllantheae to allow a wider evaluation of the position of the species included in the ingroup given the uncertainties from the phylogenies published so far, which lack a sufficient representation covering the morphological variation found in the group. Finally, an accession of *Astrocasia neurocarpa* was used to root the trees, representing Wielandieae, the sister tribe of Phyllantheae according to other phylogenetic studies of the tribe (Kathriarachchi et al. 2006; Wurdack et al. 2004; Falcón et al. 2020; Bouman et al. 2021).

Thus, 22 accessions representing 14 from the total of 19 phyllocladiferous species of *Phyllanthus* are covered in this work, 11 of them newly generated. The complete list of samples, including those obtained from Genbank, as well as their vouchers and other informations, are presented in Appendix. We also provide a plate with photos of the new section proposed here (see Fig. 1).

DNA extraction and sequencing

DNA was extracted from fresh material dried in silica-gel (Chase and Hills 1991), or herborized material following the CTAB protocol by Tel-Zur et al. (1999) (Online Resource 1). We selected the internal transcribed spacer 1, 5.8S intron and the internal transcribed spacer 2 (hereafter referred as ITS) and the maturase K gene (hereafter referred as *matK*) based on variability and to complement the data generated by Kathriarachchi et al. (2006), Falcón et al. (2020) and Bouman et al. (2021). Due to its length, for *matK* we further analyzed previous alignments provided in the works cited above with Noisy (Dress et al. 2008) to look for more variable and informative regions that would optimize our amplification efforts given most of our samples were not successful to get a complete sequence of this region.

The ITS sequences were generated employing primers 17SE and 26SE (Sun et al. 1994). with an annealing temperature of 58 °C. For the partial *matK*, the primers used were 530R and 570F, according to Samuel et al. (2005), with annealing temperatures of 48 °C, resulting in a fragment of c. 706 bp. A detailed description of the volumes and amplification cycles for each region is presented in Table 1.

The length of the PCR fragments and inspection for multiple bands, especially in the case of ITS, were verified on a 1% agarose gel with electrophoresis. Sequencing was subsequently analyzed on either an ABI3500 and POP-7 polymer (Applied Biosystems, Forsters City, California, USA) using ABI BigDye Terminator V3.1 and the same primers employed for amplification at Helixxa Laboratory.

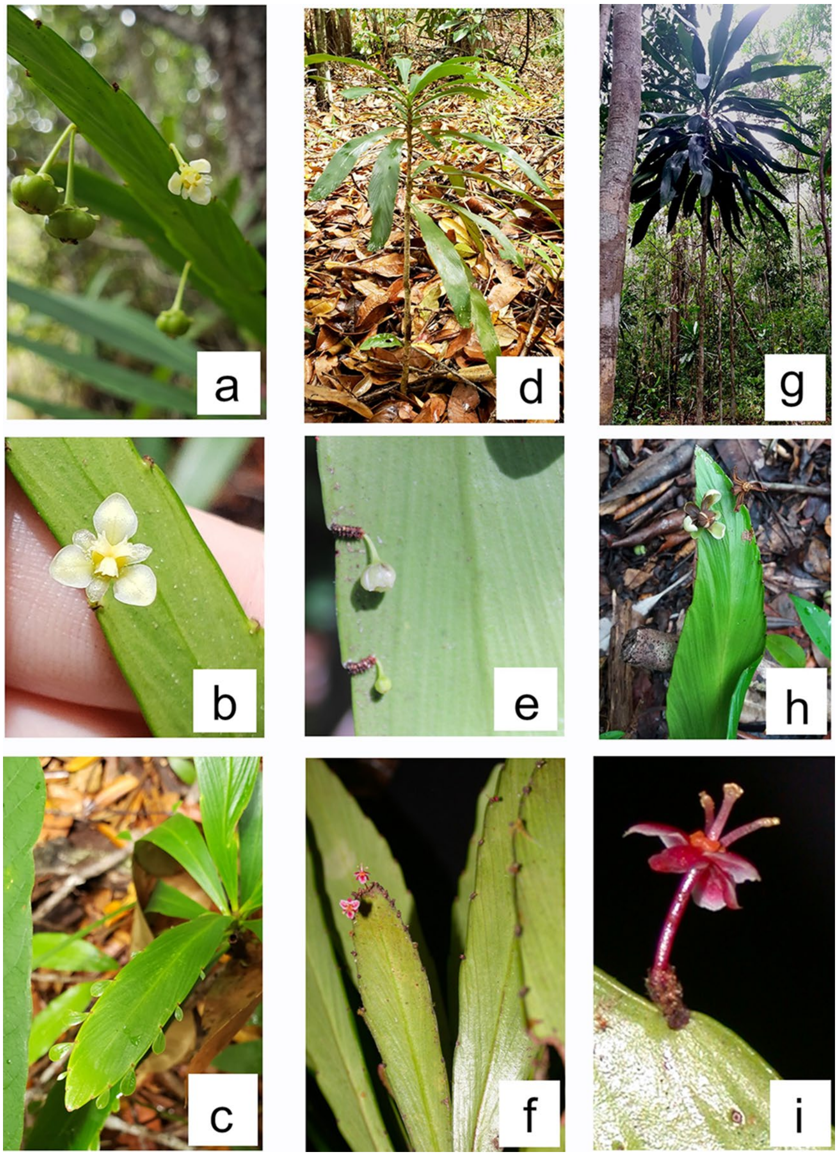

Fig. 1 Species of *Phyllanthus* sect. *Gladiatus*. **a** *Phyllanthus gladiatus*. Phylloclade with female flower and fruits; pedicel with 1.2 cm long. **b** *Phyllanthus gladiatus*. Female flower with flattened stigmas; phylloclade with 2 cm wide. **c** *Phyllanthus gladiatus*. Phylloclade with persistent leaves; leaves with 0.5 × 0.5 cm. **d** *Phyllanthus gladiatus*. Habit; young plant with 1 m height. **e** *Phyllanthus dracaenoides*. Vermiform cincinni with male flower; pedicel with 1 mm long. **f** *Phyllanthus pedicellatus*. Phylloclades with flowers; phylloclades with 20 cm long. **g** *Phyllanthus dracaenoides*. Habit; plant with 3 m height. **h** *Phyllanthus dracaenoides*. Female flower; flower with 1.5 cm long. **i** *Phyllanthus pedicellatus*. Male Flower; pedicel with 2 cm long. (Photos a–d: Priscila Orlandini; f, i: André Márcio Amorim; e, g, h: Lukas Halla Daneu)

Forward and reverse sequences were then analyzed in the Phred/Phrap/Consed package (Ewing and Green 1998; Ewing et al. 1998; Gordon et al. 1998), and contigs were assembled using phred 20 as the minimum quality standard.

Sequence alignment and phylogenetic analyses

Sequences were aligned using MAFFT online (https://mafft.cbrc.jp/alignment/server/) (Katoh et al. 2019; Kuraku et al. 2013) adopting the standard parameters. with posterior manual verification following the similarity criterion (Simmons

Table 1 Detailed description of the volumes and amplification cycles for each region

Primer	Foward or reverse primer	Sequence (5′–3′)	Annealing temperature (°C)	Volume (μ)	Source
trnK 570F	Foward	TCCAAAATCAAAAGAGCGATTGG	48	0.75	Samuel et al. (2005)
530R	Reverse	GTTCCAATTCCAATACTCGTGAAG	48	0.75	Samuel et al. (2005)
17SE	Foward	CGAATTCATGGTCCGGTGAAGTGTTC	58	0.75	Sun et al. (1994)
26SE	Reverse	TAGAATTCCCCGGTTCGCTCGCCGTTAC	58	0.75	Sun et al. (1994)

Table 2 Summary of individual marker datasets used in the analyses

	ITS	*matK*	Combined dataset
Number of samples	101	99	105
Aligned length (bp)	708	769	1477
Variable characters (%)	89 (12.57)	120 (15.60)	209 (14.15)
Parsimony-informative characters (%)	342 (48.30)	165 (21.45)	507 (34.32)
Missing data (%)	1.61	1.83	6.49

2004). Two datasets (ITS and *matK*) were analyzed individually and then incongruence between them was evaluated visually prior to combining the datasets. The visual analysis of inconsistencies was performed considering different terminals and their supports, and for the branches of interest in this work, no strong inconsistencies were found, these being restricted to some nodes with low support and that form polytomies.

Maximum Likelihood (ML) analyzes were conducted using RAxML 1.5b2 software (Stamatakis 2014), using the GTR + I + G nucleotide substitution model, and 10,000 replicates to evaluate clade support bootstraps. Bayesian inference (BI) analyzes were performed using MrBayes v.3.2.5 (Ronquist and Huelsenbeck 2003) with substitution models estimated through functions implemented since version 3.2 (Ronquist et al. 2012). Four independent runs were held, each with four simultaneous chains (one cold and three heated), for ten million generations, sampling every 1000th generation. Burn-in was initially set to 25% in MrBayes and then checked through Tracer v.1.6 software (Rambaut and Drummond 2007). For the Estimated Sample Size (ESS), we consider values above 200. The majority (50%) rule consensus was built after a burn-in a set of 25% for Bayesian inference. The trees generated in the ML and Bayesian inference analysis were analyzed and edited in FigTree version 1.4.4. software (Rambaut 2010).

For support values, we adopted ≥ 75 to ≤ 95 BS (Bootstrap Support) or ≥ 0.75 to ≤ 0.95 PP (Bayesian Posterior Probability) as moderate support and ≥ 95 or ≥ 0.95 as strong support. The generated files (individual and combined matrices, plus individual and combined ML and Bayesian trees) are available as Online Resource 2.

Results

A summary with total sequences, length, missing data and evaluation of variable characters for each dataset, as well for the combined dataset, is presented in Table 2. All species from our ingroup were recovered within a monophyletic *Phyllanthus* s.str. for both datasets, with high support on BI trees (0.98 PP for *matK*, see Fig. 2 and 0.95 PP for ITS, see Fig. 3), but low support on ML trees (47 BS for *matK*, and 42 BS for ITS). Therefore, our focus will be on the relationships within this group, especially in those clades where phyllocladiferous species were recovered, as the combined tree has low resolution on its backbone (see ahead).

Regarding phylogenetic relationships, while the backbone of *Phyllanthus* s.str. is completely unresolved for the *matK* (Fig. 2), as well as the relationships within the clades recovered for that dataset, the ITS tree shows more resolved clades, also with relatively better support values in general. The phyllocladiferous species are recovered in distinct clades in the *matK* tree with variable support on the ML tree (57–99 BS) but are all highly supported (1 PP) on the BI tree, making both *P.* sects. *Xylophylla* and *Choretropsis* paraphyletic. On the other hand, although the ITS tree (Fig. 3) recovered phyllocladiferous species in distinct clades as well as in the *matK*, species from *P.* sect. *Xylophylla* are recovered as monophyletic in this dataset, instead of two in the *matK* tree. Also, the clades are recovered with mostly high support values (1 PP/100 BS) on both analyzes of the ITS dataset.

Both individual datasets recovered the species of *Phyllanthus* sect. *Choretropsis* in four distinct clades. The first is composed by *P. chapadensis* (sampled only on the ITS dataset), *P. choretroides*, *P. klotzchianus*, *P. sarothamnoides* and *P. spartioides*. These species are recovered either as moderately supported (0.75 PP/85 BS) sister to *P. dawsonii* (*P.* sect. *Antipodanthus*) in the ITS tree, forming a clade with high support (1 PP/100 BS) (Clade 1), or as a polytomy in the *matK* tree, although the close relationship among all samples included in this polytomy are hightly supported (1 PP/99 BS). The clade 4, composed by *P. dracenoides*, *P. gladiatus* and *P. pedicellatus*, is recovered with high support (1PP/100BS) on the ITS tree, and as sister to *P. symphoricarpoides* (*P.* sect. *Pytorocladus*). On ther other hand, the *matK* tree recovered all these species as a polytomy with high (1 PP) or low (57 BS) support.

Phyllanthus flagelliformis (Clade 2) is recovered isolated from the other species of *P.* sect. *Choretropsis* in both datasets, and most closely related to the samples of *P. claussenii* (*P.* sect. *Phyllanthus* subsect. *Clausseniani*), either as a sister to these samples (ITS) or among them (*matK*). Lastly, *P. angustissimus* (Clade 3) was sampled only for the ITS dataset, in which it was recovered as sister to *P. caparaoensis* (*P.* sect. *Phyllanthus* subsect. *Clausseniani*).

Relationships within each of the clades containing species of *Phyllanthus* sect. *Choretropsis* are inconclusive on the *matK* tree due to polytomies, while species represented by two samples on the ITS tree are recovered together, with the exception of *P. klotzschianus* due to unresolved relationships.

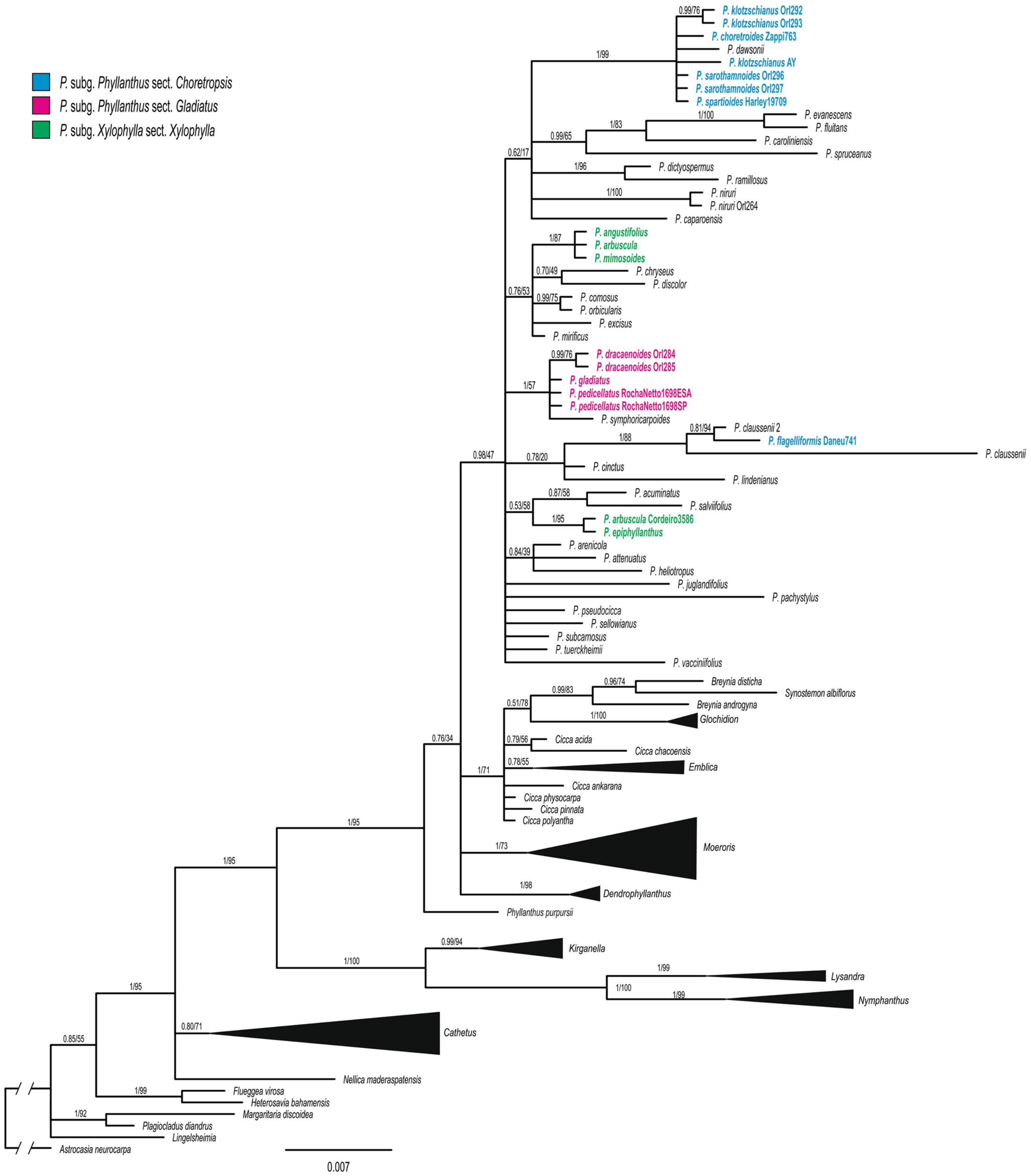

Fig. 2 Majority rule (50%) consensus tree obtained from Bayesian analysis of *matK* dataset. Values above branches represent Bayesian posterior probabilities/maximum likelihood bootstrap percentages. Samples of other genera from tribe Phyllantheae are show as collapsed clades. Species with phylloclades and their respective sections within *Phyllanthus* s.str. are colored following the legend on the upper left corner

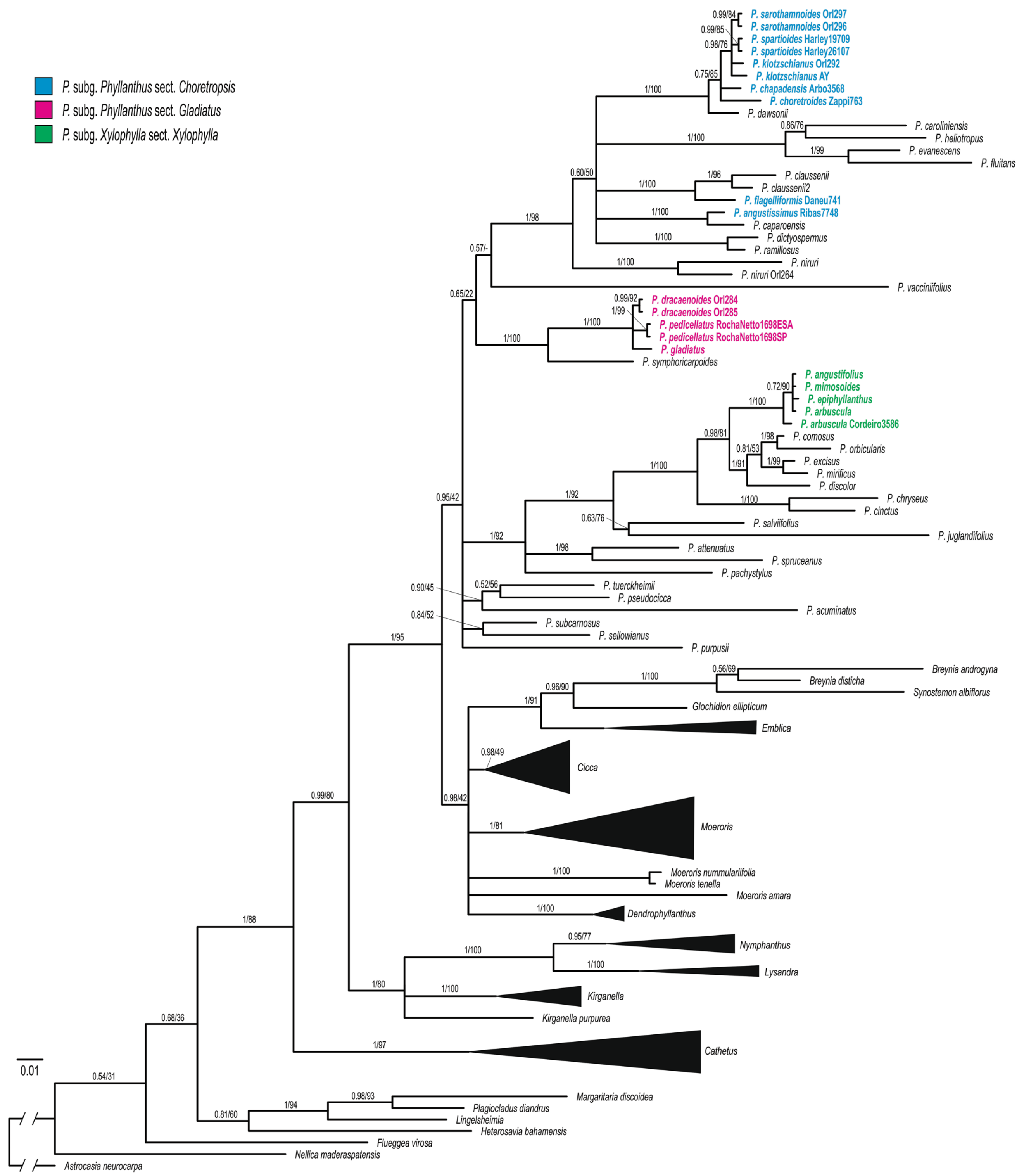

Fig. 3 Majority rule (50%) consensus tree obtained from Bayesian analysis of ITS dataset. Values above branches represent Bayesian posterior probabilities/maximum likelihood bootstrap percentages. Samples of other genera from tribe Phyllantheae are show as collapsed clades. Species with phylloclades and their respective sections within *Phyllanthus* s.str. are colored following the legend on the upper left corner

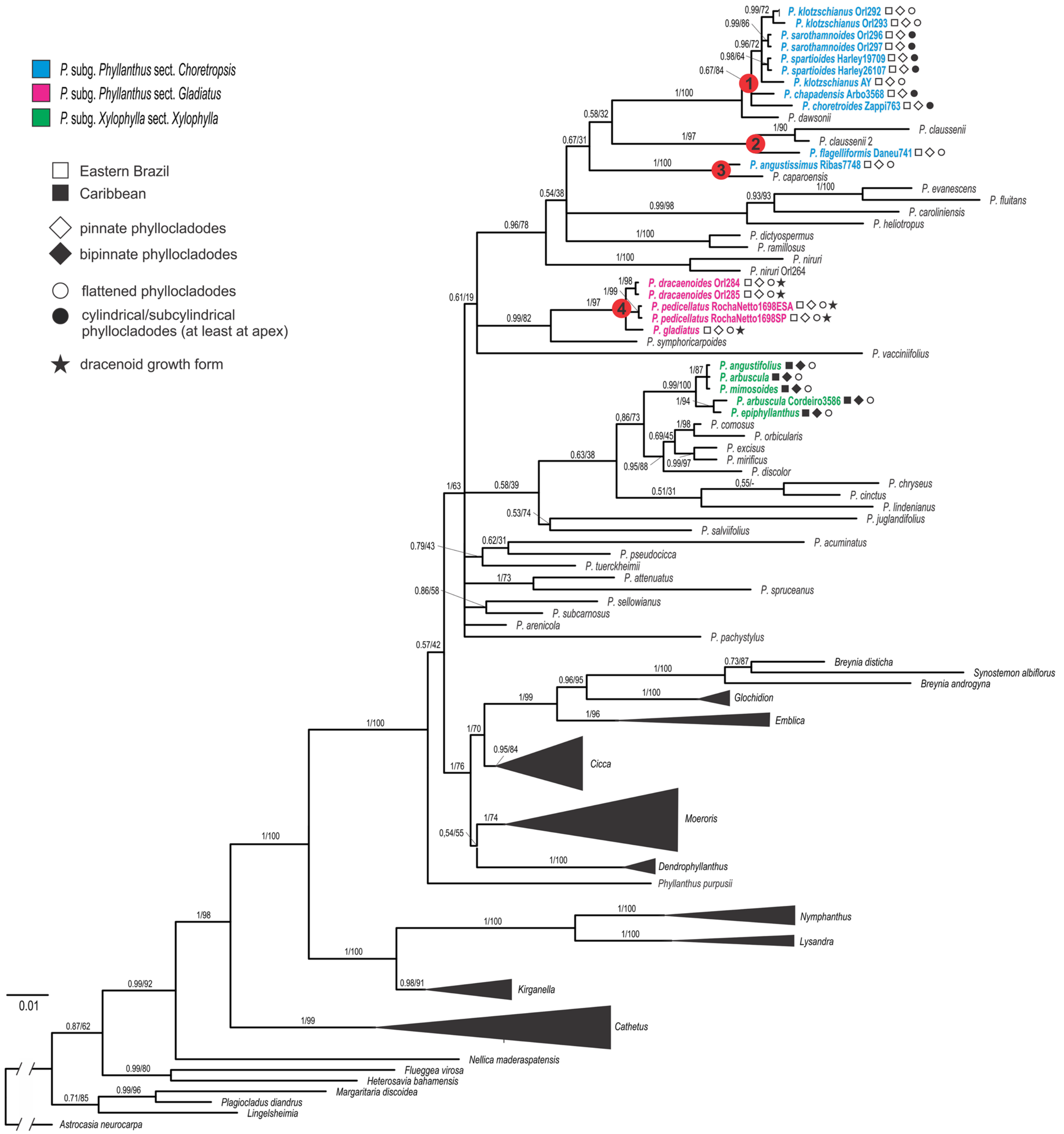

Fig. 4 Majority rule (50%) consensus tree obtained from Bayesian analysis of full combined nuclear (ITS) and chloroplast (*matK*) datasets. Values above branches represent Bayesian posterior probabilities/maximum likelihood bootstrap percentages. Samples of other genera from tribe Phyllantheae are show as collapsed clades. Species with phylloclades, their respective sections within *Phyllanthus* s.str., and morphological features are indicated following the legend on the upper left corner

Given the high number of polytomies found in the *matK*, many of them with low to moderate support on both ML and BI trees, we decided to combine the datasets for a total evidence tree (Fig. 4). In this tree, the monophyly of *P.* sect. *Xylophylla* is strongly supported (0.98 PP/100 BS), while the paraphyly of *P.* sect. *Choretropsis* is also indicated, with the species of this section recovered in four distinct clades, largely following what was described for the ITS tree. It is noteworthy, however, that the backbone of this tree is poorly resolved.

Discussion

Our results corroborate what was proposed by Webster (1958b) based on morphological and distribution data, and confirmed with molecular data by Kathriarachchi et al. (2006); Falcón et al. (2020), Bouman et al. (2021) and Bouman et al. (2022), regarding the distinction of the species bearing phylloclades in two main lineages: *Phyllanthus* sect. *Xylophylla* in the Caribbean, and *P.* sect. *Choretropsis* in eastern Brazil. Also, this distinction between these two lineages is supported by the organization of phylloclades: bippinate in the Caribbean species versus pinnate in the Brazilian species, although in rare cases we observed specimens of *P. klotzchianus* with bipinnate phylloclades.

Regarding sect. *Choretropsis*, with our wider sampling we found that although most species of the group are concentrated in the clade 1, the section is paraphyletic (Fig. 4) in their current circumscription. Therefore, phylloclades would have evolved in at least four lineages among the *Phyllanthus* species. Furthermore, the unexpected close relationship of *Choretropsis* species with *P. dawsonii* from Sect. *Antipodanthus* indicates the need of further evaluation, with a wider sampling of the other sections, to determine changes to the delimitation of infrageneric groups in *Phyllanthus* s.str.

The remaining species of Sect. *Choretropsis*, *P. angustissimus* and *P. flagelliformis*, sampled here for the first time, are also surprisingly most closely related to species of sect. *Phyllanthus* subsect. *Clausseniani*, but in two distinct clades (Clades 3 and 2, respectively), and both species apparently share no morphological similarities with species from the subsection to which they are sisters. Santiago et al. (2008) evaluated the anatomy of the phylloclades in *P.* sect. *Choretropsis* and found that *P. flagelliformis* is unique by having a combination of an open ring of vascular bundles following phylloclade shape and isodiametric photosynthetic cells. This same vascular bundle arrangement is also present in *P. edmundoi*, but we could not sample it in our phylogeny. *Phyllanthus flagelliformis* is also noteworthy among sect. *Choretropsis* because it has persistent leaves even in adult plants, unlike other species when in comparison with other species of the section. On the other hand, no anatomical feature of interest is indicated for *P. angustissimus*, and we could not sample it in the *matK* dataset. In the absence of anatomical data for the species of sect. *Phyllanthus* subsect. *Clausseniani* to which *P. angustissimus* and *P. flagelliformis* are sisters, no further suggestions may be addressed.

Our phylogenetic hypothesis does not support the division in subsections within sect. *Choretropsis* as proposed by Santiago et al. (2006). Such division is based mainly in the shape of the phylloclades in transversal section (terete or subterete in subsect. *Choretropsis* and flattened in subsect. *Applanata*) is not sustained since, although all species with terete/subterete phylloclades (*P. chapadensis*, *P. choretroides*, *P. sarothamnoides* and *P. spartioides*) were recovered within a same clade, wich also contains species with flattened phylloclades, not forming any grouping within it.

Phyllanthus dracaenoides, *P. gladiatus* and *P. pedicellatus* are noteworthy species with dracenoid habit, *i.e.,* presenting a monopodial main stem, in addition to lanceolate and flattened phylloclades concentrated at the apex, having an unique habit that looks like a *Dracaena* spp. These species also share a common habitat (humid dense forests along the Atlantic Forest domain), in which other species of sect. *Choretropsis* are usually not found (only *P. flagelligormis* and *P. klotzschianus* in seashore open vegetation as exceptions). Among these species, only *P. gladiatus* were analyzed by Santiago et al. (2006), but they indicated a distinct arrangement of the vascular tissue in the phylloclades of this species, with the presence of a central cylinder plus lateral bundles distinguishing it from the other representatives of sect. *Choretropsis*, who have a single, open or closed ring of vascular bundles. In addition to these features, they were recovered in a clade with high support in our phylogeny (1 PP/97 BS, see Fig. 4), allowing its segregation as a new section of *Phyllanthus* described here—*Phyllanthus* sect. *Gladiatus* (see formal taxonomy below). Our analyzes indicate *P. symphoricarpoides*, a species of sect. *Pityrocladus* from high elevations in Colombia and Peru, as sister to sect. *Gladiatus*. This species, however, does not share any apparent morphological feature with species of *sect. Gladiatus*, demanding further exploration.

At the subgeneric level, all phyllocladiferous species from Brazil belong to the *Phyllanthus* subgenus *Phyllanthus* according to Bouman et al. (2022). In this way, this subgenus includes the sections *Loxopodium*, *Antipodanthus*, *Choretropsis*, *Pityrocladus* (sensu Bouman et al. 2022) and here we also include the new section described here—*P.* sect. *Gladiatus*. Morphologically, no other species in the other sections has a dracenoid habit like the species of *P.* sect. *Gladiatus*, whose central stem is elongated like a stipe of varying height and whose phylloclades are all concentrated at the apex of the plant, which always presents monopodial growth. Furthermore, phylloclades are lanceolate (Radford et al. 1974), a morphological feature that is not present in other phyllocladiferous species. The other species with phylloclades of section *Xylophylla* do not occur in Brazil; however, they also do not have the dracenoid habit and the phylloclades are not lanceolate.

As the remaining species of *Phyllanthus* sect. *Chorestropsis* were recovered among species from *Phyllanthus* sects. *Antipodanthus*, *Choretropsis*, *Loxopodium* and *Phyllanthus* in a poorly resolved topology, we recommend that future works should focus on the reorganization of the taxonomy of these groups. These studies would benefit from a wider sampling of species in phylogenies, as well as investigation of micromorphological features. Such efforts could help elucidate relationships among these groups, which could not be better resolved with the more consistent dataset of Bouman et al. (2022) composed by five molecular markers. Improvements on the taxonomy of these groups that help their delimitation would also be crucial, as all these sections were recognized in the phylogenetic classification of tribe Phyllantheae by Bouman et al. (2022) in spite of their clear paraphyletic nature in previous works.

Conclusions

The species of *Phyllanthus* s.str. bearing phylloclades, circumscribed to two sections—*P.* sect. *Xylophylla* and *P.* sect. *Choretropsis*, emerged as five distinct lineages in our work. Consequently, the phylloclades evolved more times than previously thought. Although the distinction of the Caribbean (sect. *Xylophylla*) and the Brazilian phyllocladiferous species (sect. *Choretropsis*) is clear in our phylogeny and widely supported by morphological features, sect. *Choretropsis*, as currently delimited, is not monophyletic, and further studies involving sects. *Antipodanthus* and *Phyllanthus* subsect. *Clausseniani* are needed for understanding the limits of these groups, as all of them were recovered as paraphyletic in our work, as well as in previous ones. Exploration of micromorphological characters is valuable for this purpose.

As *Phyllanthus gladiatus* and two other recently described species (*P. dracenoides* and *P. pedicellatus*) with dracenoid habit clearly do not belong to sect. *Choretropsis*, we described a new section (sect. *Gladiatus*) that contains these three species that are confined to humid dense forest along the Atlantic Forest.

Taxonomic treatment (Nomenclatural changes)

Phyllanthus sect. *Gladiatus* P.Orlandini, I.Cordeiro & V.C.Souza, **sect. nov.**—TYPE: *Phyllanthus gladiatus* Müll. Arg.

–*Phyllanthus* sect. *Choretropsis* Müll.Arg. (1863: 4, 52). Santiago et al. (2006: 138), *pro parte*, excluding the type.

Phyllanthus sect. Gladiatus differs from the Phyllanthus sect. Choretropsis for having plants with a monopodial main stem (palm like plants), phylloclades always lanceolate to gladiate, and concentrated at the apex of the main stem—dracenoid habit—(versus plants with sympodial growth without an elongated axis, phylloclades never lanceolate or gladiate, and not concentrated at the apex of the main stem).

Included species (3): *P. dracaenoides* P.Orlandini & I.Cordeiro; *P. gladiatus* Müll.Arg; *P. pedicellatus* P.Orlandini, I.Cordeiro & V.C.Souza.

Appendix

Supplementary material. Voucher information for the samples included in this work, represented as follows: Taxon name, origin, collector and collection number, herbarium code, accession numbers for ITS and *matK*. Newly generated sequences are in bold.

Astrocasia: Astrocasia neurocarpa (Müll.Arg.) I.M.Johnst. ex Standl., United States (cultivated), *Wurdack 743* (DAV), AY936649, AY830261. *Breynia*: *Breynia disticha* J.R.Forst. & G.Forst., Netherlands, Utrecht Botanical Garden, *Bouman* and *Verwijs RWB024* (L), MN915814, MN916082. *Breynia androgyna* (L.) Chackrab. & N.P.Balakr., Chachoengsao, *VanWelzen 2006-4* (L), EU623563, EU643748. *Cathetus*: *Cathetus beckleri* (Müll. Arg.) I.Telford & J.J.Bruhl, Australia, *Hosking 2680* (NE), MN915861, MN916127. *Cathetus chrysanthus* (Baill.) R.W.Bouman, New Caledonia, *Munzinger* and *McPherson 796* (MO), AY936680, AY936585. *Cathetus fasciculata* Lour., China, Hong Kong, *Bouman* et al. *26* (L), MN915895, MN916154. *Cathetus kerstingii* (Jean F.Brunel) R.W.Bouman, Guinea, *Darbyshire 562* (WAG), MN915950, MN916189. *Cathetus myrtifolius* (Wight) R.W.Bouman, Sri Lanka, *Kathriarachchi* et al. *12* (K), AY936712, AY936616. *Cathetus petraeus* (A.Chev. & Beille) R.W.Bouman, Liberia, *Blyden 1037* (WAG), MN916026, MN916239. *Cathetus welwitschianus* (Müll.Arg.) R.W.Bouman, Tanzania, *Bidgood* et al. *1882* (K), AY936739, AY936640. *Cathetus wheeleri* (G.L.Webster) R.W.Bouman, Sri Lanka, *Kathriarachchi* et al. *33* (K), AY936740, AY936641. *Cicca*: *Cicca acida* (L.) Merrl., Thailand, *Samuel 702-19* (K), AY936666, AY936572. *Cicca ankarana* (Leandri) R.W.Bouman, *Ralimanana* et al. *663* (K), MN915851, MN916118. *Cicca chacoensis* (Morong.) R.W.Bouman, Paraguay, Morong, *Krapovickas* et al. *45628* (K), AY936677, AY936582. *Cicca physocarp*a (Müll.Arg.) R.W.Bouman, Gabon, *McPherson 16148* (WAG), MN916030, MN916243. *Cicca pinnat*a (Wight) R.W.Bouman, Zimbabwe, *Caster* and *Coates-Palgrave 2189* (K), AY936724, AY936626. *Cicca polyantha* (Pax) R.W.Bouman, Cameroon, *Breteler 1938* (WAG), MN916033, MN916246. *Dendrophyllanthus*: *Dendrophyllanthus cuscutiflorus* (S.Moore) R.W.Bouman, Singapore, Singapore Botanical Garden, *Yu 61* (L), MN915901, MN916299. *Dendrophyllanthus pancherianus* (Baill.) R.W.Bouman, New Caledonia, *McPherson* and *Munzinger 18264* (MO), AY936721, AY936623. *Emblica*: *Emblica officinallis* Gaertner, India, *Chase 14459* (K), AY936689, AY936594. *Emblica urinaria* (L.) R.W.Bouman, Philippines, *Majaducon 5750* (L), MN916071, MN916273. *Flueggea: Flueggea virosa* (Roxb. ex Willd.) Royle, Singapore, Singapore Botanical Garden, *Yu 64* (L), MN915825, MN916092. *Glochidion*: *Glochidion carinatum* (Beille)

R.W.Bouman, Cambodia, *Toyama* et al. *3212* (FU),_, MN916138. *Glochidion ellipticum* Wight, China, Yunnan, Xishuangbanna Tropical Botanical Garden, *Bouman* and *Yong 58* (HITBC), MN915826, MN916093. *Heterosavia*: *Heterosavia bahamensis* (Britton) Hoffm., Fairchild Tropical Garden (KW048), AY936749, AY830284. *Kirganelia: Kirganelia dinklagei* (Pax) R.W.Bouman, Gabon, *Bissiengou* (WAG), MN915908, MN916333. *Kirganelia flexuosa* (Siebold & Zuccarini) R.W.Bouman, China, *Chow 132* (L), MN915927, MN916174. *Kirganelia fuscolurida* (Müll.Arg.) R.W.Bouman, Madagascar, *Schatz 1737* (WAG), MN915934, MN916179. *Kirganelia microcarpa* (Benth.) Hurusawa and Tanaka, China, Yunan, Xishuangbanna Tropical Botanical Garden, *Bouman* and *Yong RWB056* (HITBC), MN915985, MN916207. *Kirganelia purpurea* (Müll.Arg.) R.W.Bouman, Namibia, *Ward* et al. *10442* (K), MN916042, MN916254. *Lingelsheimia: Lingelsheimia* sp., Madagascar, *Rabenantoandro* et al. *1115* (MO), AY936662, AY830272. *Lysiandra*: *Lysiandra calycina* (Labill.) R.W.Bouman, Australia, *Chase 2163* (K), AY936674, AY552446. *Lysiandra carpentariae* (Müll.Arg.) R.W.Bouman, Australia, *Clarkson* and *Neldner 8410* (L), MN915877, MN916140. *Margaritaria*: *Margaritaria discoidea* (Baill.) G.L.Webster, Mayotte, Comoro Island, Barthelat 1092 (K), AY936664, AY830274. *Moeroris*: *Moeroris amara* (Schumach. & Thonner) R.W.Bouman, Gabon, *Wieringa 8189* (WAG), MN915847, MN916114. *Moeroris boehmii* (Pax) R.W.Bouman, Kenya, *Wieringa 8841* (WAG), MN915865, MN916129. *Moeroris debilis* Klein ex Willd, Sri Lanka, *Kathriarachchi* et al. *15* (K), AY936686, AY936591. *Moeroris lokohensis* (Leandri) R.W.Bouman, Madagascar, *Ralimanana* et al. *414* (K), AY936704, AY936606. *Moeroris madagascariensis* (Müll.Arg.) R.W.Bouman, Madagascar, *McPherson 18925* (MO), MN915973, MN916317. *Moeroris nummulariifolia* (Poir.) R.W.Bouman, Madagascar, *Hoffmann* et al. *304* (K), AY936715, AY552444. *Moeroris sepialis* (Müll.Arg.) R.W.Bouman, Kenya, *Luke* et al. *7112* (K), AY936732, AY936633. *Moeroris tenella* Roxb., Comoro Island, *Hoffmann* et al. *372* (K), AY936733, AY936634. *Moeroris stipulata* Raf., Suriname, *Gietling 114* (WAG), MN916062, MN916269. *Nellica*: *Nellica maderaspatensis* (L.) Raf., Australia, *Hunter* et al. *1532* (K), AY936707, AY936609. *Nymphanthus*: *Nymphanthus glauscescens* (Baill. Ex Miquel) R.W.Bouman, China, Yunan, Xishuangbanna Tropical Botanical Garden, *Bouman* and *Yong 66* (HITBC), MN916040, MN916252. *Nymphanthus longifolius* (Miq.) R.W.Bouman, Thailand, *TRP5004102* (BK), AB550090,_. *Nymphanthus ruber* (Lour.) Spreng., China, Hainan, *Lee* et al. *2441* (CUHK), AY765298,_. *Nymphanthus watsonii* (Airy Shaw) R.W.Bouman, Malaysia, Peninsular part, *Yu 225* (L), MN916076, MN916278. *Phyllanthus: Phyllanthus acuminatus* Vahl, Venezuela, *Breteler 4238* (WAG), MN915837, MN916109. *Phyllanthus angustifolius* (Sw.) Sw., Germany, Bayreuth Botanical Garden living collection, *Lauerer 091479*, no voucher, MN915849, MN916116. *Phyllanthus angustissimus* Müll.Arg., Brazil, Minas Gerais, Serranópolis de Minas, *O.S. Ribas* and *J.M. Silva 7748* (MBM), **OP740340**,_. *Phyllanthus arbuscula* (Sw.) J.F.Gmel, Brazil, USP campus, *Cordeiro 3586* (SP), **OP740351**, **OP961939**. *Phyllanthus arbuscula* (Sw.) J.F.Gmel, Belgium, Meisse, living collection, *Reynders 19074182* (L), MN915855, MN916123. *Phyllanthus arenicola* Casar, Brazil, *Maas* and *Carauta s.n.* (U),_, MN916124. *Phyllanthus attenuatus* Miq., Venezuela, *Breteler 4696* (WAG), MN915856, MN916125. *Phyllanthus caparaoensis* G.L.Webster, Brazil, Espírito Santo, Santa Teresa, Orlandini et al. (ESA), **OP740341**, **OP961940**. *Phyllanthus caroliniensis* Walter, Guyana, *Jansen-Jacobs* et al. *4762* (K), AY936675, AY936580. *Phyllanthus chapadensis* P.Orlandini & M.J.Silva, Brazil, Goiás, Alto Paraíso de Goiás, *M.M. Arbo* et al. *3568* (MBM!), **OP740342**,_. *Phyllanthus choretroides* Müll.Arg., Brazil, Minas Gerais, Santana de Pirapama, *D.C. Zappi 763* (SPF!), **OP740348**, **OP961941**. *Phyllanthus chryseus* Howard, Cuba, *Van ee* et al. *387* (K), AY936681, AY936586. *Phyllanthus chryseus* R.A.Howard, Cuba, *T. Borsch* et al. 4280 (B, HAJB),_, LS975796. *Phyllanthus cinctus* Urb., Cuba, *Ekman 19166*, MN915892, MN916151. *Phyllanthus claussenii* Müll.Arg., Brazil, Minas Gerais, *Hatschbach 64117* (U), MN915894, MN916153. *Phyllanthus claussenii* Müll.Arg., Brazil, *Melo 2261* (HUEFS 29998), AY936683, AY936588. *Phyllanthus comosus* Urb., Cuba, *T. Borsch* et al. *4271* (HAJB), LS975727, LS975785. *Phyllanthus dawsonii* Steyerm., Brazil, *da Silva 2073* (DAV), MN915902, MN916159. *Phyllanthus discolor* Poepp. ex Spreng., Cuba, *Berazain, Rankin* and *Köhler 71878* (K), AY936688, AY936593. *Phyllanthus dictyospermus* Müll.Arg., Brazil, *Santos 5712* (DAV), MN915907, MN916162. *Phyllanthus dracaenoides* P.Orlandini & I.Cordeiro, Brazil, Bahia, Itacaré, *Orlandini* et al. *284* (ESA), **OP740335**, **OP961942**. *Phyllanthus dracaenoides* P.Orlandini & I.Cordeiro, Brazil, Bahia, Itacaré, *Orlandini* et al. *285* (ESA), **OP740336**, **OP961943**. *Phyllanthus epiphyllanthus* L., Belgium, Meisse, living collection, *Reynders 19840633* (L), MN915919, MN916169. *Phyllanthus evanescens* Brandegee, Nicaragua, *Stevens 32461* (MO), MN915921, MN916339. *Phyllanthus excisus* Urban, Cuba, *W.Greuter* et al. *28281* (B, HAJB, P-Gr), LS975746, LS975806. *Phyllanthus flagelliformis* Müll.Arg., Brazil, Bahia, Boa Nova, *L. Daneu 743* (CEPEC), **OP740349**, **OP961944**. *Phyllanthus fluitans* Benth. ex Müll.Arg., Netherlands, *Kathriarachchi 70* (WU), AY936693, AY936597. *Phyllanthus gladiatus* Müll.Arg., Brasil, Sergipe, Areia Branca, *Orlandini* (ESA), **OP740339**, **OP961945**. *Phyllanthus heliotropus* C.Wight ex Griseb, Cuba, *Maas* et al. *7762* (U), MN915946, MN916186. *Phyllanthus juglandifolius* Willd., Ecuador, *Holm-Nielsen 22881* (K), AY936699, AY936602. *Phyllanthus klotzschianus* Müll.Arg., Brazil, Bahia, Barra Grande, *Orlandini* et al. *292* (ESA), **OP740343**, **OP961946**. *Phyllanthus klotzschianus* Müll.Arg., Brazil, Bahia, Barra Grande, *Orlandini* et al. *293* (ESA),_,**OP961947**. *Phyllanthus klotzschianus* Müll.Arg., Brazil, Bahia, Mucugê, *M. Groppo Jr.* et al. *780* (K), AY936702, AY936605. *Phyllanthus lindenianus* Baill., Dominican Republic, *Fuertes 345* (K),_, MN916200. *Phyllanthus mimosoides* Sw., Belgium, Meisse living collection, *Reynders 19074179* (L), MN915989, MN916209. *Phyllanthus mirificus* G.L.Webster, Cuba, *T. Borsch* et al. *5021* (B, HAJB), LS975774, LS975835. *Phyllanthus niruri* L., Brazil, Espírito Santo, Santa Teresa, *Orlandini* et al. *264* (ESA), **OP740350**, **OP961948**. *Phyllanthus niruri* L., Costa Rica, *Cascante 1297* (K), AY936713, AY936617. *Phyllanthus orbicularis* Kunth, Borneo, *Eschevaria s.n.* (L), MN916012, MN916225. *Phyllanthus pachystylus* Urb., Cuba, *Van Ee* et al. *402* (K), AY936720, AY936622. *Phyllanthus pedicellatus* P.Orlandini, I.Cordeiro & V.C.Souza, Brazil, Minas Gerais, Santa Maria do Salto, *A. Campos-Rocha* and *N. Oleas 1698* (ESA), **OP740337**, **OP961949**. *Phyllanthus pedicellatus* P.Orlandini, I.Cordeiro & V.C.Souza, Brazil, Minas Gerais, Santa Maria do Salto, *A. Campos-Rocha* and *N. Oleas 1698* (SP), **OP740338**, **OP961950**. *Phyllanthus pseudocicca* Grisebach, Cuba, *P.A. González HFC 87681* (HAJB), LS975789, LS975820. *Phyllanthus purpusii* Brandegee, United States of America, Berkeley, cultivated from Mexico, *Breedlove 42730*, living collection Berkeley, no voucher, MN916043, MN916255. *Phyllanthus ramillosus* Müll.Arg., Brazil, *Arbo 6945* (DAV), MN916044, MN916256. *Phyllanthus salviifolius* Kunth, Ecuador, *Lewis* et al. *3500* (K), AY936730, AY936631. *Phyllanthus sarothamnoides* Govaerts & Radcl.-Sm., Brazil, Bahia, Palmeiras, *Orlandini* et al. *296* (ESA), **OP740347**, **OP961951**. *Phyllanthus sarothamnoides* Govaerts & Radcl.-Sm., Brazil, Bahia, Palmeiras, *Orlandini* et al. *297* (ESA), **OP740344**, **OP961952**. *Phyllanthus sellowianus* (Klotzsch) Müll.Arg., United Kingdom, RBG Kew, living collection, *Chase 14776* (K), MN916054, MN916263. *Phyllanthus spartioides* Pax & K.Hoffm., Brazil, Bahia, Rio de Contas, *R.M. Harley* and *D.J. Hind 26107* (SP), **OP740346**, **OP961953**. *Phyllanthus spartioides* Pax & K.Hoffm., Brazil, Bahia, Rio de Contas, *R.M. Harley* et al. *19709* (SPF), **OP740345**,_. *Phyllanthus spruceanus* Müll.Arg., Guyana, *Maas* and *Maas 474* (U), MN916061, MN916353. *Phyllanthus subcarnosus* C.Wright ex Griseb., Cuba, Mayotte, *T. Borsch* et al. *4707* (B, HAJB), LS975741, LS975800. *Phyllanthus symphoricarpoides* Kunth, *Cuatrecasas 18421* (U), MN916064, MN916321. *Phyllanthus tuerckheimii* G.L.Webster, Guatemala, *Mendez 8022* (DAV), MN916070, MN916272. *Phyllanthus vacciniifolius* (Müll.Arg.) Müll.Arg., Venezuela, *Hokche* et al. *854* (U), MN916073, MN916275. *Plagiocladus*: *Plagiocladus diandrus* (Pax & Drude) J.F.Brunel, Gabon, *de Wilde* and *de Wilde 11641* (WAG), AY936687,_. *Plagiocladus diandrus* (Pax & Drude) J.F.Brunel, Gabon, *Wieringa 2903* (WAG),_, AY936592. *Synostemon*: *Synostemon albiflorus* (F.Muell. ex Müll.Arg.) Airy Shaw, Australia, *Forster 32329* (NE), MN916077, MN916279.

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Author contributions P.O. designed and wrote the manuscript and carried out the laboratory activities. O.L.M.S. performed the bioinformatics analysis and prepared the figures. I.C. wrote and proofread the manuscript. V.C.S. wrote and proofread the manuscript.

Declarations

Competing interests This study was financed in part by the Coordination for the Improvement of Higher Education Personnel – Brazil (CAPES) – Finance Code 001, and the National Council for Scientific and Technological Development [processes 141913/2020-6 and 442162/2020-0]. PO also thanks The Mohamed bin Zayed Species Conservation Fund [grant 210528056] and IDEA WILD for support [grant number ORLABRAZ0121].

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