Plant Ecology and Evolution 156 (3): 352–364, 2023
https://doi.org/10.5091/plecevo.101657

RESEARCH ARTICLE

Molecular phylogeny and character-mapping support the synonymy of *Cordobia* and *Gallardoa* in *Mionandra* (Malpighiaceae)

Rafael F. de Almeida[1,2,3], Isa L. de Morais[1], Marco O.O. Pellegrini[2], Cassio van den Berg[3]

1 Universidade Estadual de Goiás, Quirinópolis, Goiás, Brazil
2 Royal Botanic Gardens, Kew, Richmond, Surrey, United Kingdom
3 Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil

Corresponding author: Rafael F. de Almeida (dealmeida.rafaelfelipe@gmail.com)

Academic editor: André Simões ♦ **Received** 8 February 2023 ♦ **Accepted** 21 August 2023 ♦ **Published** 4 October 2023

Abstract

Background and aims – *Cordobia*, *Gallardoa*, *Mionandra*, and *Peixotoa* (Stigmaphylloid clade, Malpighiaceae) are four small, closely related genera comprising shrubs or lianas endemic to South American savannas, dry forests, and temperate steppes. Their generic limits have significantly changed in the last century, and past molecular phylogenetic studies of Malpighiaceae have not tested the morphological characters of this group to identify synapomorphies supporting these clades/genera.
Material and methods – We sampled the monospecific *Cordobia* and *Gallardoa*, one species of *Mionandra* (out of 2 spp.), nine species of *Peixotoa* (out of 29 spp.), and a single species of *Camarea* and *Janusia* as outgroups. Bayesian and Maximum Likelihood analyses were carried out for this clade based on five molecular markers (i.e. ETS, ITS, PHYC, *matK*, and *ndhF*). A set of 16 macromorphological characters was scored and coded for identifying synapomorphies under the Maximum Likelihood criteria.
Key results – Our molecular phylogeny recovered *Peixotoa* as monophyletic and sister to the clade comprising *Cordobia* + *Gallardoa* + *Mionandra*, strongly corroborating previous phylogenetic studies of Malpighiaceae. The character-mapping analyses recovered two synapomorphies supporting the *Cordobia* + *Gallardoa* + *Mionandra* + *Peixotoa* clade, six supporting *Mionandra* s.l. (i.e. *Cordobia* + *Gallardoa* + *Mionandra*), and five supporting *Peixotoa*. *Cordobia* and *Gallardoa* are proposed as synonyms of *Mionandra*, alongside the necessary combinations, typifications, and identification keys.
Conclusions – Morphological characters related to the degree of connation of the stipules, leaf indumentum type, petiole length, inflorescence architecture, number of flowers per inflorescence, presence of a peduncle in the 1-flowered cincinni, sepal connation, posture and texture, petal width and margin integrity, staminode presence, shape and size, and the shape of the apex of styles were key in circumscribing these lineages. *Mionandra* s.l. is proposed and characterised, including a new combination, an identification key to distinguish its species, a distribution map, and taxonomy notes.

Keywords

Cono Sur, Malpighiales, *Peixotoa*, taxonomy, Stigmaphylloid clade, systematics

INTRODUCTION

Malpighiaceae has undergone unparalleled changes in its traditional classification in the last two decades due to the publication of several molecular phylogenetic studies (Cameron et al. 2001; Davis et al. 2001; Davis and Anderson 2010). Several new lineages were resolved, bringing to light taxonomic problems regarding the monophyly of its subfamilies (e.g. Byrsonimoideae W.R.Anderson, Banisterioideae A.Juss., and Malpighioideae A.Juss.), tribes (e.g. only Gaudichaudieae Horan. was recovered as monophyletic), and genera (e.g. *Banisteriopsis* C.B.Rob.,

Plant Ecology and Evolution is published by Meise Botanic Garden and Royal Botanical Society of Belgium.

Mascagnia (Bertero ex DC.) Bertero, *Stigmaphyllon* A.Juss., and *Tetrapterys* Cav.) (Cameron et al. 2001; Davis et al. 2001; Davis and Anderson 2010; Almeida et al. 2017, 2023; Almeida and van den Berg 2020, 2021). Subsequently, numerous authors have gradually proposed new genera and combinations to accommodate these newly identified relationships (Anderson 2006, 2011; Anderson et al. 2006; Almeida and van den Berg 2021). Although morphological characters were used to reconstruct the latest generic phylogeny for Malpighiaceae (Davis and Anderson 2010), no morphological characters were ever recovered and/or discussed for its newly resolved relationships (Almeida and van den Berg 2021, 2022).

The Stigmaphylloid clade is one of the new lineages recently resolved for Malpighiaceae, comprising several subclades (i.e. *Bronwenia* W.R.Anderson & C.Davis, *Diplopterys* A.Juss., *Stigmaphyllon*, *Banisteriopsis*, *Sphedamnocarpus* s.l., the Cordobioids, and the Aspicarpoids; Davis and Anderson 2010). The Cordobioids (herein referred to as the Peixotoid clade) comprise four small genera (i.e. *Cordobia* Nied., *Gallardoa* Hicken, *Mionandra* Griseb., and *Peixotoa* A.Juss.) of shrubs or lianas endemic to dry forests, savannas, and temperate steppes of South America (Davis and Anderson 2010; POWO 2023). Except for *Peixotoa*, which includes 29 species, the remaining genera of this clade are currently represented by just a single (*Cordobia* and *Gallardoa*) or two (*Mionandra*) accepted species (Anderson 1982, 2001; POWO 2023).

Their taxonomic history is quite convoluted, with most species of *Cordobia*, *Gallardoa*, and *Mionandra* having been treated under the latter. *Mionandra* was first described by Grisebach (1874) based on its bifid stipules (i.e. connate only at the base) and the presence of 5 fertile stamens alternating with 5 staminodes. This author only accepted two species (*M. argentea* Griseb. and *M. camareoides* Griseb.) as part of his new genus (Grisebach 1874). Kuntze (1898) described a new species of *Peixotoa*, *P. cordobensis* Kuntze, based on a specimen he collected from Córdoba, Argentina. It was readily synonymised by Niedenzu (1912) under the type specimen of his newly proposed genus *Cordobia* Nied., based on Grisebach's *Mionandra argentea*. Soon after, Chodat and Vischer (1917) added a new species to the recently monospecific *Mionandra*, *M. paraguariensis* Chodat, which was later combined as a variety of *M. camareoides* by Niedenzu (1928) in his revisionary study of Malpighiaceae. In the meantime, Hicken (1916) described another new genus related to *Mionandra* and *Cordobia*, the monotypic *Gallardoa* Hicken, comprising only *G. fischeri* Hicken. Finally, Niedenzu (1928) transferred *G. fischeri* to *Cordobia*, synonymising *Gallardoa* under the latter. Since then, contemporary taxonomists, such as William R. Anderson, have chosen to individually accept all three related genera, a decision followed by all major checklists and online databases to date (e.g. POWO 2023).

In this study, we reconstructed a molecular phylogeny of the Peixotoid clade based on three nuclear (ETS, ITS, and PHYC) and two plastid (*matK* and *ndhF*) genes to answer the questions: 1. Are *Cordobia*, *Gallardoa*, and *Mionandra* supported by morphological synapomorphies? 2. If not, would *Mionandra* s.l. (including *Cordobia* and *Gallardoa*) be supported by any morphological synapomorphies?

MATERIAL AND METHODS

Molecular analyses

We sampled 14 species in this study representing 12 species from the Peixotoid clade (out of 31 spp.), including the type species of all four genera and a single species of *Camarea* and *Janusia*, respectively, as outgroups, representing tribe Gaudichaudieae as their sister group (Supplementary material 1). For DNA extraction, we used leaf fragments from herbarium specimens deposited at Universidade Estadual de Feira de Santana (HUEFS). Genomic DNA was extracted using the CTAB 2× protocol, modified from Doyle and Doyle (1987). Protocols to amplify and sequence the ETS and ITS regions followed Almeida et al. (2017). PCR products were purified using PEG 11% (polyethylene glycol) and were sequenced directly with the same primers used for the PCR amplification. Sequence electropherograms were produced in an automatic sequencer (ABI 3130XL Genetic Analyzer) using Big Dye Terminator 3.1 (Applied Biosystems). Additional sequences from a single nuclear (PHYC) and two plastid (*matK* and *ndhF*) regions were retrieved from GenBank (Supplementary material 1). Sequences were edited using Geneious v.4.8.4 (Kearse et al. 2012) and aligned using Muscle v.1.0 (Edgar 2004), with subsequent adjustments in the preliminary matrices made manually by eye. The complete data matrices are available on Figshare (https://doi.org/10.6084/m9.figshare.23823105).

All trees were rooted in tribe Gaudichaudieae (*Camarea* + *Janusia*), the sister group of the Peixotoid clade, according to Davis and Anderson (2010). A combined analysis of plastid + nuclear regions was carried out using Bayesian Inference and Maximum Likelihood. We selected the model using hierarchical likelihood ratio tests (HLRT) with jModelTest2 (Darriba et al. 2012). Both model-based methods were conducted with a mixed model (GTR+G+I) and unlinked parameters, using MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003) and RAxML v.8 (Stamatakis 2014) implemented in RAxMLGUI2 (Edler et al. 2021). For the Bayesian inference, the Markov Chain Monte Carlo (MCMC) was run using two simultaneous independent runs with four chains each (one cold and three heated), saving one tree every 1,000 generations for a total of ten million generations. We excluded 20% of retained trees as 'burn in', and checked for a stationary phase of Likelihood, checking for ESS values higher than 200 for all parameters with Tracer v.1.7 (Rambaut et al. 2018). The clades' posterior probabilities (PP) were based on the majority rule consensus, using the stored trees, and calculated with MrBayes v.3.1.2. ML analyses were performed with 10 independent replicates, and default settings and support values were estimated using parametric bootstrapping with 500 replicates. Support values are presented on the branches, with bootstrap values shown above and posterior probabilities shown below the branches.

Morphological analyses

Macro-morphological characters were scored from protologues and specimens consulted in herbaria (ALCB, ASE, BHCB, CEN, CEPEC, CESJ, CGMS, COL, CVRD, CTES, EAC, ESA, F, FLOR, FUEL, FURB, G, HAS, HB, HCF, HEPH, HRB, HRCB, HUCP, HUEFS, HUEM, HUFG, HUFU, HUPG, HURB, IAC, IAN, ICN, INPA, IPA, JPB, K, MAC, MBM, MBML, MICH, MO, NY, OUPR, P, PACA, PEUFR, PMSP, R, RB, RBR, RFA, S, SI, SP, SPF, SPSF, UB, UEC, UFP, UFMS, UFMT, UFRN, UPCB, US, VIC, and VIES; herbaria acronyms according to Thiers 2023) for the 14 species sampled in this study. The indumentum terminology follows Niedenzu (1928), structure shapes follow Radford et al. (1974), inflorescence morphology and terminology follow Weberling (1965, 1989), and fruit terminology follows Spjut (1994) and Anderson (1981). Maps were made with ArcGIS v.9.3 (ESRI 2010) based on geographical coordinates obtained from GBIF (2023) and shapefiles obtained from WWF (2023). Character coding followed the recommendations for morphological analyses of Sereno (2007). Primary homology hypotheses (De Pinna 1991) were proposed for life form, leaf, inflorescence architecture, floral, fruit, and chromosomic characters. A total of 16 macromorphological characters were scored and coded (Supplementary materials 2, 3). All characters were optimised on the concatenated tree with the Maximum Likelihood function (mk1 model) using Mesquite v.2.73 (Maddison and Maddison 2010) and visualised with Winclada (Nixon 1999).

RESULTS

Phylogenetic analyses

The nuclear dataset represented 2,366 characters of the dataset, the plastid dataset represented 1,729 characters, and the combined plastid + nuclear dataset included 4,095 analysed characters. Topologies produced by BI and ML analyses, based on the individual nuclear and plastid datasets, did not exhibit incongruences among the topologies produced, so we performed a combined analysis of plastid + nuclear datasets (Fig. 1). The BI and ML analyses recovered a partially resolved tree with seven well-supported clades (> PP 0.95 / BS 65) at generic levels and six poorly-supported clades (< PP 0.95 / BS 65) within *Peixotoa* (Fig. 1). The Peixotoid clade was recovered as monophyletic and highly supported by both BI and ML analyses (1/100) comprising two major clades: the first highly supported represented by the specimens of *Cordobia* + *Gallardoa* + *Mionandra* (PP 1.0 / BS 100) and a second clade represented by the highly supported *Peixotoa* (PP 1.0 / BS 100) (Fig. 1). Combined plastid + nuclear datasets provided higher support for more clades than the results based on single plastid or nuclear datasets (Fig. 1A).

Character mapping

We recovered three synapomorphies (stipules connate at the base or up to the middle, 1-flowered cincinni lacking peduncles [i.e. sessile], and sepals revolute at apex) for the Peixotoid clade alongside the outgroups representing tribe Gaudichaudieae (Fig. 1B). The three synapomorphies recovered by us for tribe Gaudichaudieae (thyrsi, cincinnus peduncle present, and petals widely elliptic) are interpreted as sampling artefacts caused by the limited outgroup sampling of our study. These characters most likely represent plesiomorphic states in the family, but a study focusing on Malpighiaceae as a whole is necessary to address this issue.

The first clade recovered within the Peixotoid clade included the genera *Cordobia* + *Gallardoa* + *Mionandra* supported by six synapomorphies (sepals free at base, chartaceous, and entirely revolute, antherodes filiform and minute, apex of styles truncate to expanded) and a single homoplasy (1-flowered cincinni) (Fig. 1B). The second clade recovered within the Peixotoid clade comprised only species of *Peixotoa*, being supported by five synapomorphies (stipules completely connate, secondary arrangement of inflorescences [i.e. synflorescences] of umbels arranged in thyrsi, petals orbicular, petal margins dentate, and filaments of staminodes as long as fertile stamens) and two homoplasies (long petioles and leaves glabrescent) (Fig. 1B).

DISCUSSION

The Peixotoid clade was recovered as highly supported (PP 1.0 / BS 100) in our tree (Fig. 1A), corroborating previous phylogenetic studies of Malpighiaceae (Davis and Anderson 2010; Davis et al. 2014; Willis et al. 2014; Cai et al. 2016). This clade was also recovered with three morphological synapomorphies: partially to completely connate stipules, sessile 1-flowered cincinni, and sepals completely revolute. Partially connate stipules are not exclusive to the Peixotoid clade, with several genera from the distantly related Byrsonimoid clade also showing this character (Anderson 1981). In contrast, sessile 1-flowered cincinni are quite rare in Malpighiaceae, additionally found only in *Diplopterys* and *Coleostachys* A.Juss. (Almeida et al. 2020). However, the flowers in *Coleostachys* are completely sessile, lacking both peduncle and pedicel (Almeida and Hall 2016). Finally, sepals revolute at the apex are very common in Malpighiaceae (Almeida et al.

2020), but sepals completely distally revolute or involute along margins are only found in *Mionandra* s.l. (pers. obs.).

Morphologically, *Mionandra* s.l. (including *Cordobia* and *Gallardoa*) is well-circumscribed with six synapomorphies and a single homoplasy (Fig. 1B), being easily differentiated from *Peixotoa* by the sepals free at base, chartaceous and entirely revolute, antherodes filiform and minute, and apex of styles truncate to expanded. Since several morphological synapomorphies supporting *Mionandra* s.l. were recovered in our analysis, we have chosen to follow Grisebach's (1874) broader concept of *Mionandra* (including *Cordobia*) but also synonymising *Gallardoa* under it (see taxonomic treatment). For more information, see the identification key in the taxonomy

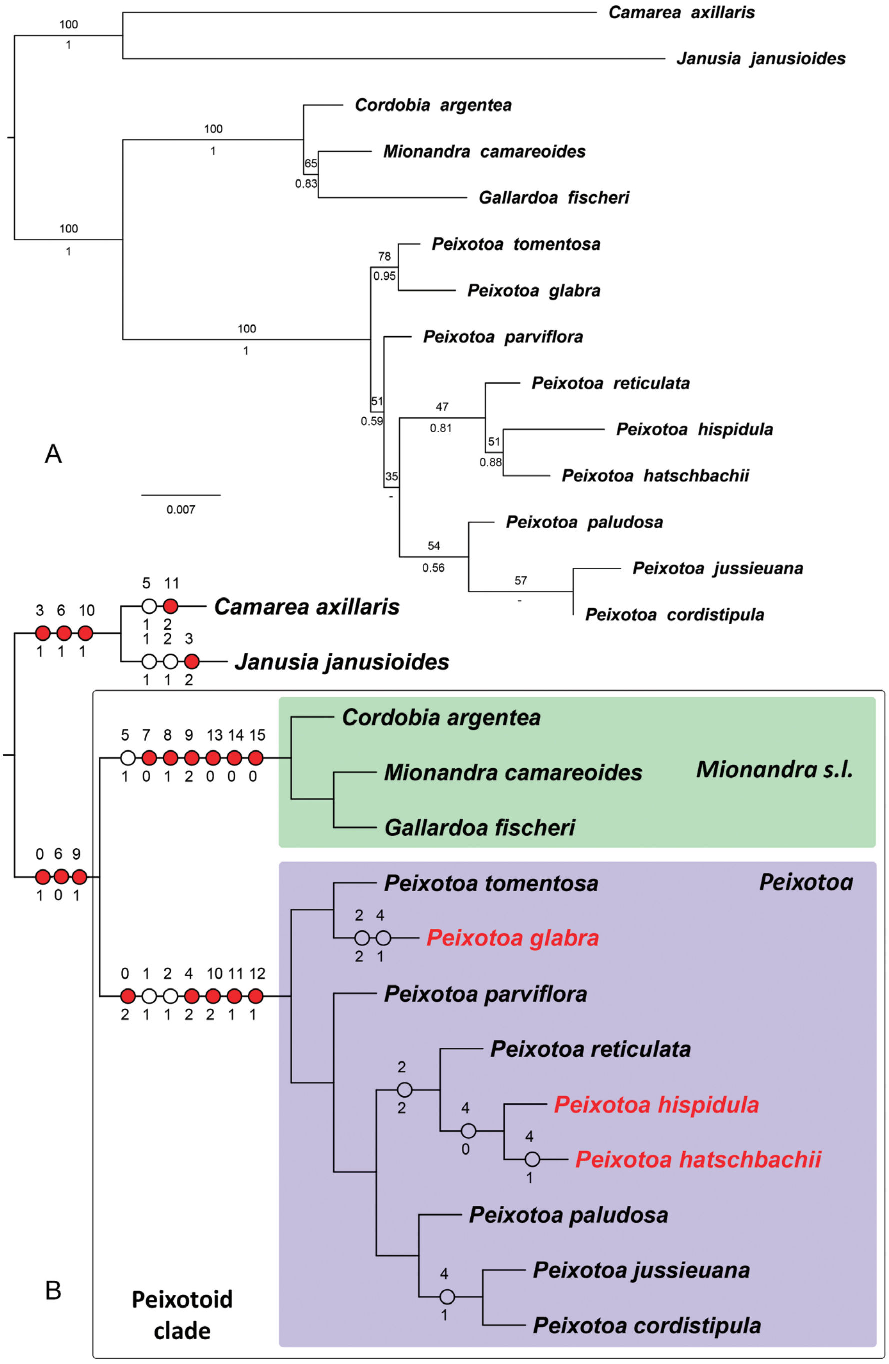

Figure 1. Phylogeny and character-mapping of the Peixotoid clade. **A**. Phylogram recovered from the Maximum Likelihood analysis showing bootstrap values above the branches and posterior probability values below the branches. **B**. Consensus tree showing the character-mapping summarisation resulting from the Mesquite Maximum Likelihood analysis and WinClada visualisation. Red circles represent synapomorphies, and white circles represent homologies. The numbers above the circles represent the character numbers, and those below the circles represent the character states provided in Supplementary materials 2 and 3. Terminals of *Peixotoa* in red represent *P.* sect. *Perinopsis* Nied. and those in black represent *P.* sect. *Balantiopsis* Nied.

Table 1. Diagnostic morphological characters differentiating both genera of the Peixotoid clade.

Character	*Mionandra*	*Peixotoa*
Habit	Erect or scandent to prostrate subshrubs	Erect to scandent shrubs or lianas
Stipules	Connate at base or up to the middle (i.e. bifid)	Completely connate (i.e. entire)
Leaves	Never reduced in the inflorescences	Reduced in the inflorescences
Petiole	Short	Long
Leaf blades	Hirsute-sericeous	Various but never hirsute-sericeous
Inflorescences	Solitary umbels	Umbels arranged in dichasia or thyrsi
Umbels	Sessile, 1-flowered	Pedunculate, 4-flowered
Bracts	Absent	Present
Bracteoles	Absent	Present
Sepals	Free, chartaceous, completely revolute or involute along margins	Connate at base, coriaceous, revolute only at apex
Petal limb	Narrowly elliptic to oblanceolate or obovate to widely obovate	Orbicular
Stamens	5	5
Staminodes	3–5	5
Antherodes	Filiform, minute	Globose, conspicuous
Style	Truncate to slightly expanded	Capitate
Fruits	Wings reduced, rarely dorsal wing well-developed, lateral wings free or fused at base	Wings well-developed, dorsal wing dominant, lateral and dorsal wings fused at base forming a basal crest

section, differentiating the genera of the Peixotoid clade accepted in this study.

Even though Anderson (1982) did not accept any infrageneric ranks in her monograph of *Peixotoa*, Niedenzu (1928) accepted two sections for this genus in his taxonomic revision for Malpighiaceae: *P.* sect. *Balantiopsis* Nied. and *P.* sect. *Perinopsis* Nied. The first was characterised by its leaves and stems pubescent and anthers with connectives 1-lobed (Niedenzu 1928). In contrast, the latter was characterised by glabrous leaves and stems, and anthers with connectives 2-lobed (Niedenzu 1928). Our analysis evidenced that the sections of *Peixotoa* proposed by Niedenzu (1928) are not monophyletic (Fig. 1B, *P. glabra*, *P. hatschbachii*, and *P. hispidula* in red represent *P.* sect. *Perinopsis*, while the remaining species in black represent *P.* sect. *Balantiopsis*) and further morphological studies must be carried out within this genus to shed light on any infrageneric classification to be proposed.

TAXONOMIC TREATMENT

Peixotoid clade

Diagnosis. Distinguished from the remaining genera of the Stigmaphylloid clade by its stipules connate, cincinni sessile and 1-flowered, and sepals completely distally revolute or involute along margins.

Notes. The Peixotoid clade currently comprises two monophyletic and morphologically well-circumscribed genera divided into a total of 32 species. *Peixotoa* is the largest genus of the two, currently with 29 species (Anderson 1982, 2001), with *Mionandra* comprising only four species (this study). As aforementioned, both genera share some peculiar morphological characters but can be easily differentiated based on both vegetative and reproductive characters (see Table 1 and the key).

Key to the genera of the Peixotoid clade

1. Stipules connate at base or up to the middle (i.e. bifid); umbels 1-flowered, bract and bracteoles absent; sepals free, completely revolute or involute along margins; antherodes filiform, minute; styles apex truncate to slightly expanded...................... ***Mionandra***
– Stipules connate (i.e. entire); umbels 4-flowered, bract and bracteoles present; sepals connate at base, revolute only at apex; antherodes globose, conspicuous; styles apex capitate...................... ***Peixotoa***

Mionandra Griseb. (Grisebach 1874: 101)

Figs 2–5

Brittonella Rusby (Rusby 1893: 429) – Type species: *Brittonella pilosa* Rusby [= *M. camareoides* Griseb.]

Cordobia Nied. (Niedenzu 1912: 41), **syn. nov.** – Type species: *Cordobia argentea* (Griseb.) Nied. [= *M. argentea* Griseb.]

Gallardoa Hicken (Hicken 1916: 102), **syn. nov.** – Type species: *Gallardoa fischeri* Hicken [= *M. fischeri* (Hicken) R.F.Almeida]

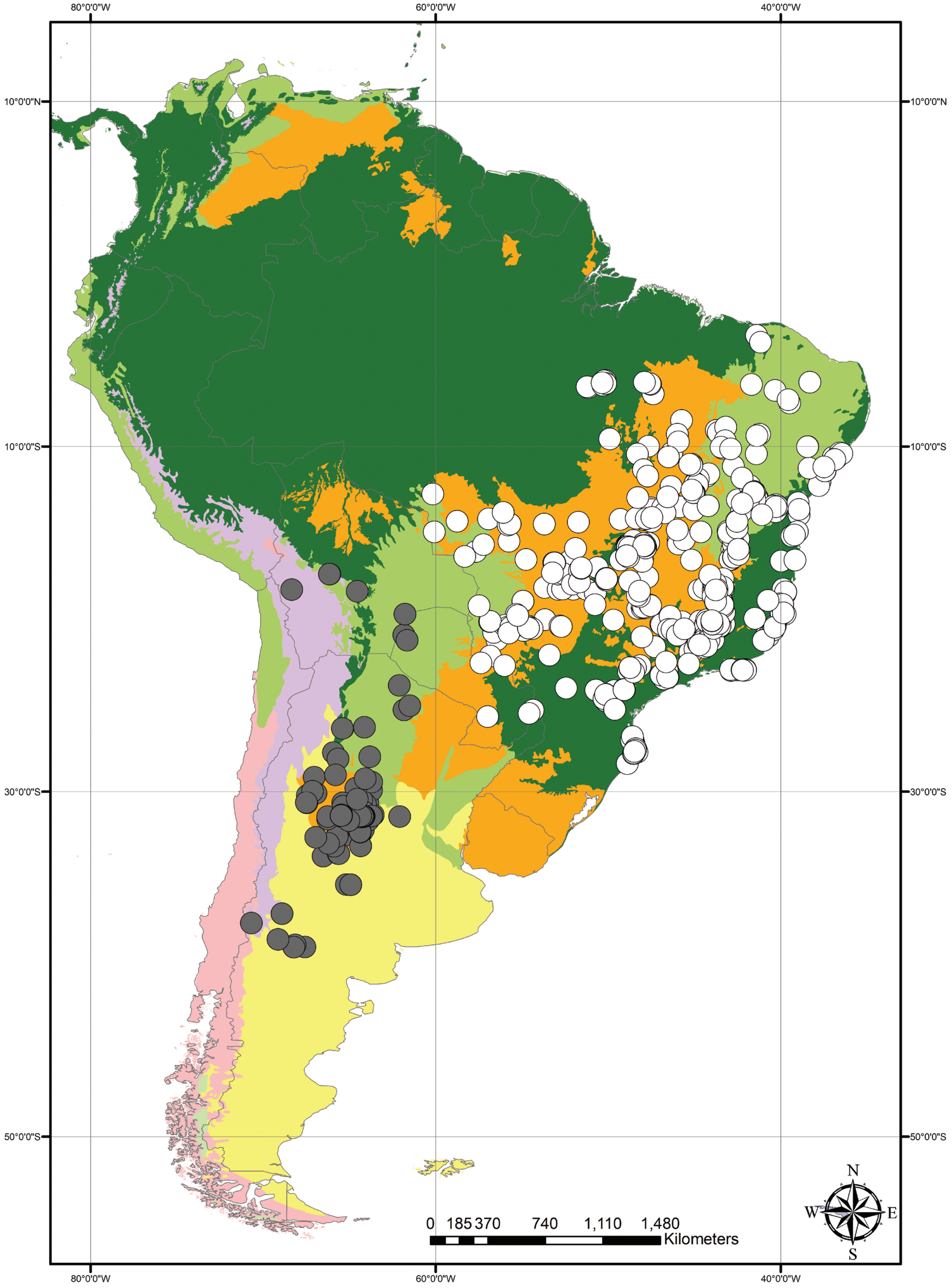

Figure 2. Distribution map of *Mionandra* (grey circles) and *Peixotoa* (white circles) in South America. Dark green: rainforests; Light green: dry forests; Orange: savannas; Lilac: Tundra/Puna; Yellow: temperate steppes; Light red: temperate forests.

Type species. *Mionandra camareoides* Griseb.

Diagnosis. Distinguished from *Peixotoa* by its stipules connate at the base or up to the middle (i.e. bifid), leaves short-petiolate, hirsute-sericeous; umbels 1-flowered, peduncles absent; sepals free, chartaceous, completely revolute or involute along margins; petals narrowly elliptic, margin glandular-fimbriate; fertile stamens 5, staminodes 3–5, antherodes filiform, minute; style apex truncate to slightly expanded; mericarps with wings reduced, rarely dorsal wing well-developed (Table 1).

Description. Erect or scandent to prostrate subshrubs; xylopodium present; indumentum throughout the plant ranging from sericeous to glabrescent; stipules expanded, connate at base or up to the middle (i.e. bifid), triangular, interpetiolar, persistent or deciduous. Leaves opposite, never reduced in the inflorescences; petioles cylindric, short-petiolate (up to 2 mm long), eglandular; blade narrowly elliptic, elliptic, lanceolate to ovate, base cuneate to obtuse, margin entire, apex acute to acuminate, abaxially 0–2-glandular near the base. Umbels solitary, terminal; cincinni 1-flowered; bracts absent; peduncles absent; bracteoles absent. Flowers bisexual, zygomorphic, chasmogamous; pedicels short to elongate; sepals concealing petals during enlargement of bud, completely revolute or involute along margins at anthesis, lateral sepals abaxially 2-glandular, the anterior usually eglandular; petals clawed, yellow, sometimes turning orange at age, both sides glabrous, limb narrowly elliptic to oblanceolate or obovate to widely obovate, base cuneate, margin glandular-fimbriate, apex round, claw plane, posterior petal erect, glandular along margins, lateral petals patent to erect. Androecium 8–10, fertile stamens 5, staminodes 3–5; filaments connate at base, straight, rarely curved, stamen filaments longer than staminode filaments, glabrous or pubescent; connective minute, inconspicuous; fertile anthers monomorphic or dimorphic, erect at apex, glabrous; antherodes absent to present, filiform, reduced to a glandular tissue, glabrous. Gynoecium with carpels connate their whole length in flower, separating during fruit development, styles thick, cylindric, erect, equal, divergent, apex of styles truncate to slightly expanded, stigma terminal to lateral, crateriform or discoid. Schizocarp breaking apart into 3 winged mericarps, separating from a short torus; mericarps with dorsal wing reduced, sometimes well-developed; lateral wings always reduced, free or fused; wings coriaceous, margin sinuate; nut ridged near areole; areole ovate to elliptic. Seeds smooth or rugose; embryos ovoid, cotyledons bent, equal or unequal.

Distribution, habitat, and ecology. *Mionandra* s.l. comprises four species confined to dry forests (Chaco), savannas, and temperate steppes (Patagonian steppes) from Argentina, southern Bolivia, and western Paraguay in South America (Fig. 2).

Notes. A comprehensive treatment for the genera comprising *Mionandra* s.l. (including *Cordobia* and *Gallardoa*) and three of their four species are presented by Aliscioni and Torretta (2017) within the Flora of Argentina project, with *M. paraguariensis* (which does not occur in Argentina) not included in the treatment. Thus, we provide an updated key to all species of *Mionandra* s.l., plus comments on the recognition of *M. paraguariensis*.

Key to the species of *Mionandra*

1. Leaves 2-glandular near base; sepals involute along margins; stamens dimorphic (the latero-posterior ones with shorter, stout and curved filaments, the posterior ones and the anterior filaments thin and straight but the anterior shorter in length); mericarps rugose, dorsal wing well-developed .... ***M. argentea***
– Leaves eglandular; sepals revolute at apex; stamen monomorphic; mericarps smooth, dorsal wing reduced to a crest **2**
2. Erect subshrubs; leaves adpressed-sericeous, margin revolute; petals turning orange at age; style apex slightly expanded; mericarps with lateral wings fused in an orbicular structure; cotyledons equal .... ***M. fischeri***
– Scandent to prostrate subshrubs; leaves hirsute-sericeous at least abaxially, margin plane; petals remaining yellow at age; apex truncate; mericarps with lateral wings free; cotyledons unequal **3**
3. Leaves adaxially hirsute-sericeous at maturity; flowers 1–1.2 cm diam.; petals narrowly elliptic to oblanceolate, apex obtuse; stamen filaments pubescent; staminodes 3, ½ the length of the stamen filaments .... ***M. camareoides***
– Leaves adaxially glabrous at maturity; flowers 2.5–3 cm diam.; petals obovate to widely obovate, apex truncate to emarginate; stamen filaments glabrous; staminodes 5, the same length as the stamen filaments .... ***M. paraguariensis***

Mionandra argentea Griseb. (Grisebach 1874: 101)

Fig. 3

Cryptolappa argentea (Griseb.) Kuntze (Kuntze 1898: 27) – Type: same as for *Mionandra argentea.*

Aspicarpa argentea (Griseb.) Nied. (Niedenzu 1912: 58), nom. illeg. – Type: same as for *Mionandra argentea.*

Cordobia argentea (Griseb.) Nied. (Niedenzu 1913: 41) – Type: same as for *Mionandra argentea.*

Gaudichaudia argentea (Griseb.) Chodat (Chodat and Vischer 1917: 204) – Type: same as for *Mionandra argentea.*

Janusia argentea Griseb., nom. not validly publ.

Peixotoa cordobensis Kuntze (Kuntze 1898: 28) – Type: ARGENTINA – **Córdoba** • 1891; fl., fr.; *Kuntze s.n.*; holotype: NY; isotypes: F, NY.

Type. ARGENTINA – **Córdoba** • in fruticetis Sierra de Córdoba, prope La Higuera; 1872; fl.; *Lorentz s.n.*; holotype: GOET; isotypes: CORD [CORD00005912], K [K000427020].

Mionandra camareoides Griseb. (Grisebach 1874: 102)

Fig. 4

Mionandra camareoides Griseb. (Grisebach 1874: 102) var. *camareoides* – Type: same as for *Mionandra camareoides.*

Brittonella pilosa Rusby (Rusby 1893: 430) – Type: BOLIVIA – **Cochabamba** • Córdoba, vic. Cochabamba; 1891; fl., fr.; *Bang 935*; lectotype (**designated here**): NY [NY00055190]; isolectotypes: GH [GH00045035], MICH [MICH1102068], MO [MO-3222744], PH [PH00008594], US [US00108637, US00603963].

Mionandra camareoides f. *prostrata* Nied. (Niedenzu 1928: 232) – Type: ARGENTINA – **Córdoba** • prop. Córdoba; 20 Apr. 1902; fl.; *Stuckert 11404*; holotype: G [G00352816].

Mionandra prostrata Stuck. ex Nied. (Niedenzu 1928: 232), pro. syn. – Type: same as for *Mionandra camareoides* f. *prostrata.*

Type. ARGENTINA – **Córdoba** • en el campo acerca de Córdoba; Dec. 1870; fl.; *Lorentz 407b*; lectotype (**designated here**): GOET [GOET007649]; isolectotype: CORD [CORD00005913].

Mionandra paraguariensis Chodat (Chodat and Vischer 1917: 165)

Mionandra camareoides var. *paraguariensis* (Chodat) Nied. (Niedenzu 1928: 232)

Type. PARAGUAY – **Cordillera** • between the municipalities of Caacupé and Tobati; s.d.; *Chodat & Vischer 238*; holotype: G [G 208718].

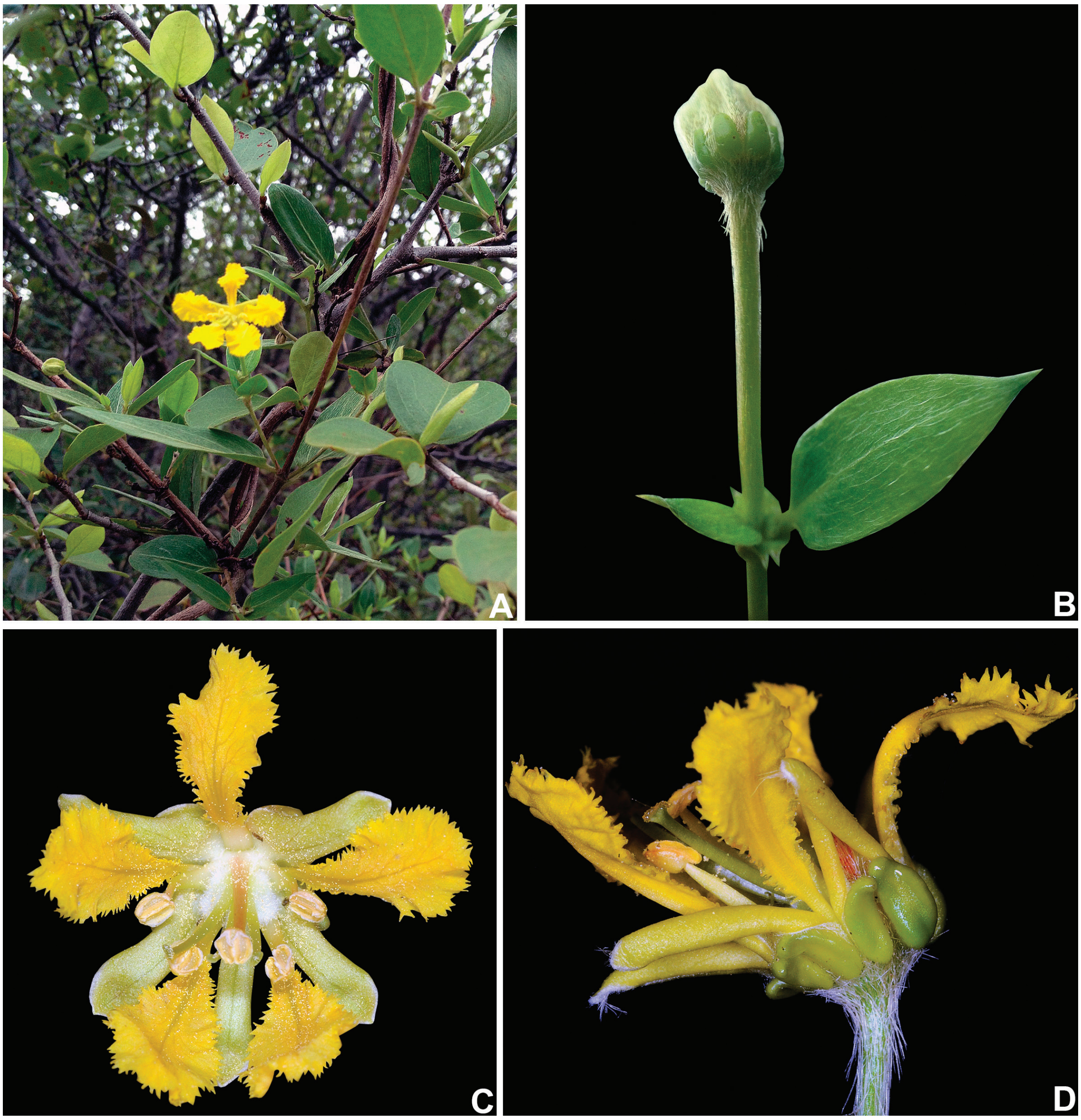

Figure 3. *Mionandra argentea*. **A**. Shrubby habit. **B**. Detail of a floral shoot showing the partially connate stipules in the node and the sessile 1-flowered cincinnus with a long-pedicellate floral bud. **C**. Flower in frontal view. **D**. Flower in lateral view showing the sepals involute along margins. Photographs A–B by Étienne Lacroix-Carignan; C–D by Andrea Cocucci.

Figure 4. *Mionandra camareoides*. **A**. Shrubby habit. **B**. Detail of floral branches. **C**. Detail of flowers. **D**. Flower in frontal view. Photographs A–C by Eduardo Alfredo; D by William Anderson.

Figure 5. *Mionandra fischeri*. **A**. Shrubby habit. **B**. Detail of a flower in frontal view. **C**. Detail of a flower in lateral view. **D**. Detail of floral branches. Photographs A–B by Anival Prina; C by Michelle Delaloye; D by Ivan Federico Ebrecht.

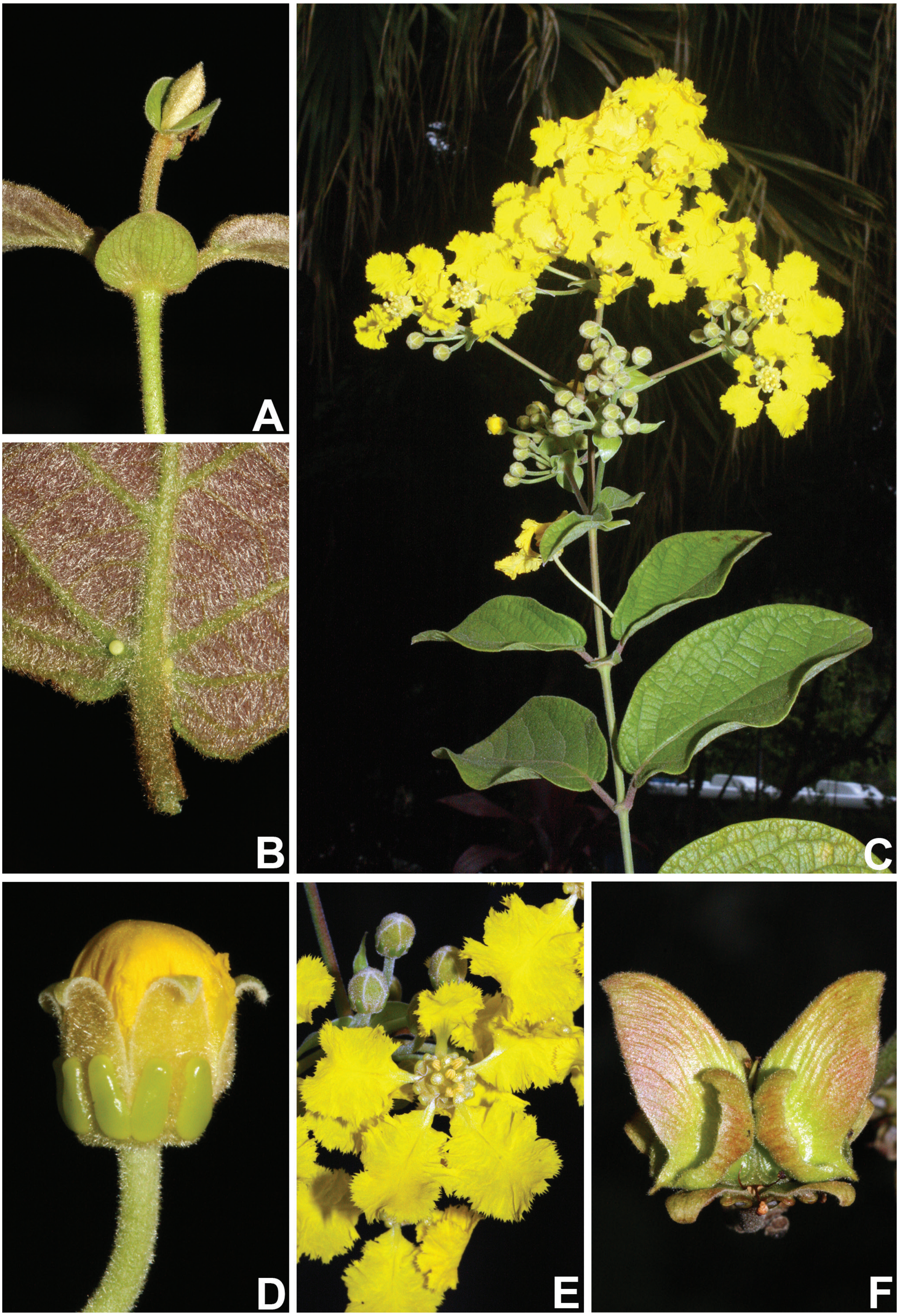

Figure 6. *Peixotoa catarinensis*. **A**. Detail of a sterile branch showing the connate stipules. **B**. Detail of the base of a leaf in abaxial view. **C**. Detail of a flowering branch. **D**. Floral bud in lateral view. **E**. Flower in frontal view. **F**. Winged mericarps in lateral view. Photographs by Marco Pellegrini.

Notes. After revisiting the original description of Chodat and Vischer (1917) and analysing the type specimen, we disagree with Niedenzu's (1928) treatment of *M. paraguariensis* as a variety of *M. camareoides*. Aside from the difference in leaf indumentum, *M. paraguariensis* differs from *M. camareoides* due to its larger flowers, differently shaped petals, stamens with pubescent filaments, and 5 staminodes the same length as the filaments. Thus, we unambiguously recognise it as a distinct species.

Mionandra fischeri (Hicken) R.F.Almeida, **comb. nov.**
urn:lsid:ipni.org:names:77327516-1

Fig. 5

Gallardoa fischeri Hicken, Physis: Revista de la Sociedad Argentina de Ciencias Naturales, Buenos Aires 2: 101. 1916. (Hicken 1916)

Cordobia fischeri (Hicken) Nied. (Niedenzu 1928: 532)

Type. ARGENTINA – **Rio Negro** • vicinity of General Roca; Dec. 1913; fl. fr.; *Fischer 10*; lectotype (**designated here**): SI [SI002629]; isolectotypes: BKL [BKL00000970], CM [CM1185], GH [GH00872231, GH00872232], K [K000427018, K000427019], SI [SI002630, SI002631, SI002632, SI002633, SI002634], US [US00108538, US00108539].

Peixotoa A.Juss. (Jussieu 1833: 59)

Figs 2, 6

Type species. *Peixotoa glabra* A.Juss.

Diagnosis. Distinguished from *Mionandra* s.l. by its stipules completely connate, leaves long-petiolate, never hirsute-sericeous; umbels 4-flowered; sepals connate at base, coriaceous, revolute only at apex; petals orbicular, margin dentate; fertile stamens 5, staminodes 5, antherodes globose, conspicuous; style apex capitate; mericarps with wings well-developed, dorsal wing dominant.

Distribution, habitat, and ecology. *Peixotoa* comprises 29 species occurring in dry forests, rainforests, and savannas in Brazil, eastern Bolivia, and eastern Paraguay in South America (Fig. 2).

Notes. *Peixotoa* has a contemporary taxonomic revision available for 28 of its species (Anderson 1982) and the taxonomic treatment for a new species endemic to Paraguay (Anderson 2001). Nonetheless, misguided morphological interpretations drawn by this author from the inflorescence architecture have made the identification keys provided in these studies challenging to use by the general public and even for Malpighiaceae specialists (pers. obs.). Since C. Anderson published more than two-thirds of the species diversity of *Peixotoa*, only species with conspicuous morphological traits (e.g. glabrous leaves – *Peixotoa glabra* A.Juss.) or specific geographical distributions (e.g. *Peixotoa catarinensis* C.E.Anderson and *P. hispidula* A.Juss.) are correctly identified in Brazilian herbaria (pers. obs.). For a preliminary revisionary study of *Peixotoa* in Brazil, see Almeida et al. (2020). A revised monograph for this genus is urgently needed to enable the correct application of names in *Peixotoa* (pers. obs.).

CONCLUSIONS

Studies mapping the evolution of macro-morphological characters in molecular phylogenies are the steppingstone to challenge traditional classifications and propose new predictive systems in Malpighiaceae, reflecting the evolutionary history of their taxa (Almeida and van den Berg 2021). As a continuation of the studies of Cameron et al. (2001), Davis et al. (2001), and Almeida and van den Berg (2021), we revised the circumscription within the genera of the Peixotoid clade based on molecular and morphological data to finally ensure the taxonomic stability of generic circumscriptions within this clade. *Cordobia* and *Gallardoa* were synonymised under *Mionandra*, and the necessary combination was made alongside typifications and identification keys.

ACKNOWLEDGEMENTS

We would like to thank the staff of the HUEFS herbaria for support with herbarium specimens and Andrea Cocucci, Anibal Prina, Eduardo Alfredo, Etienne Lacroix-Carignan, Ivan Federico Ebrecht, Michelle Delaloye, and William Anderson for allowing us to use their beautiful photographs. CVDB was sponsored by CNPq (grant #310975/2017-4), RFA was sponsored by Programa de Desenvolvimento Científico e Tecnológico Regional CNPq/FAPEG (grants #317720/2021-0 and #202110267000867), and laboratory studies were supported by PRONEX FAPESB (grant # PNX0014/2009).

REFERENCES

Aliscioni SS, Torreta JP (2017) Malpighiaceae. In: Zuloaga FO, Belgrano MJ (Eds) Flora vascular de la República Argentina 17: Dicotyledoneae-Celastrales, Cucurbitales, Fagales, Malpighiaceae, Oxalidales, volume 17. Instituto de Botánica Darwinion, Buenos Aires, 163–205.

Almeida RF, Hall CF (2016) Taxonomic revision of *Coleostachys* (Malpighiaceae). Phytotaxa 277(1): 77–84. https://doi.org/10.11646/phytotaxa.277.1.7

Almeida RF, van den Berg C (2020) Biogeography of *Stigmaphyllon* (Malpighiaceae) and a meta-analysis of vascular plant lineages diversified in the Brazilian Atlantic rainforests point to the Late Eocene origins of this megadiverse biome. Plants 9(11): 1569. https://doi.org/10.3390/plants9111569

Almeida RF, van den Berg C (2021) Molecular phylogeny and character mapping support generic adjustments in the Tetrapteroid clade (Malpighiaceae). Nordic Journal of Botany 39(1): e02876. https://doi.org/10.1111/njb.02876

Almeida RF, van den Berg C (2022) Biogeography and character-mapping of *Hiptage* (Malpighiaceae) corroborate

Indochina's rainforests as one of the main sources of plant diversity in south-eastern Asia. Nordic Journal of Botany 2022(4): e03464. https://doi.org/10.1111/njb.03464

Almeida RF, Amorim AMA, Corrêa AMS, van den Berg C (2017) A new infrageneric classification for *Amorimia* (Malpighiaceae) based on morphological, phytochemical and molecular evidence. Phytotaxa 313: 231–248. https://doi.org/10.11646/phytotaxa.313.3.1

Almeida RF, Francener A, Pessoa C, Sebastiani R, Oliveira YR, Amorim AMA, Mamede MCH (2020) Malpighiaceae in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. https://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB155 [accessed 07.02.2023]

Almeida RF, Pellegrini MO, de Morais IL, Simão-Bianchini R, Rattanakrajang P, Cheek M, Simões ARG (2023) Barking up the wrong tree: the dangers of taxonomic misidentification in molecular phylogenetic studies. Plant Ecology and Evolution 156(2): 146–159. https://doi.org/10.5091/plecevo.101135

Anderson C (1982) A monograph of the genus *Peixotoa* (Malpighiaceae). Contributions from the University of Michigan Herbarium 15: 1–92.

Anderson C (2001) *Peixotoa floribunda* (Malpighiaceae), a new species from Paraguay. Contributions from the University of Michigan Herbarium 23: 49–52.

Anderson C (2011) Revision of *Ryssopterys* and transfer to *Stigmaphyllon* (Malpighiaceae). Blumea 56: 73–104. https://doi.org/10.3767/000651911X573444

Anderson WR (1981) Malpighiaceae. In: The Botany of the Guayana Highland-Part XI. Memoirs of the New York Botanical Garden 32: 21–305.

Anderson WR (2006) Eight segregates from the neotropical genus *Mascagnia* (Malpighiaceae). Novon 16: 168–204. https://doi.org/10.3417/1055-3177(2006)16[168:ESFTNG]2.0.CO;2

Anderson WR, Anderson CE, Davis CC (2006) Malpighiaceae. https://webapps.lsa.umich.edu/herb/malpigh/index.html [accessed 07.02.2023]

Cai L, Xi Z, Peterson K, Rushworth C, Beaulieu J, Davis CC (2016) Phylogeny of Elatinaceae and the tropical Gondwanan origin of the Centroplacaceae (Malpighiaceae, Elatinaceae) clade. PLoS ONE 11(9): e0161881. https://doi.org/10.1371/journal.pone.0161881

Cameron KM, Chase MW, Anderson WR, Hills HG (2001) Molecular systematics of Malpighiaceae: evidence from plastid *rbcL* and *matK* sequences. American Journal of Botany 88: 1847–1862. https://doi.org/10.2307/3558361

Chodat R, Vischer W (1917) La végétation de Paraguay V. Malpighiacées. Bulletin de la Societe Botanique de Genève 9: 55–107.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Davis CC, Anderson WR (2010) A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. American Journal of Botany 97: 2031–2048. https://doi.org/10.3732/ajb.1000146

Davis CC, Anderson WR, Donoghue MJ (2001) Phylogeny of Malpighiaceae: evidence from chloroplast *ndhF* and *trnl-F* nucleotide sequences. American Journal of Botany 88: 1830–1846. https://doi.org/10.2307/3558360

Davis CC, Schaefer H, Xi Z, Baum DA, Donoghue MJ, Harmon LJ (2014) Long-term morphological stasis maintained by a plant-pollinator mutualism. Proceeding of the National Academy of Sciences 111: 5914–5919. https://doi.org/10.1073/pnas.1403157111

De Pinna MCC (1991) Concepts and tests of homology in the cladistic paradigm. Cladistics 7: 367–394. https://doi.org/10.1111/j.1096-0031.1991.tb00045.x

Doyle JL, Doyle JJ (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19: 11–15.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Edler D, Klein J, Antonelli A, Silvestro D (2021) raxmlGUI 2.0 beta: a graphical interface and toolkit for phylogenetic analyses using RAxML. Methods in Ecology and Evolution 12(2): 373–377. https://doi.org/10.1111/2041-210X.13512

ESRI (2010) ArcGIS, version 9.3.1. Redlands, California: Environmental Systems Research Institute. https://www.arcgis.com/index.html [accessed 07.02.2023]

GBIF (2023) Global Biodiversity Information Facility. https://www.gbif.org/ [accessed 07.02.2023]

Grisebach A (1874) Plantae lorentzianae. Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen 19: 49–278.

Hicken CM (1916) Plantae Fischerianae. Physis: Revista de la Sociedad Argentina de Ciencias Naturales, Buenos Aires 2: 101–122.

Jussieu A (1833) ["1832"]. Malpighiaceae. In: Saint-Hilaire A (Ed.) Flora brasiliae meridionalis, volume 3. A. Belin, Paris, 5–86.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organisation and analysis of sequence data. Bioinformatics 28(12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kuntze O (1898) Malpighiaceae. Revisio generum plantarum 3(3): 27–29.

Maddison WP, Maddison DR (2010) Mesquite: a modular system for evolutionary analysis. Version 2.73. https://www.mesquiteproject.org/ [accessed 07.02.2023]

Niedenzu F (1912) Malpighiaceae americanae II. Arbeiten aus dem botanischen Institut des Koniglichen Akademie Lyceum Hosianum. Druck von Heynes Buchdruckerei (G. Riebensahm), Braunsberg, 1–34.

Niedenzu F (1913) Malpighiaceae. In: Die von Dr. Th. Herzog auf seiner zweiten Reise durch Bolivien in den Jahren 1910 und 1911 gesammelten Pflanzen, T. Herzog. Mededeelingen Rijks-Herbarium Leiden 19: 70–75.

Niedenzu F (1928) Malpighiaceae. Das Pflanzenreich 141(Heft 93): 1–870.

Nixon KC (1999) Winclada (beta) version 0.9. Published by the author, Ithaca, NY. https://www.cladistics.com/ [accessed 07.02.2023]

POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. https://powo.science.kew.org/ [accessed 07.02.2023]

Radford AE, Dickison WC, Massey JR, Bell CR (1974) Vascular Plant Systematics. Harper & Row, New York, 1–891.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Tracer version 1.7. https://www.beast2.org/tracer-2/ [accessed 07.02.2023]

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rusby HH (1893) New genera of plants from Bolivia. Bulletin of the Torrey Botanical Club 20(11): 429–430.

Sereno PC (2007) Logical basis for morphological characters in phylogenetics. Cladistics 23: 565–587. https://doi.org/10.1111/j.1096-0031.2007.00161.x

Spjut RW (1994) A Systematic Treatment of Fruit Types. The New York Botanical Garden, New York, 1–181.

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Thiers B (2023) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. https://sweetgum.nybg.org/science/ih/ [accessed 07.02.2023]

Weberling F (1965) Typology of inflorescences. Botanical Journal of the Linnean Society 59: 15–221. https://doi.org/10.1111/j.1095-8339.1965.tb00058.x

Weberling F (1989) Morphology of Flowers and Inflorescences. Cambridge University, Cambridge, 1–348.

Willis CG, Franzone BF, Xi Z, Davis CC (2014) The establishment of Central American migratory corridors and the biogeographic origins of seasonally dry tropical forests in Mexico. Frontiers in Genetics 5: 00433. https://doi.org/10.3389/fgene.2014.00433

WWF (2023) Tropical and subtropical dry broadleaf forests. https://www.worldwildlife.org/biomes/tropical-and-subtropical-dry-broadleaf-forests [accessed 07.02.2023]

SUPPLEMENTARY MATERIALS

Supplementary material 1

GenBank accession numbers for all markers and species sampled in this study.
https://doi.org/10.5091/plecevo.101657.suppl1

Supplementary material 2

Morphological matrix with all 16 characters scored and coded for all species sampled.
https://doi.org/10.5091/plecevo.101657.suppl2

Supplementary material 3

Character descriptions for all 16 characters scored in the morphological matrix.
https://doi.org/10.5091/plecevo.101657.suppl3