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ADVANCES IN LEGUME SYSTEMATICS 14. CLASSIFICATION OF CAESALPINIOIDEAE PART 1: NEW GENERIC DELIMITATIONS

Edited by
Colin E. Hughes, Luciano P. de Queiroz, Gwilym P. Lewis

Hydrochorea corymbosa (Rich.) Barneby & J.W. Grimes

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EDITORIAL

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Editorial

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Since its inception in 1981, the Advances in Legume Systematics (ALS) series has provided an important outlet for publishing new results on all aspects of the systematics and classification of legumes, including papers arising from the seven International Legume Conferences. The first ten parts in the ALS series were published by the Royal Botanic Gardens, Kew, and subsequent parts as Special Issues of two botanical journals – "Australian Systematic Botany" (Part 11 in 2003 and Part 13 in 2019) and "South African Journal of Botany" (Part 12 in 2013) – a format continued here for Part 14 with this Special Issue of "PhytoKeys".

Here in ALS 14 the focus is on classification of the legume subfamily Caesalpinioideae, as it was re-circumscribed by the Legume Phylogeny Working Group (LPWG) in 2017. Caesalpinioideae is the second largest subfamily of legumes with ca. 4,600 species currently placed in 152 genera. Within the subfamily, ca. 3,400 species and 90 genera are placed in the mimosoid clade corresponding to the former subfamily Mimosoideae, which is nested within new sense Caesalpinioideae. The subfamily has a pantropical distribution and many of its lineages form diverse and ecologically abundant or dominant elements across dry, savanna and wet lowland tropical biomes. Despite major advances in the last few decades towards aligning genera with clades, generic delimitation in Caesalpinioideae remains in a state of considerable flux, especially across the mimosoid clade.

In the introductory paper of this Special Issue, a new phylogenomic framework for Caesalpinioideae built from DNA sequences of 997 nuclear genes for 420 species of 147 of the 152 genera recognized in the subfamily prior to ALS14, is presented. This

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new phylogeny reveals that 22 genera are non-monophyletic or nested within another genus and underpins a series of 15 papers focused on generic delimitation of particular subclades, which are presented here in ALS14 Part 1. This phylogeny also provides the framework for a new higher-level tribal and clade-based classification including a synopsis of genera in the subfamily which will be presented separately in ALS14 Part 2.

Here in ALS14 Part 1, the 16 papers are authored by 52 authors from 13 countries. Nine new genera are described, five genera are reinstated and three genera are subsumed into synonymy in other genera. With addition of these 14 new and reinstated genera and subtraction of three genera placed in synonymy, the total number of genera in subfamily Caesalpinioideae now stands at 163, of which 102 are in the mimosoid clade. One new species is described, several new sections of genera are erected, and 139 new nomenclatural combinations are proposed.

Given the extent of the adjustments to generic limits presented here in ALS14 Part 1, it is clear that this focus on generic delimitation was much needed. Of the 22 instances of generic non-monophyly, 15 have been reclassified here in ALS14 representing a significant step towards aligning genera with clades across Caesalpinioideae. A fully updated synopsis of the now 163 genera forms part of the new classification of Caesalpinioideae presented in ALS14 Part 2.

As editors, we thank the many people and organisations who have helped to bring this ALS14 Special Issue to fruition. The foundations for ALS14 were established through phylogenomic work started by Erik Koenen, and it was his idea to use the results of these new phylogenomic analyses to assemble a compilation of papers focused on generic delimitation authored by many different people in a single volume as part of the ALS series. We thank Erik for his vision and many contributions to making that happen. We are extremely grateful to Patrick Herendeen who acted as an additional handling editor for the introductory phylogenomics paper on which all three of us as editors are authors. We thank all the people who have promptly and willingly reviewed papers: Stephen Boatwright, Leonardo Borges, Gillian Brown, Anne Bruneau, Warren Cardinal-McTeague, Domingos Cardoso, Else Demeulenaere, Rafael Govaerts, Ethiéne Guerra, William Hawthorne, Héctor Hernández, Stefanie Ickert-Bond, Erik Koenen, Melissa Luckow, Marli Morim, Dan Murphy, Toby Pennington, Marianne Le Roux, Marcelo Simon and Jan Wieringa, and Dóra Huszár for help to compile the Index. We also very much appreciate the hard work of the Pensoft editorial team and especially the managing editor of PhytoKeys, Yasen Mutafchiev who has overseen production of this Special Issue. Finally, we thank Swiss National Science Foundation (grant 31003A_182453/1 to CEH) for support that underpinned research presented in this Special Issue, and the following organisations for contributing funds to support Open Access publication costs of ALS14 Part 1: Royal Botanic Gardens, Kew, U.K. (O'Donnell et al. and Clark et al. papers), the U.S. National Science Foundation grant number OIA-1946352 to the University of Guam (Demeulenaere et al. paper), the Australia and Pacific Science Foundation, Australia (Brown et al. paper), and especially the Department of Systematic and Evolutionary Botany at the University of Zurich, Switzerland (all other papers).

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RESEARCH ARTICLE

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Phylogenomic analysis of 997 nuclear genes reveals the need for extensive generic re-delimitation in Caesalpinioideae (Leguminosae)

Jens J. Ringelberg[1], Erik J.M. Koenen[1,2], João R. Iganci[3,4], Luciano P. de Queiroz[5], Daniel J. Murphy[6], Myriam Gaudeul[7], Anne Bruneau[8], Melissa Luckow[9], Gwilym P. Lewis[10], Colin E. Hughes[1]

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Abstract

Subfamily Caesalpinioideae with ca. 4,600 species in 152 genera is the second-largest subfamily of legumes (Leguminosae) and forms an ecologically and economically important group of trees, shrubs and lianas with a pantropical distribution. Despite major advances in the last few decades towards aligning genera with clades across Caesalpinioideae, generic delimitation remains in a state of considerable flux, especially across the mimosoid clade. We test the monophyly of genera across Caesalpinioideae via phylog-

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enomic analysis of 997 nuclear genes sequenced via targeted enrichment (Hybseq) for 420 species and 147 of the 152 genera currently recognised in the subfamily. We show that 22 genera are non-monophyletic or nested in other genera and that non-monophyly is concentrated in the mimosoid clade where ca. 25% of the 90 genera are found to be non-monophyletic. We suggest two main reasons for this pervasive generic non-monophyly: (i) extensive morphological homoplasy that we document here for a handful of important traits and, particularly, the repeated evolution of distinctive fruit types that were historically emphasised in delimiting genera and (ii) this is an artefact of the lack of pantropical taxonomic syntheses and sampling in previous phylogenies and the consequent failure to identify clades that span the Old World and New World or conversely amphi-Atlantic genera that are non-monophyletic, both of which are critical for delimiting genera across this large pantropical clade. Finally, we discuss taxon delimitation in the phylogenomic era and especially how assessing patterns of gene tree conflict can provide additional insights into generic delimitation. This new phylogenomic framework provides the foundations for a series of papers reclassifying genera that are presented here in *Advances in Legume Systematics* (ALS) 14 Part 1, for establishing a new higher-level phylogenetic tribal and clade-based classification of Caesalpinioideae that is the focus of ALS14 Part 2 and for downstream analyses of evolutionary diversification and biogeography of this important group of legumes which are presented elsewhere.

Keywords
Fabaceae, generic delimitation, mimosoid clade, monophyly, morphological homoplasy, phylogenomics

Introduction

In 2017, the Legume Phylogeny Working Group established a new subfamily classification of the Leguminosae (LPWG 2017), which dealt with the longstanding problem of the paraphyly of old sense subfamily Caesalpinioideae DC. by formally dividing the family into six subfamilies: Cercidoideae LPWG, Detarioideae Burmeist., Duparquetioideae LPWG, Dialioideae LPWG, Caesalpinioideae and Papilionoideae DC. Subfamily Caesalpinioideae was especially impacted by this new classification because several large clades previously included within it were afforded subfamily rank, while at the same time the former subfamily Mimosoideae DC., which is nested within Caesalpinioideae, was subsumed within the re-circumscribed Caesalpinioideae and is now simply referred to as the mimosoid clade (LPWG 2017). The idea that Leguminosae comprises six main lineages has since been amply confirmed by phylogenomic analyses of large nuclear gene and plastome DNA sequence datasets (Koenen et al. 2020a; Zhang et al. 2020; Zhao et al. 2021) providing robust support for the six subfamilies. Establishment of this new classification has shifted the focus of current legume systematics research to development of phylogenetically-based tribal (e.g. de la Estrella et al. 2018 for Detarioideae) and clade-based (e.g. Sinou et al. 2020 for Cercidoideae) higher-level classifications and, especially, towards establishment of robust generic systems for each subfamily. Here, we present a phylogenomic backbone for the re-circumscribed subfamily Caesalpinioideae as the basis for a new higher-level and generic classification of that subfamily.

Caesalpinioideae sensu LPWG (2017) is the second largest subfamily of legumes with ca. 4,600 species currently placed in 152 genera (LPWG 2017 plus additions, see

below). Within this subfamily, ca. 3,400 species and 90 genera are placed in the mimosoid clade corresponding to the former subfamily Mimosoideae, which is nested within new sense Caesalpinioideae (LPWG 2017). Caesalpinioideae has a pantropical distribution and many of its lineages form ecologically abundant or dominant elements across each of the major lowland tropical biomes – seasonally dry tropical forests ("the succulent biome" sensu Schrire et al. 2005 and Ringelberg et al. 2020), savannas and tropical rain forests – thus spanning the full lowland tropical rainfall spectrum from arid to hyper-wet, with just a small fraction of species extending into the warm temperate zone, a subset of which are frost tolerant. Caesalpinioideae species are infrequent above 2500 m elevation in the tropics and are notably absent from mid- and high-elevation tropical montane forests, with only a few exceptions (e.g. some *Inga* Mill. spp., *Paraserianthes lophantha* (Vent.) I.C. Nielsen subsp. *montana* (Jungh.) I.C. Nielsen). The ecological versatility of the subfamily across the lowland tropical moisture availability spectrum is matched by its great diversity of life-history strategies, from massive canopy-emergent rainforest trees to small desert shrubs, and functionally-herbaceous savanna geoxyles to woody lianas and aquatic plants (Lewis et al. 2005; LPWG 2013, 2017; Koenen et al. 2020b; Ringelberg et al. 2022). Many species are economically important because of their highly-nutritious fruits, valuable wood, nitrogen-rich leaves and other products (Lewis et al. 2005) and are especially prominent as multipurpose trees in tropical silvo-pastoral and other agro-forestry systems. Several other species constitute some of the world's most serious invasive weeds (e.g. *Leucaena leucocephala* (Lam.) de Wit, several *Mimosa* L. spp. and *Acacia* Mill. spp., *Prosopis juliflora* (Sw.) DC.). Generic diversity is highest in the Neotropics and Africa and there are important centres of species diversity in Mexico and Central America, lowland South America, Africa, Madagascar, parts of S.E. Asia and Australia. Caesalpinioideae includes some of the largest genera in the legume family, such as *Acacia* with > 1,000 species concentrated in dry parts of Australia and *Mimosa* with > 500 species mostly in the Neotropics, as well as *Chamaecrista* Moench and *Senna* Mill., each with 300+ species distributed pantropically, *Inga* Mill. with ca. 300 species restricted to the Neotropics, almost entirely in rainforests and *Vachellia* Wight & Arn. (ca. 160 species) and *Senegalia* Raf. (ca. 220 species), two pantropical genera concentrated in drier environments, within which the iconic umbrella-crown trees of African savannas are found.

Numbers of genera across Caesalpinioideae have increased progressively through the last 270 years, but are difficult to track, because of the altered delimitation of the subfamily. However, the history of generic delimitation in mimosoids illustrates the overall trajectory of numbers of genera. Linnaeus (1753) placed all known mimosoids in a single genus *Mimosa*, which was later subdivided by Willdenow (1805) into five genera: *Inga*, *Mimosa*, *Schrankia* Willd., *Desmanthus* Willd. and *Acacia*. In 1825, de Candolle added five more genera, but the real foundations for all subsequent work were established by Bentham (1842, 1875) notably in his 'Revision of suborder Mimoseae' in 1875, which recognised six tribes and 46 genera, based on examination of 1,200 species known at that time.

The legacy of Bentham's generic system has been long-lasting. At the heart of Bentham's system were a set of large, geographically widespread genera, including

Acacia, *Calliandra* Benth., *Pithecellobium* Mart. and *Prosopis* L., all of which, with the advent of molecular phylogenetics, have been shown to be non-monophyletic. The disintegration of *Acacia* into (currently) seven segregate genera (*Acacia*, *Acaciella* Britton & Rose, *Mariosousa* Seigler & Ebinger, *Parasenegalia* Seigler & Ebinger, *Pseudosenegalia* Seigler & Ebinger, *Senegalia* and *Vachellia*), based on 20 years of molecular phylogenetic studies (Clarke et al. 2000; Miller and Bayer 2000, 2001, 2003; Robinson and Harris 2000; Luckow et al. 2003; Miller et al. 2003, 2013, 2017; Murphy et al. 2003; Seigler et al. 2006a, b; Brown et al. 2008; Bouchenak-Khelladi et al. 2010; Gómez-Acevedo et al. 2010; Miller and Seigler 2012; Kyalangalilwa et al. 2013; Mishler et al. 2014; Boatwright et al. 2015; Terra et al. 2017; Koenen et al. 2020b) (Figs 1 and 6–8) has been the most prominent example in legumes of the dissolution of one of Bentham's broadly circumscribed pantropical genera. *Pithecellobium* and *Calliandra* have suffered similar fates (Barneby and Grimes 1996, 1997; Barneby 1998; de Souza et al. 2013, 2016). In contrast, although Bentham (1875) had restricted his concept of the genus *Albizia* Durazz. to just Old World species, Nielsen (1981) expanded the genus pantropically, creating the last big 'dustbin genus' of mimosoids (Koenen et al. 2020b). By far the most persistent generic delimitation problems surround those of former tribe Ingeae, where starkly contrasting generic systems and numerous generic transfers have caused much on-going confusion (reviewed by Brown 2008).

By 1981, the number of mimosoid genera had risen to 62 in *Advances in Legume Systematics* Part 1 (Elias 1981), 78 in *Legumes of the World* (Lewis et al. 2005) and in the most recent census (LPWG 2017) to 84, with 148 genera recognised in Caesalpinioideae as a whole.

Across the non-mimosoid Caesalpinioideae generic delimitation has also seen many changes. The most complex problems have been, without doubt, in the Caesalpinia Group and, especially, the genus *Caesalpinia* L. s.l. (Polhill and Vidal 1981; Lewis 1998; Gagnon et al. 2016), but these have now largely been resolved with the phylogenetically-based generic system of Gagnon et al. (2016), which recognised 26 genera, leaving just one residual generic problem in that group (see Clark et al. 2022).

Since LPWG (2017), two genera of Caesalpinioideae have been synonymised (i.e. *Cathormion* Hassk. within *Albizia* (Koenen et al. 2020b) and *Lemuropisum* H. Perrier within *Delonix* Raf. (Babineau and Bruneau 2017)) and six new genera have been segregated or resurrected (i.e. *Lachesiodendron* P.G. Ribeiro, L.P. Queiroz & Luckow (Ribeiro et al. 2018), *Parasenegalia* and *Pseudosenegalia* (Seigler et al. 2017), *Jupunba* Britton & Rose and *Punjuba* Britton & Rose (Soares et al. 2021) and *Robrichia* (Barneby & J.W. Grimes) A.R.M. Luz & E.R. Souza (de Souza et al. 2022a)), bringing the current tally of Caesalpinioideae genera to 152, of which 90 are mimosoids.

Despite this rapid on-going progress to align genera with clades in recent years, generic delimitation across Caesalpinioideae and, especially, the mimosoid clade, remains in a state of considerable flux and there is evidence to suggest that several more genera are non-monophyletic: *Prosopis* (Catalano et al. 2008), *Dichrostachys* (DC.) Wight & Arn. (Hughes et al. 2003; Luckow et al. 2005), *Balizia* Barneby & J.W. Grimes (Iganci et al. 2016; Koenen et al. 2020b), *Zygia* P. Browne (Ferm et al. 2019), *Entada* Adans.

(Luckow et al. 2003), *Caesalpinia* (Gagnon et al. 2016), *Albizia*, *Senegalia* and *Leucochloron* Barneby & J.W. Grimes (Koenen et al. 2020b; Fig. 1). One factor that has undoubtedly contributed significantly to this widespread generic non-monophyly is the potentially pervasive homoplasy of multiple morphological characters previously used for generic delimitation, as well as reliance on only a few characters for delimiting taxa. This has led to tribes defined solely on stamen number and fusion into a staminal tube (Bentham 1875) and 'fruit genera', such as *Calliandra*, which was defined by Bentham (1875), based on its characteristic elastically dehiscent fruit. All mimosoid tribes and the genus *Calliandra* have since been shown to be non-monophyletic and their defining characters shown to have evolved multiple times across the subfamily (e.g. LPWG 2013; Barneby 1998). Such over-reliance on a small number of potentially homoplasious morphological characters, such as fruit type, connation and number of stamens and floral heteromorphy have likely repeatedly misled classification and resulted in widespread generic non-monophyly.

Another issue has been delimitation of the mimosoid clade with on-going uncertainties surrounding the inclusion or not of certain genera (Luckow et al. 2000, 2003; Manzanilla and Bruneau 2012). Although lacking valvate petals in bud (the putative synapomorphy of mimosoids), morphologically some members of the informal Dimorphandra group of Polhill and Vidal (1981) and Polhill (1994) show many similarities to mimosoids, with small, often numerous, regular flowers arranged in spikes or spiciform racemes, the hypanthium contracted, the anthers sagittate and introrse, the stamens becoming the most conspicuous and attractive part of the flower and pollen in tetrads in a few genera (*Diptychandra* Tul. and *Dinizia* Ducke) with possible affinities to the polyads that characterise many mimosoid lineages (Banks et al. 2010). These mimosoid-like features have prompted inclusion of some genera such as *Dinizia* in the mimosoid clade in the past (e.g. Burkart 1943; Luckow et al. 2000). Although none of these mimosoid-like genera has flowers with petals valvate in bud, previous molecular phylogenetic analyses have unexpectedly placed two Dimorphandra group genera in the mimosoid clade: *Chidlowia* Hoyle and *Sympetalandra* Stapf. The monospecific west African genus *Chidlowia* was placed with high support within the mimosoid clade in analyses based on few genetic markers (Manzanilla and Bruneau 2012; LPWG 2017), a result which was confirmed by the phylogenomic analyses of Koenen et al. (2020b; Fig. 1). The small Asian genus *Sympetalandra* was also recovered in the mimosoid clade in the *matK* tree of LPWG (2017), but was not sampled by Koenen et al. (2020b). Although support for the mimosoid clade is robust and the branch subtending that clade is long (Koenen et al. 2020b; Fig. 1), such that the monophyly of mimosoids is not in doubt, not all Caesalpinioideae genera have been included in phylogenomic analyses. By sampling widely and densely across Caesalpinioideae as a whole, we aim to further resolve which genera are placed in the mimosoid clade.

Several other issues have hindered a more complete understanding of the phylogeny and tribal / generic classification of subfamily Caesalpinioideae. First, the legacy of the traditional subfamily classification meant that taxon sampling in previous phylogenetic studies focused primarily on either old sense Caesalpinioideae (i.e. the grade

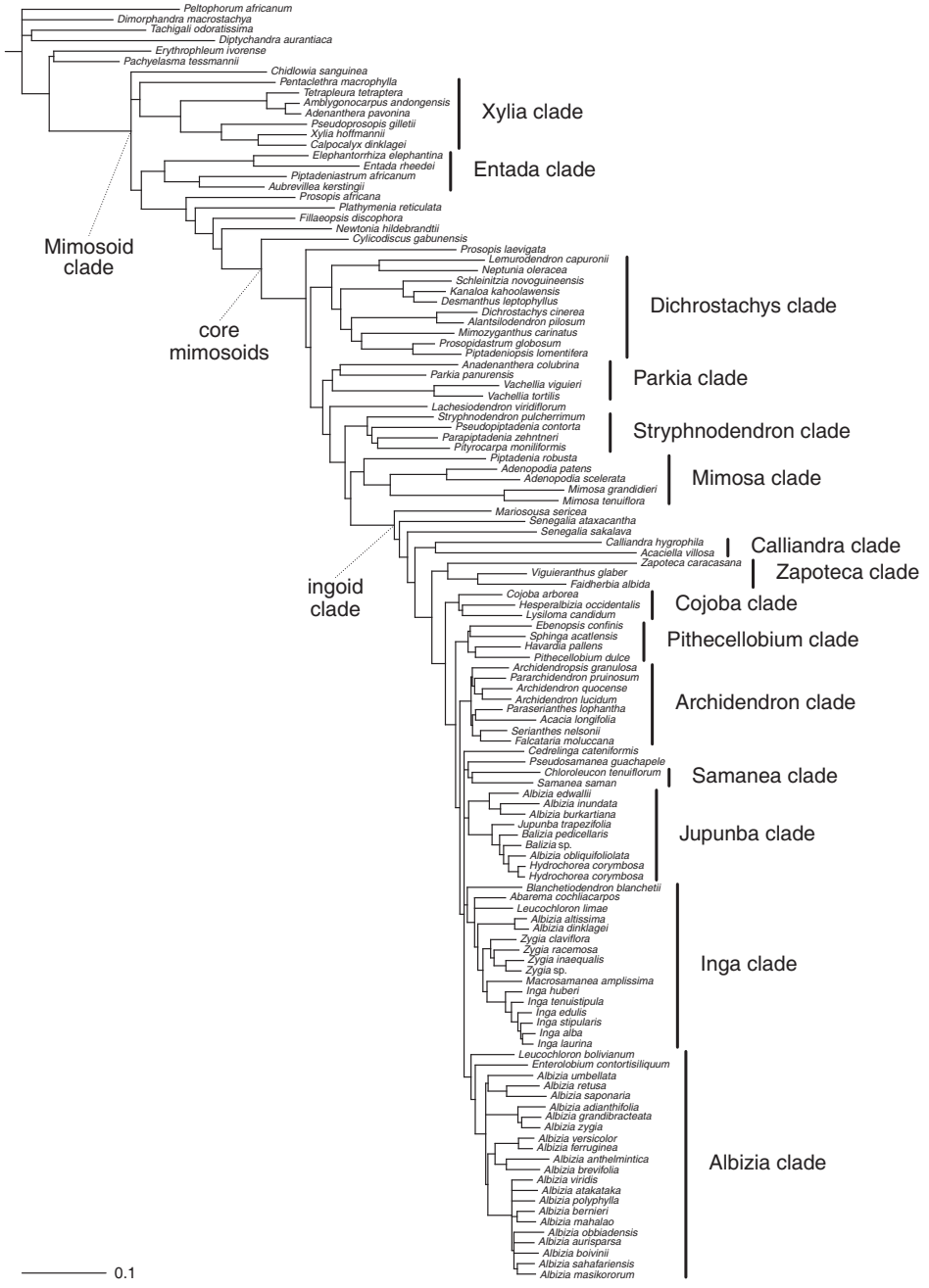

Figure 1. Phylogeny of Caesalpinioideae with clade names as inferred by Koenen et al. (2020b), the starting point for this study.

subtending mimosoids (the 'Caesalpinieae grade' of Manzanilla and Bruneau 2012) of new sense Caesalpinioideae (Bruneau et al. 2008; Manzanilla and Bruneau 2012)), or on the mimosoid clade (e.g. Luckow et al. 2003, 2005; Koenen et al. 2020b). Few studies, apart from the family-wide analysis of plastid *matK* sequences (LPWG 2017), have sampled densely and widely across Caesalpinioideae as a whole. Second, several parts of the Caesalpinioideae phylogeny have been recalcitrant to phylogenetic resolution using traditional DNA sequence loci, most notably along the backbone of the grade subtending the mimosoid clade (Bruneau et al. 2008; Manzanilla and Bruneau 2012; LPWG 2017) and across the large ingoid clade sensu Koenen et al. (2020b). Third, lack of dense pantropical sampling of taxa in previous phylogenies means that the monophyly of several key genera with wide pantropical distributions, such as the 'dustbin genus' *Albizia*, has not been adequately tested and that possible sister-group relationships between New and Old World groups that are relevant to delimitation of genera may have been missed.

More robust foundations to overcome these difficulties were established by Koenen et al. (2020b) in a phylogenomic study of the mimosoid clade. By developing a clade-specific bait set (*Mimobaits*) for targeted enrichment of 964 nuclear genes, Koenen et al. (2020b) opened the way for generating DNA sequence datasets orders of magnitude larger than those used previously, thereby providing much enhanced phylogenetic resolution. Using these new data, Koenen et al. (2020b) established a new phylogenomic framework and recognised three large informally named higher-level clades each successively nested within Caesalpinioideae (Fig. 1). The mimosoid clade, core mimosoid clade and ingoid clade were all strongly supported by high proportions of gene trees and subtended by long branches. In addition, a set of 15 smaller informally named subclades across mimosoids were proposed by Koenen et al. (2020b) (Fig. 1) to replace the previously defined tribes and informal groups and alliances, almost all of which have been shown by numerous studies to be non-monophyletic (Luckow et al. 2003; LPWG 2013, 2017; Koenen et al. 2020b). Furthermore, although the *Mimobaits* bait set was designed based on RNA-seq data from species of four mimosoid genera and used initially for the mimosoid clade, the results of Koenen et al. (2020b) suggested that they work well across the non-mimosoid Caesalpinioideae, opening the way to potentially sequence these genes across the subfamily as a whole. The Koenen et al. (2020b) study also further revealed or confirmed the non-monophyly of several genera, but it lacked sufficient taxon sampling to fully test generic monophyly and sampling was largely restricted to the mimosoid clade. Here, we capitalise on these foundations using a slightly modified version of the *Mimobaits* gene set covering 997 nuclear genes to extend taxon sampling to 420 species from 147 of the 152 genera and establish a robust phylogenomic hypothesis for subfamily Caesalpinioideae as a whole.

This new phylogeny provides the basis for testing the monophyly of genera (the main focus of this paper and of this Special Issue *Advances in Legume Systematics* (ALS) 14, Part 1), establishing a new higher-level classification of the subfamily (the focus of ALS 14, Part 2) and for downstream analyses of biogeography, trait evolution and diversification (de Faria et al. 2022; Ringelberg et al. 2022). Caesalpinioideae pro-

vides an excellent clade for investigating evolutionary diversification and phylogenetic turnover across the lowland tropics (Lavin et al. 2004; Gagnon et al. 2019; Ringelberg et al. 2020, 2022), as well as the evolution of several prominent plant functional traits including compound leaves, armature, extrafloral nectaries and ant associations (Marazzi et al. 2019), agglomeration of pollen into polyads, plant growth forms (Gagnon et al. 2019), floral morphology and pollination syndromes, fruit morphology and seed dispersal syndromes and the ability to form nitrogen-fixing root nodule symbiosis (Sprent et al. 2017; de Faria et al. 2022). However, all of these opportunities require a robust and well-sampled subfamily-wide phylogeny of Caesalpinioideae. In turn, some of these traits have been used for generic delimitation in the past and, in this paper, we also evaluate a handful of such traits in a preliminary way by mapping them on to the phylogeny.

Methods

Phylogeny: taxon and gene sampling, and tree building

To test generic monophyly as thoroughly as possible, we sampled taxa to encompass known or suspected cases of generic non-monophyly, as well as sets of representative species spanning the root nodes of larger genera in Caesalpinioideae (Suppl. material 1). The final phylogenomic dataset comprised 420 Caesalpinioideae taxa covering 147 of the 152 genera. The five missing genera are: *Stenodrepanum* Harms, the monospecific sister genus of *Hoffmannseggia* Cav. in the Caesalpinia Group (Gagnon et al. 2016); *Hultholia* Gagnon & G.P. Lewis, another monospecific genus in the Caesalpinia Group (Gagnon et al. 2016); *Microlobius* C. Presl, which is also monospecific and nested within the mimosoid genus *Stryphnodendron* Mart. (Simon et al. 2016; Ribeiro et al. 2018; Lima et al. 2022); *Vouacapoua* Aubl., a genus of three species, whose phylogenetic placement is uncertain, but most likely falls into the Cassia clade (Bruneau et al. 2008; LPWG 2017); and *Pterogyne* Tul., another monospecific genus whose placement has been uncertain (Manzanilla and Bruneau 2012; Zhang et al. 2020), but which is probably sister to all Caesalpinioideae, excluding the Arcoa and Umtiza clades (Zhao et al. 2021). In total, 89 of 90 mimosoid genera and 58 of the 62 non-mimosoid Caesalpinioideae genera were sampled.

We sequenced a set of 997 nuclear genes specifically selected for phylogenomic analyses of the mimosoid clade (Koenen et al. 2020b) via targeted enrichment and hybrid capture. This Hybseq approach has quickly become the method of choice to generate phylogenomic data because of its versatility and relatively low cost (e.g. Nicholls et al. 2015; Barrett et al. 2016; Hart et al. 2016; Dodsworth et al. 2019; Johnson et al. 2019; Koenen et al. 2020b). Library preparation, hybrid capture, enrichment and sequencing were performed by Arbor Biosciences (previously MYcroarray; Ann Arbor, USA). Full details about how the new Caesalpinioideae phylogeny was inferred are presented by Ringelberg et al. (2022), but briefly, HybPiper (Johnson et al. 2016)

was used to assemble the loci and the pipeline of Yang and Smith (2014) was used for data cleaning and orthology assessment. Various phylogenetic methods, including the multi-species coalescent approach using individual gene trees with ASTRAL (Zhang et al. 2018), Maximum Likelihood based on concatenated alignments with RAxML (Stamatakis 2014) and Bayesian gene jack-knifing with PhyloBayes (Lartillot et al. 2013), were used to infer ten nuclear species trees, which also differ in whether nucleotide or amino acid sequences were used and in the way orthology was assessed (Ringelberg et al. 2022). In addition, a chloroplast phylogeny was inferred using off-target plastid sequences, bringing the total number of phylogenies to eleven. Topological congruence between these eleven different phylogenies was assessed. Support for relationships was expressed in numbers of supporting and conflicting gene trees using PhyParts (Smith et al. 2015) and QuartetScores (Zhou et al. 2020) (Figs 2–12), rather than conventional bootstrap or posterior support values that are known to be inflated in large phylogenomic datasets (Rokas and Carroll 2006; Pease et al. 2018).

Character evolution

To explore evolution of morphological traits that have been important for generic delimitation, we scored variation in armature, aspects of floral heteromorphy and mode of fruit dehiscence and mapped their distribution across the Caesalpinioideae phylogeny. Our goal was to highlight how an over-reliance on broadly-defined character complexes or functional traits may have misled classification in the past, rather than to perform detailed reconstructions of character evolution through time or to thoroughly assess the homology of various character states.

The three character complexes and their states were defined as follows:

- armature (six states): unarmed; nodal or internodal prickles on stem; stipular spines; nodal axillary thorns, including the axillary inflorescence axes which are modified into spines in *Chloroleucon* (Benth.) Britton & Rose; spinescent shoots.
- floral heteromorphy (three states): homomorphic, i.e. with no conspicuous modification or variation amongst flowers within an inflorescence (here we include inflorescences that do not show any conspicuous phenotypic variation beyond the very common occurrence of variable proportions of male and bisexual flowers within inflorescences of many mimosoid genera); heteromorphic 1 = basal flowers of the inflorescence with showy staminodia; heteromorphic 2 = the central flower (or flowers) enlarged/sessile cf. the peripheral (sometimes pedicellate) flowers.
- pod dehiscence (six states): indehiscent; inertly dehiscent along one or both sutures; explosively dehiscent, the woody valves twisting and splitting along both sutures along whole length of pod simultaneously; elastically dehiscent from the apex, the valves recurving, but not laterally twisting; craspedium, fruits breaking up into free-falling one-seeded articles leaving a persistent replum or whole valve breaking away intact from replum (valvately dehiscent); lomentiform fruit, the valves readily cracking between the seeds into one-seeded articles, taken here to include crypto-lomentiform fruits.

Data were assembled from taxonomic monographs, revisions and floras. Character evolution was simulated across the phylogeny using the 'make.simmap' function in the phytools (Revell 2012) R (R Core Team 2022) package, with 300 independent simulations and a 'symmetrical rates' (SYM) model. In each analysis, the character complex of interest (i.e. armature, floral heteromorphy and pod dehiscence) was treated as a single character with multiple states. A rooted phylogeny, without outgroups, was used for the analyses. The root character state was assigned an uninformed prior (i.e. each character state had the same initial probability of occurrence).

Data availability

A tree file of the ASTRAL phylogeny based on the single-copy genes (depicted in Figs 2–12) is included as online Suppl. material 4. In this tree file, all taxon names have been updated to reflect taxonomic changes made in all the entries in Advances in Legume Systematics 14 Part 1.

Results

Phylogenomics

For full results of the sequencing, orthology assembly and phylogenetic inference, see Ringelberg et al. (2022). Here a brief overview is provided.

Hybrid capture and sequencing yielded a large phylogenomic dataset with little missing data: the concatenated nucleotide alignment of the 821 single-copy nuclear genes (a subset of all 997 genes, see below) contains 944,871 sites, 824,713 alignment patterns (i.e. an indication of the phylogenetic informativeness of the alignment, determined by RAxML) and only 11.88% gaps. The ten nuclear species trees that were inferred using different phylogenetic methods are well-supported in terms of gene tree congruence measures (Figs 2–12) and largely congruent with each other. The few topological differences between different phylogenies typically involve only small numbers of species within relatively recent radiations, or deeper putative polytomies such as along the backbone of the ingoid clade, characterised by lack of phylogenetic signal across almost all genes (Koenen et al. 2020b), or the backbone of the Archidendron clade (Fig. 8), characterised by both lack of signal and high conflict amongst gene trees. These minor topological differences do not affect any of the findings of generic non-monophyly discussed below.

The plastid phylogeny (Suppl. material 3) differs more substantially from the nuclear species trees, reflecting the fact that nuclear and chloroplast genomes have unique and sometimes conflicting evolutionary histories (Bruun-Lund et al. 2017; Lee-Yaw et al. 2019; Rose et al. 2021). Cytonuclear discordance affects the monophyly of *Senegalia* Raf. (Terra et al. 2022), *Archidendron* F. Muell. (Brown et al. 2022), *Dimorphandra* Schott, the placement of *Desmanthus balsensis* J.L. Contreras (Hughes et al. 2022b) and whether *Zygia inundata* (Ducke) H.C. Lima ex

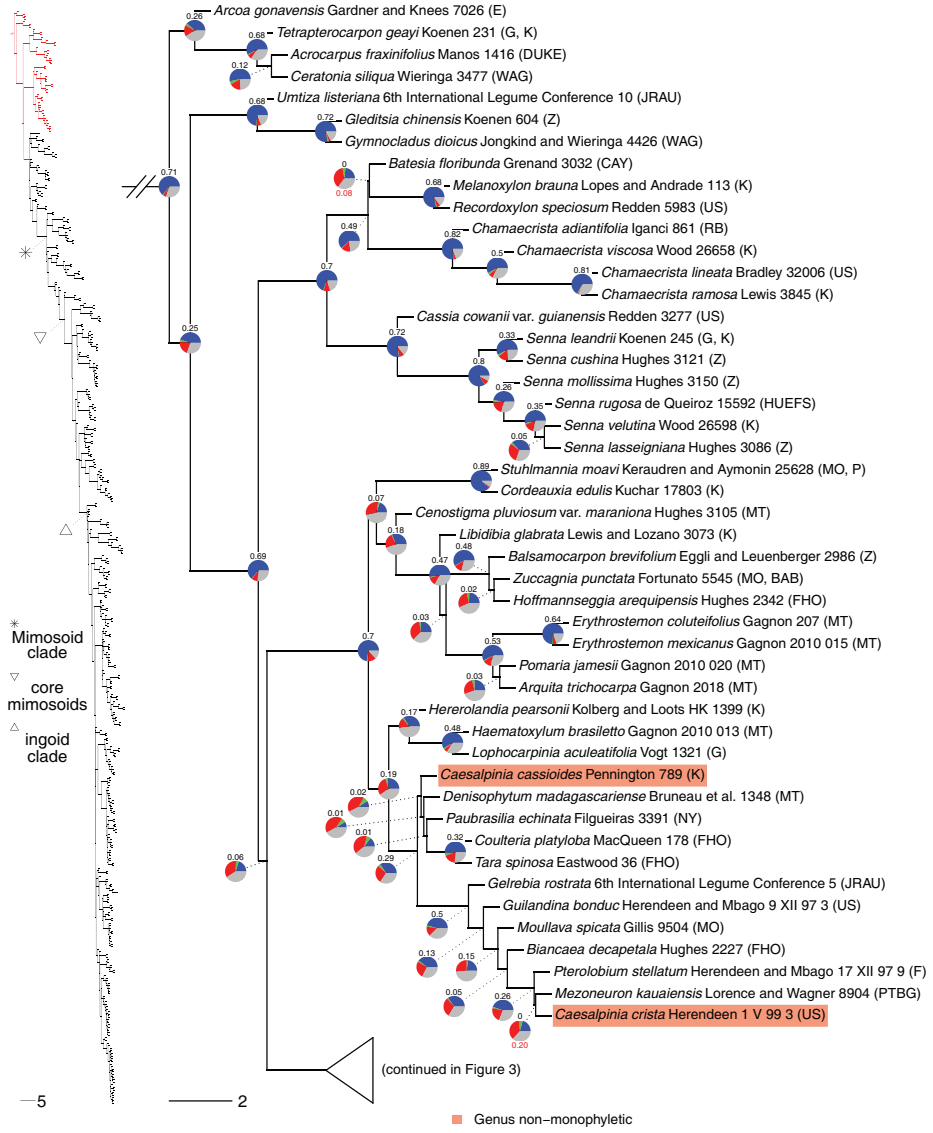

Figure 2. Phylogeny of Caesalpinioideae, part 1 (continued in Figs 3–12). Left part of figure shows complete Caesalpinioideae phylogeny with highlighted in red the part shown in detail on the right. Depicted phylogeny is the ASTRAL (Zhang et al. 2018) phylogeny based on 821 single-copy nuclear gene trees, with branch lengths expressed in coalescent units and terminal branches assigned an arbitrary uniform length for visual clarity. Genera resolved as (potentially) non-monophyletic are highlighted and clades recognised by Koenen et al. (2020b) are labelled. Support for relationships is based on gene tree conflict: pie charts show the fractions of supporting and conflicting gene trees per node calculated using PhyParts (Smith et al. 2015), with blue representing supporting gene trees, green gene trees supporting the most common alternative topology, red gene trees supporting further alternative topologies and grey gene trees uninformative for this node. Numbers above nodes are Extended Quadripartition Internode Certainty scores calculated with QuartetScores (Zhou et al. 2020). Numbers below nodes are the outcome of ASTRAL's polytomy test (Sayyari and Mirarab 2018), which tests for each node whether the polytomy null model can be rejected. Only non-significant (i.e. > 0.05) scores are shown, i.e. only for nodes that are better regarded as polytomies according to the test.

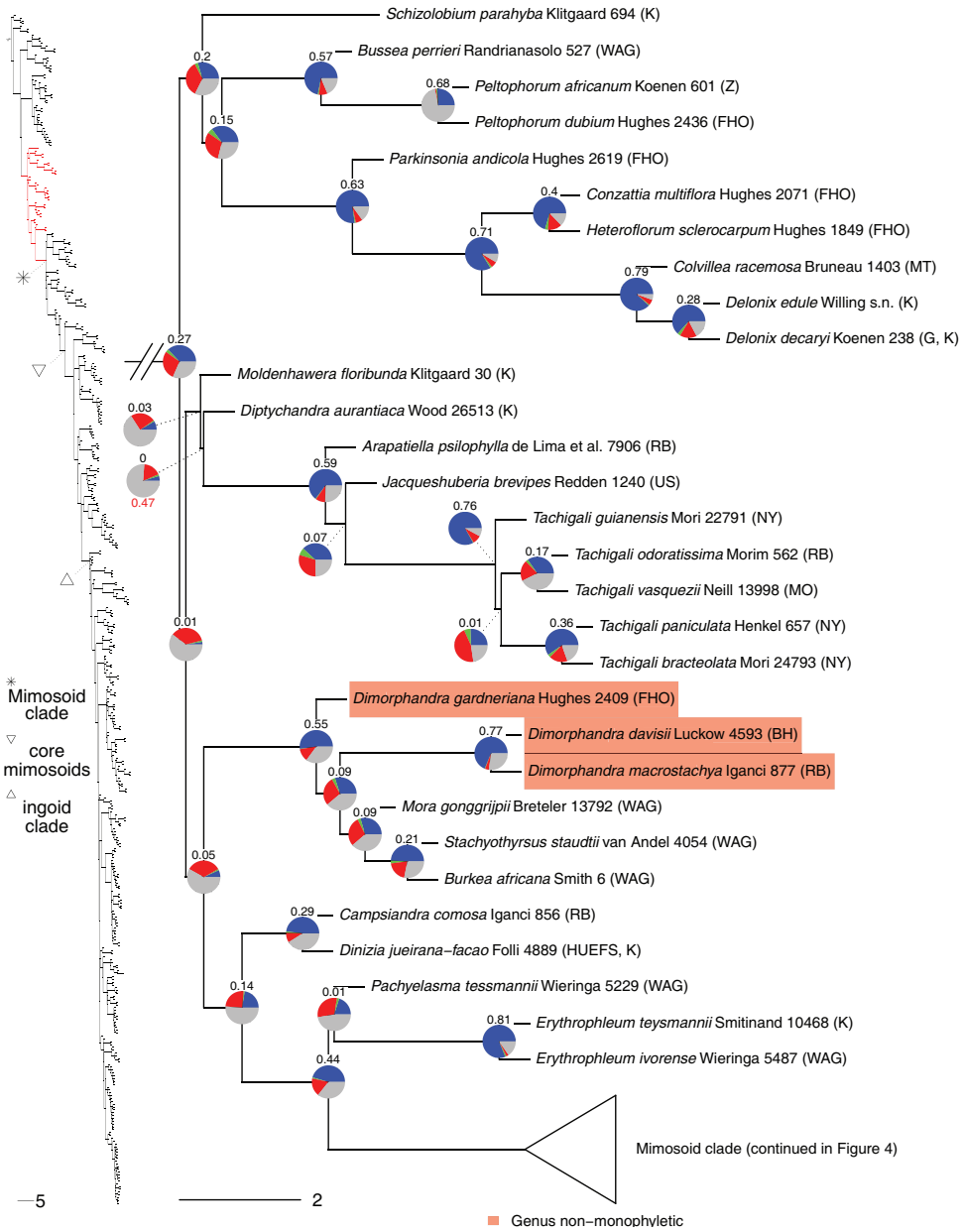

Figure 3. Phylogeny of Caesalpinioideae (continued). See Figure 2 for caption.

Barneby & J.W. Grimes and *Z. sabatieri* Barneby & J.W. Grimes form the sister clade of *Inga* or a grade subtending *Inga*.

Hereafter the ASTRAL phylogeny based on the subset of 821 single-copy nuclear gene trees is used as the 'reference' Caesalpinioideae backbone phylogeny (Figs 2–12). We use this particular tree over the plastome phylogeny because the nuclear dataset is

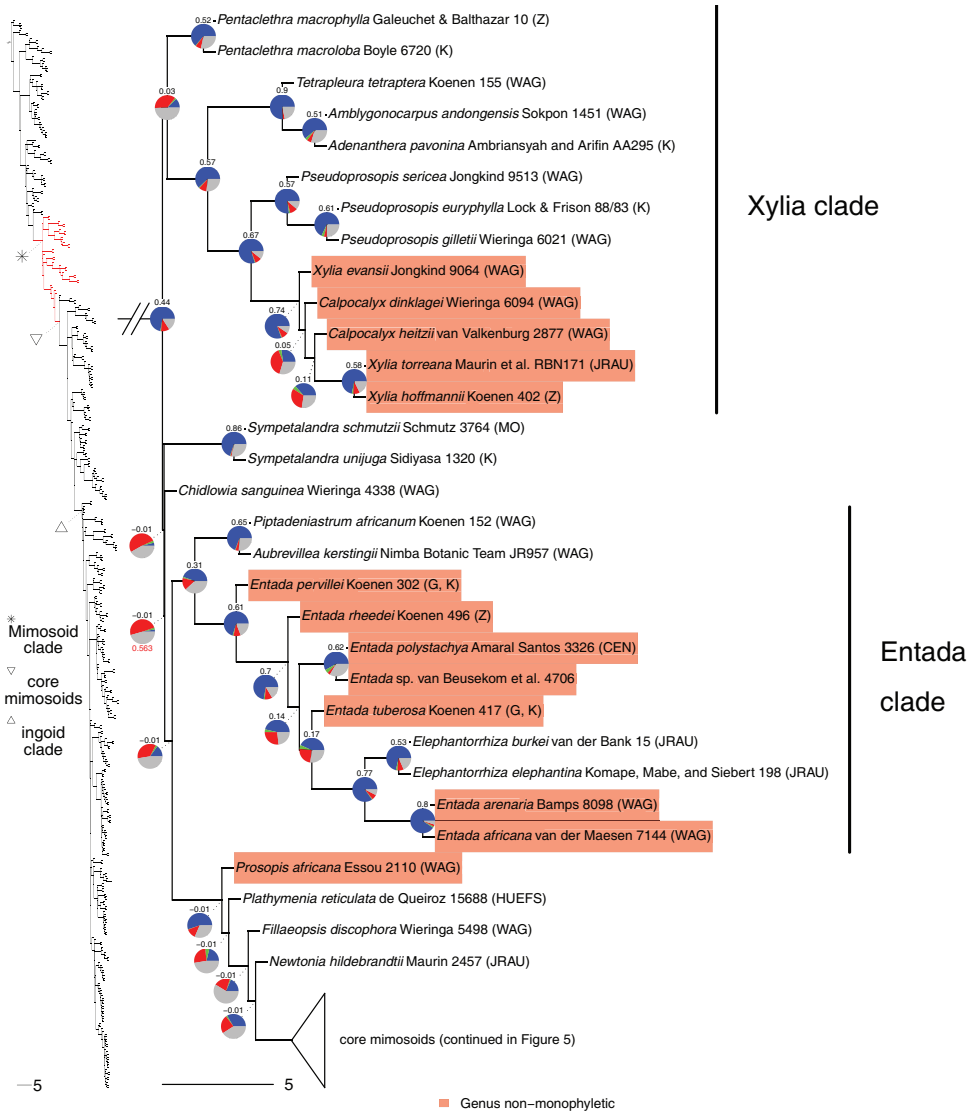

Figure 4. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

based on hundreds of independent loci and contains considerably more sites, taxa and fewer gaps, while the plastome phylogeny is based on a single non-recombining locus. The nuclear trees, therefore, likely better represent an approximation of the true evolutionary history of Caesalpinioideae than the phylogeny based on maternally inherited plastid data. Of the various nuclear trees, we select the ASTRAL phylogeny because we find extensive conflict amongst individual gene trees in certain parts of the phylogeny (Figs 2–12), which violates the central assumption of the concatenation model (Jiang et al. 2020) and because the multi-species coalescent model has been shown to consistently

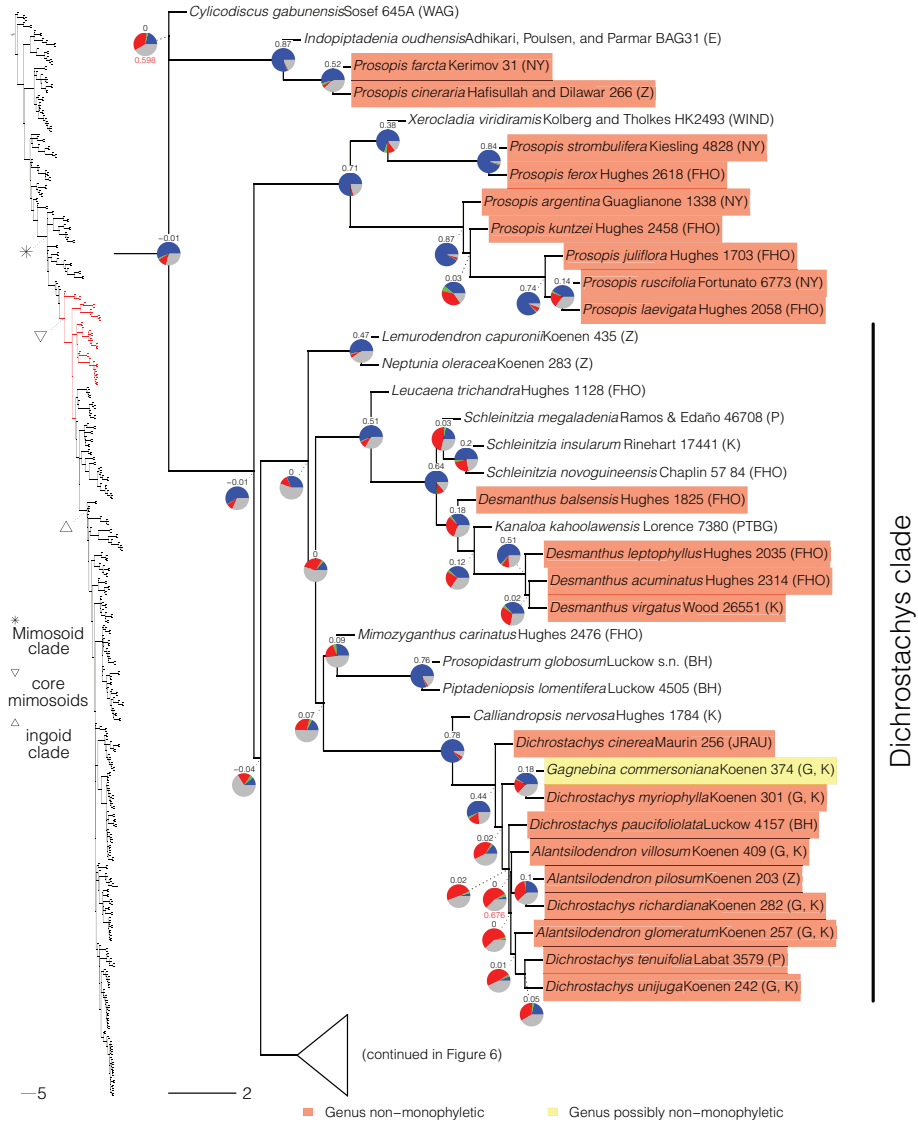

Figure 5. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

outperform the concatenation model on a range of phylogenomic datasets (Jiang et al. 2020). Our analyses reveal that different approaches to orthology assessment have a very minor impact on the final Caesalpinioideae phylogeny, likely because the vast majority of nuclear genes in our dataset are single-copy (i.e. 821 of 997) (see Ringelberg et al. 2022 for details). Nevertheless, how to deal with multi-copy genes is a contentious topic in phylogenetics (Yang and Smith 2014; Moore et al. 2018; Karimi et al. 2019) and we, therefore, focus on the ASTRAL phylogeny based on just the 821 single-copy genes.

The resultant ASTRAL phylogeny is, in general, robustly supported across the majority of nodes using measures of gene tree support and conflict (Figs 2–12). However,

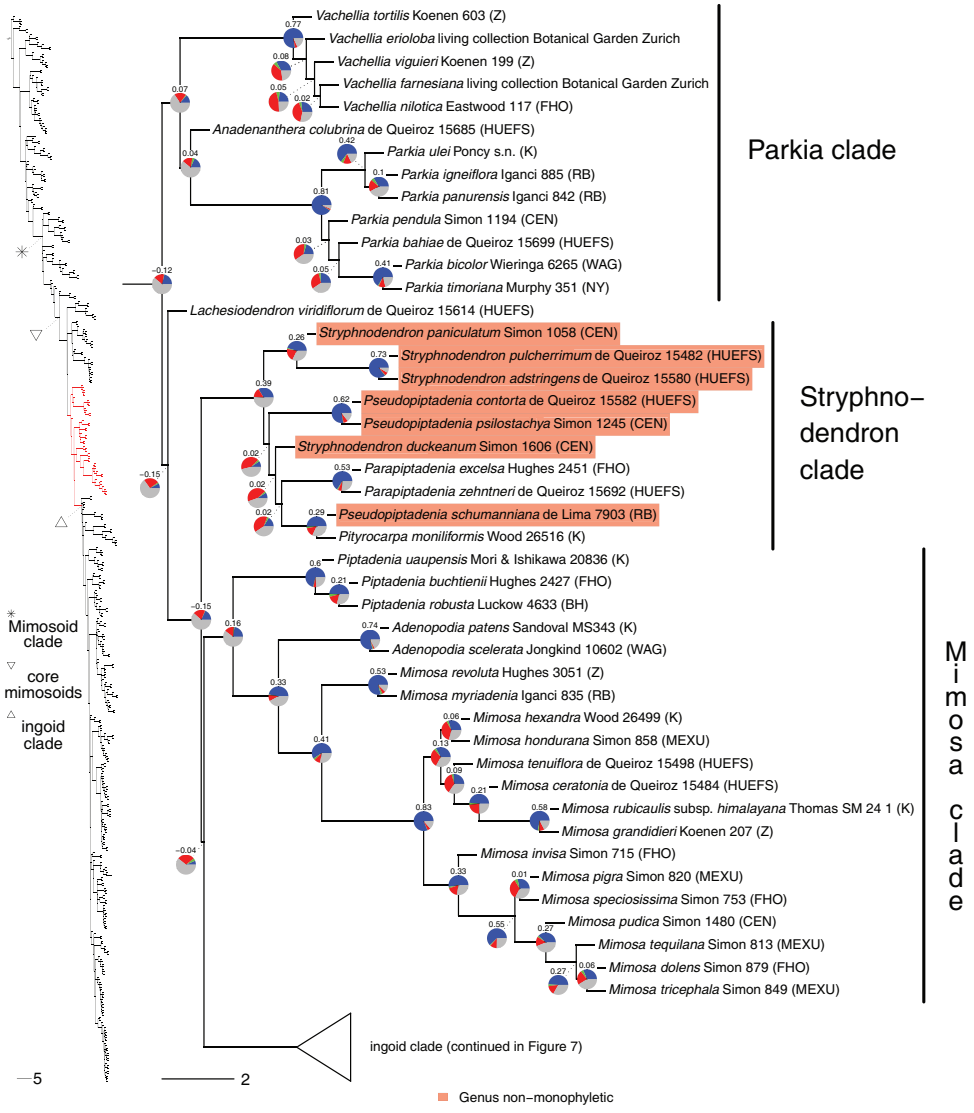

Figure 6. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

there are also some specific parts of the phylogeny which show high levels of gene tree conflict and/or lack of phylogenetic signal across large fractions of genes, which appears to be a feature of most phylogenies based on large phylogenomic datasets (Salichos and Rokas 2013; Wang et al. 2019; Jiang et al. 2020; Koenen et al. 2020a,b; Yang et al. 2020). In most cases, the primary source of gene tree conflict is limited signal in individual gene trees rather than the presence of strongly-supported alternative topologies amongst the gene trees (Figs 2–12, Koenen et al. 2020b), suggesting that the conflict

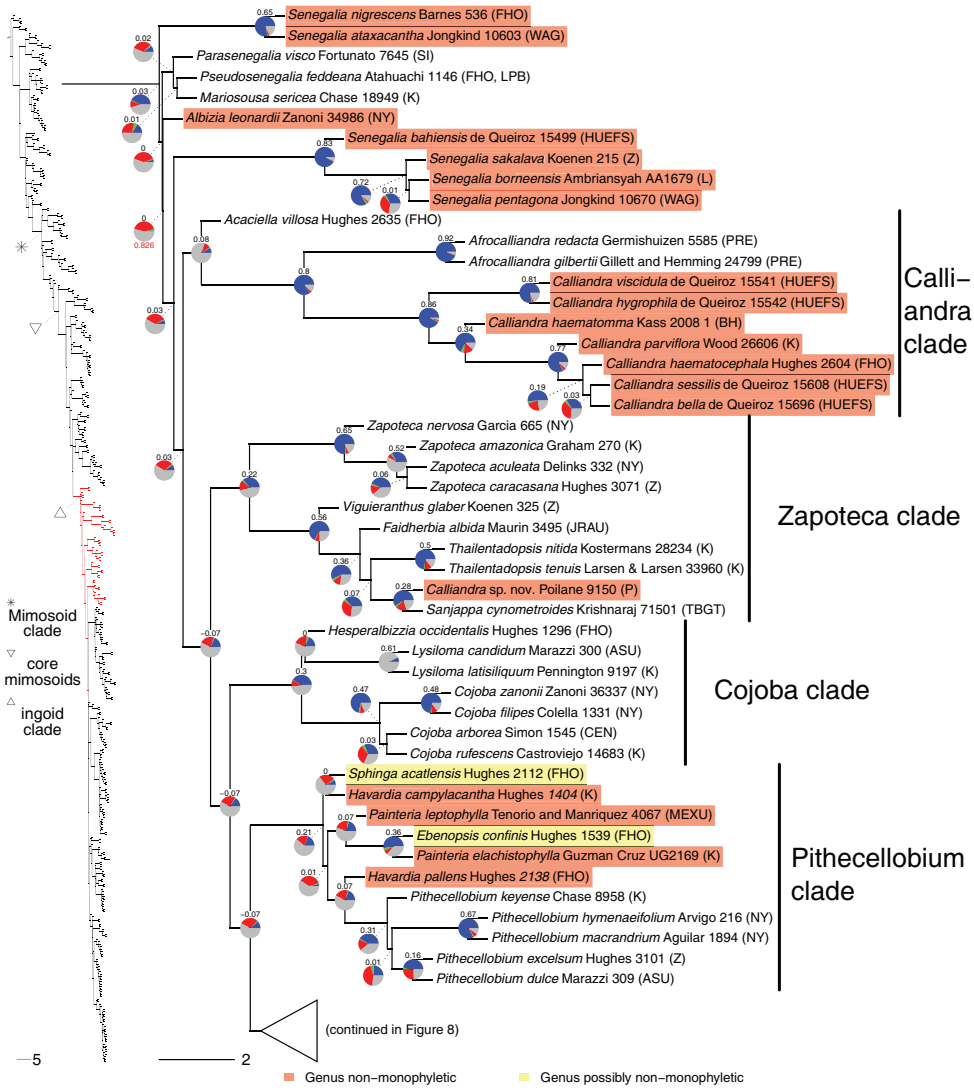

Figure 7. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

often has methodological rather than biological causes and implying that the presence of conflict per se is no reason for doubts about the recovered Caesalpinioideae topology. However, some parts of the phylogeny with high levels of gene tree conflict or lack of signal may be better viewed as potential polytomies, including the previously identified putative hard polytomy subtending a set of six or seven lineages along the backbone of the ingoid clade (Koenen et al. 2020b) and a putative polytomy across the backbone of the large Archidendron clade (see Appendix 1). These parts of the phylogeny showing

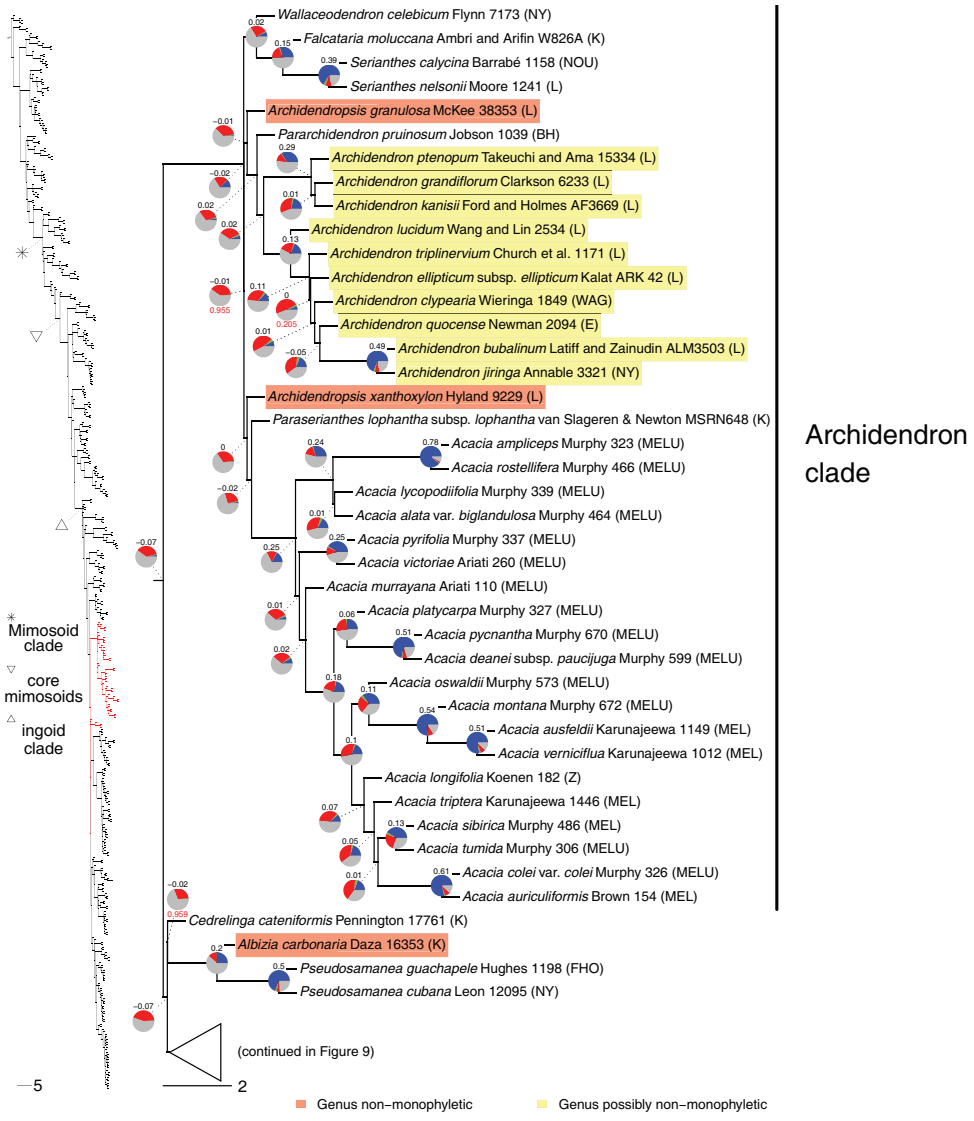

Figure 8. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

high gene tree conflict affect only a few decisions about generic delimitation, most notably across the grade comprising *Senegalia* and allies (Fig. 7; Terra et al. 2022) and across the backbone of the Archidendron clade (Fig. 8; Brown et al. 2022).

All the informally named clades of Koenen et al. (2020b; Fig. 1) are here confirmed with robust support in this new phylogeny (Figs 2–12), including the mimosoid clade that is robustly supported and subtended by a long branch (Fig. 4). Our results confirm placement of *Chidlowia* and *Sympetalandra* within the mimosoid clade and *Dinizia* outside the mimosoid clade, with high support (Fig. 4). Higher-level relationships that

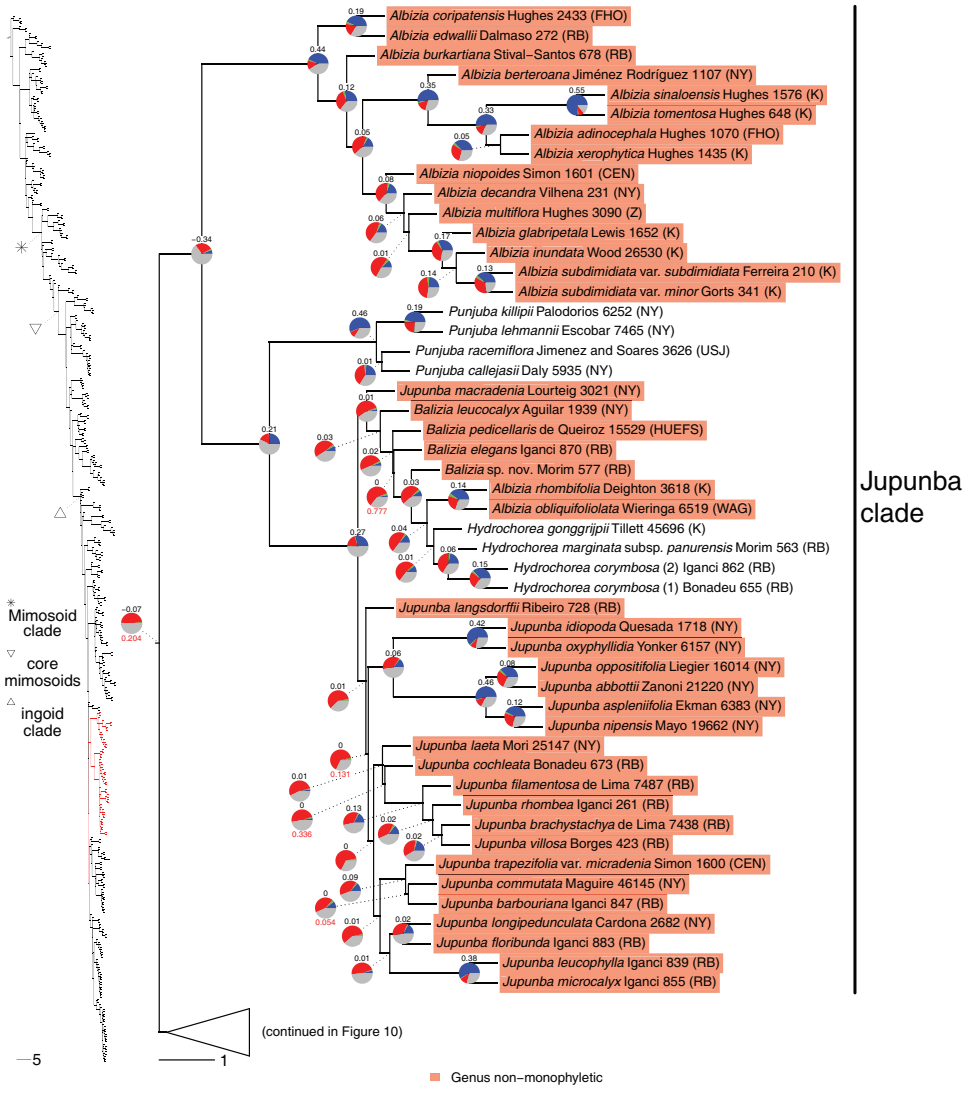

Figure 9. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

form the basis for the clade- and tribal-based classification of Caesalpinioideae presented in "Advances in Legume Systematics 14, Part 2", are not further discussed here.

Generic non-monophyly

Twenty-two genera were recovered as non-monophyletic or were nested within another genus and, therefore, likely require generic re-delimitation (Figs 2–12; Appendix 1). In addition, based on our results, the taxonomic status of *Gagnebina* Neck. ex DC.,

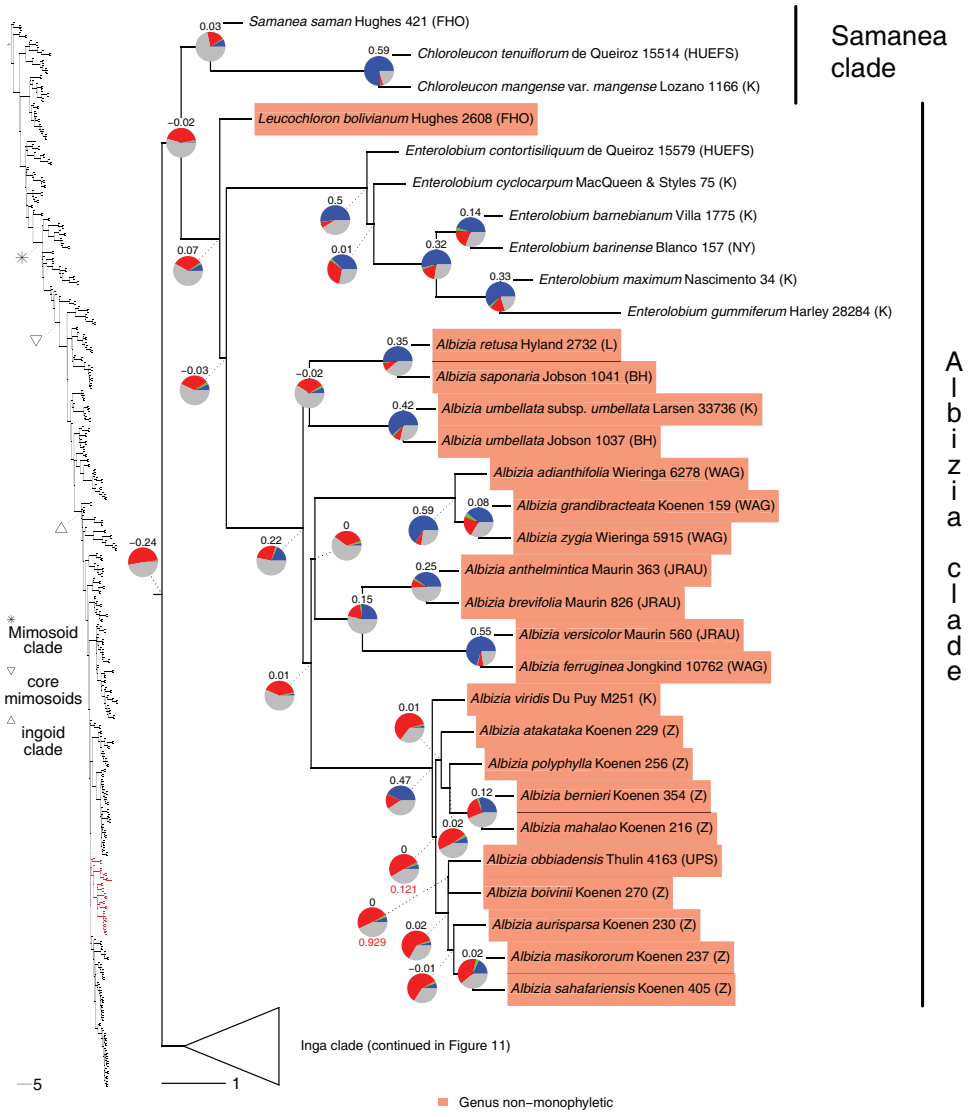

Figure 10. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

Sphinga Barneby & J.W. Grimes and *Ebenopsis* Britton & Rose, each represented here by a single taxon and nested in clades with complex generic relationships, require additional species sampling. Furthermore, although *Archidendron* species form a clade (Fig. 8), the genus is not supported as monophyletic in a substantial fraction of the individual gene trees (Fig. 8), nor in the plastid tree (Suppl. material 3) (see Brown et al. 2022). Overall, our results therefore show that 14(–17)% of the 152 Caesalpinioideae genera require re-delimitation and taxonomic updating. Only two of these genera are non-mimosoid Caesalpinioideae: *Dimorphandra* Schott and *Caesalpinia*. Almost all

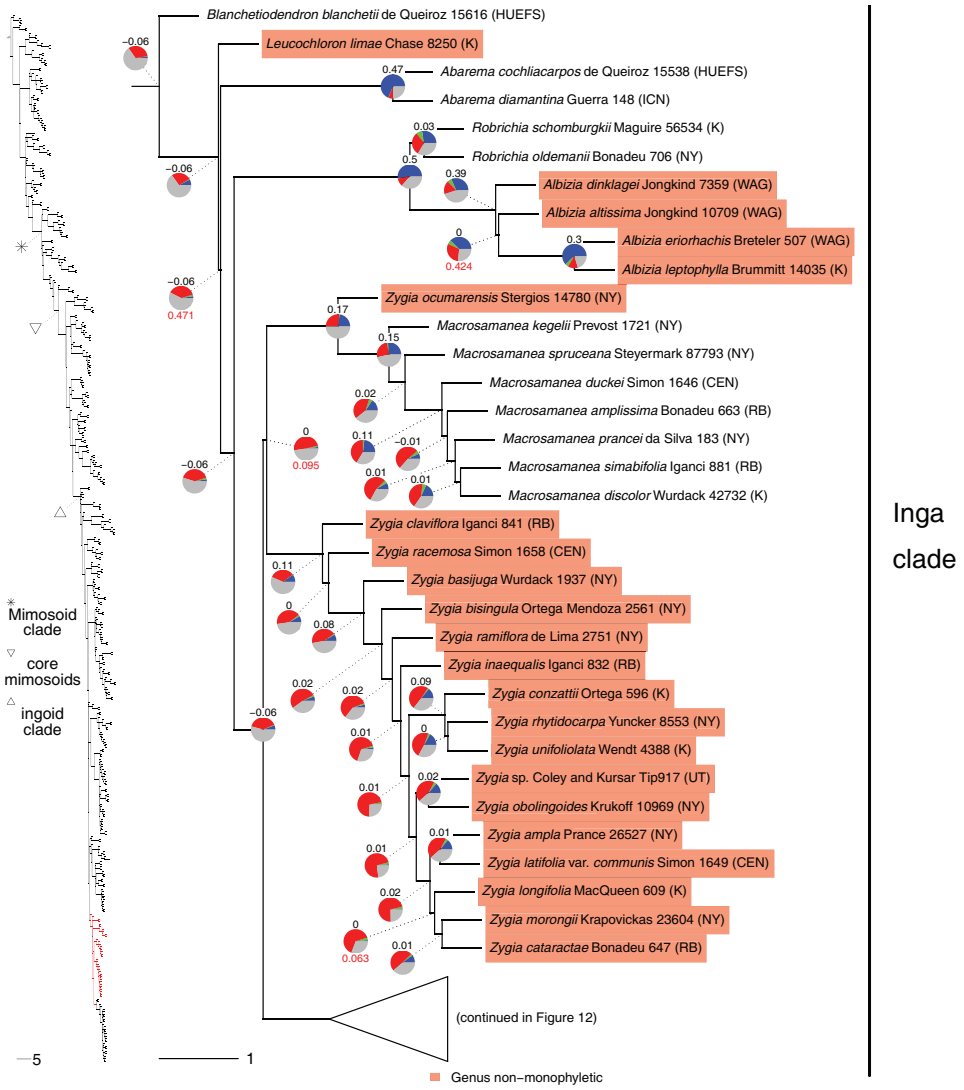

Figure 11. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

the non-monophyly issues are, therefore, in the mimosoid clade, where 22(–27)% of the 90 genera will require name changes.

Appendix 1 lists all (potentially) non-monophyletic genera with notes and pointers to papers in this Special Issue that discuss these genera and, in many cases, propose nomenclatural changes that resolve many of the non-monophyly issues revealed in our analyses. In some cases, it is clear that formal taxonomic re-circumscription must await more densely-sampled phylogenies and detailed morphological analyses. It is also important to note that, unless explicitly stated otherwise, the reported generic non-monophyly is recovered in all trees (i.e. the nuclear ASTRAL, RAxML and Phy-

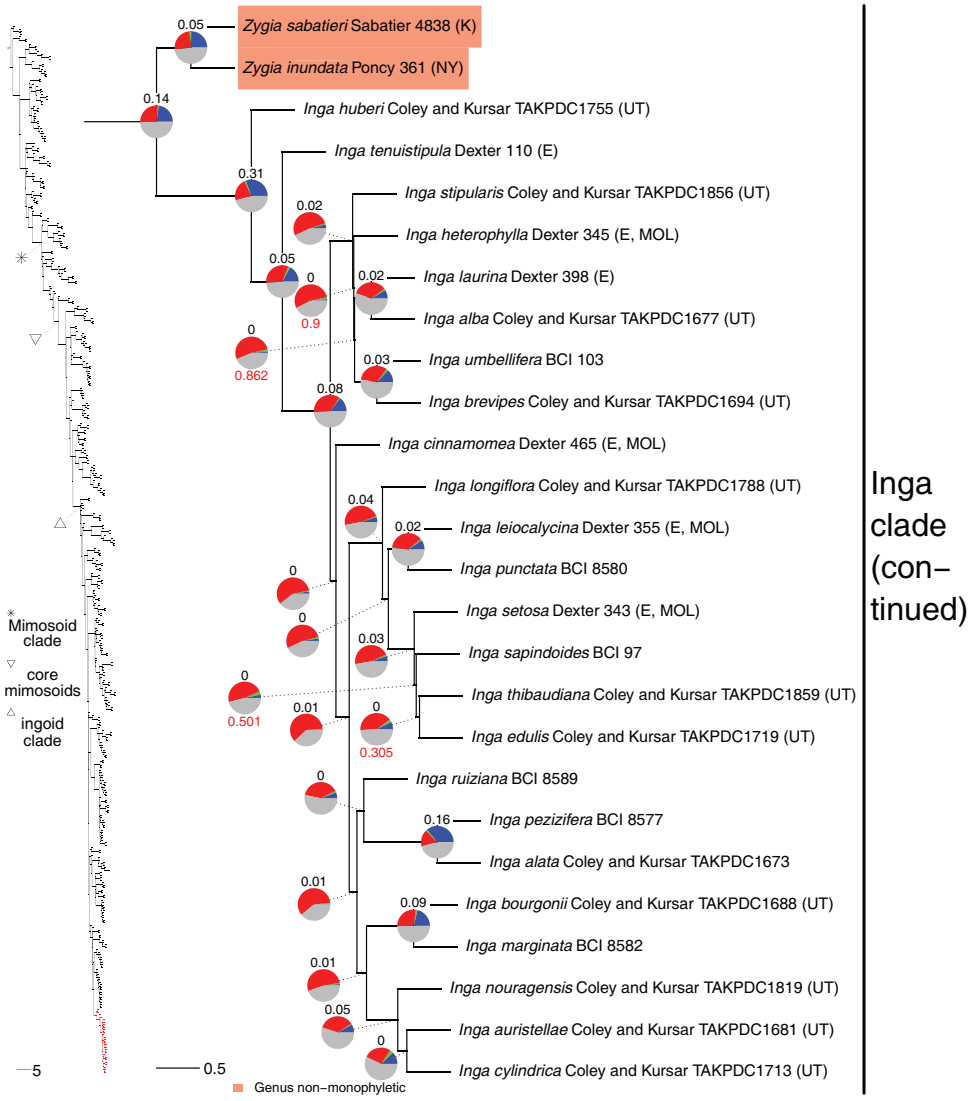

Figure 12. Phylogeny of Caesalpinioideae (continued). See Fig. 2 for caption.

loBayes species trees and chloroplast phylogeny) with high support values expressed and assessed in terms of numbers or fractions of supporting or conflicting genes.

Character evolution

Armature, types of inflorescence heteromorphy and pod dehiscence type each show high levels of homoplasy (Figs 13–15, Table S2) with all types of armature, floral heteromorphy and pod dehiscence hypothesised to have evolved multiple times.

Discussion

Generic non-monophyly

The new Caesalpinioideae phylogeny (Figs 2–12) reveals extensive generic non-monophyly: 22 genera are non-monophyletic or nested within another genus and four other genera could likely also be non-monophyletic (Appendix 1). Notably, there are just two non-monophyletic genera (3% of the 62) across the non-mimosoid Caesalpinioideae, while 20 (to 24) mimosoid genera (i.e. 22(–27)% of 90 genera) are non-monophyletic. The discovery of such a high level of generic non-monophyly in the mimosoid clade is likely attributable to the denser taxon sampling in mimosoids than non-mimosoids in our analyses; the greater species-richness of mimosoids, which account for ca. 75% of the ca. 4,600 Caesalpinioideae species (LPWG 2017), but only 59% of the 152 genera, indicating that, on average, mimosoid genera are more species-rich and, therefore, more likely to have monophyly issues than non-mimosoid Caesalpinioideae genera; the fact that the Caesalpinia Group, the most problematic clade of non-mimosoid Caesalpinioideae in terms of generic delimitation, was already largely resolved by Gagnon et al. (2016), further reducing the likelihood of non-monophyly issues across non-mimosoid Caesalpinioideae; and finally, the continued legacy of Bentham's broadly circumscribed mimosoid genera which has still not been fully resolved. For example, *Acacia*, which as indicated earlier, was once a pantropical genus with over 1,400 species (Miller and Seigler 2012) and now comprises seven genera, yet one of these genera, *Senegalia*, is here recovered as non-monophyletic (Fig. 7) and further subdivision of *Senegalia* seems likely (Terra et al. 2022). Similarly, *Calliandra* once had a pantropical distribution until Barneby (1998) restricted it to the New World (de Souza et al. 2013). However, not all Old World *Calliandra* species have yet been assigned to other genera and *Calliandra*, therefore, also remains non-monophyletic (Fig. 7). Finally, *Albizia*, the last mimosoid 'dustbin genus' (Barneby and Grimes 1996; Brown 2008; Koenen et al. 2020b) is here confirmed to be non-monophyletic in line with previous findings (Koenen et al. 2020b) (Figs 7–11), but with two previously unsampled Neotropical species each representing additional evolutionary lineages (Terra et al. 2022; Koenen 2022b). Nevertheless, most African, Madagascan and Asian *Albizia* species do form a single clade (Fig. 10; Koenen et al., unpublished data), while most Neotropical species are also in a single clade (Aviles et al. 2022) (Fig. 9, see Appendix 1).

Morphological homoplasy

Given the extensive re-arrangements of genera in Caesalpinioideae over the last two decades, the question arises why such a significant fraction of genera is still non-monophyletic in these new phylogenomic analyses. We identify two main reasons for this. First, extensive morphological homoplasy has misled generic delimitation and second, lack of pantropical taxonomic synthesis and phylogenetic sampling have resulted in

failure to identify clades that span the Old World and New World or, conversely, amphi-Atlantic genera that are non-monophyletic, i.e. potential trans-continental connections and disconnects.

First, and most importantly, the likely extent of homoplasy of morphology and functional traits across Caesalpinioideae is only now starting to be revealed using this new phylogeny (Figs 13–15; de Faria et al. 2022). Here, we reconstructed hypotheses for the evolutionary trajectories of three trait syndromes – armature, mode of fruit dehiscence and aspects of floral heteromorphy – to demonstrate the extent of homoplasy and to show how the repeated evolution of distinctive types of, for example, fruit dehiscence has misled generic delimitation.

Fruits are highly diverse across Caesalpinioideae reflecting adaptations for hydrochory, anemochory, endozoochory, ornithochory, and myrmecochory, as well as several forms of mechanical seed dispersal via explosively, elastically and inertly dehiscent fruits. Here, we show that fruit dehiscence type shows extensive homoplasy across the mimosoid clade, with repeated evolution of, for example, pods elastically dehiscent from the apex, craspedia and lomentiform fruits (Fig. 13). It is now clear that repeated, potentially convergent evolution of fruit types has repeatedly misled generic delimitation and provided the basis for 'fruit genera' that have subsequently been shown to be non-monophyletic.

For example, as pointed out by Barneby (1998), the only character uniting Bentham's (1875) broadly circumscribed pantropical *Calliandra* was the elastically dehiscent fruit, opening from the apex with the valves recurving, but not laterally twisting (Fig. 13a–e). Just how misplaced this reliance on fruit type as a generic synapomorphy was, is evident from the long parade of new genera segregated from *Calliandra*, most of them in the two decades after Barneby (1998) restricted the genus to just the New World species: *Zapoteca* H.M. Hern. (Hernández 1986), *Viguieranthus* Villiers (Du Puy et al. 2002), *Thailentadopsis* Kostermans (Lewis and Schrire 2003), *Afrocalliandra* E.R. Souza & L.P. Queiroz (de Souza et al. 2013) and *Sanjappa* E.R. Souza & M.V. Krishnaraj (de Souza et al. 2016). This procession is still incomplete given that *Calliandra* is still non-monophyletic (Fig. 7), pending phylogenetic placement of the Asian *Calliandra umbrosa* (Wall.) Benth. (see de Souza et al. 2016) and an, as yet, undescribed species (Fig. 7), the last remaining of the species excluded from *Calliandra* by Barneby (1998) that have not yet been placed in a segregate genus. It is clear that the distinctive '*Calliandra* pod' has evolved at least six times independently across Caesalpinioideae (Fig. 13) and occurs in at least 12 phylogenetically scattered genera including *Jaqueshuberia* Ducke, *Bussea* Harms, *Pseudoprosopis* Harms, some species of *Dichrostachys* (DC.) Wight & Arn., *Alantsilodendron* Villiers, *Calliandropsis* H.M. Hern. & P. Guinet, *Calliandra*, *Zapoteca*, *Viguieranthus*, *Sanjappa*, *Afrocalliandra* and a small subset of species of *Acacia*. Of course, it is possible that more detailed anatomical investigation of these morphologically and functionally similar fruits will reveal anatomical differences that show that the homology of this fruit type is misplaced, but the structure of the pod valves and raised sutures of most of these are remarkably similar (Fig. 13a–e).

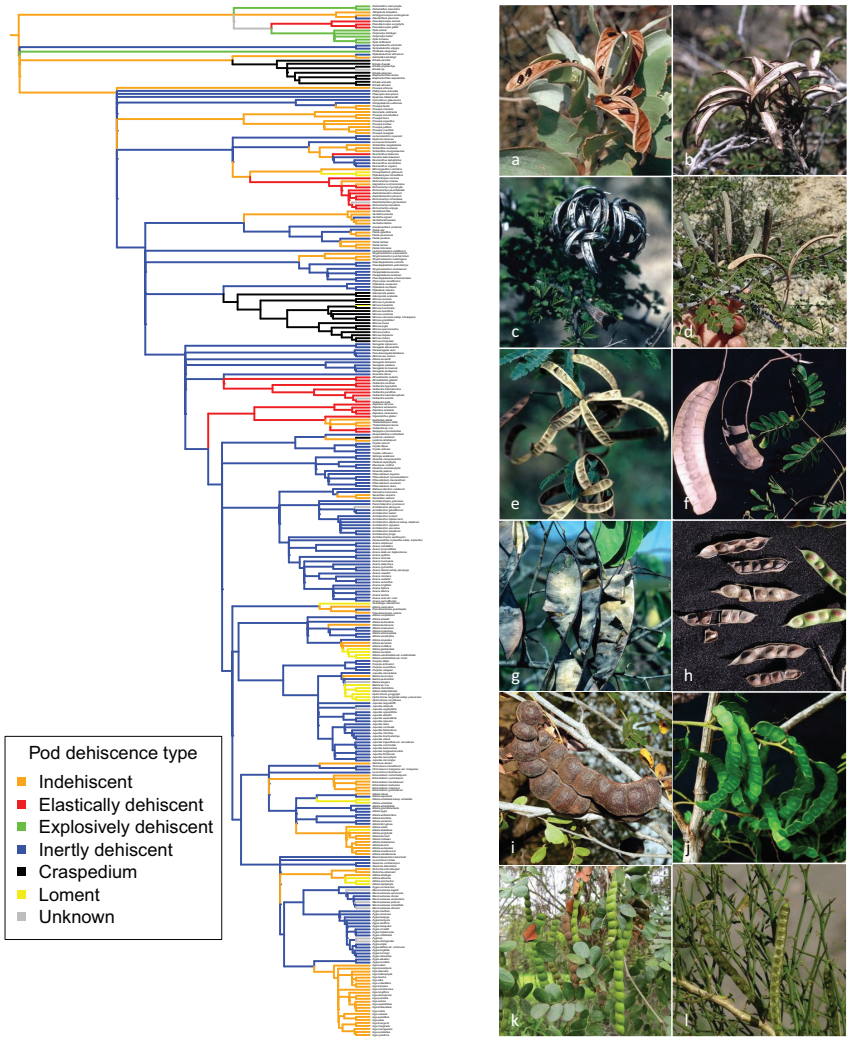

Figure 13. Evolution of fruit dehiscence types across the mimosoid clade. Character states were defined as: *indehiscent*; *inertly dehiscent* along one or both sutures; *explosively dehiscent*, whereby the woody valves twist and split along both sutures along whole length of pod simultaneously; *elastically dehiscent* from the apex, the valves recurving, but not laterally twisting; *craspedium*, i.e. fruits breaking up into free-falling one-seeded articles leaving a persistent replum or whole valve breaking away intact from replum (valvately dehiscent); *lomentiform* fruit, i.e. the valves readily cracking between the seeds into one-seeded articles, taken here to include crypto-lomentiform fruits. Branch lengths are not informative in this figure. Photos **a–e** elastically dehiscent **a** *Acacia argyraea* Tindale **b** *Calliandra prostrata* Benth. **c** *Calliandropsis nervosa* (Britton & Rose) H.M. Hern. & P. Guinet **d** *Alantsilodendron mahafalense* (R. Vig.) Villiers **e** *Zapoteca portoricensis* (Jacq.) H.M. Hern **f–h** craspedium **f** *Entada polystachya* (L.) DC. **g** *Lysiloma tergeminum* Benth. **h** *Mimosa montana* Kunth. var. *sandemanii* Barneby **i–l** lomentiform **i** *Albizia moniliformis* (DC.) F. Muell. **j** *Albizia subdimidiata* (Splitg.) Barneby & J.W. Grimes **k** *Albizia pistaciifolia* (Willd.) Barneby & J.W. Grimes **l** *Prosopidastrum globosum* (Gillies ex Hook. & Arn.) Burkart. Photos **a** Bruce Maslin **b, c, e–h** Colin Hughes **d** http://clubbotatoliara.e-monsite.com/pages/posters-films-rapports/photos.html **i** Garry Sankowsky http://www.rainforestmagic.com.au **j** Marcelo Simon **k** Xavier Cornejo **l** https://www.floramendocina.com.ar.

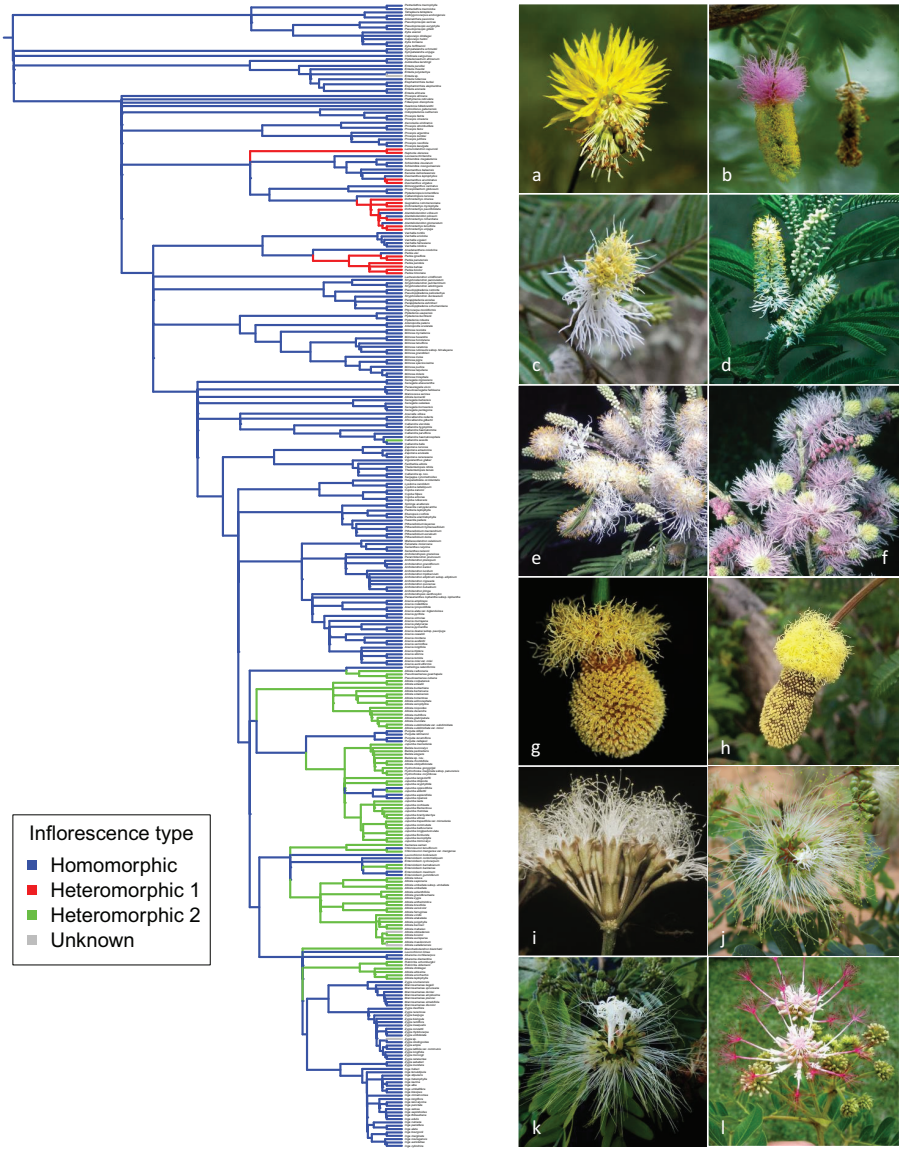

Figure 14. Evolution of types of floral heteromorphy across the mimosoid clade. Character states were defined as: *homomorphic*, i.e. with no conspicuous modification or variation amongst flowers within an inflorescence (here we include inflorescences that can comprise proportions of male and bisexual flowers, but no other more conspicuous variation); *heteromorphic 1* = basal flowers of the inflorescence with showy staminodia; *heteromorphic 2* = flowers dimorphic within an inflorescence, the central flower (or flowers) enlarged/sessile cf. the peripheral (sometimes pedicellate) flowers. Branch lengths are not informative in this figure. Photos **a–h** heteromorphic 1 **a** *Neptunia plena* (L.) Benth. **b** *Dichrostachys cinerea* (L.) Wight & Arn. **c** *Dichrostachys myriophylla* Baker **d** *Gagnebina pterocarpa* (Lam.) Baill. **e** *Dichrostachys bernieriana* Baill. **f** *Dichrostachys akataensis* Villiers **g** *Parkia bahiae* H.C. Hopkins **h** *Parkia nitida* Miq. **i–l** heteromorphic 2 **i** *Pseudosamanea guachapele* (Kunth) Harms **j** *Albizia obliquifoliolata* De Wild. **k** *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes **l** *Albizia grandibracteata* Taub. Photos **a, b, g, i** Colin Hughes **c, k, l** Erik Koenen **d** Melissa Luckow **e, f** Dave Du Puy **h** Giacomo Sellan https://identify.plantnet.org/the-plant-list/observations/1012799991 **j** Jan Wieringa.

There are several other examples of classifications and especially genera being misled by parallel evolution of fruit types. For example, the polyphyly of the genus *Enterolobium* Mart. (de Souza et al. 2022a; Figs 10–11) was unexpected because the two clades of *Enterolobium* species share the distinctive indehiscent thickened and curled 'ear pod' fruit type. Similarly, it also seems clear that septate lomentiform fruits with valves readily cracking between the seeds and breaking up into one-seeded articles have also evolved multiple times (Fig. 13), often within genera (e.g. Capuron 1970; Aviles et al. 2022; Koenen 2022a; Soares et al. 2022) associated with hydrochory in species adapted to grow in seasonally inundated habitats and this has impacted on generic delimitation. For example, Barneby and Grimes (1996) separated their newly-segregated genera *Balizia* and *Hydrochorea* Barneby & J.W. Grimes on fruit types, yet it is clear that *Hydrochorea* is nested within a paraphyletic *Balizia* (Fig. 9; Soares et al. 2022) and that the distinctive lomentiform fruits of *Hydrochorea* are derived from non-lomentiform indehiscent or follicularly dehiscent pods within this clade (Aviles et al. 2022; Soares et al. 2022). This prevalence of homoplasy associated with fruit types across the mimosoid clade matches that seen across other legume clades (e.g. in subfamily Papilionoideae; Geesink 1984; Hu et al. 2000; Lavin et al. 2001) suggesting that the late developmental stages of the legume pod and associated legume seed dispersal syndromes are prone to convergent evolution, as previously suggested (Geesink 1984; Hu et al. 2000).

Of course, homoplasy per se in no way negates the value and importance of morphology for classification, but instead prompts re-evaluation of homology and the utility of specific morphological characters via reciprocal illumination with new molecular phylogenetic evidence. For example, armature is also homoplasious across Caesalpinioideae with repeated evolution of stipular spines, nodal and internodal prickles, axillary thorns and spinescent shoots (Fig. 15). While armature has been little used as the basis for defining genera because vegetative characters were generally downplayed compared to floral and fruit characters (e.g. Bentham 1875; Burkart 1976), the utility of armature for delimiting some groups within individual clades is increasingly apparent. For example, the four genera segregated from the non-monophyletic *Prosopis* s.l. by Hughes et al. (2022a) are diagnosed by different types of armature (Fig. 15). Similarly, armature is an important character distinguishing the segregates of *Acacia* s.l. (spinescent stipules in *Vachellia*, nodal and internodal prickles in *Senegalia*, unarmed in *Acacia* s.s., *Parasenegalia*, *Pseudosenegalia*, *Mariosousa* and *Acaciella*) and the distribution of prickles (nodal vs. internodal) is discussed in relation to the non-monophyly of *Senegalia* (Terra et al. 2022). Similarly, the two major clades of genera that make up the Caesalpinia Group (Figs 2 and 15) are separated by differences in armature.

Detailed phylogenetic reconstructions for other characters, based on more rigorous and detailed anatomical assessment of homology, will undoubtedly be worthwhile, but it is already clear that the three traits mapped here (Figs 13–15) are not exceptional in terms of their high levels of homoplasy. Leaves also show evolutionarily labile patterns with numerous repeated transitions from micro- to macrophyllidinous leaves within a large majority of Caesalpinioideae genera. Even the more prominent leaf type innovations of bipinnate

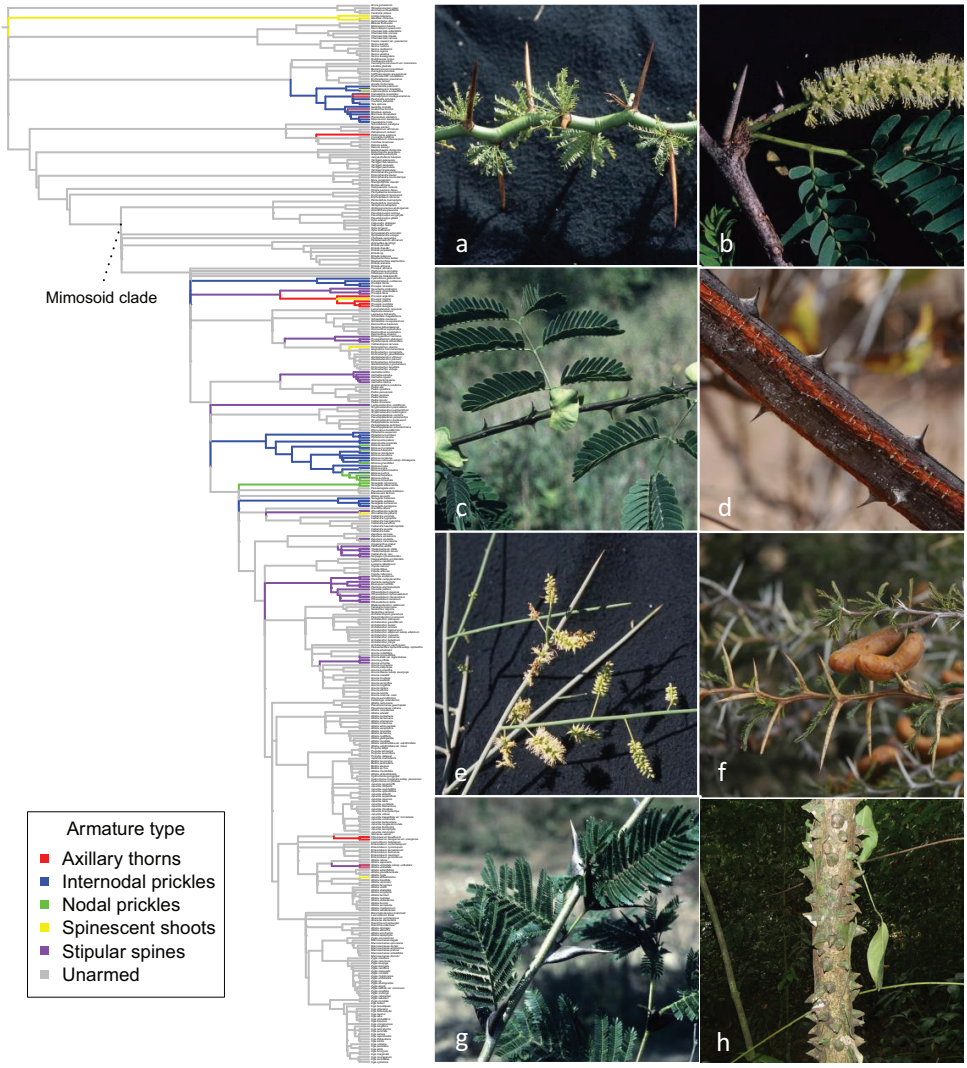

Figure 15. Evolution of different types of armature across Caesalpinioideae. Character states were defined as: *unarmed*; *nodal or internodal prickles on stem*; *stipular spines*; *nodal axillary thorns* including modified inflorescence axes of *Chloroleucon*; *spinescent shoots*. Branch lengths are not informative in this figure. Photos **a** and **b** axillary thorns **a** *Parkinsonia andicola* (Griseb.) Varjão & Mansano **b** *Prosopis juliflora* (Sw.) DC. **c, d, h** internodal prickles **c** *Senegalia tamarindifolia* (L.) Britton & Rose **d** *Mimosa ophthalmocentra* Mart. ex Benth. **e** spinescent shoots, *Prosopis kuntzei* Harms **f** and **g** stipular spines **f** *Prosopis ferox* Griseb. **g** *Vachellia cornigera* (L.) Seigler & Ebinger **h** *Cylicodiscus gabunensis* Harms. All photos Colin Hughes, except **h** William Hawthorne.

vs. pinnate leaves, presence of phyllodes and presence or absence of extrafloral leaf nectaries (EFNs) are all hypothesised to be homoplasious. Multiple reversals to once-pinnate leaves within mimosoids (*Inga*, *Calliandra hymenaeodes* (Persoon) Benth., *Sanjappa cyn-*

ometroides (Bedd.) E.R. Souza & M.V. Krishnaraj and *Cojoba rufescens* (Benth.) Britton & Rose), multiple origins of phyllodes (in *Acacia* pro parte, species of *Senna* including *S. phyllodinea* (R. Br.) Symon and some varieties of *S. artemisoides* (Gaudich. ex DC.) Randell and *Mimosa* species including, for example, *M. extranea* Benth. and *M. phyllodinea* Benth. (Barneby 1991)), and multiple losses of EFNs (Marazzi et al. 2019) need to be hypothesised to account for the phylogenetic distributions of these traits. Floral traits show similar extensive homoplasy with multiple derivations of different types of floral heteromorphy (Fig. 14), numerous switches between spikes and capitula and repeated evolution of diverse compound inflorescence conformations (Grimes 1999), homoplasious occurrences of different types of anther glands (Luckow and Grimes 1997) and extremely diverse and evolutionarily labile shapes and sizes of polyads, even within some genera (e.g. Hughes 1997). As indicated above, number of stamens and their connation or not into a staminal tube, the two androecial traits that underpinned the tribal classification of mimosoids first established by Bentham (1875), are also homoplasious across mimosoids such that the tribal classification has not stood the test of time and molecular phylogenetics. Plant functional traits including nodulation (de Faria et al. 2022) and growth forms (Gagnon et al. 2019) also show high levels of homoplasy. Indeed, it appears that nearly all Caesalpinioideae morphological characters and functional traits are homoplasious, given that collectively we, as authors familiar with Caesalpinioideae, have been unable to come up with any morphological characters or functional traits that provide robust synapomorphies subtending larger subclades within Caesalpinioideae, due to either multiple evolutionary origins or repeated independent losses or reversals. Perhaps the one exception to this would be the aquatic habit in *Neptunia* Lour. spp., which is unique within Caesalpinioideae, although many mimosoids are rheophytes, tolerant of seasonal flooding. This is very much in line with the idea that vegetative, flower and fruit characters may be equally homoplasious, as found in other legume groups such as the dalbergioid clade in Papilionoideae (Lavin et al. 2001).

Pre-eminence of certain morphological characters over others in classification of a group and the prevalence of 'organogenera' (sensu Nielsen 1981) united by just a single character, in situations where morphology is pervasively homoplasious, has been at the root of many of the disagreements about generic delimitation in mimosoids, as pointed out by Guinet (1981).

Trans-continental sampling

A second important reason for the extensive generic non-monophyly is the lack of pantropical synthesis and integration that has been the hallmark of much taxonomic work on Caesalpinioideae up to now and the lack of adequate pantropical sampling of taxa in previous phylogenies. In this light, it is notable that two of the most productive and influential mimosoid taxonomists of the twentieth century, both of whom significantly reshaped the generic classification – Rupert Barneby and Ivan Nielsen – worked largely independently in different geographical areas, especially on genera of the former tribe Ingeae. While both were very much aware of the wider pantropical dimensions and elements of their groups, Barneby focused primarily on New World mimosoids (e.g.

Barneby 1991, 1998; Barneby and Grimes 1996, 1997), while Nielsen concentrated on Australasian mimosoids (e.g. Nielsen 1981, 1992) and neither was fully familiar with the details of species of the other (see e.g. Barneby and Grimes 1996), such that no pantropical synthesis across mimosoids was fully achieved and New World – Old World clades that span the Old World and New World or conversely, amphi-Atlantic genera that are non-monophyletic, although hypothesised by both authors, were not resolved.

Our new phylogeny with its near-complete generic sampling reveals several instances of Old World – New World connections and disconnects that have important implications for generic delimitation and which were not fully apparent before. First, the amphi-Atlantic genus *Prosopis* is shown to be non-monophyletic (Figs 4 and 5), confirming earlier evidence of Catalano et al. (2008). *Prosopis africana* (Guill. & Perr.) Taub. forms a monospecific lineage unrelated to the rest of *Prosopis*, while the remaining three Old World species are sister to the Indo-Nepalese *Indopiptadenia* Brenan and New World *Prosopis* has the Namibian-Namaqualand monospecific *Xerocladia* Harv. nested within it (Fig. 5). It is, therefore, clear that Burkart's (1976) broad trans-continental concept of *Prosopis* s.l., which followed Bentham's (1842, 1875) circumscription, is not sustainable (see Hughes et al. 2022a). A second example of disconnection between Old and New World elements of a pantropical genus is *Albizia*, where species of New World section *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes form a clade quite separate from Old World *Albizia* s.s. (Figs 9 and 10; Koenen et al. 2020b: see Aviles et al. 2022). Conversely, two previously poorly understood New World – Old World connections have been revealed. First, it is now clear that the African rainforest species *Albizia obliquifoliolata* De Willd. and *A. rhombifolia* Benth. (previously often referred to the genus *Cathormion*) are nested within the New World *Balizia* / *Hydrochorea* clade (Fig. 9), which is the focus of generic re-delimitation by Soares et al. (2022). Similarly, the recently segregated Neotropical *Robrichia* (formerly *Enterolobium* section *Robrichia* – see de Souza et al. 2022a) is sister to a clade of African mainly rainforest species (*Albizia dinklagei* (Harms) Harms / *A. altissima* Hook. f. / *A. eriorhachis* Harms / *A. leptophylla* Harms) whose generic placements in *Albizia*, *Cathormion* or *Samanea* (Benth.) Merr. have long been uncertain and neglected (Fig. 11), also prompting further generic re-arrangement in this Special Issue by Koenen (2022a). For the first time, the pantropical sampling employed here is more fully documenting these issues.

The mimosoid clade

We recover both *Chidlowia* and *Sympetalandra* as firmly nested in the mimosoid clade (Fig. 4), confirming previous molecular phylogenetic studies (*Chidlowia*: Manzanilla and Bruneau 2012; LPWG 2017; Koenen et al. 2020b; *Sympetalandra*: LPWG 2017). Of the ten genera previously included in the Dimorphandra group (sensu Polhill and Vidal 1981), *Sympetalandra*, comprising five species (van Steenis 1975; Hou 1996) in the forests of Malaya, Borneo, the Philippine Islands and the Lesser Sunda Islands, is unique in having its stamens shortly joined to the petals and *Chidlowia* Hoyle (Hoyle 1932) from West Africa (Sierra Leone to Ghana) stands out by having dorsifixed (rather than basi-

fixed) anthers. These two genera are placed between the Xylia and Entada clades of the early-diverging lineages of the mimosoid clade (Fig. 4), outside the core mimosoid clade sensu Koenen et al. (2020b). For *Chidlowia*, once-pinnate leaves and relatively large flowers with showy red petals which are strongly imbricate in bud are more suggestive of placement outside the mimosoids. For example, Hoyle (1932) suggested an affinity with the detarioid genus *Schotia* Jacq., but the regular flowers with equally-sized petals, the showy red stamen filaments partly joined at the base (they were described as free in the genus protologue (Hoyle 1932)) and the small campanulate, gamosepalous calyces, support placement in the mimosoid clade. The placement of *Sympetalandra* in the mimosoid clade, based on molecular analyses, is supported by its racemose or paniculate inflorescences of small, essentially regular, flowers. Finally, the genus *Dinizia*, which on morphological grounds has sometimes been included in mimosoids in the past (Burkart 1943), is here placed in the grade of genera directly subtending the mimosoid clade, confirming the results of previous molecular phylogenetic studies (Luckow et al. 2005; Bouchenak-Khelladi et al. 2010; Marazzi and Sanderson 2010; Manzanilla and Bruneau 2012; Cardoso et al. 2013; Kyalangalilwa et al. 2013; LPWG 2017; Zhang et al. 2020).

The mimosoid clade, i.e. the subfamily formerly known as the mimosoideae, was traditionally diagnosed by petals valvate, as opposed to imbricate, in bud. Valvate petal aestivation is mostly a reflection of whether or not the flowers are actinomorphic vs. zygomorphic, i.e. as the flowers become radially symmetrical the petals become valvate in bud. Across the non-mimosoid grade of Caesalpinioideae subtending the mimosoid clade, taxa with imbricate and valvate aestivation are phylogenetically intermingled. Although the vast majority of mimosoids do, indeed, have valvate petal aestivation, three exceptions: *Chidlowia* (as indicated above), alongside *Mimozyganthus* Burkart and *Parkia* R.Br., both of which are deeply nested within the mimosoid clade, show imbricate petal aestivation, providing further evidence of the homoplasy of this character. Further work to characterise petal aestivation across all relevant genera of Caesalpinioideae is needed, but it is clear that valvate aestivation does not provide a unique diagnostic synapomorphy for the mimosoid clade.

All other aspects of higher-level relationships are discussed in ALS14 Part 2.

Taxonomy in the age of phylogenomics

Once purely the domain of morphological analyses (e.g. Barneby and Grimes 1996, 1997; Barneby 1998), decisions on delimiting and naming taxa have increasingly been based on genes rather than morphology (Muñoz-Rodríguez et al. 2019). Employing a large phylogenomic dataset and explicitly considering numbers of genes that support particular generic configurations contribute to naming taxa that are more likely to be robust to future sampling of additional species and genomic regions and, hence, to taxonomic stability (Orthia et al. 2005; Pfeil and Crisp 2005; Humphreys and Linder 2009). However, use of ever larger phylogenomic datasets also raises questions about how to delimit taxa and especially about how conflict amongst gene trees reflecting the widely different evolutionary histories of different parts of the genome (e.g. Salichos and

Rokas 2013; Wang et al. 2019; Jiang et al. 2020; Koenen et al. 2020a, b) should inform delimitation of taxa. For example, what fraction of genes supporting a clade should be used as a cut-off for delimiting taxa? To what extent does it matter if there are alternative topologies that are supported by a substantial fraction of genes, even if that number is lower than the number of genes that supports the 'main' topology and what are the classificatory implications when only a small fraction of genes is informative for certain relationships (Shen et al. 2017)? Employing large numbers of genes is also enhancing our ability to identify putative hard polytomies on nodes where all, or almost all, genes lack phylogenetic signal (e.g. Koenen et al. 2020b), raising questions about whether it is justified to delimit multiple segregate genera when the relationships amongst them are unresolved and potentially form a polytomy. Large phylogenomic datasets also highlight cases of cytonuclear discordance even more starkly than before, raising questions about what is the best approach when different genomes (i.e. nuclear, plastid and mitochondrial) have different evolutionary histories, as is often the case (e.g. Bruun-Lund et al. 2017; Thielsch et al. 2017; Lee-Yaw et al. 2019; Rose et al. 2021; Debray et al. 2022)? Finally, we might also ask what, fundamentally, is now the role of morphology in delimiting taxa in the phylogenomic era (Muñoz-Rodríguez et al. 2019)?

The phylogeny of Caesalpinioideae presented here (Figs 2–12) poses many of these questions and provides some possible answers. First, the ubiquity of gene tree conflict found here and more generally in phylogenomics (Salichos and Rokas 2013; Wang et al. 2019; Jiang et al. 2020; Koenen et al. 2020b; Yang et al. 2020), suggests that the presence of conflicting topologies for a particular node alone is not sufficient reason to avoid naming the clade subtended by that node. If many conflicting topologies exist, but none of these occurs at a high frequency amongst the gene trees, low support values are indicative of lack of signal rather than true conflict (Koenen et al. 2020b) and do not need to affect classificatory decisions if there is support for the species tree topology amongst a sizable fraction of the gene trees. The nodes subtending *Macrosamanea* Britton & Rose, *Zygia* and *Inga* (Figs 11 and 12) are good examples of an abundance of conflicting topologies none of which is widespread and the monophyly of these genera is, therefore, not in question (except for a few outlier species of *Zygia* – see Appendix 1). However, if low support for a node in the species tree is caused by an alternative topology that is common across gene trees, the situation is more complex and the clade in question should probably not be named pending further study with additional accessions and genomic regions. The crown node of *Archidendron* (Fig. 8) provides an example of a node with a relatively abundant alternative topology, raising doubts about the monophyly of *Archidendron* (see Appendix 1; Brown et al. 2022). Second, in cases of cytonuclear discordance (as we see across several key nodes that affect decisions about generic delimitation), the smaller size of the plastid dataset and the fact that the chloroplast genome can be considered as a single, albeit large, uniparentally-inherited locus, suggest that, in most cases, nuclear phylogenies provide a more accurate approximation of the true species tree (see Terra et al. 2022).

Finally, despite providing the main (usually sole) source of information for classification for centuries, morphology was rapidly eclipsed as a source of data for phylogeny

reconstruction with the advent of molecular data (e.g. Scotland et al. 2003). Nevertheless, despite the dominance of phylogenomic data for building accurate and robust trees, morphology continues to play a central role as a complementary source of evidence for delimiting taxa in the light of monophyly inferred from phylogenomic data (Humphreys and Linder 2009; Gagnon et al. 2016). For example, placement of *Zygia sabatieri* and *Z. inundata* not in a clade with the remainder of *Zygia*, but instead as the sister clade of *Inga* in the nuclear ASTRAL phylogeny (Fig. 12) or in a grade subtending *Inga* in the plastome phylogeny (Suppl. material 3; Ferm et al. 2019), presents several options for delimiting genera: transfer these two species to the genus *Inga*, place both species in a new segregate genus or place each species in separate segregate genera. All three options are valid from the perspective of monophyly, but not from a morphological standpoint, because *Z. sabatieri* and *Z. inundata* have dehiscent pods and *Z. sabatieri* has bipinnate leaves, in contrast to the once-pinnate leaves and indehiscent pods that are diagnostic of the genus *Inga*. From a morphological perspective, it will be preferable to assign *Z. inundata* and *Z. sabatieri* to a new segregate genus rather than to transfer them to *Inga*, thereby retaining the morphological integrity and diagnosability of the genus *Inga* (see Appendix 1). This example demonstrates the important role that morphology continues to play in the era of phylogenomics: not to determine relationships and infer monophyly, but to inform and guide decisions about how to partition a phylogeny into monophyletic taxa (see also Terra et al. 2022 for another example).

Conclusions and future work

Here, we present a series of phylogenomic analyses including detailed assessment of gene tree conflict and support that suggest that about one quarter of mimosoid genera are non-monophyletic (Figs 2–12). This new backbone phylogeny, building on the 122-taxon version of Koenen et al. (2020b), provides robust foundations for aligning genera with monophyletic groups across a clade where generic delimitation has long been contentious with starkly contrasting generic systems (Lewis et al. 2005; Brown 2008) and for the higher-level classification presented in *Advances in Legume Systematics* 14, Part 2. The limitations of previous work focused either just on the Old World (e.g. Nielsen 1981, 1992) or just on the New World (e.g. Barneby and Grimes 1996, 1997; Barneby 1998) have become more starkly apparent now that pantropical sampling has been achieved, revealing the non-monophyly of well-known pantropical genera, such as *Albizia* (Koenen et al. 2020b; Aviles et al. 2022) and *Prosopis* (Hughes et al. 2022a), as well as previously unrecognised clades with trans-Atlantic distributions (Soares et al. 2022; Koenen 2022a). Our analyses provide a glimpse of the likely extent of morphological homoplasy (Figs 13–15).

However, despite including 420 taxa in the current analyses, it is clear that additional taxon sampling will be needed to fully resolve all the possible non-monophyly issues within Caesalpinioideae. Several priorities for future research are apparent. First, denser taxon sampling across *Senegalia* and allies is needed to address the unusual dilemmas

posed by extreme lack of resolution and cytonuclear discordance surrounding delimitation of the genera across the paraphyletic grade comprising *Senegalia*, *Pseudosenegalia*, *Parasenegalia* and *Mariosousa* (Fig. 7) that are explored here by Terra et al. (2022) who provided a list of priority taxa for future sampling with molecular data. Second, the likely non-monophyly of *Archidendron* (see Brown et al. 2022 and Appendix 1) also remains unresolved with a clear need for additional work, especially as many species are known from incomplete material. *Archidendron* and *Senegalia* are now the largest genera in Caesalpinioideae where doubts remain about their monophyly and delimitation. Third, a much more comprehensively sampled study is needed to address the longstanding non-monophyly of *Dimorphandra* Schott (Fig. 3). Fourth, the generic affinities of *Calliandra umbrosa* (Fig. 7; de Souza et al. 2016) and *Calliandra* sp. nov., the last species removed from *Calliandra* by Barneby (1998) yet to be placed in another genus, remain to be assessed. Finally, the taxonomic implications of the non-monophyly of *Zygia* revealed by Ferm et al. (2019) and confirmed here (Figs 11 and 12) have not yet been addressed. Like *Archidendron*, many species of *Zygia* remain poorly understood.

Furthermore, although there is no evidence that any large clades in Caesalpinioideae are subtended by whole genome duplication (WGD) events (Koenen et al. 2020a), it is clear that polyploidisation events have happened many times more recently, scattered across the phylogeny of Caesalpinioideae, for example in *Leucaena* (Govindarajulu et al. 2011; Bailey et al., in prep.), *Vachellia* and *Mimosa* (Dahmer et al. 2011; Simon et al. 2011). Furthermore, high numbers of gene duplications detected on branches subtending, for example, *Sympetalandra*, *Lemurodendron* Villiers & P. Guinet and *Schleinitzia* Warb. point to possible additional WGDs (Ringelberg et al., unpublished data). More work is needed to understand all these possible polyploidisation events, whether they involved auto- or allopolyploidisation and how such events affect assessments of character evolution, homoplasy and generic delimitation.

Finally, our preliminary assessments of homoplasy (Figs 13–15) notwithstanding, there is a clear need for rigorous analysis and comparison of morphological traits across the subfamily, based on more detailed homology assessment of morphological, developmental and genomic data. Morphological diagnosability of taxa is centrally important, especially for the acceptance of novel taxonomy by the end-users of scientific names, a group that is much larger than that of the scientific taxonomic community. We hope that the new phylogeny presented here can provide the evolutionary framework for future morphological studies that assess character evolution and homoplasy in greater detail.

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Appendix 1

Generic non-monophyly in Caesalpinioideae – towards a new generic system for the subfamily

Caesalpinia

Divergent circumscriptions of the genus *Caesalpinia* L. were largely resolved by Gagnon et al. (2016) who reduced *Caesalpinia* to ca. nine species and established a new generic system for the Caesalpinia Group as a whole, with 26 genera plus their 'Ticanto clade' (*Caesalpinia crista* L. and allies) as a putative 27th genus. This 27th genus accounts for the non-monophyly of *Caesalpinia* in our analysis (Fig. 2) with *Caesalpinia crista* representing the Ticanto clade that is re-instated as a genus in this Special Issue by Clark et al. (2022).

Dimorphandra

In line with previous studies (Luckow et al. 2005; LPWG 2017), *Dimorphandra* Schott is non-monophyletic in the nuclear phylogeny (Fig. 3), but robustly supported (99% bootstrap support (BS)) as monophyletic in the plastid tree (Suppl. material 3), indicating cytonuclear discordance. This implies either splitting *Dimorphandra* into two genera or sinking *Mora* Schomb. ex Benth., *Stachyothyrsus* Harms and *Burkea*

Benth. into *Dimorphandra* (which predates these other three genera). Evidence suggests splitting *Dimorphandra* as the preferred option. First, the three *Dimorphandra* species sampled here represent the three morphologically delimited subgenera (da Silva 1986) with representatives of these subgenera intermingled with other genera rendering *Dimorphandra* polyphyletic in the legume-wide *matK* phylogeny (LPWG 2017) and *Burkea* and *Mora* are not closely related to *Dimorphandra* in the plastid phylogeny (Suppl. material 3; *Stachyothyrsus* is not included in the plastid analysis). Second, while *Mora* has been included in *Dimorphandra* based on morphological similarities (Sandwith 1932; van Steenis 1975), the two genera differ in floral, seed and pod morphology and have generally been treated as distinct (Sandwith 1932; van Steenis 1975; da Silva 1986). African *Stachyothyrsus* and *Burkea* are morphologically (van Steenis 1975) and geographically distinct from South American *Dimorphandra* and *Mora*. All of this suggests that *Dimorphandra* will need to be split into two genera or potentially three, although the robustly supported sister group relationship between *D. davisii* and *D. macrostachya* (internode certainty 0.77, subtended by a long branch) would perhaps favour two genera, rather than three. Additional taxon sampling, to test the monophyly of the three subgenera, is required before taxonomic re-arrangements can be made. If the genus is to be split, the name *Dimorphandra* would remain attached to subgenus *Dimorphandra*, here represented by *D. gardneriana* Tul. *Dimorphandra exaltata* Schott is the type species of the genus. The names of the other two subgenera, *Phaneropsia* Tulasne and *Pocillum* Tulasne, would be available for the remaining species. Both names originate from the same publication (Tulasne 1844), but since *Pocillum* also refers to a genus of fungi (Kirk et al. 2008), *Phaneropsia* would be the more suitable generic name for the species not in *Dimorphandra* s.s. However, as taxon names have no priority at different rank (Turland et al. 2018), a new generic name may also be proposed.

Xylia and *Calpocalyx*

The non-monophyly of *Xylia* with *Calpocalyx* nested within it was documented using *matK* sequences (LPWG 2017) and is confirmed here (Fig. 4). This does not come as a great surprise, as these genera have always been considered closely related (Villiers 1984; Lewis et al. 2005). They have overlapping geographical and ecological distributions mainly in the tropical rainforests of central and western Africa (although *Xylia* has a wider distribution in Africa, Madagascar and Asia). The two genera also share a suite of morphological characteristics (Villiers 1984; Luckow et al. 2003), including robust woody sickle-shaped explosively dehiscent fruits (Fig. 13), a chromosome count of 2n = 12 (Goldblatt and Davidse 1977) and pollen grains in small-sized polyads (Jumah 1991). Since the name *Xylia* (Bentham 1841) predates *Calpocalyx* (Engler and Prantl 1897) and given the morphological and ecological similarities of the two genera, the most straightforward solution to the non-monophyly presented here would be the transfer of the species of *Calpocalyx* to *Xylia*. However, this apparently straightforward incorporation of *Calpocalyx* into *Xylia* is complicated by the name *Esclerona* Raf., an apparently valid name predating *Xylia*, raising the possibility of proposing conservation of the name *Xylia* prior to merging these two genera.

Entada and *Elephantorrhiza*

A close relationship between *Entada* Adans. and *Elephantorrhiza* Benth. has long been suggested in all molecular phylogenies that sampled these genera (e.g. Luckow et al. 2003; Koenen et al. 2020b). With denser sampling of species, it has become clear that *Elephantorrhiza* is nested within *Entada* (LPWG 2017), a result that is confirmed here (Fig. 4) and which provides the basis for re-circumscription of *Entada* to include *Elephantorrhiza* by O'Donnell et al. (2022) in this Special Issue.

Prosopis

One of the most striking and robustly supported examples of generic non-monophyly in our analyses is *Prosopis* s.l. whose species are placed in four separate lineages (Figs 4 and 5). The nodes supporting this non-monophyly are some of the most robustly supported across the Caesalpinioideae phylogeny as a whole (Fig. 5). This shows that *P. africana* is not closely related to the rest of *Prosopis* s.l., but is placed in a grade with other monospecific or species-poor genera subtending the core mimosoid clade (Fig. 4), confirming results from earlier studies (Catalano et al. 2008; LPWG 2017; Koenen et al. 2020b). The rest of Old World *Prosopis* (three species) is sister to the Indo-Nepalese genus *Indopiptadenia* and New World *Prosopis* has the Namibian – S. African *Xerocladia* nested within it (Fig. 5). A new generic classification of *Prosopis* s.l., accounting for this non-monophyly, is presented in this Special Issue by Hughes et al. (2022a).

Desmanthus

The non-monophyly of *Desmanthus* with the monospecific Hawaiian endemic *Kanaloa* Lorence & K.R. Wood nested within it (Fig. 5) mirrors earlier phylogenies (Hughes et al. 2003; Luckow et al. 2003, 2005) and is in line with the morphological distinctiveness of *Desmanthus balsensis* J.L. Contreras from the remaining species of *Desmanthus* (Contreras Jiménez 1986; Luckow 1993). A new monospecific segregate genus to account for this non-monophyly is proposed in this Special Issue by Hughes et al. (2022b).

Dichrostachys, *Gagnebina* and *Alantsilodendron*

Dichrostachys (DC.) Wight & Arn. and *Alantsilodendron* Villiers are both recovered as non-monophyletic in our sparsely sampled analysis (Fig. 5), raising questions about the monophyly of *Gagnebina* Neck. ex DC., here represented by just a single species. The Malagasy members of these three genera (all species in our phylogeny, except *D. cinerea* R. Vig.) cluster together in a clade characterised by very short branches and extensive gene tree conflict (Fig. 5) suggestive of an early burst model of diversification typical of a rapid radiation on Madagascar (Aebli 2015). Previous molecular phylogenetic studies have also found at least some of these genera to be non-monophyletic (Hughes et al. 2003; Luckow et al. 2003, 2005; Aebli 2015) and some species have been transferred between genera based on morphology (Lewis and Guinet 1986). Each of these genera contains several other species from Madagascar not sampled here. While a parsimonious solution could be to merge the three genera into *Gagnebina* (de Candolle 1825) (a name predating *Dichrostachys* (Wight and Walker-Arnott 1834) and *Alantsilodendron*

(Villiers 1994)), such a move would result in a highly variable genus, with no consistent morphological character to distinguish it. A forthcoming monograph (Luckow, unpublished data) will resolve the non-monophyly of these genera by transferring two species of *Dichrostachys* to *Alantsilodendron* and seven to a new genus (Phillipson et al. 2022). Additional sampling of non-Malagasy species of *Dichrostachys* would also be important, especially Australian *D. spicata*, as it has been placed as sister to the combined *Dichrostachys* / *Gagnebina* / *Alantsilodendron* + *Calliandropsis nervosa* (Britton & Rose) H.M. Hern. & Guinet clade in several studies (Hughes et al. 2003; Luckow et al. 2003, 2005; Aebli 2015). The African species *D. dehiscens* Balf. f. and *D. kirkii* Benth. also need to be sampled as they share a dehiscent fruit type with members of the new Madagascan genus.

Stryphnodendron and *Pseudopiptadenia*

Our analyses support the monophyly of the Stryphnodendron clade sensu Koenen et al. (2020b) comprising the genera *Parapiptadenia* Brenan, *Pityrocarpa* (Benth. & Hook.f.) Britton & Rose, *Pseudopiptadenia* Rauschert and *Stryphnodendron* Mart. (Fig. 6) and presumably *Microlobius* C. Presl., which, although not sampled here, has been shown to be nested within or sister to *Stryphnodendron* (Ribeiro et al. 2018; Simon et al. 2016; see also Lima et al. 2022). Of these genera, only *Parapiptadenia* is monophyletic in our analyses, although *Pityrocarpa* is here only represented by a single taxon (Fig. 6). *Stryphnodendron* is non-monophyletic as *S. duckeanum* Occhioni does not group with the rest of the genus (Fig. 6), in line with flower, fruit and branching characteristics that suggested transfer of *S. duckeanum* to another genus (Scalon 2007) and with previous molecular phylogenies showing *S. duckeanum* separated from the rest of *Stryphnodendron* (Jobson and Luckow 2007; Simon et al. 2016; Ribeiro et al. 2018; Sauter 2019). Similarly, *Pseudopiptadenia* is also non-monophyletic with *P. schumanniana* placed as sister to the single sampled species of *Pityrocarpa*, rather than forming a clade with *Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima and *P. psilostachya* (DC.) G.P. Lewis & M.P. Lima (Fig. 6). Several previous molecular phylogenies also found *Pseudopiptadenia* to be non-monophyletic – however, those studies did not include *P. schumanniana* and found *P. brenanii* G.P. Lewis & M.P. Lima (not sampled here) to be the outlier instead (Simon et al. 2016; Ribeiro et al. 2018). The sparsely sampled backbone phylogeny of the Stryphnodendron clade presented here provides the foundations for more densely sampled analyses and re-delimitation of both *Stryphnodendron* (Lima et al. 2022) and *Pseudopiptadenia* / *Pityrocarpa* (Borges et al. 2022) in this Special Issue.
The remaining genera in the Stryphnodendron and Mimosa clades are all monophyletic (Fig. 6), confirming previous phylogenetic studies and taxonomic rearrangements, including segregation of *Lachesiodendron* P.G. Ribeiro, L.P. Queiroz & Luckow from *Piptadenia* (Ribeiro et al. 2018), as well as placement of amphi-Atlantic *Adenopodia* C. Presl as sister to *Mimosa* and the sister group relationships amongst the main clades of *Mimosa* (Simon et al. 2011).

Senegalia and allied genera

The striking cytonuclear discordance whereby *Senegalia* Raf. appears as non-monophyletic in the analyses of nuclear gene sequences, but as monophyletic in the analyses

of plastomes, was first revealed by Koenen et al. (2020b), a result confirmed here by sampling more species of *Senegalia*, plus the closely related *Mariosousa*, *Parasenegalia* and *Pseudosenegalia* (Fig. 7). In the nuclear gene analyses, the two clades of *Senegalia* plus these three other genera and the incompletely known *Albizia leonardii* Britton & Rose ex Barneby & J.W. Grimes form a paraphyletic grade with very short and poorly supported or unsupported internal branches (Fig. 7). The complex and intriguing issues these features raise for delimitation of *Senegalia* are explored by Terra et al. (2022), who conclude that sequencing of more species is required.

Calliandra

Following reduction of Bentham's (1875) broad trans-continental circumscription of *Calliandra* Benth. to just the New World species by Barneby (1998), five genera have been segregated to account for the majority of the Old World species. Now just a handful of Old World species remain to be resolved, including the Asian *Calliandra* sp. nov. (*Poilane 9150*), that, as expected, does not group together with the New World *Calliandra* s.s., but is instead sister to the Indian monospecific genus *Sanjappa* É.R. Souza & M.V. Krishnaraj in the Zapoteca clade (Fig. 7). Bentham (1875) included four Asian species in *Calliandra* (de Souza et al. 2013), which share the apically dehiscent pods of *Calliandra* (Fig. 13a–f), but in other respects present anomalies, especially in the configuration of their polyads. The identities of these Asian *Calliandra* species have long been considered ambiguous (Barneby 1998). Two of these Asian species have been assigned to different genera (*C. cynometroides* Bedd. to *Sanjappa* (de Souza et al. 2016) and *C. geminata* (Wight & Arn.) Benth. to *Thailentadopsis* Kosterm. (Lewis and Schrire 2003)), while the generic placement of the remaining species, *C. umbrosa* (Wall.) Benth., remains unknown. The fourth species, *C. griffithii* Baker ex Benth., is now considered a subspecies of *C. umbrosa* (Paul 1979). *Calliandra umbrosa* has never been included in a molecular phylogenetic analysis (de Souza et al. 2013, 2016) and, unfortunately, sequencing of *C. umbrosa* was unsuccessful in this study. However, polyad, leaf, corolla and pod morphology, plus the presence of facultatively spinescent stipules, distinguish *C. umbrosa* from other genera, suggesting that it should potentially be assigned to a new genus (de Souza et al. 2013, 2016). Until DNA sequences of *C. umbrosa* can be obtained to ascertain its relationship to *Calliandra* sp. nov., this residual non-monophyly of the genus *Calliandra* cannot be resolved.

***Pithecellobium* and allies**

While the Pithecellobium alliance is the only one of the informal alliances of Barneby and Grimes (1996) whose monophyly has withstood the test of phylogenomic analysis (Koenen et al. 2020b), other than *Pithecellobium* Mart. itself, our sparsely sampled phylogeny of this clade suggests that the monophyly of the four other genera placed in the Pithecellobium clade (*Painteria* Britton & Rose, *Havardia* Small, *Ebenopsis* Britton & Rose and *Sphinga* Barneby & J.W. Grimes) is doubtful and needs to be further tested with more complete taxon sampling (Fig. 7). Even with our limited taxon sampling, *Painteria* and *Havardia* are clearly non-monophyletic (Fig. 7), raising

significant doubts about the taxonomic status of *Ebenopsis* and *Sphinga*, which are both represented by only one species in our trees. *Painteria* is especially poorly distinguished from *Havardia*; *Sphinga* was originally described in *Havardia* and previous studies (Nielsen 1981; Polhill 1994) placed all four genera in a more broadly defined *Havardia* (Brown 2008). Such a solution might, therefore, seem sensible, but together they form a paraphyletic grade in our phylogenies (Fig. 7), suggesting that unless all four genera were to be sunk back into *Pithecellobium* (from which they were segregated (Barneby and Grimes 1996)), these four genera require at least three names, as they are divided over three (poorly-supported) lineages: one comprising *Spinga acatlensis* (Benth.) Barneby & J.W. Grimes and *Havardia campylacantha* (L. Rico & M. Sousa) Barneby & J.W. Grimes, one *Painteria leptophylla* (DC.) Britton & Rose, *Pa. elachistophylla* (A. Gray ex S. Watson) Britton & Rose and *Ebenopsis confinis* (Standl.) Britton & Rose and one *H. pallens* (Benth.) Britton & Rose, which is the type species of *Havardia* and sister to *Pithecellobium*. Clearly, taxon sampling in our phylogeny is too limited to draw firm taxonomic conclusions. A new phylogeny of the Pithecellobium clade, presented here in this Special Issue, is used as the basis for erecting two new genera to account for these generic non-monophyly issues (Tamayo-Cen et al. 2022). This new phylogeny, based on a small set of DNA sequence loci, but with denser taxon sampling than that encompassed here, is not fully congruent with the phylogenomic backbone presented in Fig. 7.

The Archidendron clade

The genera and lineages of the large Archidendron clade comprising *Acacia* Mill., *Archidendron* F. Muell. and six smaller genera (Fig. 8; Koenen et al. 2020b), together make up over one third of all mimosoid species and are restricted to Australasia. Relationships across the backbone of this clade are complex and generally poorly resolved with very short branches and high levels of gene tree conflict and lack of phylogenetic signal across a significant fraction of genes (Fig. 8), such that the topologies across different analytical approaches can differ. This suggests that some nodes across this backbone should better be viewed as putative polytomies. Three genera in this clade, *Wallaceodendron* Koord., *Pararchidendron* I.C. Nielsen and *Paraserianthes* I.C. Nielsen, are monospecific. *Falcataria* (I.C. Nielsen) Barneby & J.W. Grimes comprises three species but is represented by only one taxon in our phylogeny, so no conclusion can, therefore, be made about its monophyly, although our results support the segregation of this genus from *Paraserianthes* (Barneby and Grimes 1996; Brown et al. 2011). Three of the four remaining genera are monophyletic: *Acacia*, *Archidendron* and *Serianthes* Benth. (confirming the results of Demeulenaere et al. (2022) in this Special Issue). However, the monophyly of *Archidendron* remains doubtful as it is supported by few gene trees and opposed by many (Fig. 8) and the genus is not monophyletic in the plastid tree (Suppl. material 3). This is very much in line with previous findings of a non-monophyletic *Archidendron* (Brown et al. 2008, 2011; Iganci et al. 2016; LPWG 2017). The likely non-monophyly of *Archidendron* is explored in more detail in this Special Issue by Brown et al. (2022). It is notable that the two well-supported *Archidendron* subclades found

here are replicated by Brown et al. (2022), where their morphological and geographical identities are discussed in detail. Finally, the non-monophyly of *Archidendropsis* I.C. Nielsen, documented and addressed in this Special Issue by Brown et al. (2022), is confirmed by the much larger phylogenomic dataset analysed here (Fig. 8).

Our results weakly support *Paraserianthes lophantha* as sister to *Acacia* (Fig. 8), in line with earlier findings (Brown et al. 2008, 2011; Koenen et al. 2020b) and shared morphological similarities including hard seeds that are stimulated to germinate by fire (Brown et al. 2011), minute anthers and numerous stamens (Barneby and Grimes 1996). As *P. lophantha* contains two geographically disjunct subspecies, *P. lophantha* subsp. *montana* (Jungh.) I.C. Nielsen in Indonesia and *P. lophantha* subsp. *lophantha* (the subspecies sequenced here) in southern Australia (Brown et al. 2011), sequencing the missing subspecies would be worthwhile to check that the two cluster together as sister to *Acacia*. However, it is important to note that this relationship is sensitive to the type of dataset and phylogenetic method: the ASTRAL trees (Fig. 8) recover *P. lophantha* as the sister of *Acacia*, whereas the nuclear RAxML phylogenies (Ringelberg et al. 2022) find a sister relationship between *Acacia* and *Archidendron* plus *Archidendropsis xanthoxylon* (C.T. White & W.D. Francis) I.C. Nielsen, the PhyloBayes gene jack-knifing phylogeny (Ringelberg et al. 2022) resolves the whole Archidendron clade as one large polytomy lacking a clear sister lineage to *Acacia* and the plastid tree (Suppl. material 3) recovers *Archidendropsis xanthoxylon* as sole sister of *Acacia*. Furthermore, *P. lophantha* and several species of *Archidendron* are also identified as species often changing positions across trees by RogueNarok (Aberer et al. 2013). The high levels of intergenic conflict, very short branches, extremely low bootstrap support values especially in the nucleotide RAxML phylogenies, lack of concordance and signal amongst the gene trees and failure to reject a polytomy by ASTRAL (Fig. 8), all suggest that the backbone of the Archidendron clade should perhaps best be viewed as one large polytomy, as depicted in the PhyloBayes consensus tree (Ringelberg et al. 2022). However, the number (eight in the PhyloBayes phylogeny) and precise identity of lineages arising from this tangle remain unclear and relationships amongst the genera of this clade remain highly uncertain pending additional taxon sampling and detailed investigation of the causes of gene tree conflict and possible evidence for introgression.

Albizia

At the start of this study, the genus *Albizia* was dubbed the last pantropical so-called 'dustbin' genus pending resolution (Koenen et al. 2020b). Here, we show that *Albizia* s.l. is rampantly non-monophyletic, most notably because the bulk of the Old and New World species are placed in separate clades (Figs 9 and 10). This Old World – New World split is remedied in this Special Issue by Aviles et al. (2022) who resurrect the genus *Pseudalbizzia* Britton & Rose for the majority of the New World species placed in Barneby's *Albizia* section *Arthrosamanea*, with *Albizia* s.s. now restricted to just the Old World species, which still includes ca. 90 spp. (Koenen et al., unpubl. data). Furthermore, the disparate placements of several other species of *Albizia* across the phylogeny, viz: *Albizia carbonaria* Britton (Fig. 8), the long-neglected African *Albizia* species previously often

placed in *Cathormion* or *Samanea* (Benth.) Merr. (Figs 9 and 11) and *Albizia leonardii* (Fig. 7), are all accounted for with new generic placements and nomenclatural combinations (Koenen 2022b; Soares et al. 2022), one synonymisation (Terra et al. 2022) and a new segregate genus (Koenen 2022a), all of them being published in this Special Issue.

Abarema*, *Hydrochorea* and *Balizia

The recent re-circumscription of *Abarema* Pittier to include just two species and transfer of the remaining species to the re-instated *Punjuba* Britton & Rose and *Jupunba* Britton & Rose (Guerra et al. 2016, 2019; Iganci et al. 2016; Soares et al. 2021), is broadly supported here (Figs 9 and 11), except for the anomalous placement of *Jupunba macradenia* (Pittier) M.V.B. Soares, M.P. Morim & Iganci which is sister to the *Hydrochorea* + *Balizia* clade (Fig. 9). This placement is unexpected and somewhat suspect considering *J. macradenia* is firmly placed in *Jupunba* in Soares et al. (2021). As found by Iganci et al. (2016), Koenen et al. (2020b) and Soares et al. (2021), *Balizia* is non-monophyletic with the genus *Hydrochorea* plus two African species of *Albizia* nested within it (Fig. 9). *Hydrochorea* is re-circumscribed to accommodate all these elements by Soares et al. (2022) in this Special Issue.

Leucochloron

Koenen et al. (2020b) showed that *Leucochloron* is polyphyletic and that result is confirmed here, split between the Albizia and Inga clades (Figs 10 and 11). A new segregate genus to account for this non-monophyly is proposed in this Special Issue by de Souza et al. (2022b).

Zygia*, *Macrosamanea* and *Inga

Alongside *Archidendron*, the large Neotropical, mainly rainforest genus *Zygia* remains one of the least well-documented genera of mimosoids, with many species known from incomplete material (Barneby and Grimes 1997). Previous work by Ferm et al. (2019) showed that, while the bulk of genus *Zygia* is monophyletic, a handful of outlier species have affinities to other genera: *Zygia ocumarensis* (Pittier) Barneby & J.W. Grimes is sister to *Macrosamanea* Britton & Rose ex Britton & Killip, *Marmaroxylon magdalenae* Killip ex. L. Rico (treated as a synonym of *Z. ocumarensis* by Barneby and Grimes (1997)) is nested in *Jupunba* and *Z. inundata* and *Z. sabatieri* are together sister to *Inga*. With the exception of *M. magdalenae*, which is not included in this study, these placements are confirmed here with phylogenomic data (Figs 11 and 12) and reflect the morphological distinctiveness of these species from the rest of the genus (Barneby and Grimes 1997; Ferm et al. 2019) which prompted placements in their own separate monospecific sections of *Zygia* (Barneby and Grimes 1997). New nomenclatural combinations to deal with these outlier *Zygia* species are still pending. We suggest that *Zygia ocumarensis* should best be transferred to *Macrosamanea*, as it shares bipinnate leaves with multiple pairs of pinnae and an absence of cauli-/ramiflory (which is almost universal in *Zygia*) with several species of *Macrosamanea* (Barneby and Grimes 1996; Ferm et al. 2019). The identity of *Marmaroxylon magdalenae* needs to be re-evaluated, but the evidence of Ferm et al. (2019), who sampled the type material, suggests it should be transferred to *Jupunba*. The generic placements of *Z. inundata* and *Z. sabatieri* are more contentious.

Arguments can be made to transfer *Z. inundata* to *Inga* (Ferm et al. 2019): it was originally described in *Inga* and it shares once-pinnate leaves and absence of cauli-/ramiflory with *Inga* (Barneby and Grimes 1997; Ferm et al. 2019). However, *Z. inundata* was placed as the sole sister of *Inga* in the plastid tree (Suppl. material 3) and by Ferm et al. (2019), whereas the nuclear gene data suggest that *Z. inundata* is sister to *Z. sabatieri* and together these two species form the sister clade of *Inga* (Fig. 12). *Zygia sabatieri* has bipinnate leaves and both *Z. sabatieri* and *Z. inundata* have dehiscent pods, characteristics that distinguish these species from *Inga* with its uniformly once-pinnate leaves and indehiscent pods. In order to maintain a morphologically coherent and homogeneous *Inga* with respect to these diagnostic characters, segregating *Z. inundata* and *Z. sabatieri* as a new genus would appear to be advantageous. *Ingopsis* Barneby & J.W. Grimes and *Pseudocojoba* Barneby & J.W. Grimes, the names for the monospecific sections containing *Z. inundata* and *Z. sabatieri*, respectively (Barneby and Grimes 1997), are two available names, of which *Ingopsis* would be preferable given the morphological and phylogenetic proximity of this clade to *Inga* and the lack of a close relationship to *Cojoba* Britton & Rose. However, since these sectional names have no priority at generic rank (Turland et al. 2018), alternatively, a new name could equally be proposed. Finally, while *Zygia* s.s. was reasonably well sampled by Ferm et al. (2019) and also in the current study (Fig. 12), alongside further herbarium taxonomic work and field studies to clarify species, denser phylogenetic taxon sampling is desirable, in particular to include *Z. eperuetorum* (Sandwith) Barneby & J.W. Grimes. This species is known only from the Essequibo Valley in Guyana, was placed in its own section by Barneby and Grimes (1997), has an unusual combination of morphological characters not found elsewhere in *Zygia* and the fruit remains unknown. *Zygia eperuetorum* may well, therefore, represent an additional separate lineage that could potentially merit recognition as a distinct genus.

Supplementary material 1

Table S1

Authors: Jens J. Ringelberg, Erik J.M. Koenen, João R. Iganci, Luciano P. de Queiroz, Daniel J. Murphy, Myriam Gaudeul, Anne Bruneau, Melissa Luckow, Gwilym P. Lewis, Colin E. Hughes

Data type: excel file.

Explanation note: Samples included in this study.

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Link: https://doi.org/10.3897/phytokeys.205.85866.suppl1

Supplementary material 2

Table S2

Authors: Jens J. Ringelberg, Erik J.M. Koenen, João R. Iganci, Luciano P. de Queiroz, Daniel J. Murphy, Myriam Gaudeul, Anne Bruneau, Melissa Luckow, Gwilym P. Lewis, Colin E. Hughes

Data type: excel file.

Explanation note: Trait data used for character evolution analyses.

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Link: https://doi.org/10.3897/phytokeys.205.85866.suppl2

Supplementary material 3

Figure S1

Authors: Jens J. Ringelberg, Erik J.M. Koenen, João R. Iganci, Luciano P. de Queiroz, Daniel J. Murphy, Myriam Gaudeul, Anne Bruneau, Melissa Luckow, Gwilym P. Lewis, Colin E. Hughes

Data type: Pdf file.

Explanation note: Chloroplast phylogeny of Caesalpinioideae. Only bootstrap support values lower than 100% are shown.

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Link: https://doi.org/10.3897/phytokeys.205.85866.suppl3

Supplementary material 4

Supplementary tree file

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Data type: Tree file (Newick format).

Explanation note: Tree file of the ASTRAL phylogeny based on the single-copy genes (depicted in Figs 2–12), in which taxon labels have been updated to reflect taxonomic changes made in all the entries in Advances in Legume Systematics 14 Part 1.

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Reinstatement of *Ticanto* (Leguminosae-Caesalpinioideae) – the final piece in the Caesalpinia group puzzle

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Abstract

A recent molecular phylogenetic analysis of the Caesalpinia group demonstrated that it comprises 26 genera, but the recognition of a putative 27th genus, *Ticanto*, remained in doubt. This study presents a phylogenetic analysis of ITS and five plastid loci revealing a robustly supported monophyletic group representing the Ticanto clade, sister to the morphologically distinct genus *Pterolobium*. Based upon this evidence, along with a morphological evaluation, the genus *Ticanto* is here reinstated. Descriptions are provided for all nine species of *Ticanto*, together with a key to the species, maps, and colour photographs. Nine new combinations are made: *Ticanto caesia* (Hand.-Mazz.) R. Clark & Gagnon, *T. crista* (L.) R. Clark & Gagnon, *T. elliptifolia* (S. J. Li, Z. Y. Chen & D. X. Zhang) R. Clark & Gagnon, *T. magnifoliolata* (Metcalf) R. Clark & Gagnon, *T. rhombifolia* R. Clark & Gagnon, *T. sinensis* (Hemsl.) R. Clark & Gagnon, *T. szechuenensis* (Craib) R. Clark & Gagnon, *T. vernalis* (Champion ex Benth.) R. Clark & Gagnon and *T. yunnanensis* (S. J. Li, D. X. Zhang & Z.Y. Chen) R. Clark & Gagnon. The final major question in the delimitation of segregate genera from within *Caesalpinia sensu lato* and the Caesalpinia group is thus resolved.

Keywords

Biancaea, *Caesalpinia crista*, Caesalpinieae, China, Fabaceae, *Guilandina bonduc*, *Mezoneuron*, phylogeny, *Pterolobium*, South-East Asia, winged fruit

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Introduction

Caesalpinia s.l., and the Caesalpinia group more broadly, for a long time defied taxonomic classification, their circumscriptions and generic limits being difficult to define. This was due in part to high levels of morphological homoplasy and the consequent lack of defining characteristic synapomorphies available to delineate segregate genera. *Caesalpinia* s.l. has most often been treated as a single, pantropical genus with up to ca. 150 species encompassing a great diversity of morphological forms, but it has also been considered to comprise numerous smaller genera under as many as 30 generic synonyms (Lewis 1998, 2005). Resolution of generic limits in the Caesalpinia group using molecular phylogenetic data was impeded by a lack of adequate material for molecular sampling and the wide distribution of the taxa. Molecular phylogenetic studies of the group tended to sample from a small range of species to evaluate higher level relationships (Lewis and Schrire 1995; Simpson and Miao 1997; Haston et al. 2005; Bruneau et al. 2008; Manzanilla and Bruneau 2012; Nores et al. 2012) or more densely from selected subgroups (Simpson et al. 2004; Simpson and Ulibarri 2006) until Gagnon et al. (2013) published a densely sampled phylogeny representing 120 species from 18 of the 21 genera, based on a single plastid marker (*rps16*). This study was followed by a comprehensive investigation of the Caesalpinia group by Gagnon et al. (2016) based on one nuclear and five plastid markers which sampled 172 species (equivalent to 84% of taxa in the group at that time), encompassing the morphological diversity of the Caesalpinia group and most of its geographical range, to present a phylogeny that resolved most of the generic limits. The results demonstrated that 26 genera, representing robustly supported clades within the phylogeny, and including nine genera segregated from *Caesalpinia* s.l., should be recognised within the group (Gagnon et al. 2016).

Despite the dense sampling achieved by Gagnon et al. (2016), a lack of available material resulted in uncertain status for a proposed 27th genus, represented in their phylogeny by a single species, *C. crista* L. Nine species distributed primarily in southern China were indicated as potential candidates for inclusion in this putative genus, for which the name *Ticanto* Adans. was identified as the earliest available. The authors lacked the necessary evidence to formally reinstate this genus and highlighted the need for further investigations including thorough molecular sampling.

The difficulties inherent in morphologically defining the elements of the Caesalpinia group are exemplified by *Ticanto*. It lacks obvious diagnostic synapomorphies and was not morphologically characterised by Gagnon et al. (2016) apart from a brief discussion of the presence or absence of a wing on the fruit in comparison with the samaroid winged fruit of the proposed sister genus, *Pterolobium*.

The aim of our study is to test the monophyly of the putative genus *Ticanto* using molecular phylogenetic methods and detailed investigation of morphological characters compared with those of the most closely related genera in the Caesalpinia group, particularly *Pterolobium*, *Mezoneuron* and *Biancaea* (Gagnon et al. 2016). The morphological and molecular phylogenetic analyses presented here support the reinstatement of *Ticanto*, thus resolving the final major question in the reclassification of the complex

and taxonomically challenging pantropical *Caesalpinia* s.l. into monophyletic segregate genera. Species descriptions and a key to the species are presented, and new combinations are made for each species.

Methods

The species descriptions were developed using herbarium specimens studied at HITBC, IBK, K, and KUN, NPH, and from online specimen images at A, AU, BM, C, CDBI, CSFI, CZH, E, FJSI, GXMG, GXMI, GZAC, GZTM, HGAS, HHBG, IBSC, IMC, IMDY, JIU, L, MO, NAS, NF, NY, P, PE, PEY, SM, SN, SYS, SZG, TAIF, TNM, UC, US, W, WAG, WUK, ZM, via the Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/index.php), National Specimen Information Infrastructure (NSII, http://nsii.org.cn/2017/), Plant Photo Bank of China (PPBC, http://ppbc.iplant.cn/), and JSTOR https://plants.jstor.org), in combination with data from protologues and other relevant literature (Hattink 1974; Vidal and Hul Thol 1976; Larsen et al. 1980, 1984; Hou et al. 1996; Chen et al. 2010). The level of detail presented here in the species descriptions varies depending on the availability of material for study.

Due to the relative homogeneity of vegetative and floral characters between *T. crista*, *T. magnifoliolata*, *T. sinensis* and *T. szechuenensis*, the descriptions of these species were generated using a subset of the available specimens consisting of fruiting specimens and selected flowering or sterile specimens that could be confidently identified.

The x-ray images of fruit for study of the venation patterns were taken using a Faxitron MX101 machine with a 4-inch square digital plate.

A representative selection of specimens that were consulted, or for which the identification could be verified via a digital specimen image, contributed the primary data set used to generate the distribution maps. To encompass the full geographical range of the species, additional records were downloaded from the Global Biodiversity Information Facility (GBIF 2021). The GBIF data were cleaned by excluding records not derived from preserved specimens, those that were from capital cities or country centroids, and duplicate specimens or localities. Points that were clearly erroneous (primarily those located in the sea) were either removed or the coordinates were updated following manual georeferencing. Records lacking latitude and longitude coordinates were generally excluded; however, where records existed for areas in which a species was known to occur and for which georeferenced specimens were otherwise unavailable, a few records were manually georeferenced when sufficient locality information was provided.

Tools used for georeferencing were Google Earth Pro, Google Maps (https://www.google.com/maps) and online gazetteers (GEOLocate, https://geo-locate.org/; Falling Rain Global Gazetteer, http://www.fallingrain.com/world/; and Getty Thesaurus of Geographic Names, https://www.getty.edu/research/tools/vocabularies/tgn/). Preliminary mapping of point localities was carried out using GeoCAT (http://geocat.kew.org/editor). The distribution maps were created using ArcMap 10.5 (Redlands 2011). The specimens used to make the maps are listed in Suppl. material 1.

Molecular methods

DNA samples were taken from field-collected specimens dried in silica gel or from herbarium specimens. A total of 19 accessions were sequenced, representing six species of *Ticanto*, two of *Pterolobium*, one of *Mezoneuron* and one of *Biancaea* (Table 1).

Five genetic markers were amplified: the nuclear internal transcribed spacer (ITS) region of the 18S–5.8S–26S nuclear ribosomal cistron, and four plastid loci, namely *rps16*, the *trnD-trnT* intergenic spacer, the *matK* gene and flanking *3'-trnK* intron, and the *trnL-trnF* intron-spacer region. DNA was extracted from ca. 0.1–0.2 g silica gel-dried leaves or 0.1–0.2 g leaves from herbarium sheets using either: (1) QIAGEN DNeasy Plant Mini Kit, following the manufacturer's instructions; or (2) 2× CTAB (hexadecyltrimethylammonium bromide) method modified from Doyle and Doyle (1987). DNA was precipitated in 2.5 vol. ethanol or 2/3 vol. isopropanol for dried herbarium specimens and DNA samples were purified on caesium chloride/ethidium bromide gradients (1.55 g/mL) and stored at -20 °C until amplification.

The PCR reactions were carried out in 25 µl volumes, using 2× PCR Premix 'Dream Taq' DNA polymerase buffer (4.0 mM $MgCl_2$) (Thermo Fisher Scientific), 5×TBT (Samarakoon et al. 2013), and 2 µM of each primer. For samples that did not amplify well initially, the reaction was repeated with 50 µl reaction volume. For ITS only, 2% DMSO (D_2H_6OS) was added. For all markers except *matK-trnK*, PCR was initially carried out using standard protocols with a single set of primers. For

Table 1. Accessions sequenced and used to generate the molecular based phylogeny, with GenBank numbers.

Genus	species	Collector name	Collector number	Country	Herbarium	*ITS*	*trnL-F*	*matK*	*rps16*	*trnDT*
Biancaea	*millettii*	Zhi-Ming Zhong	ZZM003	China	IBSC	ON922869	ON932059	-	ON971386	ON971410
Caesalpinia	*crista*	Kai-Wen Jiang	KwT033	China	NPH	ON922872	ON932062	ON971417	ON971381	ON971400
Caesalpinia	*crista*	Kai-Wen Jiang	TH101	China	NPH	-	ON932064	ON971418	ON971383	ON971407
Caesalpinia	*crista*	Zhong-Cheng Liu et al.	LXP-13-23687	China	SYS	ON922873	ON932063	-	-	-
Caesalpinia	*crista*	Zhu-Qiu Song	2021057	China	IBSC	ON922871	ON932061	ON971419	ON971396	ON971411
Caesalpinia	*magnifoliolata*	Kiyama et al.	1233	China	KUN	ON922868	ON932058	-	ON971387	-
Caesalpinia	*sinensis*	Clark	415	China	K, IBK	ON922875	ON932066	ON971423	ON971390	ON971399
Caesalpinia	*sinensis*	Clark	429	China	K, IBK	ON922876	ON932067	ON971413	ON971394	ON971405
Caesalpinia	*sinensis*	Hang Sun	1672	China	KUN	ON922874	ON932065	ON971415	ON971388	-
Caesalpinia	*sinensis*	Yun-Hong Tan	s.n.	China	HITBC	ON922877	ON932068	ON971428	ON971397	-
Caesalpinia	aff. *szechuenensis*	Clark	422	China	K, IBK	ON922870	ON932060	ON971426	ON971392	ON971398
Caesalpinia	*vernalis*	Shi-Jin Li	787	China	IBSC	ON922880	ON932071	ON971425	ON971389	ON971412
Caesalpinia	*vernalis*	Ya-Min Zhang	YS023	China	NPH	ON922881	ON932072	ON971422	ON971384	ON971408
Caesalpinia	*vernalis*	Zhu-Qiu Song	2021061	China	IBSC	ON922879	ON932070	ON971420	ON971382	ON971406
Caesalpinia	sp.	Yong-Mei Yi	YYM05	China	NPH	ON922878	ON932069	ON971421	ON971385	ON971409
Mezoneuron	*scortechinii*	Wieringa et al.	4195	Australia	WAG	ON922882	ON932073	ON971424	ON971391	ON971401
Pterolobium	*punctatum*	Clark	424	China	K	ON922883	ON932074	ON971427	ON971393	ON971404
Pterolobium	*stellatum*	MPU	39	South Africa	NGB	ON922884	ON932075	ON971416	-	ON971402
Pterolobium	*stellatum*	RBGKewMSB	145895	Kenya	K	ON922885	ON932076	ON971414	ON971395	ON971403

Table 2. Primer pairs used for standard and nested PCR.

		Forward	Reverse	Reference
ITS		AB101	AB102	Douzery et al. 1999
	***ITS* nested**	ITS2	ITS3	White et al. 1990
rps16		rpsF	rpsR2	Oxelman et al. 1997
trnD-T		trnD	trnT	Shaw et al. 2005 ex Demesure et al. 1995
	***trnD-T* nested**	trnD	trnE	Shaw et al. 2005
	***trnD-T* nested**	trnY	trnT	Shaw et al. 2005
matK-trnK	**nested**	trnK685F	matKC6-Caesalpinia	Wojciechowski et al. 2004; Gagnon et al. 2016
	nested	trnK4La	trnK2R	Wojciechowski et al. 2004
trnL-F		trnL	trnF	Taberlet et al. 1991
	***trnL-F* nested**	trnLc	trnLd	Taberlet et al. 1991
	***trnL-F* nested**	trnLe	trnLf	Taberlet et al. 1991

matK-trnK, a nested approach was taken, using two sets of primers to amplify shorter regions within the target. Following initially unsuccessful results using standard protocol with a single pair of primers, a nested approach was similarly adopted for *trnL-F*, and *trnD-T*, and for one sample for ITS. The primer pairs used for each marker are listed in Table 2. PCR products were cleaned using a Macherey-Nagel NucleoSpin Purification Kit, following the manufacturer's instructions.

The concentration and quality of DNA in each sample was assessed using a Nanodrop 2000 Spectrophotometer (Thermo Fisher Scientific). Amplification products were sequenced directly with modified dideoxy cycle sequencing with dye terminators (according to the manufacturer's protocol; Thermo Fisher Scientific). Cycle sequencing reactions were run on an ABI 3730 automated sequencer (according to the manufacturer's protocols; Thermo Fisher Scientific), using 5× Sequencing Buffer, DMSO, BigDye Premix 3.1, primers diluted 1/10, and 50–300 ng of genomic DNA, depending on quality and concentration. Sequencing was performed with 26 cycles using the standard settings: 0.10 minutes at 96 °C, 0.05 minutes at 50 °C, and 4.00 minutes at 60 °C. Automated sequence output files were edited and assembled using Geneious (version 8.1.9, Biomatters, Auckland, New Zealand).

Phylogenetic analyses

Sequences of the same five genetic markers generated as described above (ITS, *rps16*, *trnD-T*, *matK-trnK* and *trnL-F*) from 60 accessions representing 51 Caesalpinia group species and two outgroups were downloaded from GenBank and incorporated into the analysis (Suppl. material 2: Table S2). A sixth genetic marker used in previous studies, *ycf6-psbM* (Gagnon et al. 2016), was also added to our dataset because sequences were available for 45 species covering most of the major groups in the phylogeny (except *Lophocarpinia* and *Stenodrepanum*), including two samples from the putative genus *Ticanto* (*Herendeen 1-V-99-3* and *Wieringa et al. 4199*, both representing *T. crista*).

Sequences were aligned using MUSCLE (Edgar 2004), with subsequent manual adjustments carried out in Geneious. A concatenated matrix of the five plastid loci

comprising 7231 bp and a separate matrix of the nuclear ITS locus comprising 940 bp were analysed independently using both Maximum Likelihood (ML) and Bayesian phylogenetic methods.

The ML analyses were implemented using RaxML-HPC2 v. 8.2.10 (Stamatakis 2014) on XSEDE via the CIPRES Science Gateway (Miller et al. 2010). Node support was estimated using the standard nonparametric MLBS procedure, with 100 replicates. Bayesian analyses were carried out using MrBayes 3.2 (Ronquist et al. 2012) via the CIPRES Science Gateway (Miller et al. 2010), with parameters of two parallel runs of four Markov Chain Monte Carlo (MCMC) chains, four swaps per swapping cycle, for 28,000,000 generations, and trees sampled every 1000 generations. The stop criterion, ensuring that convergence of the runs had been achieved, was set to an average standard deviation of split frequencies that dropped to below 0.01. The burn-in fraction was set to 25%.

Following visual comparison of the resulting phylogenies, all sequences were concatenated to create a six-locus matrix (ITS + plastid) of 8171 bp and the combined dataset was analysed using both ML and Bayesian methods as described above. In the preliminary RaxML analyses of this six-locus matrix, each accession was separate in the matrix and represented by a separate terminal in the tree. Where accessions were missing two or more loci, multiple accessions of single species were concatenated for subsequent analyses if they appeared in the same clade in the initial analyses, thus minimising missing data for each species. Accessions were concatenated in this way for six species, and these are highlighted in bold in Suppl. material 2: Table S2.

Results from the phylogenetic trees were visualised using Figtree v1.4.2 (Rambaut 2014), and figures were generated using the packages "Biocmanager", "treeio", "ggtree" and "ggplot2" in R, with final edits in Adobe Illustrator. Statistics were obtained using MEGA 11 (Tamura et al. 2021).

Results

Molecular phylogeny

The concatenated five-locus matrix included 79 accessions (17 newly sequenced, and two of the accessions used by Gagnon et al. 2016 were re-sequenced) representing 60 species (five newly sequenced). In total there were 1207 (=6.8%) parsimony-informative characters in the matrix.

Separate analyses of the plastid and nuclear datasets revealed the same major clades in both the ML and Bayesian analyses. Incongruences between the nuclear and plastid trees were found at the interspecific level within clades but were unsupported in the nuclear analyses by either bootstrap or posterior probability values; these discrepancies are therefore considered non-contradictory. The three major clades that are of most relevance to this study represent the genera *Ticanto*, *Pterolobium* and *Mezoneuron*, and these were recovered in both the ML and Bayesian analyses (Fig. 1; Suppl. material 3). The recovery of intergeneric relationships is consistent between the ML and Bayesian phylogenies, with two exceptions; in the Bayesian phylogeny, the relative positions of

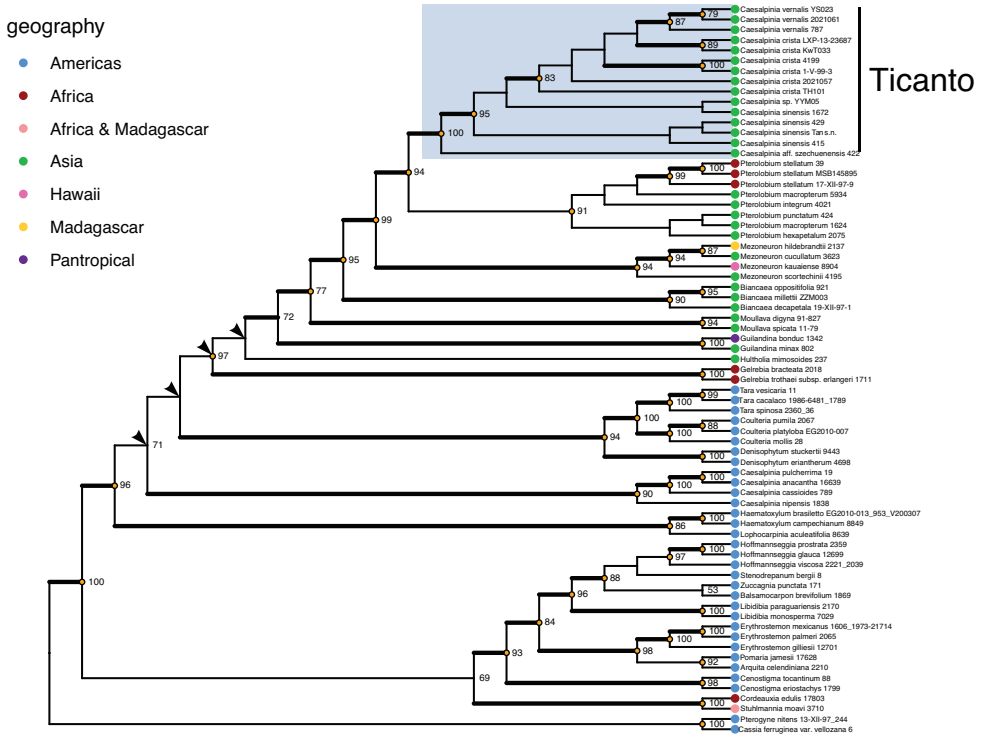


Figure 1. Caesalpinia group ML phylogeny from the combined dataset. Bootstrap values above 50 are shown, values > 75 are indicated with an orange dot at the node. Branches in bold indicate Posterior Probability greater than 0.95 in equivalent BI analysis. Arrows indicate nodes not recovered in BI analysis. The collector number of the corresponding voucher for each terminal is included with the species name. Where a terminal results from analysis of multiple vouchers, the collector numbers are separated by an underscore (see Suppl. material 2).

Gelrebia, *Hultholia* and the broad clade containing *Ticanto* are unresolved, forming a polytomy, and the position of *Caesalpinia* s.s. is also unresolved, forming a polytomy with the broad *Ticanto* clade and the *Coulteria-Tara-Denisophytum* clade.

Sequences of *Biancaea millettii* and *Caesalpinia vernalis* are incorporated into our analyses. These two species were initially included in the phylogeny of Gagnon et al. (2016) but were subsequently excluded because they were each represented by only a single sequence. The position of *Biancaea millettii* is here revealed to form a clade with *B. oppositifolia* and *B. decapetala*, whilst *Caesalpinia vernalis* is resolved as part of the *Ticanto* clade. The species *Pterolobium punctatum* is newly sequenced here and is resolved as belonging to a clade with the other sampled species of *Pterolobium*.

The six (including accession *Yi YYM05*, determined as *Ticanto* sp.) sampled species of the proposed genus *Ticanto* are resolved as a monophyletic group in all analyses (Fig. 1; Suppl. materials 3, 4). In the combined dataset analysis the genus is robustly supported as monophyletic and sister (bootstrap = 94%, PP = 1.0) to the genus *Pterolobium*. These genera together comprise a clade that is robustly supported (bootstrap = 99%, PP =

1.0) as sister to *Mezoneuron*. Some resolution of the interspecific relationships within *Ticanto* is achieved; three accessions of *T. sinensis* group together (bootstrap = 95%, PP = 1.0), sister to the clade comprising *T. crista*, *T. vernalis*, and *Yi YYM05* (*Ticanto* sp.), and a further accession of *T. sinensis*. The accession *Clark 422*, determined as *Ticanto* aff. *szechuenensis*, is resolved as sister to all other species in the clade (bootstrap = 100%, PP = 1.0). *T. crista* and *T. vernalis* are indicated as probably being sister species, but the relationships between accessions determined as *T. crista* are unresolved.

Partial sequences of ITS, *rps16* and *trnL-F* were obtained from a single accession of *T. magnifoliolata* (*Kiyama et al. 1233*), which in both the ML and Bayesian analyses was resolved as part of the *Ticanto* clade. Because the position of this accession is poorly supported due to a high proportion of missing data (80.8%), the version of the phylogeny including this accession is presented separately (Suppl. material 4).

Taxonomic treatment

***Ticanto* Adans., Fam. Pl. 2: 319. 1763.**

Caesalpinia sect. *Nugaria* DC., Prodr. 2: 481, 1825.
Nugaria Prain, J. As. Soc. Beng. 66(ii): 470, 1897 *nom. inval. nom. provis*.

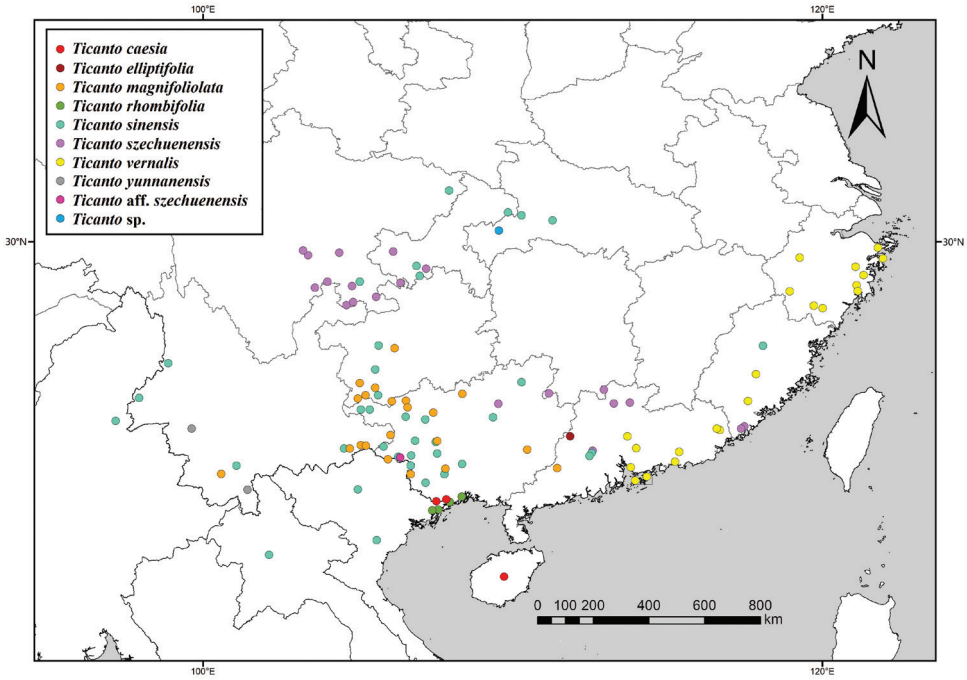
Type. *Guilandina paniculata* Lam.

Etymology and type notes. Despite reference in the protologue of *Ticanto* to the plate H.M. 6. *t.* 19, this did not constitute typification of the name because Adanson did not mention a previously or simultaneously published species name, nor the type of such a name (Turland et al. 2018; Art. 10.2; https://www.iapt-taxon.org/nomen/pages/main/art_10.html). The rules of the *Code* (Turland et al. 2018) state that a type must therefore be otherwise chosen, which in this case has been achieved in the published card index of *Index Nominum Genericorum* (https://naturalhistory2.si.edu/botany/ing/) by reference to *Guilandina paniculata* Lam. (1785). The application of the name *Ticanto* is therefore fixed by the type of *G. paniculata* Lam., H.M. 6. *t.* 19, now a heterotypic synonym of *Caesalpinia crista* L.

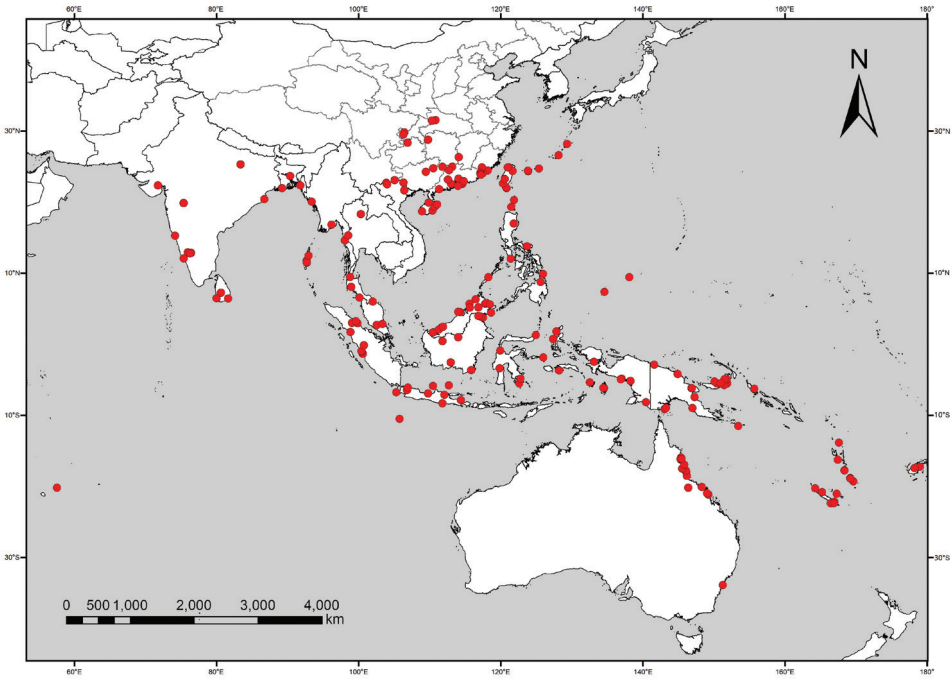
The name *Ticanto* was a vernacular name used for these plants by the Brachmanes, also known as Brahmanas, Brahmans, or Brahmins, a sector of Hinduism. This was referenced by Rheede (1686: 33) as "*Ticanto* Brachmanes" and subsequently in the protologue of *Ticanto* (Adanson 1763) as '*Ticanto. Bram.*'. The name was without gender. The only combination to have been published in *Ticanto* is *T. nuga* (L.) Medik. (1786), the epithet of which derives from the description of the plants by Rumphius in his Herbarium Amboinense (1747) as "nugae silvarum", or 'trifles [i.e., trivial plants] of the woods'. Linnaeus adopted this term in creating the epithet *Guilandina nuga* L. (1762), using it as a noun in apposition. The creation of *Ticanto nuga* (L.) Medik. therefore did not assign a gender to the genus name *Ticanto*, and in the absence of other species published under that name it remained ungendered. We hereby assign the feminine gender to the genus name *Ticanto*, thus avoiding changes to the species epithets and maintaining nomenclatural stability.

Genus description. Scandent shrubs or lianas to 15 m. Stems usually with scattered, recurved prickles. ***Leaves*** pari-bipinnate, pinnae 1–16 opposite pairs, leaflets 2–15 opposite pairs, leaf rachis with recurved prickles at base of pinnae and usually scattered in between. ***Stipules*** 0.25–3 mm long. Leaflets elliptic to ovate or obovate, oblong or rhombic. ***Inflorescence*** a terminal or axillary raceme or panicle 7–42 cm long; pedicels articulated; bracts at base of racemes, caducous, bracteoles at base of pedicels, caducous. ***Flowers*** zygomorphic, with a hypanthium, calyx lobes 5, free, the lower lobe cucullate over the others in bud; petals 5, 3.5–12 × 2–7 mm, the median petal distinct from the others in shape, usually with an approximately circular patch of hairs on the inner surface, the lateral petals glabrous or with few hairs; stamens 10, free, 4–14 mm long, the basal half tomentose; ovary 1–2-ovuled, glabrous or hairy; style 4–12 mm long; stigma funnel-shaped and more or less papillate, or truncate. Fruit coriaceous or ligneous, dehiscent or indehiscent, elliptic, lunate, or sub-circular, 1.5–7 × 1.5–5 cm, apex acute or beaked, with or without a stipe, the upper suture with or without a narrow wing 0.5–4 mm wide, or a carinate wing 5–6 mm deep, 1(–2)-seeded.

Distribution. Andaman Islands, Australia, Cambodia, China (Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hong Kong, Hubei, Hunan, Sichuan, Taiwan, Yunnan, Zhejiang), India, Indonesia, Japan (Ryukyu Islands), Malaysia, Mauritius, Micronesia, Myanmar, New Caledonia, Papua New Guinea, Philippines, Polynesia, Sri Lanka, Thailand, Vietnam (Maps 1, 2).



Map 1. Distribution of all species (excluding *T. crista*).



Map 2. Distribution of *T. crista*.

Key to the species

1 Pinnae 8–16 pairs, fruit dehiscent, ligneous ..... ***T. vernalis***
– Pinnae 1–8(–9) pairs; fruit usually indehiscent, coriaceous or ligneous **2**
2 Leaflets 8–15 pairs; 0.8–1.5 × 0.4–0.6 cm ..... ***T. caesia***
– Leaflets 2–7 pairs; (1.2–)1.5–13(–15) × 0.8–8 cm **3**
3 Leaflets rhombic, 1.5–2 × 0.8–1.3 cm; fruit without a wing..... ***T. rhombifolia***
– Leaflets elliptic, ovate or obovate, 1.2–13(–15) × 0.8–8 cm; fruit with or without a wing..... **4**
4 Fruit dehiscent, ligneous; without a wing; fruit venation not prominent..... ..... ***T. yunnanensis***
– Fruit indehiscent, coriaceous; with or without a wing; fruit venation prominent **5**
5 Fruit without a wing, slightly asymmetrical to sub-lunate **6**
– Fruit usually with a flat or carinate wing along the upper suture, strongly asymmetrical, sub-circular to lunate or teardrop-shaped..... **7**
6 Leaflets 7–13 × 4.5–8 cm, underside of leaflets with brown hairs..... ..... ***T. elliptifolia***
– Leaflets 2.1–7.2 × 1–3.3 cm, underside of leaflets usually glabrous or occasionally with sparse ferruginous hairs ..... ***T. crista***

7 Leaflets 3.5–10.8(–15) × 2.1–7 cm, apex usually rounded; ovary glabrous; fruit wing carinate..... ***T. magnifoliolata***
– Leaflets 1.2–10.7 × 0.8–5.1 cm, apex usually acute or acuminate; ovary sparsely to densely tomentose, or subglabrous; fruit wing flat or absent **8**
8 Leaflets 1.2–6 × 0.8–3 cm, leaflet apex usually acute; fruit 1.5–3.4 × 1.5–3 cm, wing 1–3 mm wide, present only along part of the fruit length or absent ..... ***T. szechuenensis***
– Leaflets 1.8–10.7 × 0.8–5.1 cm, leaflet apex usually acuminate; fruit 3–5.8 × 1.9–4.1 cm, wing 0.5–4 mm wide ..... ***T. sinensis***

Species descriptions

1. *Ticanto caesia* (Hand.-Mazz.) R. Clark & Gagnon, comb. nov.
urn:lsid:ipni.org:names:77303538-1

Caesalpinia hypoglauca Chun & F. C. How., Acta Phytotax. Sin. 7: 20 pl. 6. 1958. Type: China. Kwangtung, Sup Man Ta Shan [Mt. Shiwandashan], 26 Jul. 1933, *H.Y. Liang 69864* (lectotype: (designated by Vidal and Hul Thol 1976): A [A00059892!], isolectotypes IBK [IBK00190838!, IBK00190839!]) (note: the locality of this specimen is in Qinzhou, which has been considered part of Guangxi since 1952).

Basionym. *Caesalpinia caesia* Hand.-Mazz., Oesterr. Bot. Z. 85: 215. 1936.

Type. China. Kwangsi, *Fenzel 3* (W!).

Description. ***Habit*** a climber. ***Stems*** with sparse recurved prickles, puberulent. ***Stipules*** unknown. ***Leaves*** with 5–8(–9) pairs opposite pinnae; leaf rachis and petiole 15–20 cm, leaf rachis and pinnae rachises pilose; leaflets 8–12(–15) opposite pairs per pinna, subsessile, chartaceous, oblong, base strongly asymmetric, apex truncate or obtuse-rounded, emarginate, 0.8–1.5 × 0.4–0.6 cm, both surfaces glabrous. ***Inflorescence*** a panicle, supra-axillary or terminal, 10–15 cm, the axes brown puberulent; pedicels 4–7 mm, articulated. ***Flowers*** with a hypanthium, this glabrous, lower calyx lobe ca. 6 mm long, others 3.5–4 mm, all lobes glabrous; petals obovate-oblong, ca. 3.5–5.5 mm long, median petal with rhombic patch of dense hairs on the inner surface at base of blade, other petals pubescent, shortly clawed; stamen filaments ca. 6 mm long, ferruginous pilose at base; ovary glabrous, 2-ovuled, style ca. 4 mm long. ***Fruit*** blackish when dry, indehiscent, ligneous, elliptic, inflated at maturity, venation prominent, glabrous, ca. 4.5–5 × 2.3–5 cm, ventral suture narrowly winged. ***Seed*** 1, lenticulate, 1.5 × 2.0 cm, blackish.

Ecology. Sparse forests along rivers, elevation 200–1000 m.

Phenology. Flowering July-September, fruiting August.

Distribution. China (Guangxi, Hainan) (Map 1).

Notes. Only one specimen collected from Hainan was seen by the current authors (*H. Fenzel s.n.*, see the citation below), of which the detailed locality is unknown (not recorded on the specimen). To include Hainan in the species distribution, we georeferenced this specimen in the centre of the island.

Selected specimens examined. China. Guangxi: Fangcheng, Naliang, *s. coll.*, *s.n.* (PEY). Fangcheng, Dongzhong, Dakeng Village, *Shiwandashan Exped. 3224* (IBK). Shiwandashan, *C.L. Tso 23669* (IBSC). **Hainan:** *H. Fenzel s.n.* (IBSC).

2. *Ticanto crista* (L.) R. Clark & Gagnon, comb. nov.
urn:lsid:ipni.org:names:77303539-1

= *Guilandina nuga* L., Sp. Pl., 2. 1: 545. 1762. Type: [Indonesia]. East Indies, Ambon, *Nugae silvarum* Rumph. Herb. Am. 5. p.95, t. 50. 1750.
= *Guilandina axillaris* Lam., Encycl. 1(2): 435. 1785. Type: [India]. Rheede. Hort. Mal. 6: t. 20. 1686.
= *Ticanto nuga* (L.) Medik., Theodora 52. 1786. Type: based on *Guilandina nuga* L.
= *Guilandina paniculata* Lam., Encycl. 1(2): 435. 1785. Type: [India]. Malabar, Kaka Mullu vel Kaka Moullou (in caption Kaka Mullu) Rheede, Hort. Mal. 6: t. 19. 1686.
= *Genista scandens* Lour., Fl. Cochinch. 2: 428. 1790. Type: Cochinchina (*n.v.*).
= *Guilandina parvifolia* Stokes, Bot. Mat. Med. 2: 466. 1812. Type: [Indonesia]. East Indies, Ambon, *Nugae silvarum* Rumph. Herb. Am. 5. p.95, t.50. 1750.
= *Caesalpinia nuga* (L.) W.T. Aiton, Hort. Kew, ed 2, 3: 32. 1811. Type: based on *Guilandina nuga* L.
= *Caesalpinia paniculata* (Lam.) Roxb., Hort. Beng. 32. 1814. Type: based on *Guilandina paniculata* Lam.
= *Caesalpinia scandens* Heyne ex Roth, Nov. Pl. Sp. 209. 1821. Neotype: (designated by Turner 2021): India, Samalcott, Mar 1811, *B. Heyne s.n.* [K: K000789355!].
= *Caesalpinia axillaris* (Lam.) DC., Prodr. 2: 481. 1825. Type: based on *Guilandina axillaris* Lam.
= *Caesalpinia laevigata* Perr., Mém. Soc. Linn. Paris 3: 104. 1825. Type: Philippines. *Perrottet s.n.* (*n.v.*).
= *Caesalpinia crista* var. *parvistipula* Urb., Symb. Antill. 2(2): 271. 1900. Type: Trinidad. Cult. Hort. Trinidad, *Broadway 5589* (*n.v.*).

Basionym. *Caesalpinia crista* L. Sp. Pl. 1: 380. 1753, emend Dandy & Exell in J. Bot. 76: 179. 1938. ≡ *Guilandina crista* (L.) Small, Fl. S.E. U.S. 591, 1331 (1903).

Type. [Sri Lanka] Ceylon ("Ceylan"), *Herb. Hermann* vol. 1, fol. 68, no. 157 (lectotype (designated by Skeels in Science, n.s., 37: 922. 1913): BM [BM000621459!]) (note: the sheet bearing this specimen was previously identified by a single barcode, BM000594500, which was subsequently replaced with four barcodes representing the four separate specimens on the sheet).

Description. ***Habit*** a liana or scrambling shrub to 15 m. ***Stems*** with few, scattered recurved prickles to 5 mm, sometimes with spine-tipped corky tubercles on older stems, or unarmed, glabrous or occasionally sparsely tomentose. ***Stipules*** persistent, triangular, ca. 1 × 1 mm. ***Leaves*** with 3–6(–8) pairs pinnae, these opposite to occasionally

slightly subopposite; petiole 1.8–5 cm; rachis 4–31 cm, usually armed with recurved prickles, these sometimes also on pinnae rachises, petiole and rachis usually glabrous, occasionally sparsely to moderately ferruginous tomentose; leaflets 2–4(–7) pairs per pinna, coriaceous, opposite, elliptic, base cuneate to obtuse, apex rounded to obtuse, less commonly acute, obtuse, or acuminate, terminal leaflets 2.1–7.2 × 1–3.3 cm, lateral leaflets 2.1–5.8 × 1–3.1 cm, upper surface glabrous, often glossy, lower surface glabrous or occasionally sparsely ferruginous tomentose, venation reticulate, anastomosing, visible on both surfaces. ***Inflorescence*** a raceme or panicle, axillary or terminal, 8–40 cm, axes glabrous or sparsely tomentose; pedicels 5–15 mm; bracts persistent, triangular or lunate, 1–1.5 × 1 mm; bracteoles caducous, broadly elliptic, apex acute, margins sometimes with small teeth, 1–2.5 × 0.5–1 mm. ***Flowers*** with a hypanthium 1–2 × 3–6 mm, glabrous or sparsely ferruginous tomentose; lower calyx lobe 6–8(–10) × 3–4 mm, other lobes 5–6(– 8) × 2–3 mm, all lobes glabrous, or margins ciliate, or sparsely ferruginous tomentose; median petal 6–9 × 3–7 mm, with dense circular patch of hairs on inner surface at base of blade; upper laterals 6–10 × 3–5 mm, including claw ca. 1 mm, glabrous or inner surface of claw sparsely hairy; lower laterals 7–11 × 3–6 mm, including claw ca. 1 mm, glabrous or inner surface of claw sparsely hairy; stamen filaments 4–12 mm, the vexillary shorter than the lower ones, orange tomentose on lower ½–¾ on inner surface; anthers 1–1.5 mm; ovary 2–4 mm long, glabrous or sparsely or partially tomentose; style 4–11 mm; stigma cupular or funnel-shaped, the rim papillate, sometimes only slightly so, 0.5–1 mm wide. ***Fruit*** indehiscent, coriaceous, elliptic to lunate, subsymmetrical to somewhat asymmetrical, slightly inflated, base cuneate, stipe 2–5 mm, apex acute to beaked, beak 1–10 mm, venation reticulate, prominent, glabrous or very sparsely tomentose, (2–)2.7–7 × 2.2–3.7 × 0.3–0.8 cm, lacking a wing. ***Seeds*** 1, rarely 2, circular to reniform in outline, flat, ca. 2–2.5 × 1.5–2 × 0.5–1 cm. (Fig. 3A).

Ecology. Riverbanks, sandy beaches, in and behind sandy parts of mangroves, on chalk rocks and limestone, at low altitude, elevation rarely up to 350 m.

Phenology. The flowering and fruiting time of this species varies throughout its distribution and may be correlated with latitude or biome as indicated below; however, the periodicity listed below derives in some cases from few records and thus may be incomplete.

China, Japan: Flowering February-April, fruiting April-October;

Bangladesh, India, Myanmar: Flowering August-December, fruiting December-October;

Thailand, Vietnam: Flowering January-June, fruiting January-June;

Malaysia, Indonesia, Palau Islands: Flowering February-December, fruiting February-January;

Philippines: Flowering December-March, fruiting May-December;

New Guinea: Flowering January-November, fruiting February-November;

New Hebrides, Solomon Islands: Flowering February-December, fruiting February-December;

New Caledonia: Flowering May, fruiting unknown;

Mauritius: Flowering unknown, fruiting February.

Distribution. Andaman Islands, Australia, Cambodia, China (Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hong Kong, Hubei, Hunan, Sichuan, Taiwan, Yunnan), India, Indonesia, Japan (Ryukyu Islands), Malaysia, Mauritius, Micronesia, Myanmar, New Caledonia, Papua New Guinea, Philippines, Solomon Islands, Sri Lanka, Thailand, Vanuatu, Vietnam (Map 2).

Notes. The current authors have not seen any specimens or specimen records from Cambodia (other than a single record in GBIF which is not from a preserved specimen), but Vidal and Hul Thol (1976) list Cambodia within the range for this species, citing two specimens from Kampot Province (*Geoffray 62*, *62 bis*) and that information is retained here. As these specimens could not be traced by the current authors, they are not included on the map. See also Nomenclatural notes on *Caesalpinia* (*Ticanto*) *crista*, below.

Selected specimens examined. Australia. Queensland: Daintree area, Noah Creek, Mangroves, *J.J. Wieringa 4199* (WAG). **Bangladesh.** Chittagong, *Flagstaff 255* (K). **China. Chongqing:** Jiulongpo, Jinfeng, Baihe Village, *Jiulongpo Exped. 500107150402-289LY* (IMC). Mt. Jinyunshan, *Z.Y. Liu 182996* (IMC). **Fujian:** Hua'an, Wenhua, *W.D. Han 20667* (NF). Pinghe, Daxi, Jiangzhai Village, *H.B. Chen s.n.* (FJSI). Xiamen, Yunding Cliff, *G.D. Ye 1208* (IBSC). Yunxiao, Huotian, Baihuayang Reservoir, *G.D. Ye 2482* (FJSI). Zhangzhou, Zhaoan, Wushan, *X.F. Zeng ZXF19839* (CZH). Zhangzhou, Zhaoan, Wushan, Jinshui Village, *X.F. Zeng ZXF41029* (CZH). Zhao'an, Jinshui Village, *s. coll.*, *s.n.* (AU). **Guangdong.** Boluo, Mt. Luofushan, near Damiao, *Yue78 5714* (IBSC). Dianbai, Luokeng, Mt. Shuangjiling, *H.G. Ye 6379* (IBSC). Huidong, Pingshan Forest Farm, Mt. Chenshuishan, Zhulian?, *P.Y. Chen*, *B.H. Chen & G.C. Zhang 46* (IBSC). Jiangmen, Mt. Guifengshan, *J.Y. Chen 20165220* (SN). Qingyuan, Yangshan, near Qincaitang Reservoir, *K.W. Jiang KwT033* (NPH). Ruyuan, Daqiao Health Center, back mountain, *Yue73 1182* (CSFI). Shenzhen, Longgang, Nan'ao, Yangmeikeng, *S.Z. Zhang*, *L.Q. Li et al. 185* (SZG). Xin'an, Ng-tung Shan, *T.M. Tsui 231* (NAS). Zhaoqing, Mt. Dinghushan, *S.J. Li 30* (IBSC). *ibid.*, *Z.Q. Song 2021057* (IBSC). **Guangxi:** Liuzhou, Longtan Park, Mt. Jiaodingshan, *Longtan & Dule Exped. 242* (IBK). Yang-shoh, *H. Fung 21112* (SYS). **Guizhou:** Tungtze, *Y. Tsiang 4894* (IBSC). **Hainan:** Kan-en, Chim Fung Ling, near Sam Mo Watt Village, *S.K. Lau 3582* (IBSC). Lin'gao, Maniao, Wende Village, *Z.X. Li et al. 911* (IBSC). Qionghai, Lehui, near Shuangbang Village, *Y. Zhong 4472* (IBSC). Wanning, Mt. Dongshan, the second mountain range, *S.P. Kao 52115* (IBSC). Wenchang, Longlou, nera Mt. Beijianshan, *G.W. Tang*, *Z.M. Li & J. Li TangGW2525* (IBSC). **Hubei:** Shennongjia, Xingshan to Yangri, *D.G. Zhang ZB130226624* (JIU). Xingshan, Xiakou, Jianyangping, Lifangyan to Huangliang, *D.G. Zhang zdg4185* (JIU). **Hunan:** Jianghua, *C.J. Qi 3822* (CSFI, IBSC). Xiangxi, Yongshun, Zejia, Donglu Village, *K.D. Lei ZZ40516121* (JIU). **Jiangxi:** Ji'an, Suichuan, Daijiapu, Xianmo, *Z.C. Liu*, *W.J. Xiong*, *F. Ye*, *L. Deng*, *M. Tu*, *X.J. Zhang*, *L. Feng*, *Q.Y. Yin & N.N. Liu LXP-13-23687* (SYS). **Taiwan:** Hsinchu, Hsienchiaoshih, *Z.-H. Chen 277* (TAIF). **Yunnan:** Hekou, Erqu, *W.X. Liu 277* (HITBC). **Micronesia.** Caroline Islands, Yap

Group, Gorror Island, Central Plateau, *E.Y. Hosaka 3319* (K). **India.** Kaswar, *R.J. Bell 7750* (K). Kuppam River, Taliparamba, *C.A. Barber 8788* (K). North Kanara, *W.A. Talbot 1256* (K). S. Andaman, *Dr King's Collector s.n.* (K). **Myanmar.** Myebon, *H.S. McKee 6069* (K). Rangoon, *D.R. Khant 1079* (K). **Mauritius.** The Pouce, *J. Gueko s.n.* (K). **New Caledonia.** Yate, Touaourou, *s. coll. s.n.* (K). **Thailand.** Narithiwat: Kulok river mouth next to bridge on road from Tak Bai to Sungai Ko-lok, *P.S. Herendeen & R. Pooma 1-V-1999-3* (US). **Vanuatu.** Aniwa Island, Isavai village, *P. Curry 1447* (K). Banks Islands, Port Patterson, *A. Morrison s.n.* (K). New Hebrides, Erromanga, between Nouanko Camp and Ipota, about 10 km E of Ipota, *P.S. Green RSNH1318* (K). New Hebrides, Port Vila, *A. Morrison s.n.* (K).

3. *Ticanto elliptifolia* (S. J. Li, Z. Y. Chen & D. X. Zhang) R. Clark & Gagnon, comb. nov.
urn:lsid:ipni.org:names:77303540-1

Basionym. *Caesalpinia elliptifolia* S. J. Li, Z. Y. Chen & D. X. Zhang, Nordic J. Bot. 22: 349. 2003.

Type. China Guangdong, Fengkai, Qixing, alt. 120m, 20 July 2000, *Shijin Li 026* (holotype: IBSC!)

Description. ***Habit*** a liana to 15 m. ***Stems*** occasionally with scattered, recurved prickles to 2 mm. ***Stipules*** caducous. ***Leaves*** with 1–2 pairs opposite pinnae; leaf rachis 20–30 cm, leaf rachis and pinnae rachises with recurved prickles; petiolules 2–3 mm; leaflets 2 opposite pairs per pinna, coriaceous, broadly elliptic, base cuneate to rounded, apex rounded, obtuse or acute, 7–13 × 4.5–8 cm, upper surface glabrous, glossy, lower surface with brown hairs especially on midvein; venation anastomosing, finely reticulate. ***Inflorescence*** a panicle, supra-axillary or terminal, 15–25 cm, all parts densely hairy; pedicels 8–12 mm, articulated; bracts caducous, lanceolate, 1–3 mm; bracteoles caducous, ca. 1.5 mm. ***Flowers*** with a hypanthium, this with brown hairs; calyx lobes ca. 6 × 2 mm, with brown hairs; median petal blade reflexed, claw ca. 3.5 × 1 mm, blade ca. 7 × 6–7 mm, circular patch of brown hairs at base of blade, otherwise glabrous; lateral petals 10–12 × 4–5 mm, claw ca. 1 mm, glabrous; stamen filaments 9–14 mm, the basal ca. ½ tomentose, anthers 2 mm; ovary subsessile, ca. 2 mm long, tomentose, 1- or 2-ovuled; style (2–)7–10 mm, occasionally as short as 2 mm, glabrous; stigma truncate, papillate. ***Fruit*** indehiscent, coriaceous, oblong-elliptic to sub-lunate, sub-symmetrical, compressed but slightly inflated when mature, base cuneate, stipe short, apex acute to attenuate, beak ca. 1–5 mm, veins prominent and reticulate, ca. 4.5–5 × 2.2–2.5 cm, lacking a wing. ***Seeds*** 1 or 2, brownish black, compressed, sub-circular, ca. 10–15 mm cm in diameter.

Ecology. Beside ditches, elevation ca. 100 m.

Phenology. Flowering April, fruiting May-June.

Distribution. China (Guangdong) (Map 1).

4. *Ticanto magnifoliolata* (Metcalf) R. Clark & Gagnon, comb. nov.
urn:lsid:ipni.org:names:77303541-1

Basionym. *Caesalpinia magnifoliolata* Metcalf. Lingnan Sci. J. 19: 553. 1940.

Type. China. Kwangsi, Ling Yun Hsien, *Steward*, *A.N. & Cheo, H.C. 583* (holotype: A [A00059894!]).

Description. ***Habit*** a scrambling shrub. ***Stems*** with scattered recurved prickles, ferruginous puberulent, glabrescent. ***Stipules*** not seen. ***Leaves*** with 2–3(–4) pairs opposite pinnae; petiole 3.5–9 cm; leaf rachis 3.3–18.5 cm, with paired recurved prickles at the pinna insertion points and scattered in between, or unarmed; pinnae 2–9 cm; leaflets 2(–3) opposite pairs per pinna, coriaceous, elliptic to obovate, base oblique, apex usually rounded or obtuse, retuse to emarginate, occasionally acute; terminal leaflets 3.5–10.8(–15) × 2.1–7 cm; lateral leaflets 3.5–9.3 × 2.1–4.6 cm; both leaf surfaces glabrous, or lower surface sparsely puberulent; venation reticulate, anastomosing. ***Inflorescence*** a raceme or panicle, axillary or terminal, 15–30 cm; axes and pedicels sparsely to moderately ferruginous tomentose; pedicels 5–11 mm, articulated, glabrous; bracts and bracteoles not seen. ***Flowers*** with a hypanthium ca. 1 × 2–4 mm, glabrous to sparsely orange tomentose; lower calyx lobe ca. 7 × 3 mm; other calyx lobes ca. 5–6 × 2 mm; all calyx lobes with ciliate margins; median petal inrolled, with a patch of hairs at base of blade on inner surface, ca. 7–10 × 3–5 mm; upper laterals ca. 7–10 × 3–5 mm, hairy on the claw inner surface; lower laterals ca. 7–10 × 3–5 mm, hairy on the claw inner surface. Stamen filaments ca. 5–9(–10) mm, the basal ½ tomentose; ovary ca. 3 mm long, glabrous, subsessile; style 5–10 mm, glabrous; stigma funnel-shaped, papillate, sometimes laterally placed. ***Fruit*** dark brown, indehiscent, coriaceous, lunate, stipe ca. 1 mm, beak 2–7 mm, venation prominent, glabrous, 2.8–4.2 × 2.2–3.1(–3.5) × 0.4–0.7 cm, wing on ventral suture carinate, 5–6 mm deep. ***Seed*** 1, brownish black, compressed, sub-circular, ca. 2 × 2.5 cm (Fig. 2B).

Ecology. Forests, scrubland; 400–1800 m.

Phenology. Flowering February-July, fruiting May-November.

Distribution. China (Guangdong, Guangxi, Guizhou, Yunnan) (Map 1).

Selected specimens examined. China. Guangdong: Luoding, Caotang, Lianshi Village, *B.H. Chen et al. 1793* (IBSC). **Guangxi:** Donglan, Sannong, Xiangtiandong Village, Haoyantun, *H.Z. Lü*, *Z.Z. Lan & H.F. Cen 451224180425005LY* (GXMG). Fusui, Zhongdong, Luhan?, near Mt. Damingshan, *S.H. Chun 12435* (IBSC). Huanjiang, Mulun Nature Reserve, Xiazhai Observation Deck, *W.B. Xu*, *R.C. Hu & M.Q. Han ML1296* (IBK). Leye, on the way from Gantian to Daping, *M. Shi s.n.* (NPH). Lingle, Xinhua, Sanhe, *Lingle Exped. 34420* (IBK). Longzhou, Jinlong, Jinmei, Nongqiao, *W.B. Xu*, *Y.S. Huang et al. LZ1370* (IBK). Napo, Bing Mung, Rong La Shan, *H. Akiyama*, *H. Kudo*, *J. Murata*, *T. Sugawara*, *N. Tanaka*, *Y. Tateishi*, *Y.G. Wei & S.G. Wu 1233* (KUN). Pingguo, Taiping, Chami Village, Chajiangtun, *H.Z. Lü*, *Y. Lin*, *L.L. Mo & B.Z. Ban 451023150325048LY* (GXMG). Pingnan, Yaoshan, Luoxiang, Mt. Lingdingshan, *C. Wang 39106* (IBK). **Guizhou:** Anlong, Huali, Dewo, *Guizhou*

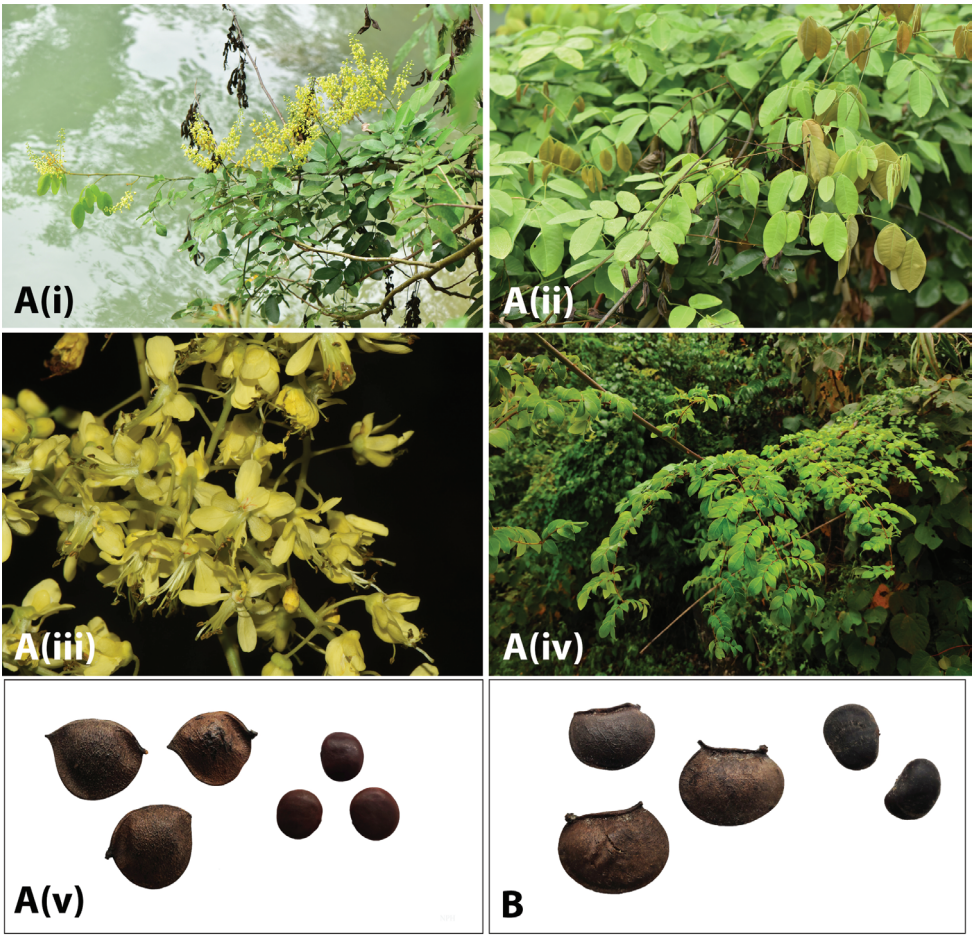


Figure 2. Photos of *Ticanto* **A** *T. crista* (i) habit (ii) leaves (iii) flowers (*E.D. Liu 8629*, Yunnan, China (KUN)) (iv) leaves (*K.W. Jiang KwT033* (NPH)) (v) fruit and seeds (*Z.Q. Song s.n.* (fruit and seeds in NPH)) **B** *T. magnifoliolata* fruit and seeds (*Q. Meng s.n.*, Guizhou, China (fruit and seeds in NPH)) .

Exped. (*C.S. Chang & Y.T. Chang*) *3543* (HGAS). Anlong, Longshan, Dushan, *Guizhou Exped.* (*C.S. Chang & Y.T. Chang*) *3138* (HGAS, IBSC, KUN, NAS, PE). Ceheng, Shuanghe, Jishanlin, *C.Z. Dang 1684* (HGAS). Pingba, Qibo, Taohua Village, Baidong, *R. Yang & L.B. Yan PB1356* (GZAC). Xingren, Nongchang, near Shanhe, *Guizhou Exped.* (*C.S. Chang & Y.T. Chang*) *7790* (HGAS, IBSC, KUN, NAS, PE, WUK). Xingyi, Qingnan, Yangping, Bajiaoping?, *Anshun Exped. 744* (HGAS). **Yunnan:** Funing, Zhesang, Nonguo Village, *J. Cai*, *J.D. Ya*, *X.Q. Yu*, *Y. Su & C.H. Li 14CS9136* (KUN). Mali, Xialiangshuijing, *Malipo Exped. 5326240386* (IMDY). Malipo, on the way from Huilong to Mabiao, *X.X. Zhu*, *B. Xiao*, *G.S. Wang & J. Wang LiuED8612* (KUN). Si-chour-hsien, Ping-chai, *K.M. Feng 12522* (KUN). Simao, Simaogang, *H. Wang 3842* (HITBC).

5. *Ticanto rhombifolia* (J. E. Vidal) R. Clark & Gagnon, comb. nov.

urn:lsid:ipni.org:names:77303542-1

Basionym. *Caesalpinia rhombifolia* J. E. Vidal, Adansonia, n.s., 15: 394. 1976.

Type. Vietnam. Quang Ninh, Dam Ha, *W.T. Tsang 29830* (holotype: P [P02142684!]; isotypes: C [C10011919!], E [E00313521!], G, K [K000789332!], L [L0018793!], SING).

Description. ***Habit*** a liana. ***Stems*** with sparse recurved prickles, glabrous. ***Stipules*** caducous, not seen. ***Leaves*** with 3–6 pairs opposite pinnae; petiole 2.5–3 cm; leaf rachis ca. 10–15 cm, with paired recurved prickles at base of pinnae and scattered in between, glabrous; pinna rachis 3.5–6 cm, glabrous; petiolules ca. 1 mm; leaflets 3–5 opposite pairs per pinna; chartaceous, slightly rhombic, base broadly cuneate, apex acute, rarely slightly emarginate, 1.5–2 × 0.8–1.3 cm, both surfaces glabrous; venation reticulate, anastomosing. ***Inflorescence*** a panicle, axillary or terminal, 10–20 cm; axes glabrous; pedicels 6–9 mm, articulated, glabrous or subglabrous. ***Flowers*** with a hypanthium that is sparsely ferruginous tomentose or glabrous; calyx lobes with ciliate margins; petals ca. 7 mm long, median petal smaller than the others, rounded at apex, with a patch of hairs at base of blade, other petals hairy on inner surface of claw; stamen filaments ca. 7 mm long, pale orange tomentose on basal ca. ½ on inner surface; anthers ca. 1.5 mm long; ovary glabrous, 1- or 2-ovuled; style ca. 10 mm, glabrous. ***Fruit*** indehiscent, coriaceous, asymmetrical, sub-lunate, inflated when mature, stipe ca. 3 mm, apex slightly beaked, venation prominent, glabrous, ca. 3–4 × 2.3–2.5 cm, lacking a wing. ***Seed*** 1, broadly ellipsoid, ca. 1.8–2 × 1–1.5 × 1.1 cm, matt black.

Ecology. Thickets.

Phenology. Flowering May-July, fruiting October-November.

Distribution. China (Guangxi), Vietnam (Map 1).

Selected specimens examined. China. Guangxi: Dongxing, Jiangping, Hezhou, *Dongxing Exped. 450681180510051LY* (IBK). Fangcheng, Dawangjiang Village, *Y.S. Huang & L. Wu H110397* (IBK).

6. *Ticanto sinensis* (Hemsl.) R. Clark & Gagnon, comb. nov.

urn:lsid:ipni.org:names:77303545-1

= *Caesalpinia chinensis* Roxb. in Fl. Ind. ed. 2: 361. 1832., *nom. rej.* Li et al. Taxon 51: 816. 2002. Type: not designated.

= *Mezoneuron sinense* var. *parvifolium* Hemsl., J. Linn. Soc., Bot. 23: 205. 1887. Type: China. Hupeh Province, Ichang, *Henry*, *A. 2238* (lectotype, designated here: K [K000264687!]; isolectotype: P [P00751902!])

= *Caesalpinia tsoongii* Merr., Philipp. J. Sci. 27: 162. 1925. Type: China. Szechuen, *Tsoong 4190*. (holotype: UC [UC227358!]; isotype: GH [A00059897!]).

= *Caesalpinia stenoptera* Merr., J. Arnold Arbor. 19: 35. 1938. Type: Indo-China. Tonkin, Cao Bang, Ban Gioc, Jun. 1933, *Petelot*, *A. 4757* (lectotype, designated here: A

[A00059899!], isolectotypes: P [P02142685!, P02142686!], NY [NY00003575!, NY00003576!, NY00003577!]).

Basionym. *Mezoneuron sinense* Hemsl., J. Linn. Soc., Bot. 23: 204. 1887. ≡ *Caesalpinia sinensis* (Hemsl.) J.E. Vidal in J.E. Vidal & S. Hul Thol, Bull. Mus. Natl. Hist. Nat., ser. 3, 395 (Bot. 27): 90. 1976. *nom. cons.* Li et al. Taxon 51: 816. 2002.

Type. China. Hupeh, Ichang, *A. Henry*, (Herb. Kew) (lectotype (designated by Larsen et al. 1980): China, *Henry*, *A. 3113* [K 000264688!]).

Description. ***Habit*** a scandent shrub or vine to 13 m. ***Stems*** with scattered recurved prickles to 4 mm, glabrous or sparsely whitish to pale orange tomentose. ***Stipules*** persistent, triangular, 1–3 × 1–2.5 mm. ***Leaves*** with 2–4(–5) pairs opposite pinnae; petiole (1.3–)3–7 cm; leaf rachis 2.5–24 cm, with paired recurved prickles at pinna insertion points and scattered in between, sometimes densely; pinnae 2.5–12.5 cm, sometimes with recurved prickles in pairs at the leaflet insertion points and scattered in between; leaf rachis and petiole glabrous to sparsely whitish to pale orange tomentose; pinna rachis glabrous to sparsely pale orange tomentose; leaflets 2–5 opposite pairs per pinna; elliptic, base cuneate to rounded, sometimes oblique, apex usually acuminate, or acute, occasionally rounded; terminal leaflets 1.8–10.7 × 0.9–5.1 cm; lateral leaflets 1.9–9.2 × 0.8–4.7 cm; all leaflets glabrous on both surfaces or lower surface sparsely orange tomentose at base and on midvein, sometimes at margins, glossy above; venation reticulate, anastomosing. ***Inflorescence*** a panicle, axillary, supra-axillary or terminal, 7–42 cm long, axes sparsely to densely ferruginous tomentose, axis sometimes with small, recurved prickles; pedicels (3–)4–12(–17 in fruit) mm, articulated, sparsely to moderately ferruginous tomentose; bracts caducous, triangular, 0.5–2 × 1–1.5 mm; clusters of triangular scale-like bracts sometimes below base of raceme; bracteoles caducous, broad, elliptic, acute, 2–3 × 1–1.5 mm. ***Flowers*** with a hypanthium 1–2 × 3–5 mm, sparsely to moderately ferruginous tomentose; lower calyx lobe 6–8 × 3–5 mm, other lobes 5–6 × 2–3 mm, all lobes sparsely to densely pale orange to ferruginous tomentose on inner and outer surface; median petal obovate, sometimes reflexed backwards, inrolled, 6–8 × 3–4 mm, including claw 1–2 mm long, a circular patch of orange hairs between claw and blade, hairs on margins of claw; upper laterals obovate, 6–10 × 2–6 mm, including claw ca. 1 mm long, petal glabrous or with a few hairs on inner surface of claw; lower laterals 6–10 × 2–6 mm, including claw ca. 1 mm long, glabrous or with a few hairs on inner surface of claw; stamen filaments flattened, 5–12 mm long, densely orange villous on basal ½; anthers 1–2 mm long; ovary 2–5 mm long, sparsely to densely, sometimes partially, orange tomentose, occasionally glabrous; style 6–12 mm long, sparsely hairy on basal ½; stigma funnel-shaped, not or very slightly papillate, sometimes slightly laterally placed. ***Fruit*** light green, indehiscent, coriaceous, sub-circular to lunate, base cuneate to rounded, not stipitate or stipe 0–2 mm, apex with a pronounced beak to 25 mm, venation prominent, sparsely ferruginous tomentose, the indumentum most dense at base and on margins, glabrescent or glabrous, 3–5.8 × 1.9–3.6(–4.1) cm × ca. 4–8 mm deep, wing on ventral suture 0.5–4 mm wide. ***Seed*** 1, ca. 1.8–2.5 cm diameter, matt or glossy dark brown. (Fig. 3A).

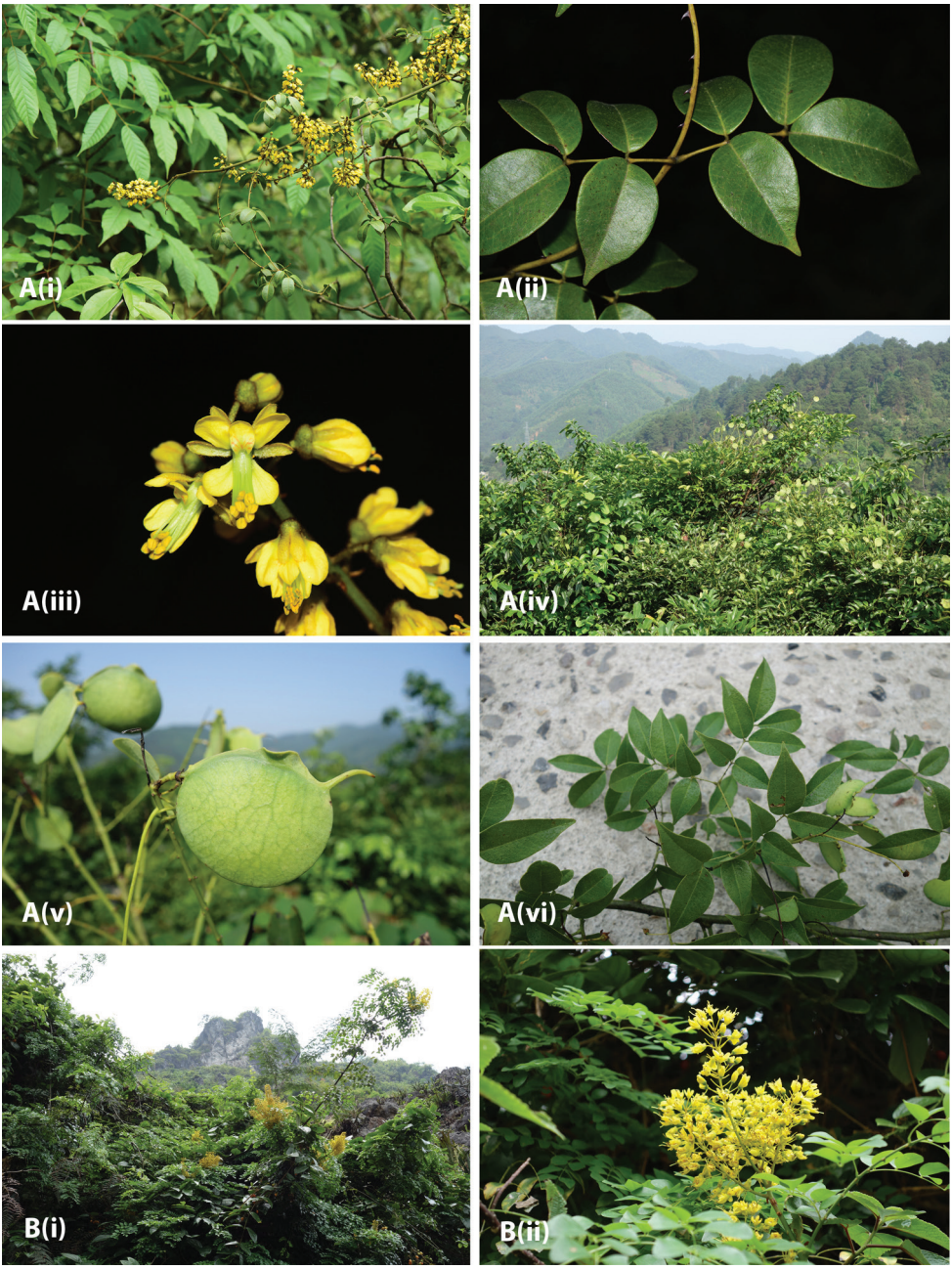


Figure 3. A *T. sinensis* (i) habit (ii) leaves (iii) flowers (photos by Xin-Xin Zhu, Guizhou, China, *unvouchered*) (iv) habit (v) fruit (*R.P. Clark 429*, Guangxi, China, (IBK, K)) (vi) leaves (*R.P. Clark 415*, Guangxi, China (IBK, K) **B** *T.* aff. *szechuenensis* (i) habit (ii) inflorescence and leaves (*R.P. Clark 422*, Guangxi, China (IBK, K)).

Ecology. Forest and thicket, on limestone. Elevation 100–1500m.

Phenology. Flowering March-May, fruiting March-October.

Distribution. China (Chongqing, Guangxi, Guangdong, Hong Kong, Hubei, Sichuan, Yunnan), Laos, Myanmar, Vietnam (Map 1).

Notes. The current authors have not seen any specimens or specimen records from Hong Kong but the area is included within the distribution listed by Vidal and Hul Thol (1976) and that information is retained here. The identity of the few available specimens from Laos and Myanmar is unconfirmed and these could be individuals of *T. crista*, although based on morphological affinities and the preference of *T. crista* for coastal habitats they are retained here as *T. sinensis* pending further analysis of the species limits.

Selected specimens examined. China. Chongqing: Qijiang, Wansheng, Heishangu Ave., opposite of Yaqulou, *S.R. Yi YSR9620* (NPH). Shimiaoxiangzhai, *S.G. Tang s.n.* (SM). Wushan, Guandu River, *T.P. Wang 10431* (WUK). **Fujian:** Mengtongyang, Chengmenkan, *H.Y. Zou 0931* (NF). **Guangdong:** Dinghu, Xinghu, Yuping Peak, *K.C. Ting & G.L. Shi 1337* (WUK). Zhaoqing, Qixingyan, *F.C. How 74128* (IBK). **Guangxi:** Bama, Xishan, *Z.T. Li 601739* (KUN). Donglan, Ma'an mountain, *R.P. Clark 429* (K, IBK). Debao, Longguang, Miaohuai Village, *Debao Exped. 451024160516009LY* (IBK). Fusui, Quli, Jidao Village, *B.Y. Huang*, *Y.Y. Xie & H.F. Cen 451421160523025LY* (GXMG). Jingxi, Longlin to Ande, *R.P. Clark 415* (K, IBK). Liuzhou Longtan Park, *W.E. Qun 150* (K). Long'an, Nanxu, Longxintun, *Long'an Exped. 450123130506007LY* (IBK). Longlin, Kechang, Haichang Village, Dankuntun, *L.Y. Yu*, *Y.D. Peng & X.Y. Hu 451031140410083LY* (GXMG). Napo, county town, Hongshui River Exped. 400 (TNM). Ningming, W Tingliang, *C.C. Huang et al. 2111* (GXMI). On the slopes of the limestone mountain near the county seat of Lingle, *Z.T. Li 603637* (IBK). S Nanning, Dar Shan, Seh-Feng, Me-Jon, *R.C. Ching 8435* (US). Tianyang, Wucun, Dalu Village, Longlitun, *Tianyang Exped. 451021150410060LY* (GXMG). **Guizhou:** Ceheng, Rongxian, Huangtian to Maoping, *Z.Y. Cao 544* (PE). Kwanlin, Kwanlinchow, Da-Swee-Tzi, *S.W. Teng 1641* (IBSC). Zhenfeng, Beipanjiang, Shuiyanba Village, *Y. Jia 522325190716483LY* (GZTM). **Hubei:** Badong, *T.P. Wang 10830* (IBK). **Sichuan:** Jiang'an, Nanyan, Hongfo Temple, *K.Y. Lang 3033* (PE). Xuanhan, Dong'an, *Xuanhan Exped. 1498* (SM). **Yunnan:** Between Szemao and Puerhfu, *J.F. Rock 2849* (NY, US). Lushui, near Nujiang River, *H. Sun 1672* (KUN). Xichou, Changqing, *C.W. Wang 81282* (KUN). Yingjiang, 23 km milestone on X309 Road from Pingyuan to Kachang, *Y.J. Guo*, *W.L. Zhao*, *P.X. Tang*, *X.L. Jin & X.Q. Zhang 13CS7525* (KUN). **Laos.** Phou Phung pres de Louang Prabang, *M. Poilane 20257* (K, L). **Myanmar.** Bhamo District, Lapycke to Sinlum Kabo, *J.H. Lace 5769* (K). **Vietnam.** Indo-China, Tonkin, *A. Petelot 4757* (NY). **Ninh Binh:** Cuc Phuong National Park, *N.M. Cuong 464* (MO).

7. *Ticanto szechuenensis* (Craib) R. Clark & Gagnon, comb. nov.

urn:lsid:ipni.org:names:77303565-1

= *Caesalpinia kwangtungensis* Merr., J. Arnold Arbor. 8: 7. 1927; Herkl. in Hong Kong Naturalist ix. 32. 1938, descr. ampl. Type: China. Kwangtung, *Wilson in Canton Christ. Coll. 12838* (lectotype, designated here: (GH [A00059893!], isolectotypes: BM [BM000958803!], E [E00313522!], LU, NAS, [NAS00071304!, NAS00071305!], P [P02142689!], US [US00002578!]).

Basionym. *Caesalpinia szechuenensis* Craib, Pl. Wilson. (Sargent) 2(1): 92. 1914.

Type. China. Western Szechuan, Kiating Fu, May 1908, *E.H. Wilson 3255*. (lectotype, designated here: K [K000980490], isolectotypes: A [A00059895!, A00059896!], BM [BM000958802!], E [E00313523!], GH, NY [NY00003572!], US.)

Description. ***Habit*** a scandent shrub. ***Stems*** with sparse, scattered recurved prickles, glabrous. ***Stipules*** minute, ca. 0.5 × 0.25 mm, triangular, subglabrous. ***Leaves*** with 3–6 pairs opposite to strongly subopposite pinnae; petiole 1.8–7 cm, leaf rachis with prickle at the base of each pinna and scattered in between pinnae insertions, 6–22 cm; pinnae 3.8–8.5 cm, occasionally with prickle at base of petiolule; leaflets 3–6 opposite pairs per pinna, elliptic to slightly ovate, the apex usually acute, occasionally slightly rounded; terminal leaflets 2–6 × 1–3 cm, lateral leaflets 1.2–6 × 0.8–3 cm, upper surface glabrous, lower surface glabrous or with a few ferruginous tomentose hairs on midvein at base or with sparse short ferruginous hairs; venation prominent on both surfaces, reticulate, anastomosing. ***Inflorescence*** a terminal, few-branched panicle, 11–15 cm long, axes subglabrous to sparsely to moderately ferruginous tomentose; pedicels (5–)9–11 mm, articulated, glabrous to sparsely ferruginous tomentose; bracts not seen; bracteoles caducous, 1 × 0.25 mm, lanceolate-acuminate. ***Flowers*** with a hypanthium ca. 1–2 × 3–4 mm, sparsely ferruginous tomentose; lower calyx lobe 8 mm long, other lobes 5 mm long; median petal 6–9.5 × 2.5–5 mm, with a patch of hairs at base of blade and few hairs on the claw; upper laterals ca. 5–10 × 3–4 mm, glabrous or with a few hairs on inner surface of the claw; lower laterals ca. 5–10 × 3–4 mm, glabrous or with a few hairs on inner surface of claw; stamen filaments flattened, ca. 9 mm long, densely orange villous on basal ½; ovary ca. 2.5 mm long, sparsely to moderately densely pale orange tomentose; style 10–12 mm, with a few hairs at the base, otherwise glabrous, ovules 2; stigma funnel-shaped, papillate, ca. 1 mm wide. ***Fruit*** indehiscent, coriaceous, strongly asymmetrical, sub-lunate to subcircular or teardrop-shaped, stipe 0–1 mm, beak 1–5 mm, venation prominent, glabrous, 1.5–3.4 × 1.5–3 cm × 0.4–0.6 cm, wing sometimes present along part of length of ventral suture, 1–3 mm wide. ***Seed*** 1, circular, dark brown, 1.4–1.7 cm diameter (Fig. 3B).

Ecology. Mountain forest, thicket, on limestone, elevation 260–1500 m.

Phenology. Flowering April-August, fruiting June-October.

Distribution. China (Chongqing, Fujian, Guangdong, Guangxi, Hong Kong, Hunan, Sichuan) (Map 1).

Notes. The current authors have seen no specimens or specimen records from Hong Kong and inclusion of the species in that area follows Vidal and Hul Thol (1976).

Selected specimens examined. China. Chongqing: Jiangjin, Mt. Simianshan, Sunzigang, *Z.Y. Liu*, *J. Zhang et al. S-2006* (IMC). Nanchuan, Mt. Jinfoshan, Sanquan, Lengshuixi, *Z.Y. Liu 960468* (IMC). **Fujian:** Yunxiao, Xiaban, Mt. Dachenshan, *G.D. Ye 2038* (PE). Zhangzhou, Yunxiao, Mt. Liangshan, Yunliang Reservoir, *X.F. Zeng ZXF36083* (CZH). **Guangdong:** Gaoyao, at the foot of Mt. Dinghushan, *C. Huang 161752* (IBSC). Ruyuan, Daqiao, *Yue71 466* (IBSC). **Guangxi:** Jingxi to Longbang, *R.P. Clark 422* (K, IBK). Liuzhou, Rongan, Banqiao, Guban Village, *Rong'an Exped. 450224170806001LY* (GXMG). **Hunan:** Yizhang, Changle, Mt. Xinpingshan, *S.K. Lau 29560* (IBSC). Yongzhou, Jiangyong, Lanxi, Shangjin Village, *X.C. Jiang*, *G.H. Tang & X.W. Pan SCSB-HNJ-0051* (KUN). **Sichuan:** Changning, Xiangling, Liushuiyan, *s. coll. 704* (SM). Gongxian, Luobiao, Wangjia, *s. coll. 278* (SM). Hongya, Liujiang, Shuguang, Laoyingzui, *Hongya Group 420* (SM). Junlian, Tuanjie, Lüzhu Temple, *Sichuan Economic Plants 0281* (PE). Leibo, Zhongshanping, Xining, *Sichuan Economic Plants 487* (CDBI). Mt. Emei, Heilongjiang, *K.T. Fu 12134* (WUK). Pingshan [Pingshan], *F.T. Wang 22721* (PE). Tongliang, Xiquan, Xiafeng, *Tongliang Exped. 267* (SM). Xuyong, Shuiwei, Guandou Village, across the Qiaogoutou River, *X.F. Gao*, *Y.D. Gao & W.B. Ju HGX10640* (CDBI).

8. *Ticanto vernalis* (Champion ex Benth.) R. Clark & Gagnon, comb. nov.

urn:lsid:ipni.org:names:77303566-1

Basionym. *Caesalpinia vernalis* Champion ex Benth., Hooker's J. Bot. Kew Gard. Misc. 4: 77. 1852.

Type. China. Hong Kong, *Champion in Herb. Bentham 502* (neotype (designated by Vidal and Hul Thol 1976): K [K000789359!])

Description. ***Habit*** a liana. ***Stems*** moderately to densely ferruginous tomentose, glabrescent when old, sometimes with scattered recurved prickles. ***Stipules*** triangular, 1–2 × ca. 1 mm. ***Leaves*** with 8–16 pairs opposite to strongly subopposite pinnae; petiole 1–2.5 cm; rachis 20–43 cm long, with a recurved prickle at the base of each pinna and scattered along the rachis between the pinnae insertions, moderately to densely ferruginous tomentose; pinnae 4.5–8 cm; leaflets 5–10 opposite pairs per pinna, coriaceous, elliptic to ovate, apex acute, mucronulate, terminal leaflets 1.4–2.8 × 0.5–1.5 cm, lateral leaflets 1.2–2.5 × 0.5–1.3 cm, both surfaces glabrous, or lower surface sparsely ferruginous tomentose, or only on midvein; venation reticulate, anastomosing, obscure. ***Inflorescence*** a raceme or many-branched panicle 12–35 cm long, in axils of upper leaves or terminal, axes and pedicels densely ferruginous tomentose; bracts not seen, bracteoles ca. 1–2 × 1 mm, apex acuminate, sparsely to densely ferruginous tomentose; pedicels 6–12(–16 in fruit) mm. ***Flowers*** with a hypanthium ca. 2 × 4 mm, this moderately to densely ferruginous tomentose; lower (cucullate) lobe ca. 7–11 × 4 mm, sparsely to moderately ferruginous tomentose on centre of outer surface, becoming glabrous towards the edges, other lobes ca. 6–12 × 2 mm, (very) sparsely ferruginous tomentose inner and outer surfaces sparsely ferruginous

tomentose; median petal (6–)9 × 2 mm, inrolled, with dense circular patch of hairs at base of blade, and some hairs on claw, particularly on the margins; upper laterals ca. 9 × 3 mm, sparsely tomentose on inner surface of claw; lower laterals ca. 10–11 × 3 mm, sparsely tomentose on inner surface of claw; stamen filaments flattened, ca. 9–12 mm, pale orange tomentose on lower ca. $^{2}/_{3}$ on inner surface; anthers ca. 1.5–2 mm long; ovary ca. 2.5 mm long, densely ferruginous tomentose, stipe ca. 1 mm long, style ca. 6 mm, glabrous, ovary 2-ovuled; stigma funnel-shaped, slightly papillate, ca. 1 mm wide. ***Fruit*** dehiscent, ligneous, obliquely oblong or sub-elliptic, slightly asymmetrical, apex beaked, venation obscure, sparsely to densely ferruginous tomentose, 4–6 × 2.5–4 × 1–1.3 cm, ventral suture lacking a wing. ***Seeds*** (1–)2, lunate, ca. 2.1–2.7 × 1.3–2.1 cm, matt black (Fig. 4).

Ecology. Moist sandy soils, beside rocks along valleys, in thickets; elevation ca. 600 m.

Phenology. Flowering February-April, fruiting September-December.

Distribution. China (Fujian, Guangdong, Hong Kong, Zhejiang) (Map 1).

Selected specimens examined. China. Fujian: Hua'an, Eshan, *W.D. Han 20542* (NF). Yunxiao, Datian, *G.D. Ye s.n.* (FJSI). **Guangdong:** Baoan, Shatian, *T. Chung M185* (IBSC). Chaochow, Raoping, Fenghuangshan, *N.K. Chun 42662* (IBSC). Guangzhou, Conghua, Daling, Shanshizao, *S.J. Li 787* (IBSC). Haifeng, Lianhua, Lügong, Dakeng, *G.X. Chen 24* (IBSC). Huidong, *Z.Q. Song 2021061* (IBSC). Luofushan, Sulao Taoist Temple, on the way to Dachashan, *Y. Tsiang 1751* (IBSC).

Figure 4. *T. vernalis* (**i**) habit (**ii**) leaves (**iii**) flowers (**iv**) fruit (photos by Jian-Ping Wu, Zhejiang, China, *unvouchered*).

Meizhou, Fengshun, Yanping, Fengbei Village, *X.F. Zeng ZXF01805* (CZH). **Hong Kong:** Lantau, Tung Chung, *S.Y. Hu 12897* (PE). N. T. Lan Nai Chung, Sai Kong, *S.Y. Hu 8570* (PE). **Zhejiang:** Huangyan, Western part, Shidun, *N.Z. Wang s.n.* (NAS). Jiande, Jiande Forest Farm, *J. Zhao et al. 8524205* (PE). Jingning, Wangkeng, *M.L. Yu et al. 25125* (HHBG). Jiansae, Laufuyoh, *K.W. Jiang*, *J.P. Wu*, *Y.F. Zhang*, *M.S. Zhang et al. YS022* (NPH). *ibid.*, *Y.M. Zhang YS023* (IBSC). Linhai, Yongdongkou, Dakeng, *s. coll. 196* (HHBG). Ningpo, Tientungssu, *H. Migo s.n.* (NAS). Suichang, Daban, Yakoumen, *M.L. Yu 25756* (NAS). Tiantai, Gaoming, *L.S. Que 28517* (ZM). Wencheng, Shuiyanhu, *J.P. Feng 499* (HHBG). Yueqing, Dajing, Dianling, Dazhuyuan, mountainside, *Hangzhou Botanical Garden Herbarium 2493* (HHBG).

9. *Ticanto yunnanensis* (S. J. Li, D. X. Zhang & Z.Y. Chen) R. Clark & Gagnon, comb. nov.

urn:lsid:ipni.org:names:77303567-1

Basionym. *Caesalpinia yunnanensis* S. J. Li, D. X. Zhang & Z.Y. Chen. Novon 16(1): 78–80. 2006.

Type. China. Yunnan, Xishuangbanna, *T. P. Zhu* (*Zhu Tai-Ping*) *139* (holotype KUN: [1206956!], isotype IBSC [0162107!]).

Description. ***Habit*** a liana. ***Stems*** with recurved prickles to ca. 2 mm long, glabrous. ***Stipules*** caducous, not seen. ***Leaves*** with 3 pairs opposite pinnae, petiole 7–8 cm, rachis 15–20 cm long, rachis with recurved prickles at the base of each pinna and scattered in between the pinnae insertions, pinnae 5–6.5 cm long; leaflets 2–3 opposite pairs per pinna, blade coriaceous, elliptic or narrowly elliptic, base obtuse to cuneate, apex bluntly acuminate, margin incurved abaxially, 6–11.5 × 2.5–4.5 cm, upper surface glossy, lower surface dull, both surfaces glabrous, 2° venation anastomosing, 3° venation finely reticulate. ***Inflorescence*** an axillary raceme, more than 20 cm long; pedicels ca. 7 mm. ***Flowers*** unknown; receptacle remnant ca. 3 mm wide. ***Fruit*** dehiscent, ligneous, oblong to elliptic, slightly asymmetrical, base widely cuneate, apex with beak ca. 2 mm long, venation reticulate, not prominent; 5–7 × 2.8–3.5 cm, ventral suture lacking a wing. ***Seed*** 1.

Ecology. Thickets along riversides, sparse woodlands along roadsides, elevation ca. 600 m.

Phenology. Flowering unknown, fruiting October.

Distribution. China (Yunnan) (Map 1).

Notes. Specimen *Chen 0066* which is listed as a paratype of *T. yunnanensis* has leaflets that are asymmetrical, with an asymmetrical base and distinctly acuminate tip, and the secondary veins are at a more acute angle to the midvein when compared with typical *T. yunnanensis*. It is sufficiently morphologically divergent from the concept of *T. yunnanensis* to be considered by the current authors to represent a different taxon (not determined), and the characters of that specimen are therefore not included in the description above.

Selected specimens examined. China. Yunnan: Xishuangbanna, Mengla, Yiwu, *J.H. Zhang 19335* (HITBC).

Excluded names

Guilandina rotunda Noronha, Verh. Batav. Genootsch. Kunst. 5(Art. 4): 16 (1790), *nom. inval. nom. nud.*

Butea loureiroi Spreng., Syst. Veg., ed. 16(3): 186. 1826. *nom. inval. nom. superfl.*

Caesalpinia scandens J. Koenig ex Baker in Hook. F., Fl. Brit. India 2(5): 255 (1878), *nom. inval.*

Fossil taxa

Although there are no fossils definitively attributed to *Ticanto*, some partial leaf fossils from the Upper Tochiwara Formation of Japan, dating to the mid Miocene, have been tentatively likened to *Caesalpinia crista* and assigned the name *Caesalpinia hokiana* Ozaki (1980). However, it is not clear from the text of that publication, or the fossil material itself, whether the *C. crista* under comparison is the species here included in *Ticanto* or the alternative species to which that name is commonly (though erroneously) applied, *Guilandina bonduc* L. The fossil material is also compared with *Caesalpinia japonica* Siebold & Zucc. (= *Biancaea decapetala* (Roth) O. Deg.), but is in fact inadequate to be attributed confidently even to *Caesalpinia* s.l. No combination for *Caesalpinia hokiana* is therefore made here in *Ticanto*, but the possibility that the species belongs within the genus cannot be eliminated.

Nomenclatural notes on *Caesalpinia* (*Ticanto*) *crista*

The protologue of *Caesalpinia crista* L. lists three type elements: *Fl. Zeyl.* 157; *Pluk. alm.* 4. *t.* 2. *f.* 2.; *Breyn. ic.* 58. *t.* 28. Of these, only the *Flora Zeylandica* element references material (in Hermann's Herbarium) attributable to *Caesalpinia crista* L. whilst the Plukenet figure and Breynius plate are representative of *Guilandina bonduc* L. (1753) (see Dandy and Exell 1938). This has been a source of nomenclatural confusion, resulting in the name *Caesalpinia crista* being erroneously applied to *G. bonduc*. In addition, names synonymous with *G. bonduc* L. have been mistakenly placed in synonymy with *C. crista* L. by various authors. Adding to the confusion, the name *Guilandina crista* (L.) Small was based on the name *Caesalpinia crista* L., and is therefore a synonym of that name, although the protologue of *G. crista* clearly describes a species of *Guilandina* (features include large, prickly fruits, grey seeds, and distribution including the Florida Keys).

The impact of the application of the name *Caesalpinia crista* to two widespread species, both of which have medicinal uses, is significant. A wide range of studies record the presence of numerous phytochemicals in *C. crista* along with a wealth of reported pharmacological benefits including antioxidant, antibacterial, antiviral (including for treatment of Covid-19 [Ahmad et al. 2021]), anti-malarial, anti-tumour, anticancer, anti-diabetic, anti-inflammatory, analgesic, hepatoprotective,

cardioprotective, anti-amyloidogenic, nootropic, wound healing, anthelmintic, insecticidal, antipyretic and antiulcer activities (Ramesh et al. 2010; Sarkar et al. 2012; Kumar et al. 2017; Chan et al. 2018; Chethana et al. 2018; Srinivasa et al. 2019; Amirtharaj and Sivashankar 2021). These apparent benefits reflect long-standing and diverse traditional medicinal uses in countries including India, Myanmar, Sri Lanka and Indonesia of the so-called 'fever nut', a name often used for the species *Guilandina bonduc* L. (also known as nickar bean or grey nickar bean). Although the majority of published phytochemical and pharmacological analyses referring to *Caesalpinia crista* appear to concern the species *Guilandina bonduc* L., a review of these studies reveals widespread lack of clarity surrounding the identity of the taxon under study. Details of the material under investigation include mixed lists of synonyms, species descriptions that appear to combine elements of the morphology of both *C. crista* and *G. bonduc*, or photos of *C. crista* presented to represent studies of *G. bonduc* (Chan et al. 2018; Upadhyay et al. 2019). Several studies lack reference to a voucher specimen (although the material is usually said to have been verified by a botanist; Gupta et al. 2013; Sharma et al. 2013; Chauhan et al. 2015; Srinivasa et al. 2019), or the voucher reference is incomplete (Yang et al. 2009; Kumar et al. 2017) and thus the identity of the material cannot be easily verified. Most studies that cite a voucher specimen do not present photographs of the plant material used (Kalauni et al. 2004; Cheenpracha et al. 2005; Linn et al. 2005; Patil 2005; Awale et al. 2006; Jabbar et al. 2007; Satnami and Yadava 2011; Sarkar et al. 2012; Chethana et al. 2018; Amirtharaj and Sivashankar 2021). If provided these may be too poor to enable identification (Upadhyay et al. 2019), and digital images of the voucher specimens are rarely available online. Confusion of the species' identity is also apparent on web resources such as the India Biodiversity Portal (https://indiabiodiversity.org), Tropical Plants Database (http://tropical.theferns.info/), Mangroves of Odisha (https://odishamangroves.in/) and those describing or retailing traditional medicine (e.g., https://ayushvedah.com/, https://www.planetayurveda.com/) which provide synonyms and photos of *C. crista* alongside descriptions of *G. bonduc*. Other resources present details of true *Caesalpinia crista* (e.g., Flora and Fauna Web, a Singapore Government agency website, https://www.nparks.gov.sg/) without reference to the common, though erroneous, application of the name to *G. bonduc*. Compounding the nomenclatural issue between the two species is the morphological similarity between them (both are prickly, scrambling shrubs with yellow generalised caesalpinioid flowers and fruit with 1–2 seeds), and by their mutual tendency to inhabit coastal areas.

The implications of misidentification of samples used to test for the presence of biologically active phytochemicals and to evaluate medicinal properties are clear. Taxonomic uncertainty could lead to false assumptions of the properties of a species or inclusion of the wrong species in medical preparations, and potential harm to human health. Reiteration of the correct application of the name *Caesalpinia crista* L. provided here will contribute to avoidance of this issue in future studies.

Discussion

Recognition of *Ticanto*

Genera segregated from *Caesalpinia* s.l. are most often morphologically characterised by fruit and floral characters, as well as by glands and trichomes (Gagnon et al. 2016). However, certain genera recognised by Lewis (2005) including *Caesalpinia* s.s., *Denisophytum* and *Erythrostemon*, and *Arquita*, recognised by Gagnon et al. (2015), were recircumscribed by Gagnon et al. 2016 to reflect true phylogenetic relationships, and these have been more difficult to define morphologically. Nonetheless, recognition of these genera is justified given that the alternative would be to continue to recognise a massive Caesalpinia Group that also lacks clear morphological diagnostic characters to distinguish it from other groups and genera in the Caesalpinieae tribe.

Gagnon et al. (2016) refrained from reinstating the genus *Ticanto* because of the limited amount of sampling in their phylogeny of this genus. Furthermore, no diagnostic synapomorphies were identified to distinguish the species provisionally ascribed to *Ticanto* from the genera to which they are most closely related, *Pterolobium*, *Mezoneuron* and *Biancaea*. It was noted that two species putatively placed in *Ticanto* (*Caesalpinia caesia* and *Mezoneuron sinense*) sometimes have a winged fruit, but that character also occurs in these three related genera. However, the phylogenies reconstructed here show that by sampling multiple species that were putatively attributed to this group, a strongly supported monophyletic clade is recovered, (bootstrap = 94%, PP = 1.0) sister to the long-recognised genus *Pterolobium* (Fig. 1). The very robust values supporting the clades containing *Ticanto* species and the most closely related genera provide strong justification for recognising *Ticanto* as a distinct genus. Our thorough revision of the group also allows us to verify that the group is morphologically distinct from the most closely related genera.

The morphological resemblance of species now included in *Ticanto* was detected as long ago as the 19th century, when Prain (1897) suggested that *Caesalpinia nuga* (= *T. crista*) and *Mezoneuron sinense* (= *T. sinensis*) may be better placed together in a proposed new genus, *Nugaria*. Later, Clark (2016) observed the similarity of fruits of *Mezoneuron sinense* to those of five species here attributed to Ticanto, and commented on the possible generic misplacement of that species in *Mezoneuron*. Although there are no unique morphological synapomorphies to define *Ticanto* as circumscribed in this account, the species are united by a combination of characters: the lianescent or scrambling habit, armature of recurved prickles, a pari-bipinnate leaf, a laterally compressed fruit with 1(–2) seeds that is usually indehiscent and is with or without a narrow sutural wing, and relatively small, unspecialised flowers. The capacity of each of these features to diagnose the genus will now be discussed.

The vegetative characters of *Ticanto* do not distinguish it clearly from *Pterolobium*, *Mezoneuron* and *Biancaea*, all being lianas or scandent or trailing shrubs armed with recurved prickles, and with pari-bipinnate leaves (Fig. 2, 3, 4). However, some divergence can be observed between the leaves of *Ticanto* and those of *Pterolobium* in that

Ticanto usually bears few pinnae (1–8 pairs, although up to 16 pairs in *T. vernalis*) and few, relatively large leaflets (2–10 pairs, or up to 15 in *T. caesia*), whereas *Pterolobium* is characterised by numerous pinnae (4–20 pairs) and numerous, small leaflets (4–25 pairs per pinna). The leaflets of *Ticanto* are usually elliptic or rhombic (except *T. caesia*) whilst those of *Pterolobium* are oblong, strongly asymmetric at the base, and regular in size. It should be noted, however, that these differences are tendencies rather than discrete states.

The flowers of all four genera can be considered as 'typical' Caesalpinia group flowers consisting of a short hypanthium and five sepals, the lower of which is cucullate over the others in bud, and five oblong, obovate or spathulate (occasionally bilobed) petals that are yellow or white, sometimes with red markings on the median petal, usually with some degree of pubescence. Stamens are free and tomentose, the ovary is glabrous or hairy, and the stigma is cupular, funnel-shaped or truncate, often papillate. The flowers of all four genera appear to be adapted for a range of generalist pollinators (mostly species of bee) and do not exhibit modifications related to novel pollination syndromes (although ambophily, i.e., pollination by both wind and insects, is reported uniquely in *T. crista* by Li et al. 2004), which seems to result in an absence of generic level floral distinctions among the four similar genera.

Like several other genera in the Caesalpinia group, *Ticanto*, and the genera to which it is most closely related (*Pterolobium*, *Mezoneuron* and *Biancaea*) are distinguished primarily by differences in fruit morphology. The fruits of *Ticanto* are elliptic, circular or lunate, compressed or inflated, coriaceous or ligneous, usually indehiscent (two dehiscent exceptions), 1–2-seeded, and with or without a narrow wing up to 4 mm wide along the upper suture (Fig. 5) (or a carinate wing 5–6 mm deep) (Table 3). The genus *Mezoneuron*, sister to the *Ticanto-Pterolobium* clade, is characterised by fruits that are elliptic to oblong, laterally compressed, chartaceous to coriaceous, indehiscent, with a wing along the upper suture 2–20 mm wide, containing one to 13 seeds (11 species multi-seeded, nine species single-seeded, three unknown). There is thus a degree of congruence between the fruits of *Ticanto* and those of *Mezoneuron* with respect to indehiscence, number of seeds and presence of a wing (variable in *Ticanto*, universal in *Mezoneuron*). However, the majority of *Mezoneuron* fruits are multi-seeded and the wing is usually broader than 3 mm, whilst the species of *Mezoneuron* bearing single-seeded and narrow-winged fruit most like those of *Ticanto* are distributed in Australia, New Caledonia and New Guinea and are thus allopatric with respect to almost all species of *Ticanto* (except *T. crista*).

The fruits of *Pterolobium* bear some structural similarities to those of *Ticanto* in that they comprise a 1(–2)-seeded locule that is always (*Pterolobium*) or sometimes (*Ticanto*) winged, and the wing is non-vascularised (no venation is conspicuous on the exterior surface or in X-ray, Fig. 5). However, the fruits of *Pterolobium* are unique within the Caesalpinia group in being samaroid, with a basal seed chamber. The surface of the fruit wing of *Pterolobium* also differs from that of *Ticanto* in having sculpturing in the form of parallel lines (the surface is smooth in *Ticanto*). The distinctiveness of the fruits of *Pterolobium* compared with all others in the Caesalpinia group, and particularly compared with those of *Ticanto*, strongly supports the recognition of two genera to represent those clades.

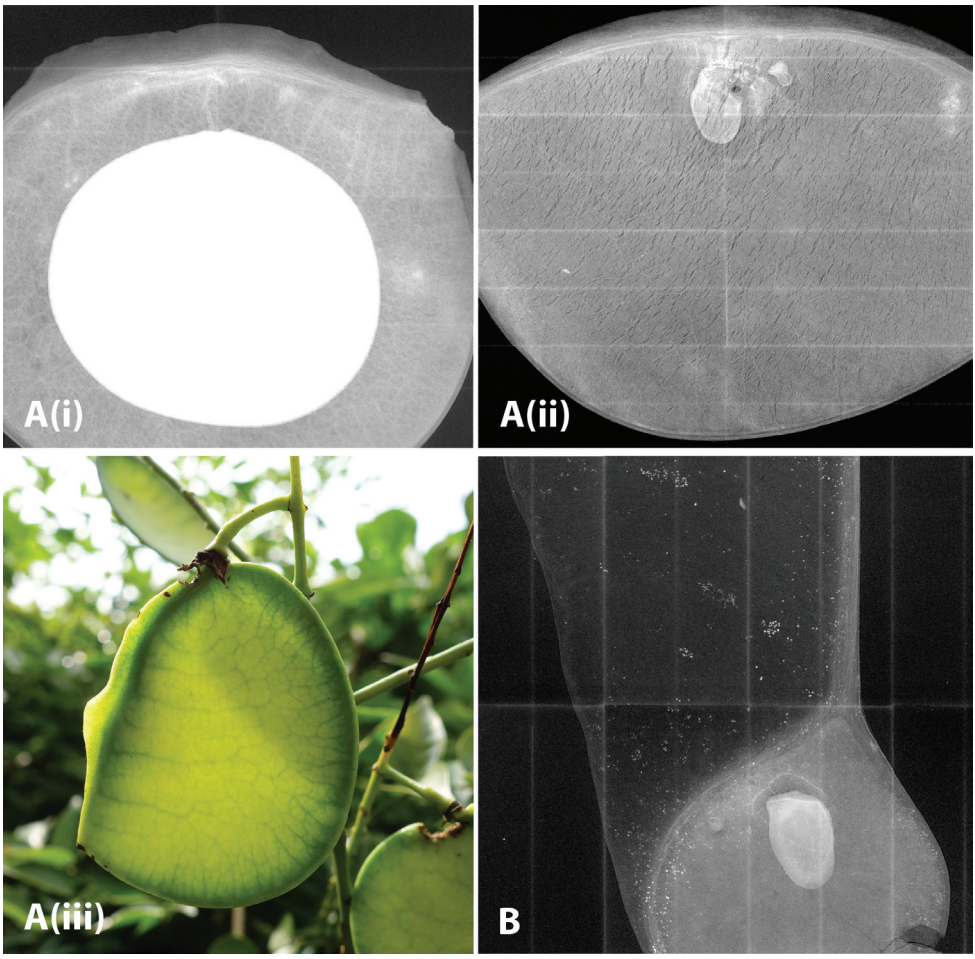


Figure 5. Fruit wing venation **A** *T. sinensis* fruit with wing (i) (X-ray) (*Z. Zhang 148*, China (MO)) (ii) (X-ray) (*W.E. Qun 150*, China (K)) (iii) (photo by R.P. Clark, Guangxi, China, *unvouchered*) **B** *Pterolobium microphyllum* fruit with wing (X-ray) (*C. Phengkhlai 682*, Thailand (K)).

The fruits of *Biancaea* differ from *Ticanto* in that they are usually dehiscent and wingless (except *B. decapetala* which may have a narrow wing or ridge along the upper suture, and *B. millettii* which may have a very narrow wing along the upper suture) whilst those of *Ticanto* are usually indehiscent (with the exceptions of *T. vernalis* and *T. yunnanensis*) and often with a narrow wing along the upper suture, although some species are wingless (*T. crista*, *T. elliptifolia*, *T. rhombifolia*, *T. vernalis*, *T. yunnanensis*). The ovary indumentum of *Biancaea* is (densely) hairy, as opposed to glabrous or sparsely to (less commonly) densely hairy in *Ticanto*. The fruits of *Biancaea* are 2–8-seeded (apart from *B. millettii* with 1 seed), versus 1(–2)-seeded in *Ticanto*. *Biancaea* usually has large stipules, ranging from 3 mm to 4.5 cm long (except for *B. millettii* in which they are 2 mm long), whilst those of *Ticanto* are

Table 3. Comparative characters of *Ticanto* species (characters considered to be most taxonomically informative are in bold).

	T. caesia	*T. crista*	*T. elliptifolia*	*T. magnifoliolata*	*T. rhombifolia*	*T. sinensis*	*T. szechuenensis*	*T. vernalis*	*T. yunnanensis*
Pairs pinnae	**5–8(–9)**	**3–6(–8)**	**1–2**	**2–3(–4)**	**3–6**	**2–4(–5)**	**3–6**	**8–16**	**3**
Position of pinnae	opposite	opposite (occasionally slightly subopposite)	opposite	opposite	opposite	opposite	opposite (rarely subopposite)	opposite to strongly subopposite	opposite
Pairs leaflets	**8–15**	**2–4(–7)**	**2**	**2–3**	**3–5**	**2–5**	**3–6**	**5–10**	**2–3**
Leaflet size	**0.8–1.5 × 0.4–0.6**	**2.1–7.2 × 1–3.3**	**7–13 × 4.5–8**	**3.5–10.8(–15) × 2.1–7**	**1.5–2 × 0.8–1.3**	**1.8–10.7 × 0.8–5.1**	**1.2–6 × 0.8–3**	**1.2–2.8 × 0.5–1.5**	**6.0–11.5 × 2.5–4.5**
Leaflet apex	**truncate, obtuse, rounded, emarginate**	**obtuse or rounded to retuse, acute, or acuminate**	**rounded, obtuse or acute**	**usually obtuse, rounded, retuse or emarginate, occasionally acute**	**acute**	**usually acuminate or acute, occasionally rounded**	**usually acute, occasionally slightly rounded**	**acute**	**bluntly acuminate**
Inflorescence indumentum	brown puberulent	glabrous or sparsely tomentose	densely hairy	sparsely to moderately tomentose	glabrous or subglabrous	sparsely to densely ferruginous tomentose	subglabrous to moderately tomentose	densely tomentose	unknown
Inflorescence length cm	10–15	8–40	unknown	15–30	10–20	7–42	11–15	12–35	>20
Pedicel length mm	4–7	5–15	8–12	5–11	6–9	3–12(–17 in fruit)	5–11	6–12(–16 in fruit)	ca. 7
Bracteoles mm	unknown	1 – 2.5 × 0.5 – 1	unknown	unknown	unknown	broad, 2–3 × 1–1.5	caducous, 1 × 0.25 mm, lanceolate-acuminate	1.2 × 1	unknown
Median petal size mm	3.5–5.5 (L)	6–9 × 3–7	ca. 10.5 × 6–7	ca. 7–10 × 3–5	ca. 7 (L)	6–8 × 3–4	6–9.5 × 2.5–5	6–9 × 2	unknown
Lateral petals size mm	3.5–5.5 (L)	6–11 × 3–6	10–12 × 4–5	ca. 7–10 × 3–5	ca. 7 (L)	6–10 × 2–6	5–10 × 3–4	9–11 × 3	unknown
Median petal indumentum (inner surface)	rhombic patch of hairs	dense circular patch of hairs in middle	circular patch of hairs	patch of hairs	patch of hairs	circular patch of orange hairs in middle, hairs on margins of claw	patch of hairs in middle; few hairs on margins of claw	dense circular patch of hairs in middle, some hairs on claw	unknown
Stamen length mm	ca. 6	4 – 12	9–14	5–10	7	5–12	ca. 9	9–12	unknown
Style length mm	ca. 4	ca. 4–11	7–10	ca. 5–10	10	6–12	10–12	6	unknown
Ovary indumentum	**glabrous**	**glabrous or sparsely or patchily hairy**	**tomentose**	**glabrous**	**glabrous**	**sparsely to densely tomentose or glabrous**	**sparsely to moderately tomentose**	**densely pilose**	unknown
Fruit dehiscence	**indehiscent**	**indehiscent**	**indehiscent**	**indehiscent**	**indehiscent**	**indehiscent**	**indehiscent**	**dehiscent**	**dehiscent**
Fruit size cm	**4.5–5 × 2.3–5**	**2.7–7 × 2.2–3.7**	**4.5–5 × 2.2–2.5**	**2.8–4.2 × 2.2–3.5**	**3–4 × 2.3–2.5**	**3–5.8 × 1.9–4.1**	**1.5–3.4 × 1.5–3**	**4–6 × 2.5–4 × 1–1.3**	**5–7 × 2.8–3.5**
Fruit wing	**narrow**	**absent**	**absent**	**carinate, 5–6 mm**	**absent**	**0.5–4 mm wide**	**sometimes present, 1–3 mm wide, along part of fruit length**	**absent**	**absent**

	T. caesia	*T. crista*	*T. elliptifolia*	*T. magnifoliolata*	*T. rhombifolia*	*T. sinensis*	*T. szechuenensis*	*T. vernalis*	*T. yunnanensis*
Fruit shape	**elliptic**	**elliptic to lunate, sub-symmetrical to somewhat asymmetrical**	**oblong-elliptic, sub-symmetrical to sub-lunate**	**lunate**	**asymmetrical, sub-lunate**	**Sub-circular to lunate**	**strongly asymmetrical, sub-lunate to sub-circular or teardrop-shaped**	**obliquely oblong or sub-elliptic, slightly asymmetrical**	**oblong to elliptic, slightly asymmetrical**
Fruit stipe mm	unknown	2–5	short	ca. 1	ca. 3	0–2	0–1	unknown	unknown
Fruit beak mm	unknown	1–10	1–5	2–7	slight beak	pronounced beak to 25	1–5	beak present	ca. 2
Fruit venation	prominent	prominent	prominent	prominent	prominent	prominent	prominent	not prominent	not prominent
Fruit indumentum	glabrous	glabrous or very sparsely tomentose	unknown	glabrous	glabrous	glabrous or glabrescent	glabrous	sparsely to densely tomentose	unknown
Fruit texture	ligneous	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous	coriaceous	ligneous	ligneous
Ecology & elevation	forests along rivers, 200–1000 m	often coastal; limestone, up to 350 m	ca. 100 m	forests, 400–1800 m	thickets	forest, thicket, limestone, 100–1500 m	forest, thicket, limestone, 260–1500 m	Moist sandy soils, thickets, ca. 600 m	unknown

0.25–3 mm long. *Biancaea millettii* has morphological affinities with *Ticanto* in having small stipules and single-seeded fruits that sometimes have a narrow wing, and its distribution (Guangdong, Guangxi, Hunan, Jiangxi in China) is congruent with the centre of diversity of *Ticanto*. The leaves of *B. millettii*, which bear numerous pinnae and numerous, small, oblong leaflets, resemble those of *Ticanto caesia*. The morphological affinities of *B. millettii* with *T. caesia* (including certain fruit characters), and the distribution of the former in southern China (the centre of diversity of *Ticanto*), raised the question of whether *B. millettii* might belong in *Ticanto*; however, the molecular phylogenetic analysis here presented demonstrates it to be correctly placed in *Biancaea*. The fruit of *B. millettii*, despite some similarity with *Ticanto* fruits, exhibits features typical of *Biancaea* fruits in being dehiscent and with a puberulent indumentum. This supports the hypothesis that fruit characters are important in delineating segregate genera of *Caesalpinia* s.l.

Geographical distribution of *Ticanto*

The distribution of *Ticanto* compared with closely related genera suggests it to be a distinct evolutionary lineage. The centre of diversity of *Ticanto* is Southern China, where all species are present and six are endemic (*T. caesia*, *T. elliptifolia*, *T. magnifoliolata*, *T. szechuenensis*, *T. vernalis*, and *T. yunnanensis*). Of the three remaining species, *T. rhombifolia* occurs also in northern Vietnam, *T. sinensis* extends into northern Laos, Myanmar and Vietnam, and only *T. crista* is more widely distributed throughout South-East Asia. The centre of diversity of its sister genus *Pterolobium* is South-East Asia (and a single species in Africa) from India through Myanmar into Indochina, and to Indonesia, Borneo, the Philippines, and Malaysia. Only two species of *Pterolobium* are found in China, namely *P. macropterum* Kurz, in Yunnan and Hainan provinces, and *P. punctatum* Hemsl., which is a broadly distributed Chinese endemic extending into at least nine provinces (International Legume Database and Information Service, https://ildis.org/LegumeWeb/). The distribution of *Ticanto* reflects its preferred ecological niche, characterised by a drier and more seasonal climate and scrub or dry forest habitat, and that of *Pterolobium* likewise reflects its preference for a warmer, moister climate and lowland forest habitat. *Mezoneuron* occurs (like *Pterolobium*) predominantly in the moist tropics, but with a more widespread and disjunct distribution (across South East Asia, two species in Africa, six species endemic to New Caledonia, one endemic in Madagascar, and one endemic in Hawaii), with only two species (*M. cucullatum* and *M. enneaphyllum*) present in southern China, represented by just a few specimens collected close to the borders. Of the six species in the Asian genus *Biancaea*, *B. millettii* is endemic to a few provinces in southern China, whilst the widely distributed *B. decapetala* is present throughout southern China, and the remaining four species occur in moist tropical areas from India to Thailand, Cambodia, Vietnam, and Malesia. *Ticanto* is therefore the only genus in the Caesalpinia Group of which most species occur either partially or exclusively in China.

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Supplementary material 1

Appendix 1
Authors: Ruth P. Clark, Kai-Wen Jiang, Edeline Gagnon
Data type: Occurrences.
Explanation note: **Table S1.** Specimens used for mapping point localities.
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Link: https://doi.org/10.3897/phytokeys.205.82300.suppl1

Supplementary material 2

Appendix 2
Authors: Ruth P. Clark
Data type: Docx file.
Explanation note: **Table S2**. Sequences obtained from GenBank.
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Supplementary material 3

Caesalpinia group Bayesian phylogeny
Authors: Ruth P. Clark
Data type: Phylogeny.
Explanation note: Caesalpinia group Bayesian phylogeny based on the combined dataset.
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Supplementary material 4

Caesalpinia group ML phylogeny

Authors: Ruth P. Clark

Data type: Phylogeny.

Explanation note: Caesalpinia group ML phylogeny based on the combined dataset, including the accession Kiyama et al. 1233, *Ticanto magnifoliolata*.

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RESEARCH ARTICLE

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Re-circumscription of the mimosoid genus *Entada* including new combinations for all species of the phylogenetically nested *Elephantorrhiza* (Leguminosae, Caesalpinioideae, mimosoid clade)

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Abstract

Recent phylogenomic analyses of 997 nuclear genes support the long-held view that the genus *Entada* is congeneric with *Elephantorrhiza*. *Entada* is resolved as monophyletic only if the genus *Elephantorrhiza* is subsumed within it. The two genera were distinguished solely by relatively minor differences in the mode of dehiscence of the fruits (a craspedium separating into one-seeded endocarp segments in *Entada* versus a craspedium with the whole fruit valve breaking away from the persistent replum in *Elephantorrhiza*) and the craspedial fruit type itself provides a shared synapomorphy for the re-circumscribed *Entada*. Here, we provide a synopsis of *Entada*, including 11 new combinations in total, for the eight species, one subspecies and one variety previously placed in *Elephantorrhiza*, as well as a new combination for a subspecies of *Entada rheedei* Spreng. not previously dealt with when *Entada pursaetha* DC. was placed in synonymy. These new combinations are: *Entada burkei* (Benth.) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada elephantina* (Burch.) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada goetzei* (Harms) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada goetzei* subsp. *lata* (Brenan & Brummitt) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada obliqua* (Burtt Davy) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada praetermissa* (J.H. Ross) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada rangei* (Harms) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada rheedei* subsp. *sinohimalensis* (Grierson & D.G. Long) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada schinziana* (Dinter) S.A. O'Donnell & G.P. Lewis, **comb. nov.**; *Entada woodii* (E. Phillips)

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S.A. O'Donnell & G.P. Lewis, **comb. nov.**; and *Entada woodii* var. *pubescens* (E. Phillips) S.A. O'Donnell & G.P. Lewis, **comb. nov.** We provide a revised circumscription of the genus *Entada* which now comprises 40 species distributed pantropically, with the greatest diversity of species in tropical Africa. We present a complete taxonomic synopsis, including a map showing the global distribution of the genus and photographs showing variation amongst species in habit, foliage, flowers and fruits. A short discussion about extrafloral nectaries, mainly observed in the Madagascan species, is presented.

Keywords
extrafloral nectaries, Fabaceae, generic delimitation, monophyly, nomenclature, taxonomy

Introduction

Traditional circumscriptions of the mimosoid genus *Entada* Adans. encompass around 30 species of large woody lianas to 75 m long, thin woody climbers, scandent shrubs, small trees and geoxylic suffrutices to < 0.5 m height, pantropical to subtropical in distribution and with a centre of species diversity in Africa south of the Sahara (Lungu 1995; Lewis et al. 2005). The species are as diverse in their ecologies as they are in growth forms, with many species occupying lowland rainforest, especially in riverine and littoral habitats, while others are adapted to savannah grassland, open woodland or seasonally dry tropical forest. To illustrate this range in habit and ecology, consider the large palaeotropical lianas *Entada rheedei* Spreng. and *E. phaseoloides* (L.) Merr., which produce pods up to two metres in length from flowers less than a centimetre long, involving impressive post-pollination mechanical reinforcement of fruit-bearing structures. These species and those with large fruits and seeds thought to be closely related, are often found in riparian forest and along the landward fringes of mangroves associated with hydrochory, i.e. they have riverine and oceanic seed dispersal. Mature pods of these and most other *Entada* species, split transversely and break up into one-seeded segments that break away from the persistent woody frame (the replum) – a fruit type referred to as a craspedium. In the large-fruited species inhabiting riparian forest, these one-seeded articles often wash into rivers which then carry the buoyant seed-bearing envelopes downstream and out to sea, where they can drift on ocean currents for at least a year and remain viable (Ridley 1930, p. 284), enabling dispersal across enormous distances. In addition to landing on shores in the tropics conducive to establishment, seeds of *E. gigas* (L.) Fawc. & Rendle, *E. rheedei* and *E. phaseoloides* frequently wash up on temperate coasts in northern Europe (Nelson 1978; Cadée and Piersma 1990; Alm 2003), southern South Africa (Muir 1933) and southeast Australia (Smith 1991), well outside their known ranges and bioclimatic niche limits. Presence of fossilised seeds of *Entada palaeoscandens* (Awasthi & Prasad) Antal & Awasthi in late Oligocene facies from New Zealand (Conran et al. 2014) and similar in Oligocene and Miocene units from India and Nepal (Awasthi and Prasad 1990; Antal and Awasthi 1993), suggest that *Entada*

seeds have been drifting on ocean currents for tens of millions of years. Contrast this with the species adapted to the fire-prone savannahs and seasonal edaphic grasslands on poorly drained Kalahari sands of south-central Africa, such as the geoxylic *E. arenaria* Schinz, *E. hockii* De Wild. and *E. dolichorrhachis* Brenan, the woody tissues of which are confined to subterranean stems from which sprout annual aerial shoots. This 'underground tree' life history strategy apparently represents an adaptation to the fire-prone and frequently burnt savannah environments in which they live and to the nutrient-poor soils with impeded drainage on which they occur (White 1976; Maurin et al. 2014; Pennington and Hughes 2014).

Species of *Entada* form keystone elements of coastal ecosystems under threat from climate change (Wong et al. 2014). Roots of *Entada* species form nodules that house 'rhizobia'-bacteria (Sprent 2009), facilitating nitrogen-fixation and soil enrichment which, in turn, enables *Entada* plants to colonise impoverished soils and promote ecological succession (e.g. Bush et al. 1995). Many species also have promising medicinal potential. *Entada* seeds, roots, stems and leaves are rich in bioactive compounds, especially saponins, explaining their ethnopharmacological and domestic uses in many indigenous African and Southeast Asian cultures (Lungu 1995, pp. 69–72), as well as their broader pharmaceutical and economic potential. For example, Fabry et al. (1998) demonstrated the antibacterial activity of bark extract from *E. abyssinica* Steud. ex A. Rich. against 105 bacterial strains; Cioffi et al. (2006) showed the capacity of saponins extracted from the roots of *E. africana* Guill. & Perr. to inhibit the development of pre-cancerous kidney cell lines; and Zheng et al. (2012) demonstrated in type 2 diabetic rats the antidiabetic effects of saponins extracted from the seeds of *E. phaseoloides*.

Generic delimitation

Delimitation of the genus *Entada* has remained relatively stable since Brenan (1986) transferred the five species of his short-lived subgenus of *Entada*, *Acanthentada* Brenan to the genus *Adenopodia* C. Presl. This revised placement of these species was based on palynological (Guinet 1969) and wider morphological evidence from pollen dispersal unit, armature, petiolar nectaries, ovary indumentum and stylar morphology (Lewis and Elias 1981), published in the 15 years after Brenan tentatively described subgenus *Acanthentada* (Brenan 1966). Although species of *Entada* and *Adenopodia* share similar craspedial pods that break up to leave a persistent replum, species of *Adenopodia* disperse their pollen as polyads (vs. monads in *Entada*), have prickles on stems and leaves (*Entada* are unarmed, save for *E. spinescens* Brenan which has spinescent stipules), display petiolar nectaries (absent in *Entada*, although see 'Note on extrafloral nectaries' below), have pubescent ovaries (glabrous in *Entada*) and styles that taper to a porate stigma (vs. tubular to cupuliform in *Entada*). Additionally, Brenan (1966, 1986) noted that the epicarp of *Adenopodia* pods remains attached

to the endocarp, whereas these structures separate in the mature pods of *Entada*. In their review of the genera of tribe Mimoseae, Lewis and Elias (1981) used this suite of characters to argue for a more parsimonious placement of *Adenopodia* within the informal Piptadenia group of genera. This placement of *Adenopodia*, separate from *Entada* in the *Piptadenia*-containing Mimosa clade (*sensu* Koenen et al. 2020), is supported by recent large-scale phylogenomic analyses (Koenen et al. 2020; Ringelberg et al. 2022). In that same review of Mimoseae genera, Lewis and Elias (1981) highlighted the close affinity between *Entada* and *Elephantorrhiza* Benth., an essentially southern African genus of eight species of geoxylic suffrutices, shrubs or small trees and placed them in their informal Entada group. Both genera share craspedial fruits, leaflets in mostly opposite pairs, a perigynous stemonozone, pollen released as monads and a tubular to cup-shaped stigma. The primary distinguishing character is that the craspedia in species of *Elephantorrhiza* lack the transverse septa between seeds that are present in *Entada* and, hence, do not split into one-seeded segments along these septa upon ripening as in *Entada*. Rather, in *Elephantorrhiza*, the two valves separate from the replum, the epicarp usually peeling off the endocarp, with the valves otherwise remaining entire or breaking up irregularly. These two types of craspedia are also found within the large monophyletic genus *Mimosa* (Simon et al. 2011; Ringelberg et al. 2022), where species with craspedia in which the entire valve breaks away from the replum are phylogenetically deeply nested within the genus (Simon et al. 2010), just as found here in *Entada* / *Elephantorrhiza*, suggesting this switch is an evolutionarily easy one in mimosoid fruits and that this character is not useful for generic delimitation.

Molecular phylogenetic analyses over the past twenty years have repeatedly supported a close relationship between *Entada* and *Elephantorrhiza* (e.g. Luckow et al. 2003; LPWG 2013, 2017; Koenen et al. 2020; Ringelberg et al. 2022), with generally greater resolution achieved as locus- and taxon-sampling and tree-building methods have improved. Luckow et al.'s (2003) strict-consensus tree of 134 mimosoid taxa, based upon two chloroplast regions, recovered *Elephantorrhiza elephantina* (Burch.) Skeels and *Entada abyssinica* as sister species, the pair, in turn, sister to *Entada rheedei*, suggesting that *Elephantorrhiza* might be nested within *Entada*. The LPWG (2017) family-wide *matK* phylogeny included eight species of *Entada* and three species of *Elephantorrhiza* and also showed the latter to be phylogenetically nested within *Entada*. Ringelberg et al.'s (2022) phylogenomic analyses of subfamily Caesalpinioideae (*sensu* LPWG 2017) used 997 nuclear genes and included eight species from across the two genera, again showing robust support for *Elephantorrhiza* being nested within *Entada* (Fig. 1). The combined morphological and molecular evidence thus overwhelmingly supports sinking *Elephantorrhiza* into *Entada*.

We present a synopsis of the here re-circumscribed genus *Entada*, including a synthesis of species descriptions from existing literature, and propose new combinations in *Entada* for all eight species of *Elephantorrhiza*, based upon the strong molecular evidence discussed above. This formal transfer of species resolves the non-monophyly of traditional circumscriptions of *Entada*.

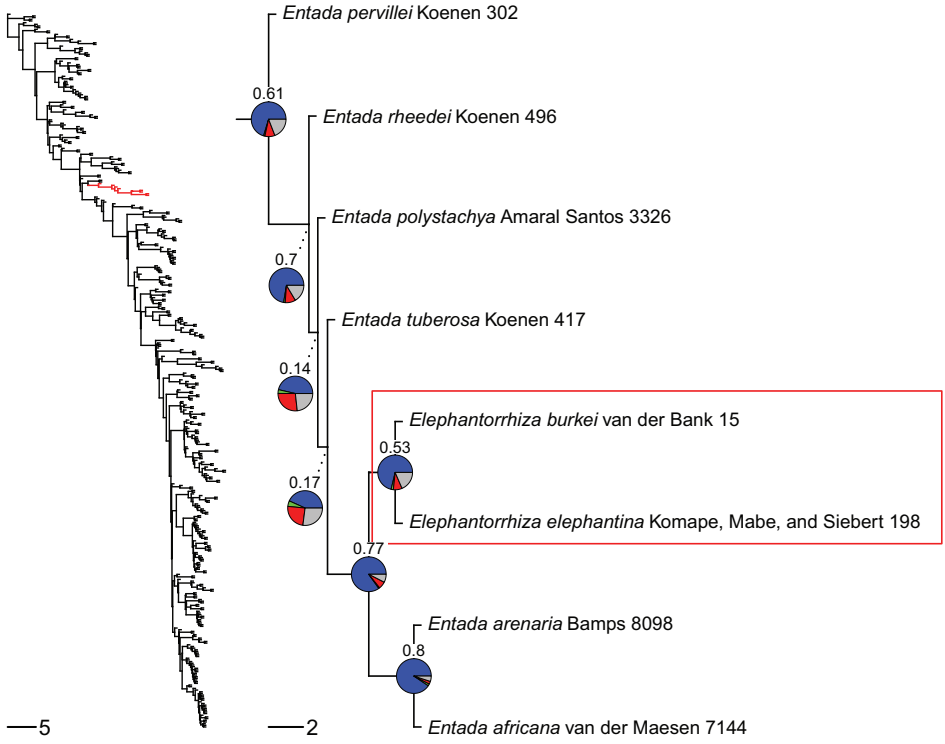

Figure 1. Non-monophyly of *Entada,* based on the ASTRAL (Zhang et al. 2018) single-copy genes phylogeny of Ringelberg et al. (2022). Red branches in the Caesalpinioideae subfamily-wide tree at left denote the phylogenetic position of the magnified *Entada* + *Elephantorrhiza* subtree at right. Red rectangular outline highlights the nested *Elephantorrhiza* species. Pie charts on nodes show the fraction of gene trees supporting each bipartition in blue, the fraction of gene trees supporting the most likely alternative configuration in green, the fraction of gene trees supporting additional conflicting configurations in red and the fraction of uninformative gene trees in grey, based on a total of 821 unique gene trees. Numbers above pie charts are Extended Quadripartition Internode Certainty scores (Zhou et al. 2020). Branch lengths are expressed in coalescent units and terminal branches were assigned an arbitrary uniform length for visual clarity. Tree: J Ringelberg.

Taxonomy

Entada Adans., Fam. Pl. 2: 318. 1763, emended S.A. O`Donnell & G.P. Lewis.

Gigalobium P. Browne, Civ. Nat. Hist. Jamaica: 362. 1756.
Perima Raf., Sylva Tellur.: 118. 1838.
Strepsilobus Raf., Sylva Tellur.: 117. 1838.
Elephantorrhiza Benth., J. Bot. (Hooker) 4: 344. 1841. Synon. nov.
Pusaetha L. ex Kuntze, Revis. Gen. Pl. 1: 204. 1891.
Entadopsis Britton, N. Amer. Fl. 23: 191. 1928.

Type species. *Entada rheedei* Spreng.

Description. Lianas, scandent shrubs, small trees or geoxylic suffrutices, unarmed or with spinescent stipules in *E. spinescens*. **Leaves:** bipinnate; primary and secondary axes either eglandular or, in some Madagascan species, with extrafloral nectaries (see Note below) and at least in *E. phaseoloides*, with unusual 'pit' nectaries on stems at nodes adjacent to petiole; rachis in lianescent taxa terminating in a bifurcating tendril (modified terminal pinnae pair); pinnae 1–many pairs per leaf; leaflets 1–many pairs per pinna; lamina often asymmetric and apically mucronate or emarginate. **Inflorescence:** spiciform racemes or spikes, axillary to supra-axillary, solitary or clustered, sometimes into terminal panicles. **Flowers:** 5-merous, sessile to shortly pedicellate, staminate or bisexual, cream-coloured, yellow, green, red or purple; calyx gamosepalous, campanulate, the fused sepals distinctly toothed or not; petals 5, free to basally connate, adnate basally with the stamens and a perigynous disc forming a stemonozone; stamens 10, fertile, free or basally united, anthers usually with a caducous spheroidal apical gland, sessile to stipitate; pollen tricolporate, columellate, dispersed as monads; style tapering to a tubular to rarely cupuliform stigma, ovary glabrous and multi-ovulate. **Fruit:** a craspedium, torulose or not, compressed to flattened, straight to curved to rarely spirally twisted, sometimes gigantic (up to 2 m long in taxa with sea-drifted seeds); epicarp woody to thinly coriaceous; endocarp woody to parchment-like; splitting along transverse septa into one-seeded segments upon ripening or valvately dehiscent, the entire valve breaking away from the replum and the epicarp also separating from the endocarp. **Seeds:** globular to elliptic, usually laterally compressed, longest axis up to 6 cm in large-fruited taxa, dark brown, smooth, with or without areole, pleurogram (when present) usually open. Fig. 2.

As delimited here, a genus of 40 species (traditionally ± 30 species), widespread, primarily tropical, but reaching subtropical latitudes in southern Africa and eastern Asia (Fig. 3); 29 species in Africa (including Madagascar), nine species in Asia, four species in the Americas; two species (*E. rheedei* and *E. gigas*) occur in two of these regions. Frequently found in riparian and littoral vegetation, though also in savannah, open woodland, thickets or dense humid to more open and dry forest, often on sandy substrates.

Note on extrafloral nectaries

While much of the literature on *Entada* (e.g. Brenan 1966; Lewis and Elias 1981; Nielsen 1981, 1992; Villiers 2002; Wu and Nielsen 2010; Braga et al. 2016) noted the absence of petiolar and leaf rachis nectaries that are otherwise common across the mimosoid clade, examination of herbarium specimens from Madagascar uncovered several species that do appear to possess putative extrafloral nectaries. Six species of *Entada* are native to Madagascar (Villiers 2002): *E. chrysostachys* (Benth.) Drake; *E. leptostachya* Harms; *E. louvelii* (R. Vig.) Brenan; *E. pervillei* (Vatke) R. Vig.; *E. rheedei* Spreng.; and *E. tuberosa* R. Vig. Of these, *E. louvelii*, *E. pervillei* and *E. tuberosa* are endemic to the Island. Villiers (2002) noted that *E. tuberosa* "is easily recognisable by the white, glandular mucro at the tip of the leaf rachis and the axes of the pinnae (generally present)" (Villiers 2002, p. 169). Close examination of specimens at K reveals structures that are here interpreted as extra-

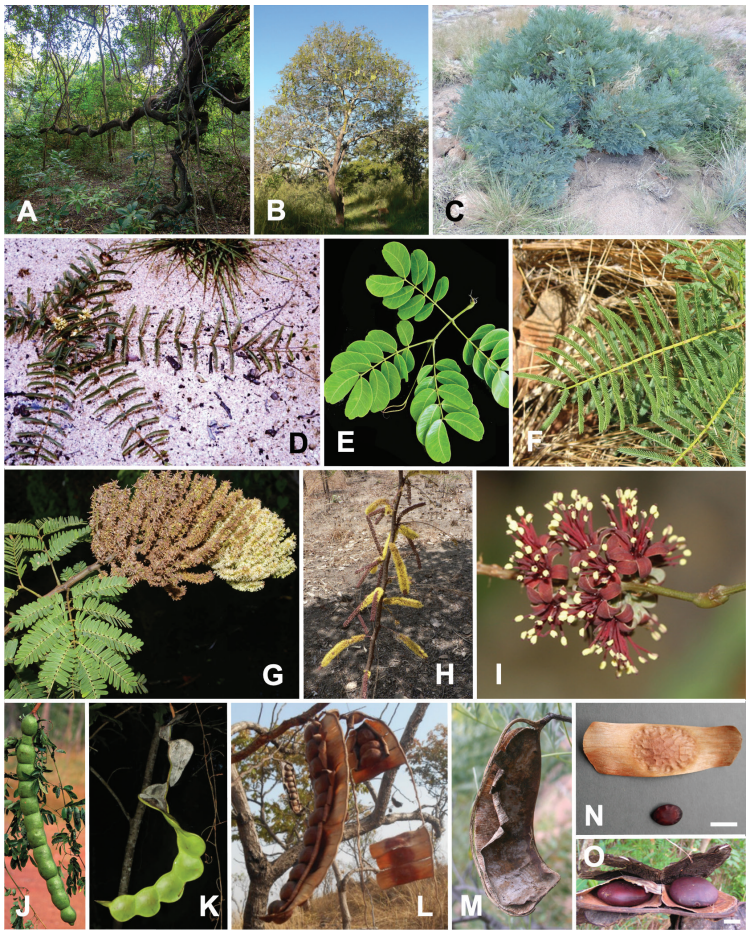

Figure 2. Genus-wide variation in morphological characters. **A–D** habit **A** large woody liana, *E. rheedei* (photo: B Wursten, Hyde et al. (2021)) **B** small tree, *E. abyssinica* (photo: G Baumann, Dressler et al. (2014a)) **C** shrub, *E. burkei* (photo: M Schmidt, Dressler et al. (2014a, b)) **D** geoxylic suffrutex, *E. dolichorrhachis* (photo: M Bingham, Bingham et al. (2021)) **E, F** leaves **E** bipinnate leaf with few pinnae, few large leaflets and ending in a bifurcating tendril, *E. rheedei* (photo: AP Balan, Balan and Predeep (2021)) **F** bipinnate leaf with many pinnae, many small leaflets and no tendril, *E. rangei* (photo: A Dreyer, Dressler et al. (2014a)) **G–I** inflorescences **G** terminal panicle of up-turned spikes, *E. polyphylla* (photo: R Vásquez Martínez, CC BY-NC-SA 3.0, MBG (2021)) **H** axillary fascicles of spiciform racemes, *E. goetzei* (photo: G Baumann, Dressler et al. (2014a)) **I** short spiciform raceme of dark red flowers, *E. wahlbergii* (photo: R Mangelsdorff, Dressler et al. (2014a)) **J–M** fruits **J** immature, weakly falcate, segmented craspedium up to 2 m long, *E. rheedei* (photo: photographer unknown, Centre for Australian National Biodiversity Research (CANBR), 2000) **K** immature, segmented, laxly spiralled craspedium up to 120 cm long, *E. gigas* (photo: R Aguilar CC BY-NC-SA 2.0, Aguilar (2021)) **L** ripe segmented craspedia breaking up into one-seeded segments with exfoliating epicarp, *E. africana* (photo: B Eichhorn, Dressler et al. (2014a)) **M** ripe unsegmented craspedium, the entire valve breaking away from the persistent replum, *E. burkei* (photo: M Kriek CC BY-SA 4.0, Ueda (2021) observation 85675968) **N, O** seeds **N** one-seeded endocarp segment and small ovoid, flattened seed with elliptic pleurogram, *E. africana* (photo: B Eichhorn, Dressler et al. (2014a)) **O** ripe one-seeded fruit segments with large circular, laterally compressed seeds lacking a pleurogram, *E. gigas* (photo: J Stevens, Dressler et al. (2014a)). Scale bars: 1 cm (**N, O**).

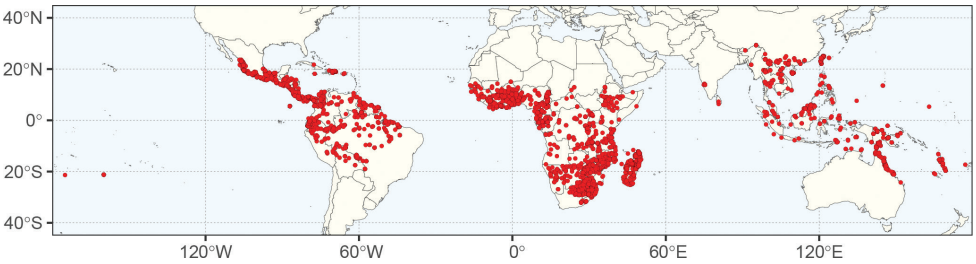

Figure 3. Global distribution of 4415 digitised, quality-controlled herbarium records of *Entada* (including those for ex-*Elephantorrhiza* species) in GBIF (www.GBIF.org), DryFlor (www.dryflor.info) and SEINet (swbiodiversity.org/seinet) from Ringelberg et al. (in prep.). Map created using R packages ggplot2 (Wickham 2016), sf (Pebesma 2018) and rnaturalearth (South 2017). Map: J Ringelberg.

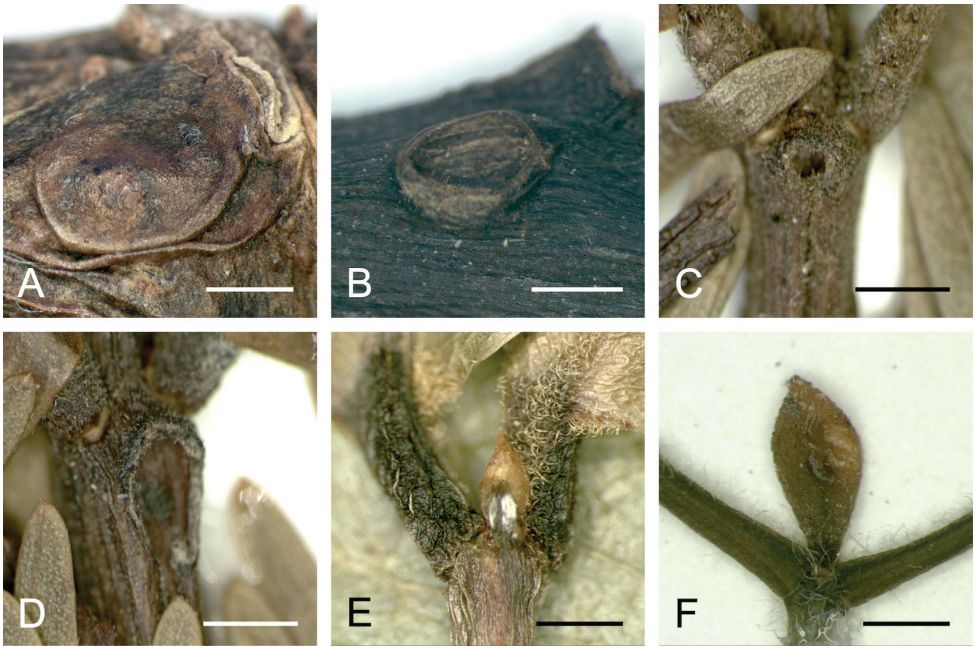

Figure 4. Putative extrafloral nectaries on herbarium specimens of five of the six native Madagascan species of *Entada* **A** *E. leptostachya, Du Puy et al. M235* **B** *E. louvelii, Réserves Naturelles RN1447* **C** *E. pervillei, Service Forestier 10525_SF* **D** *E. pervillei, Service Forestier 11481_SF* **E** *E. rheedei, Gautier LG3153* **F** *E. tuberosa, Jongkind et al. 3264*. Scale bars: 2 mm (**A–F**). Photos: S O'Donnell.

floral nectaries on five of the six Madagascan *Entada* species (*E. chrysostachys* is the only species on which these structures were not observed) (Fig. 4). These nectaries are visible as annular structures on shoots immediately beneath the base of stipules, in similar positions to those documented for *E. phaseoloides* (Blüthgen and Reifenrath 2003; Marazzi et al. 2019) (Fig. 5), in all five potentially extrafloral nectary-bearing species. In addition, multiple vouchers of *E. pervillei* contain material with small basin-like structures

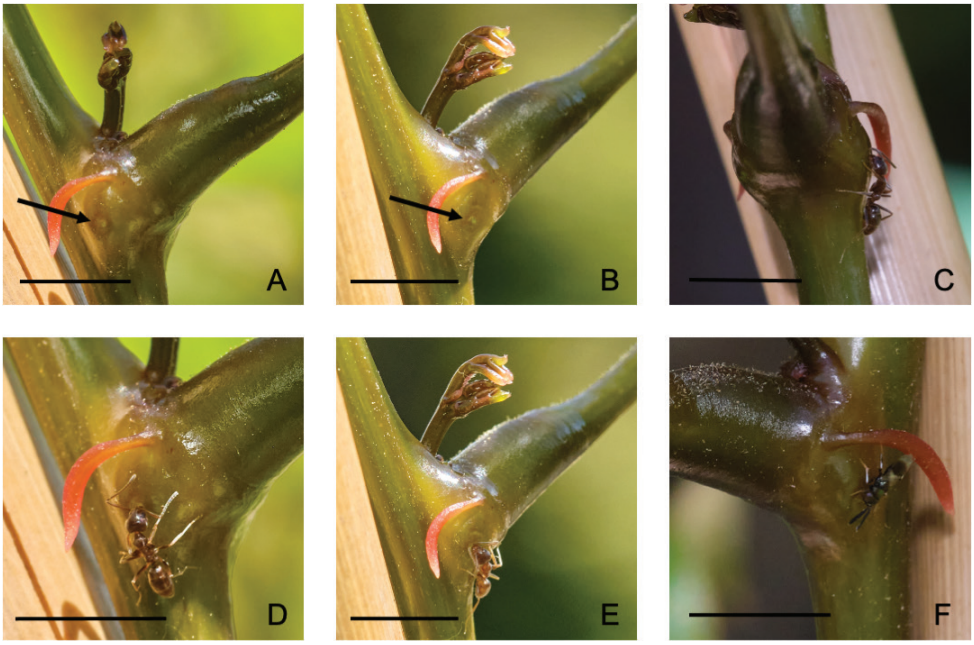

Figure 5. Extrafloral nectaries at nodes on stems of cultivated *Entada phaseoloides* grown in California from seed. **A, B** Pit nectary at node on stem adjacent to petiole, indicated by arrow **C–E** Argentine ants (*Linepithema humile*) visiting nectaries **F** dipteran nectary visitor. Scale bars: 5 mm (**A–F**). Photos: S O'Donnell.

at the distal end of adaxially grooved rachises that are also interpreted here as nectaries (Fig. 4C, D). Finally, structures comparable to those described by Villiers (2002) for *E. tuberosa* and confirmed on several K vouchers ascribed to this species (e.g. Fig. 4F), were also observed on specimens identified as *E. rheedei* (Fig. 4E). Examination of living material, chemical analyses of any exudates that might issue from all the above-mentioned structures and observations of animal visitation are needed to verify the interpretation offered here that these structures are indeed nectaries. The presence of these structures begs the question about how widespread they might be across the genus. A detailed study of extrafloral nectaries across the full geographical range of *Entada* should be carried out, this using a high-powered microscope and backed up by fieldwork.

We present no infrageneric classification at this point, pending a more densely sampled species-level molecular phylogeny and more detailed taxonomic revision which are foci of proposed future work. Instead, species are here simply alphabetically ordered. Species descriptions, species delimitation and synonymy are based on regional floristic treatments in Brenan (1959, 1966, 1970), Ross (1974, 1975a, 1975b), Nielsen (1992), Barneby (1996), Cowan (1998), Villiers (2002), Tateishi et al. (2008), Wakita et al. (2008), Ohashi et al. (2010), Wu and Nielsen (2010), Grobler (2012) and Braga et al. (2016), as well as Lungu's (1995) global synopsis and, for the ex-*Elephantorrhiza* species, rely almost entirely upon Ross (1974, 1975a) with occasional additions from Brenan (1970) and Grobler

(2012). Where opinions in literature differ, we defer to Brenan (1959, 1966, 1970), Ross (1974, 1975a), Nielsen (1992) and Villiers (2002) with any exceptions noted in the corresponding species descriptions. In addition to basionyms, we include synonyms only when these are names published in the genus *Entada*. For example, under *Entada abyssinica*, we do not present the synonyms published in the genera *Pusaetha*, *Gigalobium* or *Entadopsis*. We include type details for all accepted species, but not for synonyms.

Entada abyssinica Steud. ex A. Rich, Tent. Fl. Abyss. 1: 234. 1847.

= *Entada abyssinica* var. *microphylla* Oliv., Fl. Trop. Afr. 2: 228. 1871. Synon. nov.
= *Entada abyssinica* var. *intermedia* Fiori, L'Agricoltura Colon. 5: 170. 1911. Placed as a synonym of *E. abyssinica* by Thulin (1983) in Leguminosae of Ethiopia: 36. 1983.

Types. ETHIOPIA. Tigray region, mountains of Shire Dschogardi, *Schimper 520* (isosyntypes: BR [BR0000008378606], H [H1034939], HAL [HAL0120946], K [000232163, 000232164], LG [LG0000090027161], M [0108317], MO [MO-954247], MPU [MPU016174], P [P00418276, P00418277 & P00418278], S [S13-12046], TUB [TUB000996 & TUB000997]); ETHIOPIA. Abyssinie, *Quartin Dillon s.n.* (syntype: MPU [MPU016240 & MPU016246]).

Description. Tree 2.7–10(–15) m tall, crown spreading (Figs 2B, 6A). **Leaves:** rachis 16.3–21.7 cm long, tendrils absent; pinnae 12–20 pairs per leaf, each pinna 4.8–7.8 cm long, with 20–55 pairs of leaflets; leaflets 4–12 × 1–3 mm, linear-oblong, apex rounded to obtuse and mucronate, base rounded to sub-truncate, mid-rib oblique, closer to the distal margin, lamina appressed-pubescent above and below though sometimes glabrescent above (Fig. 6C). **Inflorescence:** a 7–16 cm long spiciform raceme, either solitary or in groups of up to 4 inserted in a supra-axillary position, inflorescence peduncle and rachis pubescent (Fig. 6B). **Flowers:** creamy white turning yellowish, sweetly scented, pedicels 0.5–1 mm long; calyx 0.75–1 mm long, shallowly toothed, glabrous; petals 1.5–3 × 1 mm; stamen filaments 3.5–6 mm long

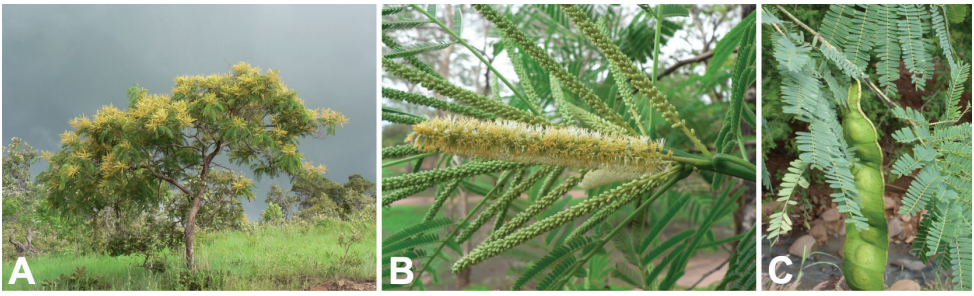

Figure 6. *Entada abyssinica* habit, vegetative and reproductive structures. **A** small tree, Malawi (photo: G Baumann, Dressler et al. (2014a)) **B** spiciform racemes both pre- and post-anthesis, Malawi (photo: G Baumann, Dressler et al. (2014a)) **C** immature fruit and leaves, Burkina Faso (photo: A Thiombiano, Dressler et al. (2014a)).

(Fig. 6B). **Fruit:** a laterally compressed, torulose, almost straight craspedium, 15–39 × 3.8–9 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments moderately umbonate over seeds (Fig. 6C). **Seeds:** 1–1.3 × 0.8–1 cm, pleurogram elliptic, C-shaped or closed.

Distribution. Tropical and southern subtropical Africa (excluding Madagascar).

Habitat and ecology. Wooded grassland (Chipya), fringes of woodland (Miombo, characterised by *Brachystegia* Benth.), riparian vegetation and – in Sierra Leone – on laterite plateaux; 430–2290 m alt.

***Entada africana* Guill. & Perr., Fl. Seneg. Tent.: 233. 1832.**

= *Entada ubanguiensis* De Wild., Pl. Bequaert. 3: 88. 1925.
= *Entada sudanica* Schweinf., Reliq. Kotschy.: 8. 1968.

Types (fide Brenan 1959: 12). SENEGAL. Tiélimane, Cayor, *Leprieur* (syntype: G; photo: K); GAMBIA. Albreda, *G.S. Perrottet 290* (isosyntypes: BM [BM000842201], G; photo: K).

Description. Shrub to small tree, 1.2–10 m tall, bark very rough (Fig. 7A). **Leaves:** variable, rachis 5.3–30 cm long, tendrils absent; pinnae 2–10 pairs per leaf, each pinna 7.1–17 cm long, with 10–24 pairs of leaflets; leaflets 1–3.1 × 0.32–0.85 cm, linear-oblong to elliptic- or obovate-oblong, apex rounded, base obtuse to oblique, mid-rib sub-central above base, lamina glabrous to slightly puberulous. **Inflorescence:** a 6.5–15 cm long, spiciform raceme, either solitary or in groups of up to 4 inserted in a supra-axillary position, peduncle and rachis usually glabrous, rarely pubescent (Fig. 7B). **Flowers:** yellow to white, sweetly scented, pedicels 1(–1.5) mm long; calyx 0.75–1.25 mm, shallowly toothed, glabrous; petals 1.5–4 × 0.6–1 mm (Fig. 7C). **Fruit:** a torulose, laterally compressed, almost straight craspedium, 38 × 5–7.3 cm; with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments distinctly umbonate over seeds (Figs 2L, 7D). **Seeds:** ovoid, 1.2 × 0.9–1 cm (Fig. 2N).

Distribution. Throughout tropical sub-Saharan Africa, north of the equator.

Figure 7. *Entada africana* habit, vegetative and reproductive structures. **A** small tree, Burkina Faso (photo: A Gockele, Dressler et al. (2014a)) **B** spiciform racemes both pre- and post-anthesis, Côte d'Ivoire (photo: S Porembski, Dressler et al. (2014a)) **C** open, pedicellate flowers, Mali (photo: P Birnbaum, Dressler et al. (2014a)) **D** mature fruits at varying ripeness, Burkina Faso (photo: Marco Schmidt, Dressler et al. (2014a)).

Habitat and ecology. Savannah grasslands and woodland, often in association with *Terminalia* L., *Combretum* Loefl., *Philenoptera laxiflora* (Guill. & Perr.) Roberty and *Pterocarpus lucens* Lepr. ex Guill. & Perr. (Lungu 1995, p. 35).

Entada arenaria Schinz, Mém. Herb. Boissier 8: 118. 1900.

Type. NAMIBIA. Hereroland, Grootfontein District, Omuramba-Omatako River, *Schinz 277* (holotype: Z).

Description. Geoxylic suffrutex with erect annual 5–120 cm stems, young stems densely pubescent (Fig. 8A). **Leaves:** petiole 6–12 cm long, grooved above, puberulous; rachis 4–17 cm long, grooved above; pinnae 2–4 pairs per leaf, 7.5–14 cm long, with 6–13 pairs of leaflets; leaflets (1.2–)2–3.5(–4) × 0.7–2 cm, narrowly oblong to obovate-oblong, apex rounded to emarginate, base asymmetric, rounded to cordate on proximal margin, cuneate to cuneate-rounded on distal margin, lamina pubescent below at least on mid-rib and often throughout (Fig. 8A, B, D). **Inflorescence:** an axillary spiciform raceme 4–12 cm long, 1–3 per axil, rachis usually glabrous (Fig. 8A–C). **Flowers:** pale cream, pedicels 1–2 mm long; calyx campanulate, 1–2 mm long, shallowly toothed; petals 3–4 mm long; stamen filaments 5–6 mm long (Fig. 8C). **Fruit:** a torulose, laterally compressed, straight to distinctly falcate craspedium, 7.5–22 × 1.5–6 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum (Fig. 8D). **Seeds:** 12.5 × 9 mm or smaller (see subsp. *microcarpa* below), dark brown, smooth.

subsp. *arenaria*

= *Entada nana* Harms, Kunene–Sambesi Exped.: 244. 1903.

Description. Stems 30–120 cm high. Fruit strongly falcate, 17–22 × 5–6 cm. Seeds 12.5 × 9 cm.

Distribution. Namibia, Botswana, Zimbabwe, Zambia, Angola.

Habitat and ecology. Woodland on Kalahari sand; ca. 900 m alt.

subsp. *microcarpa* (Brenan) J.H. Ross, Bothalia 11: 126. 1973.

Type. ZAMBIA. Mwinilunga District, Dobeka Bridge, *E. Milne-Redhead 4496* (holotype: K; isotype BR [BR0000006252199]).

Basionym. *Entada nana* Harms subsp. *microcarpa* Brenan, Kew Bull. 20(3): 373. 1966.

Description. Stems 5–25 cm high. Fruit nearly straight, 7.5–12 × 1.5–2.8 cm. Brenan (1970, p. 20) noted that he did not see mature seeds, but presumed them to be smaller than in subsp. *arenaria*.

Figure 8. *Entada arenaria* habit, vegetative and reproductive structures. **A** geoxylic suffrutex with erect annual stem, Angola (photo: D Goyder *CC BY-NC 4.0*, Ueda (2021) observation 35199077) **B** leaves and spiciform racemes pre-anthesis, Democratic Republic of Congo (photo: J Stevens, Dressler et al. (2014a)) **C** open, pedicellate flowers, Democratic Republic of Congo (photo: W McCleland, all rights reserved, iNaturalist (2021) observation 95512918) **D** leaves and immature fruits, Zambia (photo: W McCleland, Dressler et al. (2014a)).

Distribution. Zambia, Democratic Republic of Congo.

Habitat and ecology. Grassland and woodland on Kalahari sand; ca. 1200 m alt.

***Entada bacillaris* F. White, Bol. Soc. Brot., sér. 2, 33: 5. 1959.**

Type. ZAMBIA. Abercorn District, Kambole escarpment, *H.M. Richards 9986* (holotype: K [K000232144, K000232145 & K000232146]; isotypes: BR [BR0000006251895 & BR0000006252229]).

Description. Shrub 1.2–1.8 m tall, little-branched, young stems with golden to grey indumentum. **Leaves:** rachis 17–30 cm long, pubescent, tendrils absent; pinnae 3–4(–10) pairs per leaf, 10–17.5 cm long, with 8–13(–24) pairs of leaflets; leaflets (1.3–)2–4(–4.6) × (0.4–)1–1.7 cm, oblong-elliptic, apex rounded to sub-truncate, base obliquely rounded to sub-cordate, mid-rib nearly central, lamina sub-glabrous above, pubescent below. **Inflorescence:** an axillary spiciform raceme, 8–18 cm long, 1–3 per axil, peduncle and rachis pubescent. **Flowers:** greenish-white to yellow, pedicels 1–1.5 mm long; calyx 1–2 mm long, shallowly toothed, glabrous to slightly pubescent at teeth apices; petals 2.5–4 × 1–1.2 mm; stamen filaments 5–6 mm long. **Fruit:** a torulose, laterally compressed, slightly curved craspedium, 26–37 × 8–9 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments slightly umbonate over seeds. **Seeds:** ovoid, compressed, 1.2–1.5 × 0.9–1.1 × 0.3–0.4 cm, pleurogram heart-shaped, becoming diffuse near hilum.

var. *bacillaris*

= *Entada nana* Harms var. *pubescens* R.E. Fr., Schwed. Rhod.–Kongo–Exped. 1911–12, 1: 64. 1914.

Description. Young stems with yellowish to golden hairs. Pinnae 3–4 pairs per leaf. Leaflets 8–13 pairs per pinna, (2–)2.5–4(–4.6) × (0.5–)1–1.6 cm. Calyx glabrous.

Distribution. Zambia, southwest Tanzania.

Habitat and ecology. Escarpment woodland with *Brachystegia*, *Julbernardia* Pellegr. and *Isoberlinia* Craib & Stapf (Lungu, 1995, p. 38), on shallow rocky soils; 900–1520 m alt.

var. *plurijuga* Brenan, Kew Bull. 20(3): 372. 1966.

Type. ZAMBIA. Abercorn District, Inono Valley, 1 km from Mpulungu Road, *H.M. Richards 2278* (holotype: K [K000232133]).

Description. Young stems and leaves with grey to golden hairs. Pinnae 3–10 pairs per leaf. Leaflets (10–)11–24 pairs per pinna, (1–)1.6–2.7 × 0.4–0.7 cm. Calyx sometimes sparsely hairy.

Distribution. Zambia.

Habitat and ecology. Similar to var. *bacillaris*, though Brenan (1970, p. 19) also noted var. *plurijuga* sometimes occurs on sandy soils; 1220-1740 m alt. Additionally, Lungu (1995, p. 38) stated that var. *plurijuga* has also been found on deep, well-drained soils on the edges of Miombo woodland and river valleys.

Note. Brenan (1966, 1970) expressed uncertainty about the status and placement of this taxon, citing the possibility that it might represent a putative hybrid between var. *bacillaris* and *E. abyssinica* or be better placed as a variety of *E. chrysostachys*, stating that it differs from the latter only in its more numerous pinnae and longer stipe to the fruit (Brenan 1970, p. 19).

***Entada borneensis* Ridl., J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 67: 307. 1898.**

Type. MALAYSIA. Borneo, Sarawak, Sarawak River, Penkulu Ampat, *G.D. Haviland s.n.* (holotype: K [K000635744]).

Description. Liana > 40 m long. **Leaves:** rachis 5–9.5 cm, sub-glabrous to tomentose, terminating in a bifurcating tendril; pinnae 2 opposite pairs per leaf, each with 3–7 pairs of alternate to sub-opposite leaflets, except for the distal opposite pair; leaflets narrowly oblong to obovate, 1.4–4 × 0.7–1.8 cm, base asymmetrically rounded, apex rounded and emarginate, both surfaces glabrous, main vein puberulous. **Inflorescence:** a 19–40 cm long, solitary, axillary spike, rachis tomentose. **Flowers:** yellowish or greenish-white to white, sessile, staminate or bisexual; calyx cupular, 0.5–0.6 mm long, glabrous; petals 2 × 0.6–0.8 mm; stamen filaments 4–6 mm long. **Fruit:** a gigantic, torulose craspedium, 50–120 × 10–13 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments 9–10 cm long; epicarp coriaceous, endocarp chartaceous. **Seeds:** circular, laterally compressed, 4 cm in diameter, hard, brown, lacking a pleurogram.

Distribution. Borneo.

Habitat and ecology. Primary and secondary rainforest, especially along rivers; in sandy clay substrates, loams and soils derived from limestone; 0–800 m alt.

Note. Nielsen (1992) noted that *E. borneensis* is locally common but rarely collected.

***Entada burkei* (Benth.) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303568-1

Type. SOUTH AFRICA. Transvaal, Magaliesberg, *Burke & Zeyher s.n.* (holotype: K [K000232271]; presumed isotypes (fide Ross 1975a: p. 144): BM [BM000842178], MO [MO-954355], TCD, Z).

Basionym. *Elephantorrhiza burkei* Benth., London J. Bot. 5: 81. 1846.

Description. Shrub to small tree (0.3–)1–3(–6) m, with dark grey to reddish bark (Figs 2C, 9A). **Leaves:** petiole 2.6–6.5 cm long; rachis 3.6–14.5 cm long; pinnae (1–)4–8(–9) pairs, 3.5–12.5 m long, with (9–)12–23(–32) pairs of leaflets; leaflets 7–17 × 1.5–3.5(–5) mm, oblanceolate to elliptic or linear-oblong, apex obtuse to rounded, base slightly oblique, lamina glabrous. **Inflorescence:** an axillary spiciform raceme borne on lateral shoots of the current season's growth, 5–10(–12) cm long, solitary or aggregated in fascicles, rachises glabrous. **Flowers:** cream, yellow or yellowish-white, pedicels 2 mm long, articulated near the middle, with minute reddish glands at the base of the pedicels; calyx campanulate, 2.5 mm long, distinctly toothed, glabrous; petals 3–4.5 mm long; stamen filaments 5 mm long (Fig. 9B). **Fruit:** a laterally compressed, straight to slightly curved craspedium, 10–19(–28) × 2.5–4 cm, transverse veins prominent, lacking transverse septa between seeds, the valves separating from the replum intact upon ripening, the epicarp exfoliating from the endocarp (Figs 2M, 9C, D). **Seeds:** irregular in shape, 9–13 × 8–12 × 8 mm.

Distribution. Botswana, Zimbabwe, Mozambique, South Africa.

Habitat and ecology. Woodland, grassland and scrub, usually in rocky settings; 970–1370 m alt.

Figure 9. *Entada burkei* habit and reproductive structures. **A** branched shrub bearing leaves of the current season's growth alongside inflorescences near shoot tips, South Africa (photo: J Heymans *CC BY-NC-ND 4.0*, iNaturalist (2021) observation 11078242) **B** open, pedicellate flowers with minute red glands at base of pedicels, South Africa (photo: J-H Keet *CC BY-NC 4.0*, Ueda (2021) observation 11099684) **C** leaves and immature fruits, South Africa (photo: M Schmidt, Dressler et al. (2014a)) **D** leaves and mature fruits, South Africa (photo: tjeerd *CC BY-NC 4.0*, Ueda (2021) observation 38383810).

***Entada camerunensis* Villiers, Bull. Mus. Natl. Hist. Nat., B, Adansonia 4: 193. 1983.**

Type. CAMEROON. West Kongolo, on bank of River Bayo, *R. Letouzey 3534* (holotype: P [P00418283, P00418284 & P00418285]; isotype: YA [YA0023378]).

Description. Liana, sometimes sarmentose, stem twisted, to 15 cm diameter at base. **Leaves:** a conspicuous ridge at petiole base; rachis 5.5–7.9(–9.5) cm, grooved above, tendrils absent, but petioles sometimes modified for climbing; pinnae 2–4 pairs per leaf, 3.5–10(–16) cm long with 5–10 pairs of leaflets; leaflets 1–2.5 × 0.3–1.1 cm, obovate-oblong, increasing in size distally, apex truncate to retuse, base asymmetric with proximal margin rounded, distal margin attenuate, lamina pubescent. **Inflorescence:** a terminal or axillary spiciform raceme, 7–9.5 cm long, solitary or 2 per axil, peduncle and rachis pubescent. **Flowers:** yellow to greenish-yellow, staminate or bisexual, pedicels 0.5–0.75 mm long; calyx cupular, 0.75–1.25 mm long, shallowly toothed, glabrous to sparsely pubescent at tooth apices; petals 3–3.25 × 0.6–0.8 mm, elliptic to obovate; stamen filaments 3–5 mm long. **Fruit:** a torulose, laterally compressed, slightly curved craspedium, 20–29 × 7–9 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments distinctly umbonate over seeds. **Seeds:** elliptic-oblong, laterally compressed, 1.7–1.9 × 0.9–1 cm, pleurogram open.

Distribution. Cameroon, Democratic Republic of Congo, Zambia.

Habitat and ecology. Riparian forests.

***Entada chrysostachys* (Benth.) Drake, Hist. Phys. Madagascar 30: 51. 1902.**

= *Entada kirkii* Oliv., Fl. Trop. Afr. 2: 327. 1871.
= *Entada boiviniana* (Baill.) Drake, A. Grandidier, Hist. Phys. Madagascar 30: 51. 1902. (publ. 1903).
= *Entada grandidieri* (Baill.) Drake, A. Grandidier, Hist. Phys. Madagascar 30: 51. 1902. (publ. 1903).

Type. MADAGASCAR. Emirna Province [Imerina] and Imamou, *W. Bojer s.n.* (holotype: K; isotypes: M [M0218663], P [P00367635 & P00367637]).

Basionym. *Adenanthera chrysostachys* Benth., J. Bot. (Hooker) 4: 343. 1841.

Description. Shrub or small tree to 10 m tall or liana to 12 m, stem to 20 cm thick, often twisted (Fig. 10A). **Leaves:** rachis 8–16 cm long, grooved above, glabrous; pinnae (2–)3–5(–8) pairs per leaf, (4.5–)5.2–8.9(–13) cm long, with 10–17(–21) pairs of leaflets; leaflets 13–19(–29) × (3–)4.9–5.5(–10) mm, oblong to obovate-oblong, apex rounded, base asymmetric rounded on proximal margin and cuneate on distal margin, mid-rib diagonal and raised above and below, lamina appressed-pubescent to glabrous (Fig. 10B). **Inflorescence:** an axillary spiciform raceme, 4–12(–13.5) cm long, usually clustered, but sometimes solitary, rachis pubescent or glabrous (Fig. 10C). **Flowers:** white to yellow, pedicels 1–1.5 mm long, with an unpleasant odour; calyx

Figure 10. *Entada chrysostachys* habit, vegetative and reproductive structures. **A** small tree, Madagascar (photo: thierrycordenos *CC BY-NC 4.0*, Ueda (2021) observation 25108890) **B** leaf, Mozambique (photo: O Maurin *CC BY-NC-SA 3.0*, iBOL (2016) record SAFH1507–11) **C** axillary spiciform racemes of open, pedicellate flowers and closed flower buds, Madagascar (photo: D Du Puy) **D** leaves and immature pods, Madagascar (photo: D Du Puy) **E** mature pods, Mozambique (photo: O Maurin *CC BY-NC-SA 3.0*, iBOL (2016) record SAFH1507–11).

obconical, 1–1.5 mm long, glabrous to sparsely pubescent, distinctly toothed; petals 3–4 × 1–1.4 mm; stamen filaments 4–6 mm long. **Fruit:** a torulose, laterally compressed, slightly curved craspedium 20–45 × 5–10 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum (Fig. 10D, E). **Seeds:** elliptic, 14–17.7 × 10.5–12.8 × 3.3–4 mm, pleurogram elliptic, open near hilum.

Distribution. Madagascar, Comoro Islands, Mozambique, Zimbabwe, Zambia, Malawi, Tanzania.

Habitat and ecology. Disturbed forests and grassland; riparian thicket; woodland characterised by *Brachystegia glaucescens* Hutch. & Burtt Davy; and seasonally wet valley bottoms with *Combretum*; sandy soils and laterite.

Entada dolichorrhachis Brenan, Kew Bull. 20: 374. 1966. (publ. Jan. 1967).

Type. ZAMBIA. Mbala (Abercorn) District, Lufubu River, Iyendwe Valley, on path to Shulu Kwesa Village, *H.M. Richards 11952* (holotype: K; isotypes: BR [BR0000006251536], LISC [LISC001666], NY [NY00002026], SRGH).

Description. Geoxylic suffrutex with erect annual stems, 1–10 cm tall, young shoots pubescent (Figs 2D, 11A). **Leaves:** elongate and trailing on the ground; rachis (15–)42–65(–90) cm long, expanding from the apex during the growing season, tendrils lacking; pinnae 19–35 pairs on mature leaves, 2.7–5 cm long, with 6–9(–16) pairs of leaflets; leaflets (5–)8–17(–20) × 2.5–9.3 mm, ovate-oblong, asymmetric, apex rounded and mucronate, base oblique, lamina glabrous above, pubescent below (Fig. 11D). **Inflorescence:** an axillary spiciform raceme, 3.4–10 cm long, 1–2 per axil, rachis densely pubescent (Fig. 11B). **Flowers:** greenish-yellow, pedicels 1.5–2.5 mm long; calyx 1.5–2 mm long, deeply toothed, pubescent; petals pale dull yellow, 4.75–5.75 mm long; stamen filaments 7–10 mm long (Fig. 11C). **Fruit:** a torulose, straight craspedium, 3–6.5 × 1.5–1.8 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent

Figure 11. *Entada dolichorrhachis* habit, reproductive and vegetative structures. **A** uprooted geoxylic suffrutex, Zambia (photo: M Bingham, Bingham et al. (2021)) **B** spiciform racemes in axils of short, erect shoot with two young leaves expanding towards base of image, Zambia (photo: M Bingham, Bingham et al. (2021)) **C** open and unopened flowers, Zambia (photo: M Bingham, Bingham et al. (2021)) **D** mature fruits and trailing, scandent leaves with elongate rachises, Zambia (M Bingham, Bingham et al. (2021)).

replum; segments umbonate over seeds (Fig. 11D). **Seeds:** ovate, laterally compressed, 9 × 8 mm, with open pleurogram.

Distribution. Zambia.

Habitat and ecology. Woodland and open riverbanks, on sandy soil; 780–1620 m alt.

***Entada elephantina* (Burch.) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303964-1

≡ *Elephantorrhiza elephantina* (Burch.) Skeels, Bull. Bur. Pl. Industr. U.S.D.A. 176: 29. 1910.

Type. SOUTH AFRICA. Cape Province, Bechuland Division, Kuruman District, between Matlowing River and Kuru, *W.J. Burchell 2410* (holotype: K [K000232273]; isotypes: GH [GH00058379], P [P00418275]).

Basionym. *Acacia elephantina* Burch., Trav. S. Africa 2: 236. 1824.

Description. Geoxylic suffrutex with erect, annual, herbaceous stems 20–90 cm arising from the woody end of an elongate subterranean axis (Fig. 12A, B). **Leaves:** petiole 1.3–3.6(–8) cm long, rachis 3.5–13.5(–17.5) long; pinnae 2–4 pairs on lower leaves, 7–17 pairs on upper leaves, 3–9(–10.5) cm long, with (7–)12–45(–55) pairs of leaflets; leaflets (4–)5–10(–15) × (0.3–)0.5–2(–2.5) mm, linear to linear-oblong, apex acute to rarely obtuse, sometimes asymmetric, mucronate, base oblique, lamina glabrous (Fig. 12B, E). **Inflorescence:** an axillary spiciform raceme usually confined to the lower part of the stem, (2–)4–8(–12) cm long, solitary or grouped, rachises usually glabrous (Fig. 12B–D). **Flowers:** cream-coloured, yellow or yellowish-white, pedicels 1.5 mm long, articulated near the middle, with minute reddish to reddish-brown glands at the base; calyx campanulate, 1.75 mm long, distinctly toothed, glabrous; petals 2.75–3.75 mm long; stamen filaments 6.5 mm long (Fig. 12D). **Fruit:** a laterally compressed, straight to slightly curved craspedium, (5–)9.5–15(–21) × 3–5.7 cm, lacking transverse septa between seeds, thus leaving the

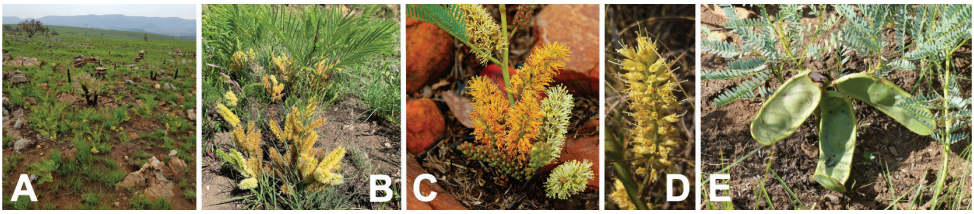

Figure 12. *Entada elephantina* habitat, habit, reproductive and vegetative structures. **A** growing in fire-prone open scrub, South Africa (photo: R Gill *CC BY-NC 4.0*, Ueda (2021) observation 32241269) **B** geoxylic suffrutex with erect herbaceous shoots bearing finely divided bipinnate leaves and producing spiciform racemes near ground level, Eswatini (photo: L Loffler *CC BY-NC 4.0*, Ueda (2021) observation 44861491) **C** spiciform racemes clustered near the base of the stem, South Africa (photo: tjeerd *CC BY-NC 4.0*, Ueda (2021) observation 62025284) **D** spiciform raceme of open flowers, South Africa (photo: J Whatmore, Ueda (2021) observation 62547631) **E** immature fruits borne near the base of the stem, South Africa (photo: G Lewis).

valves to separate from the replum intact upon ripening, the epicarp exfoliating from the endocarp; umbonate over seeds (Fig. 12E). **Seeds:** ellipsoid, 18–26 × 13–18 × 6–13 mm.

Distribution. Namibia, Botswana, Zimbabwe, Mozambique, South Africa, Eswatini, Lesotho.

Habitat and ecology. Grassland and open scrub, sometimes gregarious (Fig. 12A); 1060–1360 m alt.

Note. Brenan (1970, p. 28) and Ross (1974, p. 250; 1975a, p. 141) noted that leaf characters vary considerably across the range of *E. elephantina*. Specimens from the western portion of the range tend to have fewer pinnae and leaflets with larger leaflets; those from eastern areas bear more numerous pinnae and leaflets, with smaller leaflets. This variation appears to be continuous, so neither author attempted to subdivide the taxon.

Entada gigas (L.) Fawc. & Rendle, Fl. Jamaica 4: 124. 1920.

= *Entada gigalobium* DC., Mém. Légum.: 421. 1826.
= *Entada scandens* (L.) Benth. subsp. *planoseminata* De Wild., Pl. Bequaert. 3: 85. 1925.
= *Entada scandens* (L.) Benth. subsp. *umbonata* De Wild., Pl. Bequaert. 3: 86. 1925.
= *Entada planoseminata* (De Wild.) G.C.C. Gilbert & Boutique, Fl. Congo Belge 3: 221. 1952.
= *Entada umbonata* (De Wild.) G.C.C. Gilbert & Boutique, Fl. Congo Belge 3: 222. 1952.

Type. SWEDEN (cultivated). Uppsala Botanic Garden, *Herb. Linn. No. 1228.11* (neotype: LINN, designated by Panigrahi in Taxon 34: 714. 1985).

Basionym. *Mimosa gigas* L., Fl. Jamaic. (Linnaeus) 22. 1759.

Description. Liana to 45 m long (Fig. 13A). **Leaves:** rachis 5.9–7.5 cm long, terminating in a bifurcating tendril; pinnae (1–)2 pairs per leaf, with (3–)4(–5) pairs of leaflets; leaflets oblong to elliptic, often asymmetric, apex obtuse or

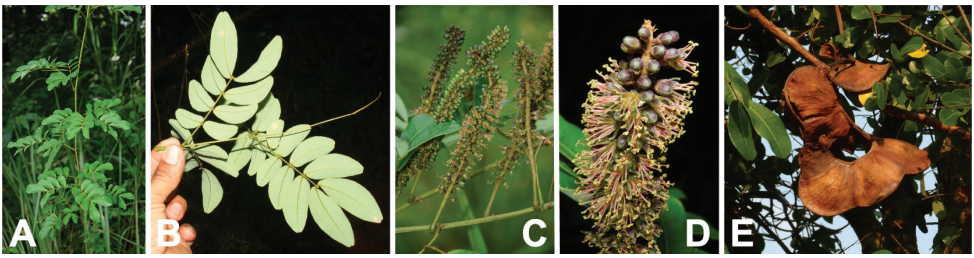

Figure 13. *Entada gigas* habit, vegetative and reproductive structure. **A** vegetative shoot of liana, Gabon (photo: E Bidault *CC BY-NC-ND 3.0*, MBG (2021)) **B** abaxial view of a leaf, Costa Rica (photo: D Janzen *CC BY-ND-SA 3.0*, iBOL (2016) record MHPAD2192–10) **C** axillary spiciform racemes, Gabon (photo: E Bidault *CC BY-NC-ND 3.0*, MBG (2021)) **D** open, pedicellate flowers, Gabon (photo: E Bidault *CC BY-NC-ND 3.0*, MBG (2021)) **E** large, mature fruit twisted into a lax spiral, Democratic Republic of Congo (photo: W McCleland, Dressler et al. (2014a)).

rounded, emarginate, both surfaces of lamina essentially glabrous, except beneath near the base and the mid-rib puberulous above and sometimes below (Fig. 13A, B). **Inflorescence:** a spiciform raceme, 8–25 cm long, solitary, supra-axillary (3–5 mm above the axil) with tufted glands between the axil and point of insertion of the rachis, ± pubescent, peduncle 1.5–6 cm long (Fig. 13C). **Flowers:** creamy white to greenish-yellow, pedicels 1–1.5 mm long; calyx 1–1.25 mm long, glabrous to pubescent; petals 2.5–3 mm long; stamen filaments 3.5–6 mm long (Fig. 13E). **Fruit:** a gigantic craspedium, 40–120 × 7.5–12 cm, less woody than in the morphologically similar *E. rheedei*, twisted into a lax spiral, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; epicarp falling away to expose an inflexible chartaceous endocarp; 10–12-seeded (Figs 2K, 13E). **Seeds:** circular to slightly cordate, laterally compressed, 4–5.5 cm in diameter, hard; cotyledons separated by an intervening air space, enabling flotation (Fig. 2O).

Distribution. Central and west Africa; Central America, Caribbean and Colombia.

Habitat and ecology. Riparian forests; Brenan (1959) noted two specimens collected from Uganda (*Jarrett 400*; *Brown 328*) at 1310 m alt. and 1183 m alt., respectively. Seeds dispersed widely by sea currents.

Entada glandulosa Pierre ex. Gagnep., Notul. Syst. (Paris) 2: 57. 1911.

= *Entada tamarindifolia* Pierre ex. Gagnep., Notul. Syst. (Paris) 2: 59. 1911.

Type. LAOS. *Massie s.n.* (lectotype: P [P02436137], designated by I.C. Nielsen in Adansonia ser. 2, 19: 342. 1980).

Description. Shrub, scandent (Fig. 14A). **Leaves:** petiole 1.8–4 cm long, rachis 4.5–10 cm long, terminating in a bifurcating tendril; pinnae 2 pairs pair leaf, 4–8 cm

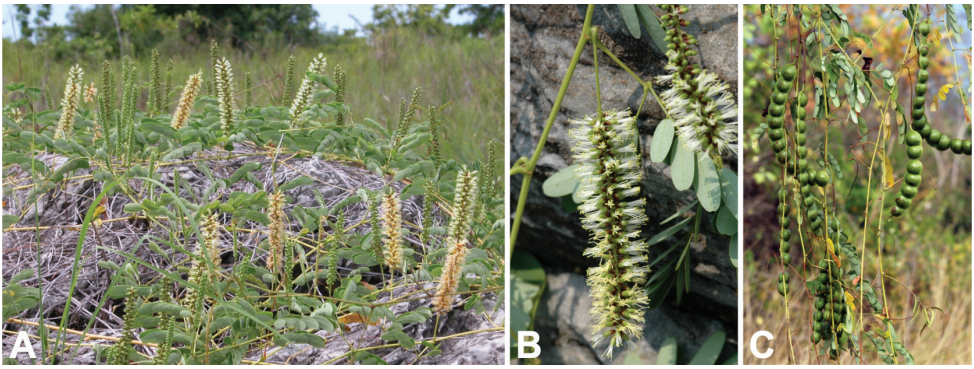

Figure 14. *Entada glandulosa* habit and reproductive structures. **A** scandent shrub with erect axillary spikes, Thailand (photo: T Boonkerd, all rights reserved) **B** solitary axillary spikes with open flowers, Thailand (photo: T Boonkerd, all rights reserved) **C** immature fruits, Thailand (photo: T Boonkerd, all rights reserved).

long, with 5–6 pairs of leaflets; leaflets 1.1–4 × 0.5–1.7 cm, elliptic to oblong, base truncate, apex emarginate or mucronate. **Inflorescence:** a spike 7–18 cm long, axillary, solitary, rachis pubescent to velutinous (Fig. 14A, B). **Flowers:** creamy white to yellowish-white, sub-sessile; calyx cupular, 2–2.5 mm long, glabrous to puberulous; petals lanceolate, 5 × 1 mm, a pair of linear glands on the lower half of the dorsal side of each petal; stamen filaments 8 mm long (Fig. 14B). **Fruit:** a torulose, curved craspedium, 35 × 2.2–2.6 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments 2.4 cm long; epicarp coriaceous, endocarp papyraceous (Fig. 14C). **Seeds:** subglobular, 1.1–1.8 cm, hard, brown, pleurogram lacking.

Distribution. Laos, Cambodia, southern Vietnam, Thailand, Myanmar.

Habitat and ecology. Seasonally dry deciduous forest, mixed forest with Dipterocarpaceae and evergreen forest, up to 500 m alt. Usually on limestone, though also in shallow sandy soils and in red soils.

***Entada goetzei* (Harms) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303569-1

≡ *Elephantorrhiza goetzei* (Harms) Harms, Veg. Erde [Engler] 9(3, 1): 400, in obs. 1915.

Type. TANZANIA. Rufiji District, *W. Goetze 82* (holotype: B†; drawing: BM [BM000842177]; isotype: K).

Basionym. *Piptadenia goetzei* Harms, Bot. Jahrb. Syst. 28: 397. 1900.

Description. Shrub to small deciduous tree 1–4(–7) m tall, young shoots often becoming blackish (Fig. 15A). **Leaves:** petiole 1–5(–7.5) cm; rachis 6–20(–45.5) cm, grooved above; pinnae 3–30(–41) pairs per leaf, 1.8–9 cm long, with 9–40(–48)

pairs of leaflets; leaflets 3.5–12(–22) × 0.7–0.8(–2.75) mm, linear-oblong to narrowly oblong, apex acute to rounded and mucronate, base oblique, mid-rib running from distal corner of leaflet base to apex centre, lamina glabrous (Fig. 15B). **Inflorescence:** a spiciform raceme, (2–)5–20(–23) cm long, axillary, solitary or aggregated in fascicles or on short lateral shoots, rachis glabrous (Figs 2H, 15C). **Flowers:** yellowish-white, sometimes tinged pink or purple, pedicels 1 mm, articulated near the middle, with minute pale yellowish-white glands at the base of the pedicels; calyx 1.5–1.75 mm long, distinctly toothed, glabrous; petals 2.5–3 mm long; stamen filaments 4.5 mm long (Fig. 15C). **Fruit:** a straight to curved craspedium, (15–)20–30(–44) × 1.3–2.2(–3) cm, lacking transverse septa between seeds, thus leaving the valves to separate from the replum intact upon ripening, the epicarp exfoliating from the endocarp; umbonate over seeds (Fig. 15D). **Seeds:** ellipsoid to lenticular, 11–20 × 9–18 × 7–12 mm.

subsp. *goetzei*

Description. Leaves with (3–)14–41 pairs of pinnae per leaf, pinna rachis 3.5–9.5 cm long. Leaflets (11–) 20–48 pairs per pinna, 3.5–12 × 0.7–3 mm.

Distribution. Tanzania, Angola, Botswana, Zambia, Zimbabwe, Malawi, Mozambique, South Africa (Transvaal).

Habitat and ecology. Woodland and scrub, usually on rocky substrates, but also on alluvial soils; 120–1460 m alt.

Note. Ross (1974, 1975a) noted that plants from the area delimited for Flora Zambesiaca (e.g. those referred to in Brenan 1970, p. 26) frequently flower when the plant is leafless, whereas those from the Transvaal produce flowers together with leaves.

subsp. *lata* (Brenan & Brummitt) S.A. O'Donnell & G.P. Lewis, comb. nov.
urn:lsid:ipni.org:names:77303965-1

Type. ZAMBIA. Katombora, *Morze 55* (holotype: FHO [00096339U]).

Basionym. *Elephantorrhiza goetzei* (Harms) Harms subsp. *lata* Brenan & Brummitt, Bol. Soc. Brot., Sér. 2, 39: 189. 1965.

Description. Leaves with 4–15 pairs of pinnae, pinna rachis 6.5–15 cm long. Leaflets 9–28 pairs per pinna, 12–22 × 4–8 mm.

Distribution. Zambia, Zimbabwe.

Habitat and ecology. Woodland of various types.

Note. Grobler (2012, p. 129) does not accept subspecific taxa within *E. goetzei* on the basis that the additional material she collected across the species range revealed the morphological variation in leaf characters to be continuous.

Figure 15. *Entada goetzei* habit, vegetative and reproductive structures. **A** shrub with mature fruits, Malawi (photo: G Baumann, Dressler et al. (2014a)) **B** leaf with linear-oblong leaflets, Malawi (photo: C Chisale, Dressler et al. (2014a)) **C** fascicles of spiciform racemes bearing open, pedicellate flowers and closed flower buds on leafless stem, Malawi (photo: C Chisale, Dressler et al. (2014a)) **D** mature fruits, Malawi (photo: C Chisale, Dressler et al. (2014a)).

Entada hockii De Wild., Repert. Spec. Nov. Regni Veg. 11: 535. 1913.

Type. DEMOCRATIC REPUBLIC OF CONGO. Haut–Katanga, Plateau de la Manika, *A. Hock s.n.* (holotype: BR [BR0000008916471]).

Description. Geoxylic suffrutex, annual stems pubescent. **Leaves:** rachis 6–9.7 cm long, pubescent; pinnae 1–2 pairs per leaf, 6–8.1 cm long, with 7–9 pairs of leaflets; leaflets 1.4–2.3 × 0.65–0.85 cm, oblong, apex obtuse to rounded, base obtuse to subtruncate, lamina glabrous above, pubescent below. **Inflorescence:** an axillary, spiciform raceme 3.5–7 cm long, 1–3 per axil, rachis densely pubescent. **Flowers:** cream-coloured, pedicels 0.5–1 mm long; calyx 1 mm long, distinctly toothed, glabrous; petals 2.8–3.4 × 1–1.3 mm; stamen filaments 2.8–3 mm long. **Fruits and seeds:** not seen.

Distribution. Democratic Republic of Congo, Angola.

Habitat and ecology. On Kalahari sands.

Entada leptostachya Harms, Bot. Jahrb. Syst. 53: 456. 1915.

Type. KENYA. Machakos District, Kibwezi, *G. Scheffler 120* (lectotype: P [P00418289], designated by J.-F. Villiers in Leguminosae of Madagascar, 2002: 165; isolectotype: K [K000232161]; original syntype: B†).

Description. Liana, shrub or small tree, 3–6 m, stems twining, with elevated nectaries at nodes (Fig. 4A). **Leaves:** rachis (4.5–)5.6–15.1(–16) cm long, tendrils absent, but plant climbing using modified, hooked pinnae on long shoots; pinnae 2–4(–5) pairs per leaf, (4–)5.6–6.8(–13) cm long, with 7–11(–14) pairs of leaflets; leaflets 9–25(–35) × 3–9(–15) mm, oblong to oblanceolate-oblong, apex rounded to emarginate, base asymmetric, lamina usually puberulous above and below though sometimes sub-glabrous to glabrous. **Inflorescence:** an axillary spike, 3–8(–16) cm long, 1–3 per axil together on short shoots, rachis glabrous. **Flowers:** yellow, sweetly scented; calyx

obconical, 0.5–1 mm long, shallowly toothed, glabrous; petals 2–2.5 × 0.8 mm; stamen filaments 2.5–4 mm long. **Fruit:** a torulose, laterally compressed craspedium, 17–23 × 4.3–8.4 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** elliptic, 10.4–14 × 9–10.6 × 3.5–3.7 mm, pleurogram oval, open.

Distribution. Ethiopia, Somalia, Kenya, Tanzania, Madagascar.

Habitat and ecology. Dry scrub, degraded woodland with scattered trees, dense *Commiphora* Jacq. Woodland; growing as small trees when on steep limestone slopes.

Entada louvelii (R. Vig.) Brenan, Kew Bull. 20: 365. 1966.

Type. MADAGASCAR. Analamazoatra, south of Moramanga, *M. Louvel 16* (lectotype: P [P00452896], designated by J.-F. Villiers in Leguminosae of Madagascar, 2002: 165).

Basionym. *Entada pervillei* (Vatke) R. Vig. var. *louvelii* R. Vig., Notul. Syst. (Paris) 13: 347. 1949.

Description. Tree 10–15 m tall, with elevated nectaries at nodes (Fig. 4B). **Leaves:** petiole 2–4 cm long, grooved above; rachis 9–18 cm long, winged, no tendril; pinnae 11–20 pairs per leaf, 3–9 cm long, with 24–46 pairs of leaflets; leaflets 3–7 × 1–1.75 mm, oblong to oblong-elliptic, apex rounded-obtuse to sub-acute and mucronate, base asymmetric and sub-truncate; lamina glabrous (Fig. 16A, B, D). **Inflorescence:** a terminal panicle of spikes, each spike 5–19 cm long, rachis pubescent (Fig. 16A, B). **Flowers:** white, 4–5 mm long, sessile to sub-sessile; calyx cream-coloured, obconical, 1.5–2 mm long, shallowly toothed, glabrous; petals 3.5–4 mm long; stamen filaments 5–7.25 mm long (Fig. 16C). **Fruit:** a torulose, laterally compressed craspedium, 15–20 × 3–6.5 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum (Fig. 16D). **Seeds:** elliptic, 1.5–2.4 × 0.6–1.2 cm, light brown, pleurogram lacking.

Figure 16. *Entada louvelii* vegetative and reproductive structures. **A** branch and shoots bearing leaves and terminal panicles of spikes, Madagascar (photo: P Antilahimena *CC BY-NC-ND 3.0*, MBG (2021)) **B** terminal panicle of flower spikes, Madagascar (photo: D Du Puy) **C** spikes bearing open, sessile flowers and closed flower buds, Madagascar (photo: D Du Puy) **D** leaves and fruits nearing maturity, Madagascar (photo: D Du Puy).

Distribution. Madagascar (east).

Habitat and ecology. Moist forest, up to 1000 m alt. (Villiers 2002, p. 167); disturbed or dry forest (Lungu 1995).

***Entada mannii* (Oliv.) Tisser., Bull. Soc. Bot. France 99: 257. 1953.**

= *Entada bequaertii* De Wild., Pl. Bequaert. 3: 79. 1925.

Type. EQUATORIAL GUINEA. Fernando Pó (Boiko), *Mann 414* (holotype: K [K000232169]).

Basionym. *Piptadenia mannii* Oliv., Fl. Trop. Afr. [Oliver et al.] 2: 329. 1871.

Description. Shrub, scandent, sometimes becoming arborescent, to 30 m, stem 15 cm diameter near base, glabrous (Fig. 17A). **Leaves:** rachis 5–20 cm long, sparsely pubescent; pinnae 3–6 pairs per leaf, one or more pinnae sometimes modified into a tendril, leaflet-bearing pinnae 4–6 cm long, with 8–13 pairs of leaflets; leaflets 4–16(–21) × 1.5–7 mm, oblong, apex retuse, base rounded, asymmetric, lamina glabrous to puberulous above, pubescent below (Fig. 17B). **Inflorescence:** an axillary spiciform raceme, 5.5–10 cm long, in panicles from the upper axils, rachis pubescent (Fig. 17D). **Flowers:** white, minutely pedicellate; calyx 0.7–1 mm, shallowly toothed, glabrous to puberulous; petals 2 mm long (Fig. 17D). **Fruit:** a torulose, laterally compressed, straight craspedium, 15–45 × 6–10 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum (Fig. 17E). **Seeds:** elliptic, 1.8 × 0.9 cm, pleurogram present.

Distribution. Tropical West Africa, from Senegal to Angola.

Habitat and ecology. Riparian forest and on rocky hills in forest.

Figure 17. *Entada mannii* habit, vegetative and reproductive structures. **A** scandent shrub with mature fruits, Mali (photo: P Birnbaum, Dressler et al. (2014a)) **B** leaf bearing oblong leaflets, Malawi (photo: C Chisale, Dressler et al. (2014a)) **C** young shoot with swollen nodes either side of petiole insertion, Mali (photo: P Birnbaum, Dressler et al. (2014a)) **D** spiciform raceme with open, pedicellate flowers and closed flower buds, Congo (photo: D Harris, Dressler et al. (2014a)) **E** leaf and nearly mature fruits, Mali (photo: P Birnbaum, Dressler et al. (2014a)).

Entada mossambicensis **Torre, Contr. Conhec. Fl. Mocamb. 2: 88. 1954.**

Type. MOZAMBIQUE. Niassa, Nampula, *A.R. Torre 4750 A* (holotype: LISC [LISC001696, LISC001697, LISC001698, LISC001699]; isotypes: BM, K [K000232129, K000232130], BR [BR0000006251864]).

Description. Shrub, sub-erect, 1–2 m tall, roots thick, fusiform. **Leaves:** rachis 6.7–8 cm long, tendrils lacking; pinnae 3–7 pairs per leaf, 7–9 cm long, with (40–)138–154 pairs of leaflets; leaflets 2.1–5.5 × 0.4–0.8 mm, linear-oblong, apex sub-acute and mucronate, base asymmetric, lamina glabrous. **Inflorescence:** an axillary spiciform raceme, 12–30 cm long, solitary. **Flowers:** purple, pedicels 2–2.5 mm long; calyx 1 mm long, glabrous; petals 4.5–5 mm long; stamen filaments 5–6 mm long. **Fruit:** a torulose, laterally compressed, falcate craspedium, 10–12 × 2–2.5 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** 1.2 × 1 cm, 2.3 mm thick, with closed pleurogram.

Distribution. Mozambique.

Habitat and ecology. Rocky habitats.

Entada nudiflora **Brenan, Kew Bull. 20: 377. 1966. (publ. Jan. 1967).**

Type. ZAMBIA. Mbala (Abercorn) District, path to Kapata village, *H.M. Richards 10192* (holotype: K [K000232154, K000232155]).

Description. Climber, slender, woody, up to 3 m. **Leaves:** rachis 4–6 cm long, terminating in bifurcating tendril or the petiolules of the terminal pinna pair modified for coiling; pinnae 1–3 pairs per leaf, 4.6–5.1 cm long, with 18–25 pairs of leaflets; leaflets 3.3–13.5 × 1–1.75 mm, linear to linear-oblong, apex sub-acute and mucronate, base oblique, lamina glabrous. **Inflorescence:** an axillary spike, 3.5–5.5 cm long, solitary or in fascicles on short shoots or occupying terminal portions of shoots and produced when the plant is leafless. **Flowers:** dark purple, sessile to sub-sessile; calyx 2.5 mm long, deeply toothed, glabrous; petals 3.5–6 mm long; stamen filaments 6–8 mm long. **Fruit:** a torulose, laterally compressed, falcate craspedium, 25–28 × 3–3.4 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** 10 × 6.5 mm, with pleurogram.

Distribution. Zambia, Tanzania.

Habitat and ecology. Rocky hillsides, especially those of the escarpment facing Lake Tanganyika, in deciduous thicket, scrub and dry evergreen woodland, occasionally on sandy soil. Leafless when flowering.

Entada obliqua **(Burtt Davy) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303570-1

= *Elephantorrhiza obliqua* Burtt Davy var. *glabra* E. Phillips, Bothalia 1: 189. 1923.

Type. SOUTH AFRICA. Transvaal, between Carolina and Oshoek, ~ 1.6 km from Robinson's Farm, *J. Burtt Davy 2976* (holotype: BM [BM000081856]; isotypes: FHO, K [K000232281]).

Basionym. *Elephantorrhiza obliqua* Burtt Davy, Bull. Misc. Inform. Kew 1921: 191. 1921.

Description. Geoxylic suffrutex with erect, annual, usually unbranched stems up to 30 cm from underground axes, stems pubescent to glabrous. **Leaves:** primary and secondary axes glabrous to sparsely pubescent; petiole 2–6 cm long; rachis (0–)1.5–9 cm long; pinnae (1–)2–6 pairs per leaf, 2–11 cm long, with 4–13(–21) pairs of leaflets; leaflets 5.5–15 × 2–6.5 mm, distinctly asymmetric, ovate to oblong-ovate, apex acute or mucronate, base oblique, mid-rib running from distal corner of leaflet base to apex centre, lamina glabrous. **Inflorescence:** an axillary spiciform raceme, 3.5–6 cm long, solitary, rachis glabrous to sparsely pubescent. **Flowers:** yellowish-white, pedicels 1.5 mm long, with minute red glands at base; calyx campanulate, 2 mm long, shallowly toothed, glabrous; petals 4.5 mm long; stamen filaments 7.5 mm long. **Fruit:** a laterally compressed, straight craspedium, 11 × 4 cm, lacking transverse septa between seeds, thus leaving the valves to separate from the replum intact upon ripening, the epicarp exfoliating from the endocarp. **Seeds:** mature seeds not seen.

Distribution. South Africa, restricted to the Transvaal.

Habitat and ecology. In grassland.

***Entada parvifolia* Merr., Philipp. J. Sci., C 3: 229. 1908.**

= *Entada philippinensis* Gagnep., Notul Syst. (Paris) 2: 58. 1911.

Type. PHILIPPINES. Luzon, Zambales Province, *M. Ramos 5067* (holotype: NY [NY00002028]; isotypes: K [K000295958], US [US01108049]).

Description. Shrub, scandent, stem swollen from base, tuberous. **Leaves:** rachis 4–7.5 cm long; pinnae 2 pairs per leaf, 4.5–7.5 cm long, with 8–11 pairs of opposite leaflets; leaflets 1.1–1.9 × 0.4–0.75 cm, obliquely oblong, asymmetric, apex rounded to truncate, retuse or mucronate, base cuneate to rounded, lamina glabrous above and below. **Inflorescence:** a supra-axillary, 15 cm long spike, axis appressed-puberulous. **Flowers:** sub-sessile, staminate or bisexual; calyx cupular, 1 mm long, with minutely deltate teeth, glabrous to sparsely puberulent; petals 3 mm long, oblong; stamen filaments 5.5–7 mm long. **Fruit:** a straight, torulose craspedium, 29.5 × 5–5.5 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; epicarp chartaceous, endocarp papyraceous. **Seeds:** irregularly ovoid, 1.8 × 1.6 × 0.8 cm, dark brown, lacking a pleurogram.

Distribution. Philippines.

Habitat and ecology. Low elevation thickets.

Entada pervillei **(Vatke) R. Vig., Notul. Syst. (Paris) 13: 347. 1949,** ***pro parte*****, var.** ***louvellii*** **excl. (see** ***E. louvellii*****)**

≡ *Entada pervillei* var. *genuina* R. Vig., Notul. Syst. (Paris) 13: 347. 1949. Nom. superfl.

Type. MADAGASCAR. Nossi Bé [Nosy Bé], *J.M. Hildebrandt 2952* (holotype: B?; isotypes: JE [JE00003317, JE00003318], K, M [M0218736], P).

Basionym. *Piptadenia*? *pervillei* Vatke, Linnea 43: 109. 1881.

Description. Tree to 15 m tall, with elevated nectaries at nodes. **Leaves:** rachis 8–18 cm long, ridged above, sometimes with elevated nectaries between distal pairs of pinnae, tendrils lacking; pinnae 7–16 pairs per leaf, 3.5–11 cm long, with 26–72 pairs of leaflets; leaflets (4–)6–10.5 × 1–1.5 mm, linear-oblong, sub-falcate, apex acute to rounded or obtuse, base asymmetric, rounded on the proximal margin, attenuate on the distal margin, lamina glabrous, margins ciliolate to ciliate at base. **Inflorescence:** a terminal panicle of spikes, each spike 7–25 cm long, spike rachis slightly pubescent. **Flowers:** white, sub-sessile; calyx obconical, 1–1.6 mm long, shallowly toothed, glabrous; petals 2.5–4 × 1 mm; stamen filaments 5–6.5 mm long. **Fruit:** a torulose, laterally compressed craspedium, 18–25 × 2.5–4.5 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** oblong-ovate, 1.7 × 1 cm, brown, pleurogram indistinct.

Distribution. Madagascar (north, northeast and west).

Habitat and ecology. Humid evergreen forest and seasonally dry deciduous woodland up to 700 m alt.; sandy or calcareous soils.

Note. The "?" in the basionym *Piptadenia*? *pervillei* Vatke is associated with the genus *Piptadenia* and not with the species name *pervillei* because Vatke was not certain about the generic position of the species. *Entada pervillei* var. *genuina* R. Vig. (i.e. equivalent to the typical variety var. *pervillei*) is a superfluous name because, once var. *louvellii* was moved to *E. louvellii*, the typical variety was effectively disbanded.

Entada phaneroneura **Brenan, Kew Bull. 32: 545. 1978.**

Type. BURUNDI. Bubanza Territory, Cibitoke, *J. Lewalle 3238* (holotype: K; isotypes: BR [BR0000008915856], FHO).

Description. Shrub, climbing to 12 m. **Leaves:** rachis (2–)4–5 cm long, glabrous, terminating in a bifurcating tendril; pinnae 2 pairs per leaf, (1.5–)3–4 cm long, with 9–15 pairs of leaflets, pinna rachis distinctly winged; leaflets 5–8(–16) × 1.5–4 mm, oblong-oblanceolate to near linear, apex rounded to obtuse and mucronate, base oblique, lamina glabrous. **Inflorescence:** an axillary spiciform raceme, 5–6 cm long, the racemes often aggregated into a panicle, rachis glabrous. **Flowers:** purple, pedicels 1–2 mm long; calyx 0.75–1 mm long, distinctly toothed, glabrous; petals 3 × 1.1–

1.2 mm; stamen filaments 4–5 mm long. **Fruit:** a torulose, laterally compressed, falcate craspedium, 20 × 3–5 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** mature seeds not seen (although several specimens in BR have fruits).

Distribution. Burundi, Democratic Republic of Congo.

Habitat and ecology. Wooded savannah, ×erophilous thickets and dry forest; 800–950 m alt.

***Entada phaseoloides* (L.) Merr., Philipp. J. Sci., C 9: 86. 1914.**

= *Entada gandu* Hoffmanns., Verz. Pfl.–Kult. 8: 274. 1824.
= *Entada parrana* Spreng., Syst. Veg. 2: 325. 1825.
= *Entada adenanthera* DC., Mém. Légum.: 422. 1826.
= *Entada scandens* (L.) Benth., J. Bot. (Hooker) 4: 332. 1841.
= *Entada rumphii* Scheff., Natuurk. Tijdschr. Ned.–Indië 32: 412. 1871.
= *Entada scandens* var. *aequilatera* Domin, Biblioth. Bot. 22(89): 247. 1926.

Type. INDONESIA. Maluku, Amboina, illustration of *Faba marina major* in Rumphius Herb. Amb. 5: 5–8, tab. 4. 1747.

Basionym. *Lens phaseoloides* L., Herb. Amboin. (Linn.) 18. 1754.

Description. Liana to 40 m long, stems often flattened and spirally twisted, with pit nectaries at nodes. **Leaves:** petiole 1.5–3.5 cm long, rachis 4.3–7.7 cm long, terminating in a bifurcating tendril; pinnae 1–2 pairs per leaf, 6–20 cm long, each pinna with 1–2(–3) pairs of leaflets; leaflets opposite, coriaceous, elliptic or narrowly obovate, sometimes asymmetrical about the mid-vein, 4.5–10 × 1.8–6.3 cm and increasing in size distally, apex acute to acuminate, retuse, base obtuse, mid-rib and margins puberulous (Fig. 18A). **Inflorescence:** a spike, 11.5–30 cm long, axillary, solitary or fascicled on short shoots, puberulous (Fig. 18B). **Flowers:** sessile to sub-sessile, staminate or bisexual, mildly fragrant; calyx cupular, glabrous, 0.8–1.2 mm long; petals green with base reddish; stamen filaments 4–6.5 mm long, white turning yellow; ovary slender, glabrous (Fig. 18C). **Fruit:** a gigantic, torulose craspedium, 100–135(–200) × 7–15 cm, straight to slightly curved, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments 6.5–7.5 cm long; epicarp woody, endocarp chartaceous; 9–16-seeded (Fig. 18D). **Seeds:** subcircular, laterally compressed, but convex with an angular margin, 3.5–5.5 × 3.3–4.5 × 1–1.5 cm, hard, reddish-brown, pleurogram lacking; an air-filled cavity between the cotyledons.

Distribution. Subtropical Japan (Ryukyu Islands), Taiwan (south), throughout Malesia, Australia (east coast of northern Queensland), Micronesia, southwest Pacific.

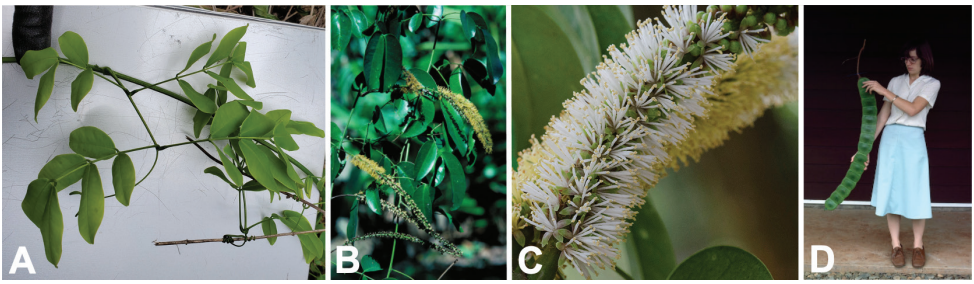

Figure 18. *Entada phaseoloides* vegetative and reproductive structures. **A** leaf with rachis terminating in a bifurcating tendril, Guam (photo: Pacific Island Network (PACN), US National Park Service (NPS) *CC BY-NC 4.0*, Ueda (2021) observation 34434359) **B** shoot bearing leaves and axillary flower spikes, Australia (photo: photographer unknown, Centre for Australian National Biodiversity Research (CANBR), 1998) **C** open, sessile flowers, Hong Kong (photo: C Chiu, all rights reserved, Chiu (2021)) **D** nearly mature pod, Australia (photo: B Gray, Centre for Australian National Biodiversity Research (CANBR), 1979).

Habitat and ecology. A wide variety of habitats from back-mangrove and lowland freshwater swamp, riparian vegetation and lowland rainforest up to montane forest, 0–1700 m alt.

***Entada polyphylla* Benth., J. Bot. (Hooker) 2: 133. 1840.**

= *Entada paranaguana* Barb. Rodr., Vellosia, ed. 2, 1: 18. 1891.
= *Entada polystachya* var. *polyphylla* (Benth.) Barneby, Brittonia 48: 175. 1996.

Type. GUYANA. Rio Quitaro, *R.H. Schomburgk 604* (holotype: K [K000504673, K000504674]; isotypes: E [E00296969], F [F0092593F], NY [NY00002025], US [US00001028]).

Description. Shrub, scandent, to 10 m. **Leaves:** rachis 7–13 cm long, puberulous, tendrils lacking; pinnae 4–7 pairs per leaf, 5–7 cm long, with (12–)13–20 pairs of leaflets; leaflets 8–20 × 3–8 mm, oblong, apex rounded to emarginate, base truncate to subtruncate, lamina pubescent above and below (Fig. 2G). **Inflorescence:** a compound, terminal, one-sided panicle of up-turned spikes, each spike 4–6.5 cm long, rachis pubescent (Fig. 2G). **Flowers:** cream to greenish-yellow, staminate or bisexual, sub-sessile; calyx cupular, 0.5–1 mm long, glabrous to sparsely puberulous; petals 2.5–3 × 0.8–1 mm; stamen filaments 3–4 mm long. **Fruit:** a torulose, laterally compressed craspedium, 20–30 × 6 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** 1.9–2.4 × 1–1.2 cm, with pleurogram.

Distribution. Amazonian Brazil, Ecuador, Peru, Venezuela, the Guianas, Puerto Rico.

Habitat and ecology. Disturbed forest, grassy fields, secondary vegetation at forest margins.

***Entada polystachya* (L.) DC., Mém. Légum. 434. t. 61. 1825.**

= *Entada chiliantha* DC., Mém. Légum. 422. 1826.
= *Entada plumeri* Spreng., Syst. Veg. 4(2): 164. 1827.
= *Entada acaciifolia* Benth., Trans. Linn. Soc. London 30: 365. 1875.

Type. illustration in Plumier, Pl. Amer. 1: tab. 12. 1755.

Basionym. *Mimosa polystachya* L., Sp. Pl. 1: 520. 1753.

Description. Liana or scandent shrub to 10 m. **Leaves:** rachis 6–13 cm long, glabrous to puberulous; pinnae (2–)3–5 pairs per leaf, 3.5–8 cm long, with 5–11 pairs of leaflets; leaflets 1.5–4 × 0.5–2 cm, oblong, apex rounded, base oblique, lamina glabrous above and below (Fig. 19A). **Inflorescence:** a terminal one-sided panicle of up-turned spikes, each spike 8–10 cm long, spike rachis glabrous to puberulous (Fig. 19A, C). **Flowers:** cream-coloured (the stamens) and reddish (the sepals and petals), with an unpleasant odour; calyx cupular, 1 mm long; petals 2.5–4 × 0.8–1 mm; stamen filaments 4 mm long (Fig. 19D). **Fruit:** a torulose, laterally compressed, falcate craspedium 15–30(–40) × (5–)5.5–9.3 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; mesocarp over seeds conspicuous and spongy (Fig. 19E). **Seeds:** elliptic, 1.2–1.7 × 0.8–1.3 × 2–4 mm, with pleurogram.

Distribution. Pacific Mexico east to Lesser Antilles and south to Bolivia.

Habitat and ecology. Seasonally dry and humid forest near the coast, especially on the margins of mangroves, occasionally reaching the forest canopy.

***Entada praetermissa* (J.H. Ross) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303571-1

Type. SOUTH AFRICA. Transvaal, Lydenburg District, Steelpoort Valley, near Sarahshof, *L.E.W. Codd 9830* (holotype: PRE [PRE0391104-0]; isotypes: BM [BM000842179], K [K000232268]).

Basionym. *Elephantorrhiza praetermissa* J.H. Ross, Bothalia 11: 252. 1974.

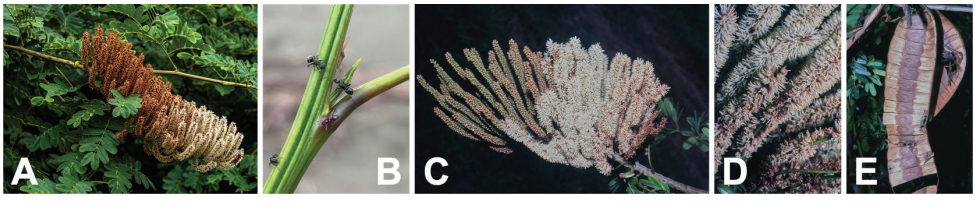

Figure 19. *Entada polystachya* vegetative and reproductive structures. **A** branch and shoots of scandent shrub bearing leaves and a terminal one-sided panicle of up-turned flower spikes, Ecuador (photo: M Alache, all rights reserved, iNaturalist (2021) observation 95175614) **B** stem node with ants accessing gland at point of petiole insertion, Costa Rica (photo: J Montero, all rights reserved, iNaturalist (2021) observation 86105886) **C** terminal panicle of up-turned flower spikes, with open flowers appearing white and buds appearing brown, Brazil (photo: G Lewis) **D** open, sessile flowers, Brazil (photo: G Lewis) **E** mature pods, Brazil (photo: G Lewis).

Description. Shrub 1–2 m tall. **Leaves:** petiole 2.2– 4 cm long; rachis 4–9 cm long, grooved above and with occasional scattered dark glands; pinnae (3–)5–10(–12) pairs per leaf, (2.8–)3.5–6(7) cm long, with 20–40 pairs of leaflets; leaflets 5–10 × 0.9–1.5 mm, linear to linear-oblong, apex rounded to acute, base oblique, mid-rib running from distal corner of leaflet base to apex centre, lamina glabrous. **Inflorescence:** a spiciform raceme, 4–5.5 cm long, solitary or aggregated in fascicles or on short lateral shoots, rachis glabrous. **Flowers:** yellowish-white; pedicels 1.5–2 mm long, articulated near or below the middle, with minute reddish glands at the base; calyx 0.75–1.25 mm long, toothed, glabrous; petals 2–3 mm long; stamen filaments 4–5 mm long. **Fruit:** a laterally compressed, straight to slightly curved craspedium, 12–18 × 2–3.2 cm, lacking transverse septa between seeds, thus leaving the valves to separate from the replum intact upon ripening, the epicarp exfoliating from the endocarp. **Seeds:** laterally compressed, 15 × 13 × 3.5 mm.

Distribution. South Africa, apparently restricted to the Transvaal.

Habitat and ecology. On dry wooded hillsides.

Entada rangei **(Harms) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303572-1

= *Elephantorrhiza suffruticosa* Schinz, Mém. Herb. Boissier 8: 117. 1900, non *Entada suffruticosa* Vatke. 1881 [= *Mimosa suffruticosa* (Vatke) Drake]. Type: ANGOLA. Huila District, "Kilevi am Kunene", south of Humbe, *Schinz 2071* (lectotype: Z, designated by J.H. Ross in Fl. Southern Afr. 16(1): 148. 1975).

Type. NAMIBIA. Keetmanshoop District, Naute, near Keetmanshoop, *P. Range 455* (holotype: B†; drawing: BM [BM000842180]; isotypes: BOL, NBG [SAM0073417-1, SAM0073417-2], SAM).

Basionym. *Elephantorrhiza rangei* Harms, Bot. Jahrb. Syst. 49(3–4): 420. 1913.

Description. Shrub or small tree, 1–6 m tall (Fig. 20A). **Leaves:** petiole (0.6–)1.5–3.5 cm long; rachis (0.5–)10–17(–25.4) cm; pinnae (2–)15–27(–42) pairs per leaf, (1.4–)2–3.5(–6.8) cm long, with (17–)27–40(–50) pairs of leaflets; leaflets 3–7.5 × 0.4–1.2 mm, linear-oblong to linear, apex obtuse to acute, asymmetric and often mucronate, base oblique with proximal margin rounded, mid-rib marginal throughout or more rarely running from the distal corner of the leaflet base to the apex centre, lamina glabrous (Fig. 20B, C). **Inflorescence:** an axillary spiciform raceme, (4–)6–14(–18) cm long, 1–3 per axil or borne on short lateral shoots, rachis pubescent or sometimes glabrous (Fig. 20C). **Flowers:** yellowish-white, golden yellow or cream-coloured; pedicels 1 mm long, articulated near the middle, with minute reddish, reddish-brown or pale yellow glands at the base of the pedicels; calyx cupular, 1 mm long, shallowly toothed, glabrous; petals 3–3.75 mm long; stamen filaments 5 mm long. **Fruit:** a laterally compressed, straight to slightly curved craspedium, 8.5–30.5 × 1.8–2.25 cm,

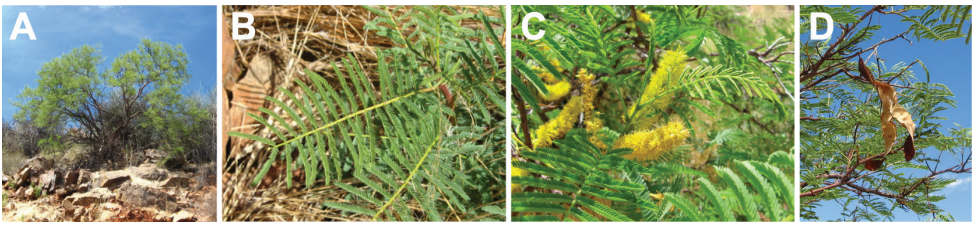

Figure 20. *Entada rangei* habit, vegetative and reproductive structures. **A** erect shrub, Namibia (photo: A Dreyer, Dressler et al. (2014a)) **B** short shoot and adaxial view of mature leaves, Namibia (photo: A Dreyer, Dressler et al. (2014a)) **C** spiciform racemes of open flowers amongst young leaves, Namibia (photo: A Dreyer, Dressler et al. (2014a)) **D** mature pods, Namibia (photo: A Dreyer, Dressler et al. (2014a)).

transverse veins usually prominent, lacking transverse septa between seeds, thus leaving the valves to separate from the replum intact upon ripening, the epicarp of both valves peeling away from the endocarp; umbonate over seeds (Fig. 20D). **Seeds:** ellipsoid, 13–15 × 9–12 mm.

Distribution. Angola, Namibia, Zimbabwe, Mozambique.

Habitat and ecology. Woodland and grassland, often in rocky areas; 1050–2130 m alt.

Note. *Elephantorrhiza rangei* Harms was treated as a distinct species by Ross (1975a), although with some hesitation because the species was known only from the type locality and displays considerable variation in leaflet size, even on a single branch. Ross also noted that it "bears a superficial resemblance to *Elephantorrhiza suffruticosa* Schinz." Plants of the World Online (POWO) places *Elephantorrhiza rangei* as a synonym of *Elephantorrhiza suffruticosa* Schinz, but when transferred to the genus *Entada*, the epithet *suffruticosa* cannot be used because the name *Entada suffruticosa* Vatke (1881, p. 108), for a Madagascan species (a synonym of *Mimosa suffruticosa* (Vatke) Drake), already exists.

Entada reticulata Gagnep., Notul. Syst. (Paris) 2: 59. 1911.

Type. LAOS. Bassac, *Thorel 1427*, *p.p.* (holotype: P [P030131, P030132]).

Description. Shrub, scandent. **Leaves:** petiole 1.3–2.3 cm long, rachis 3.5–5 cm long, terminating in a bifurcating tendril; pinnae 2 pairs per leaf, 5–7 cm long, with 8–16 pairs of opposite leaflets; leaflets 0.6–1.8 × 0.2–0.4 cm, oblong, apex mucronate, base obtuse, lamina glabrous except for pubescence on mid-rib below. **Inflorescence:** a 5–8 cm long, axillary, solitary spike, axis pubescent. **Flowers:** sessile, staminate or bisexual; calyx cupular, 0.8–1.5 mm long, shallowly toothed, glabrous; petals 3–3.5 mm long, linear-lanceolate. **Fruit:** a straight to slightly curved torulose craspedium, 5.5–11.5 × 1.5 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments 1.3–1.5 cm

long; epicarp coriaceous, endocarp parchment-like. **Seeds:** globose, 0.85 cm in diameter, hard, brown, pleurogram lacking.

Distribution. Laos, Cambodia.

Habitat and ecology. Seasonally dry deciduous forest or mixed forest with Dipterocarpaceae.

Entada rheedei Spreng., Syst. Veg. 2: 325. 1825.

= *Entada pursaetha* DC., Mém. Légum.: 421. 1826.
= *Entada monostachya* DC., Mém. Légum.: 422. 1826.
= *Entada gogo* I.M. Johnst., Sargentia 8: 137. 1949.

Type. INDIA. Malabar coast, illustration in *Rheede* Hort. Malab. 9: 151, tab. 77. 1689.

Description. Liana to 75 m long, stems to 30 cm diameter at base (Figs 2A, 21A), with elevated nectaries at nodes. **Leaves:** rachis 6.4–12.9 cm long, terminating in a bifurcating tendril; pinnae 1–2 pairs per leaf, 5–14 cm long, with 3–5 pairs of opposite leaflets, sometimes terminating in a glandular mucro (Fig. 4E); leaflets 1.8–6.6 × 1.2–2.9 cm, chartaceous, elliptic to oblanceolate, asymmetric, apex obtuse to acuminate, retuse, base rounded to attenuate, mid-rib above pubescent, lamina glabrous, except below near the base (Figs 2E, 21B). **Inflorescence:** a spike, 8–25 cm long, axillary, solitary, or sometimes several spikes from a short shoot, peduncle 1–8.5 cm long, peduncle and rachis puberulous to villose (Fig. 21C). **Flowers:** cream or greenish, sessile to subsessile, staminate or bisexual, with an unpleasant odour; calyx cupular, 0.75–1.2 mm long, shallowly toothed; petals pale green to white, 2.5–3.5 mm long; stamen filaments 2–6.5 mm long, white turning yellow; stigma shallowly cupular. **Fruit:** a gigantic, torulose craspedium, 50–200 × 7–15 cm, straight to slightly curved, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments 6.5–7.5 cm long; epicarp and endocarp woody (Figs 2J, 21D, E). **Seeds:** subcircular, laterally compressed, 5 × 3.5–5 cm, hard, brown, pleurogram lacking.

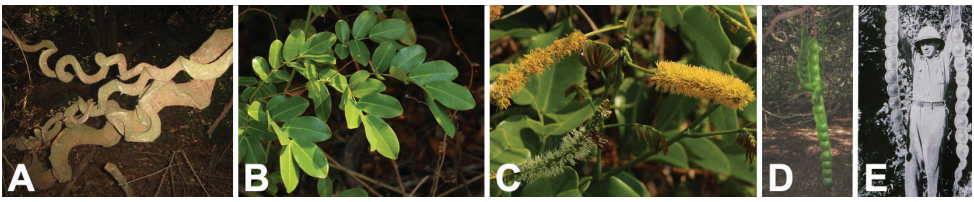

Figure 21. *Entada rheedei* habit, vegetative and reproductive structures. **A** liana with twisted woody stems, South Africa (photo: R Taylor *CC BY-NC 4.0*, Ueda (2021) observation 28499551) **B** adaxial view of mature leaf, South Africa (photo: R Taylor *CC BY-NC 4.0*, Ueda (2021) observation 11095941) **C** axillary spikes of open, sessile flowers, South Africa (photo: R Taylor *CC BY-NC 4.0*, Ueda (2021) observation 11095941) **D** immature pods, South Africa (photo: R Taylor *CC BY-NC 4.0*, Ueda (2021) observation 28499551) **E** mature pods of collection Schleiben 769a, Tanzania (photographer unknown).

subsp. *rheedei*

Description. Calyx glabrous.

Distribution. Tropical and southern subtropical Africa (including Madagascar), Mascarene Islands, Sri Lanka, India, Bangladesh, mainland South East Asia, southern China, Taiwan, Malesia, tropical northern Australia.

Habitat and ecology. Primary and secondary rainforest, especially riparian, back-mangrove and beach forest, 0–900 m alt.

subsp. *sinohimalensis* (Grierson & D.G. Long) S.A. O'Donnell & G.P. Lewis, comb. nov.
urn:lsid:ipni.org:names:77303573-1

≡ *Entada pursaetha* var. *sinohimalensis* (Grierson & D.G. Long) C. Chen & H. Sun, Fl. Yunnanica 10: 289. 2006.
= *Entada laotica* Gagnep., Bull. Soc. Bot. France 99: 46. 1952.

Type. NEPAL. Without locality, *N. Wallich 5294a* (holotype: K [K000756992]; isotypes: BM, E).

Basionym. *Entada pursaetha* subsp. *sinohimalensis* Grierson & D.G. Long, Notes Roy. Bot. Gard. Edinburgh 37: 348. 1979.

Description. Calyx puberulous to velutinous.

Distribution. Nepal, northeast India, Bangladesh, Myanmar, Laos, southwest China (Yunnan).

Habitat and ecology. Wet forest, especially riparian, up to about 1300 m alt.

***Entada schinziana* (Dinter) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303574-1

Type. NAMIBIA. Grootfontein District, Otavi, *Dinter 745* (lectotype: SAM [SAM0073418-0], designated by J.H. Ross in Fl. Southern Afr. 16(1): 148. 1975).

Basionym. *Elephantorrhiza schinziana* Dinter, Repert. Spec. Nov. Regni Veg. 17: 190. 1921.

Description. Branched shrub to 2.5 m tall. **Leaves:** petiole 2.2–3.5(–5.2) cm long; rachis (4.5–)7.5–14.5(–20.5) cm long; pinnae (2–)6–11(–14) pairs per leaf, 5.5–10(–14) cm long, with (14–)21–40 pairs of leaflets; leaflets (5–)7–14 × 1.5–3.5 mm, linear-oblong to oblong, apex rounded and sometimes mucronate, base oblique, mid-rib running from distal corner of leaflet base to apex centre, lamina glabrous, slightly glaucous. **Inflorescence:** an axillary spiciform raceme, 7–9.5 cm long, 1–2 per axil, rachis glabrous. **Flowers:** yellowish-white; pedicels 0.75 mm long, articulated towards the apex, with minute yellowish glands at the base; calyx cupular, 1.5 mm long, shallowly toothed, glabrous; petals 3–3.75 mm long; stamen filaments 5 mm long. **Fruit:** a

laterally compressed, straight to slightly curved craspedium, (15–)19–30(–40.5) × 3–3.9 cm, transverse veins prominent, lacking transverse septa between seeds, thus leaving the valves to separate from the replum intact upon ripening, the epicarp of both valves peeling away from the endocarp; umbonate over seeds. **Seeds:** mature seeds not seen.

Distribution. Namibia.

Habitat and ecology. In savannah and woodlands.

Note. Ross (1975a, p. 148) noted that the above description of the flowers of *E. schinziana* comes from the second sheet of *Dinter 1689*, which Ross regarded as of potentially ambiguous identity given that "one of the [other two] sheets of *Dinter 1689* is a mixed gathering of a vegetative shoot of *E. suffruticosa* and a pod of *E. schinziana*". The flowering specimen on the second sheet is leafless, thus preventing a more definitive identification. Ross conceded that "it is possible therefore that the flowers described are those of *E. suffruticosa* and not of *E. schinziana*."

Entada simplicata (Barneby) Sch. Rodr. & A.S. Flores, Phytotaxa 39: 47. 2012.

Type. BRAZIL. Roraima, Municipality Caracaraí, North Perimetral Road (BR–210) 10 km from the junction with the Manaus–Caracaraí Road (BR–174), near Novo Paraiso, *C.A. Cid Ferreira 9220* (holotype: INPA**;** isotype: NY [NY00038703]).

Basionym. *Entada polystachya* var. *simplicata* Barneby, Brittonia 48: 175. 1996.

Description. Liana or scandent shrub to 10 m. **Leaves:** petiole 3.7–7.7 cm long, rachis 5.8–13 cm long; pinnae 1–3 pairs per leaf, 1.6–3.7 cm long, with 1–3 pairs of leaflets; leaflets 2.5–8.3 × (1.8–)2.2–5.2 cm, obovate to broadly elliptic, apex retuse to truncate, base asymmetric, rounded to cuneate, both surfaces glabrous. **Inflorescence:** a terminal one-sided panicle of up-turned spikes, each spike rachis 16–26 cm long. **Flowers:** calyx 1–1.2 mm long, shallowly toothed; petals 2.2–3.3 mm long; stamen filaments 3.8–4.5 mm long. **Fruit:** a torulose, laterally compressed craspedium, 25.5–29 × 3.8–5.3 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** elliptic, 14–20 × 9–13 mm, with pleurogram.

Distribution. Brazil (Roraima State).

Habitat and ecology. Open margins of wet tropical forest on rocky slopes.

Entada spinescens Brenan, Kew Bull. 10: 168. 1955.

Type. TANZANIA. Mpwapwa District, near Gulwe, *B.D. Burtt 4639* (holotype: K [K000232157, K000232158]).

Description. Climber, slender, woody to 3.6 m, stipules spinescent, young shoots pubescent. **Leaves:** stipules sub-conical, spinescent, rigid, gradually spreading, rachis 3.4–10.7 cm long; pinnae 1–3 pairs per leaf, sometimes modified into a tendril or spirally twisted at base, each pinna 2.8–6 cm long, with 12–18 pairs of leaflets; leaflets 5.6–17.5 × 1.7–3.2 mm, oblong to linear-oblong, apex rounded to obtuse and mucronate, base oblique, lamina glabrous, except for puberulous mid-rib and margins.

Inflorescence: an axillary spike, 3–7 cm long, solitary, the rachis pubescent. **Flowers:** purple, sub-sessile; calyx 1 mm long, distinctly toothed, glabrous; petals 3–4 × 1.2–1.6 mm; stamen filaments 3.5–4.6 mm long. **Fruit:** a torulose, laterally compressed, falcate craspedium, 13–17 cm long, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** sub-circular to ovate, 10.4 × 9.2 × 2.3 mm, with closed pleurogram.

Distribution. Tanzania.

Habitat and ecology. Deciduous bushland and tall deciduous thickets; 910–1220 m alt.

Entada spiralis Ridl., J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 67: 305. 1898.

Type. Not specified, though Ridley's description appears to be based upon plants that are "very common in Singapore…[and] very conspicuous here from its very remarkable fruit." (Ridley 1898, p. 305).

Description. Liana more than 25 m long, stem flattened and spirally twisted, 7.5 cm wide × 2.5–5 cm thick. **Leaves:** rachis 5–9 cm long, tomentose, terminating in a bifurcating tendril; pinnae 2–3 pairs per leaf, 3.6–9.3 cm long with 2–4 pairs of opposite leaflets; leaflets 1.8–6.5 × 0.9–3 cm, obovate to narrowly obovate-elliptic, unequal-sided, apex rounded-truncate, retuse, base rounded to cuneate, asymmetrical, lamina chartaceous, glabrous (Fig. 22A, B). **Inflorescence:** a spike 15–20 cm long, axillary, solitary, tomentose (Fig. 22A, B). **Flowers:** sessile to sub-sessile, staminate or bisexual; calyx cupular, 0.5–1 mm long, glabrous to puberulous; petals white, 2.5–3 mm long; stamen filaments 5–8 mm long, white turning yellow (Fig. 22C). **Fruit:** a large, torulose, spirally coiled craspedium, 120–180 × 6 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments irregularly triangular; epicarp woody, endocarp chartaceous (Fig. 22D, E). **Seeds:** irregularly compressed and mirroring the fruit segment shape, 6–6.5 × 5 cm × 1.5–1.8 cm, hard, brown, pleurogram lacking.

Distribution. Peninsular Thailand, peninsular Malaysia, Singapore, Sumatra.

Habitat and ecology. Primary and secondary rainforest; 0–540 m alt.

Figure 22. *Entada spiralis* vegetative and reproductive structures. **A** climbing shoot bearing leaves and flower spikes, Singapore (photo: C Ng *CC BY-NC-SA 2.0*, Ng (2021)) **B** leaf and axillary flower spike, Singapore (photo: C Ng *CC BY-NC-SA 2.0*, Ng (2021)) **C** spike with open, subsessile flowers, Singapore (photo: C Ng *CC BY-NC-SA 2.0*, Ng (2021)) **D** immature, spirally coiled pod, Singapore (photo: C Ng *CC BY-NC-SA 2.0*, Ng (2021)) **E** mature, spirally coiled pod, Singapore (photo: B-C Ho).

***Entada stuhlmannii* (Taub.) Harms, Veg. Erde 9(III 1): 401. 1915.**

Types. TANZANIA. Uzaramo District, *Stuhlmann 6845*, *6939*, *6965*, *7114* (syntypes: B†); Bagamoyo District, *Stuhlmann 7197* (syntype: B†).

Basionym. *Pusaetha stuhlmannii* Taub., Pflanzenw. Ost–Afrikas, C: 196. 1895.

Description. Climber, slender, woody, to 2.5 m, young shoots glabrous and sinuous, roots tuberous. **Leaves:** rachis 5–6.2 cm long; pinnae 2(–3) pairs per leaf, sometimes modified into a tendril or spirally twisted at base, 1.9–3.6 cm long, with 4–5(–8) pairs of leaflets, pinna rachis slightly winged; leaflets 0.9–3 × 0.25–1.5 cm, obovate to oblanceolate-oblong, occasionally narrowly oblong, apex rounded to sub-truncate and with or without a mucro, base oblique, lamina glabrous, lateral venation raised below. **Inflorescence:** an axillary spiciform raceme, (2–)3.5–8 cm long, usually solitary though sometimes in fascicles, rachis glabrous. **Flowers:** purple or brownish-red, pedicels 1–1.5 mm long; calyx 1 mm long, distinctly toothed, glabrous; petals 2.5–4 mm long; stamen filaments 3–3.5 mm long. **Fruit:** a torulose, laterally compressed, falcate craspedium, 12–24(–30) × 2.7–4.3 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** 1 × 0.9 cm.

Distribution. Tanzania, Mozambique.

Habitat and ecology. Scrub around Lake Tanganyika, deciduous bushland, wooded grassland and woodland; 15–1600 m alt.

***Entada tonkinensis* Gagnep., Notul. Syst. (Paris) 2: 60. 1911.**

≡ *Entada phaseoloides* subsp. *tonkinensis* (Gagnep.) H. Ohashi, Taiwania 55: 50. 2010.

Type. VIETNAM. Banton Valley, near Tu-vu, *B. Balansa 2130* (holotype: P [P02436139, P02436140]).

Description. Robust liana, stems often flattened and spirally twisted, base up to 60 cm in diameter. **Leaves:** petiole 1.5–4 cm long, rachis 3–6.5 cm long, terminating in a bifurcating tendril; pinnae (1–)2 pairs per leaf, 10–22 cm long, proximal pinnae with 2 opposite pairs of leaflets, distal pinnae with 2–3 opposite pairs of leaflets, increasing in size distally; leaflets 5–12 × 2.5–6 cm, chartaceous, obliquely elliptic to obovate-elliptic, asymmetrical, apex acute to obtuse. **Inflorescence:** a spike, 9–25 cm long, axillary, solitary or several spikes from a short shoot; peduncle glabrous; rachis puberulous. **Flowers:** sessile to sub-sessile, distylous; short-styled flowers on proximal half of spike, long-styled flowers on distal half of spike; calyx cupular, glabrous, 1.2–2 mm long; petals pale green with a reddish base, 3–3.2 mm long; stamen filaments 5.5–7 mm long, white turning yellow; ovaries of long-styled flowers with 12–18 ovules. **Fruit:** a gigantic torulose craspedium, 50–150 × 9–12 cm, laterally compressed, straight to slightly curved, 9–16-seeded, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; segments

6.5–7.5 cm long; endocarp chartaceous. **Seeds:** subcircular, compressed with a rounded margin, 5.2–7.4 × 4.7–5.5 × 1.6–2.3 cm, hard, blackish-purple, pleurogram lacking.

Distribution. Subtropical Japan (Ryukyu Islands), Taiwan (north and central), southern China, northern Vietnam.

Habitat and ecology. Inland evergreen forests, especially riparian, from low to mid-elevations.

Entada tuberosa R. Vig., Notul. Syst. (Paris) 13: 346. 1949.

Type. MADAGASCAR. Maevarano, near Majunga (Mahajangal), *H. Perrier de la Bâthie 12906* (lectotype: P [P00367633], designated by J.-F. Villiers in Leguminosae of Madagascar: 2002: 168).

Description. Climber, slender, woody, to 6 m, stem 1 cm in diameter, glabrous or pubescent, twining, with elevated nectaries at nodes; underground tuber elongated. **Leaves:** rachis 5–12.5 cm long, grooved above, laterally winged, glabrous or pubescent, white glandular mucro at apex; pinnae 2–4 pairs per leaf, 2–6.5 cm long, with 13–22 pairs of leaflets; leaflets 5–18 × 1.5–2 mm, oblong, apex rounded to obtuse and mucronate, base oblique, lamina glabrous, mid-rib near distal margin (Fig. 23A, B). **Inflorescence:** a dense, axillary spiciform raceme, 3–7 cm long, solitary or grouped on short leafless shoots or occupying terminal portions of leafy shoots, rachis glabrous or pubescent (Fig. 23A, B). **Flowers:** maroon-red, red-brown or greenish-brown, pedicels 0.75–1.5 mm; calyx obconical, 0.8–1.5 mm long, deeply toothed, glabrous; petals greenish, 3–4.5 mm long; stamen filaments red, 3.5–6.5 mm long (Fig. 23C). **Fruit:** a torulose, laterally compressed, falcate craspedium, 11–23 × 2.9–3.8 cm, 12–14-seeded, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum. **Seeds:** ovoid, 11 × 9 mm, dark brown, with pleurogram.

Figure 23. *Entada tuberosa* vegetative and flowering structures. **A** slender climbing shoot bearing leaves and axillary spiciform racemes, Madagascar (photo: feno *CC BY-NC 4.0*, iNaturalist (2021) observation 64636058) **B** spiciform racemes and leaf with twining petiolules, Madagascar (photo: D Du Puy) **C** portion of spiciform raceme with open, pedicellate flowers, Madagascar (photo: B Schrire).

var. *tuberosa*

Description. Stem, petiole, leaf rachis, pinna rachis and inflorescence peduncle and rachis glabrous to sparsely pubescent.

Distribution. Madagascar (west, extending to northern tip).

Habitat and ecology. Dry, deciduous woodland and riparian vegetation, on limestone and granite, but not on sand; low altitudes.

var. *pubescens* Brenan, Kew Bull. 20(3): 377. 1966.

Type. MADAGASCAR. Belambo, near Maeventanana, *H. Perrier de la Bâthie 12129* (holotype: P [P00367634, P00533757]).

Description. Stem, petiole, leaf rachis, pinna rachis and inflorescence peduncle and rachis distinctly to densely pubescent.

Distribution. Madagascar (west).

Habitat and ecology. Dry woodland over granite.

***Entada wahlbergii* Harv., Fl. Cap. 2: 277. 1862.**

= *Entada flexuosa* Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 356. 1928.

Type. SOUTH AFRICA. Natal, probably Zululand, *J.A. Wahlberg s.n.* (holotype: S [S13-12053]; photos: K, PRE).

Description. Climber, slender, woody, to 3–4 m, young branches glabrous and sinuous (Fig. 24A). **Leaves:** rachis 3.4–8.4 cm long; pinnae (1–)2(–3) pairs per leaf, sometimes modified into a tendril or spirally twisted at base, 2.8–6.5 cm long, with 7–18 pairs of leaflets; leaflets 5–19 × 1.5–6 mm, oblong, apex rounded to obtuse and mucronate, base oblique, lamina glabrous (Fig. 24B). **Inflorescence:** an axillary spiciform raceme, 3–6 cm long, solitary or grouped together on short leafless shoots or occupying terminal portions of leafy shoots, rachis glabrous (Fig. 24C). **Flowers:** dark purple or red, pedicels 1–1.5 mm; calyx 1–1.5 mm long, deeply toothed, glabrous; petals 3–4.5 mm long; stamen filaments 4–6.5 mm long (Figs 2I, 24C). **Fruit:** a torulose, laterally compressed, falcate craspedium, 11–23(–30) × 2.9–3.8(–4.4) cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum (Fig. 24A, D). **Seeds:** 1–1.1 × 0.7–0.8(–1) cm, pleurogram oval, closed.

Distribution. Tropical west to southern Africa, from Guinea and Mali to Nigeria and Sudan, south through the Democratic Republic of Congo, Mozambique and South Africa.

Habitat and ecology. Wooded grassland, open forest, bushveld, valley scrub and banks of dry watercourses on dry, sandy soil; 610–1070 m alt.

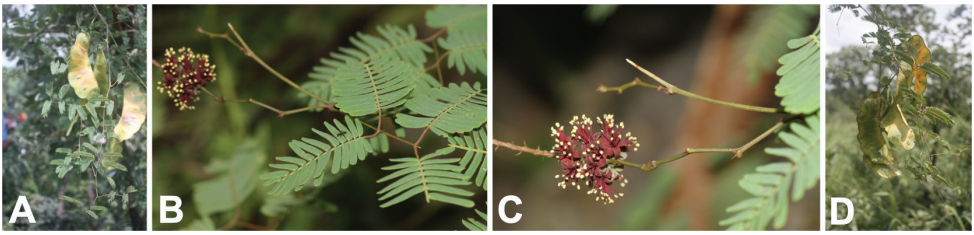

Figure 24. *Entada wahlbergii* vegetative and reproductive structures. **A** slender climbing stem bearing leaves and nearly mature pods, Benin (photo: M Schmidt, Dressler et al. (2014a)) **B** leaf and spiciform raceme, Benin (photo: R Mangelsdorff, Dressler et al. (2014a)) **C** spiciform raceme of open, pedicellate flowers, Benin (photo: R Mangelsdorff, Dressler et al. (2014a)) **D** leaves and nearly mature pods, Benin (photo: M Schmidt, Dressler et al. (2014a)).

***Entada woodii* (E. Phillips) S.A. O'Donnell & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303575-1

Type. SOUTH AFRICA. Natal, Klip River District, Pieters, near Colenso, *J. Medley-Wood 7958* (holotype: NH [NH0008767-0]; isotype: PRE [PRE0392009-0]).

Basionym. *Elephantorrhiza woodii* E. Phillips, Bothalia 1: 193. 1923.

Description. Geoxylic suffrutex with procumbent, annual, branched, longitudinally striate stems to 60 cm, arising from an elongate subterranean axis, glabrous or pubescent. **Leaves:** petiole 0.8–1.6 cm long, glabrous or pubescent; rachis (1–)3.5–8.5(–13) cm long, grooved above, glabrous or pubescent; pinnae (2–)5–10 pairs per leaf, 1.8–6 cm long, with 12–28 pairs of leaflets; leaflets 2.5–6(–9) × 1–1.8(–2.25) mm, linear to linear-oblong, apex acute to obtuse, sometimes asymmetric, mucronate, base oblique, mid-rib running from distal corner of leaflet base to apex centre, lamina glabrous. **Inflorescence:** an axillary spiciform raceme, 4.5–9.5 cm long, usually solitary, rachis glabrous to densely pubescent. **Flowers:** yellowish-white, pedicels 1.25 mm long and articulated near the middle, with minute glands at the base; calyx 1.5 mm long, shallowly toothed, glabrous; petals 3.25 × 1.25 mm; stamen filaments 6 mm long. **Fruit:** a laterally compressed falcate craspedium, 9 × 3.2 cm, transverse veins prominent, lacking transverse septa between seeds, the valves thus separating from the replum intact upon ripening, the epicarp of both valves peeling away from the endocarp; umbonate over seeds. **Seeds:** mature seeds not seen.

var. *woodii*

Description. Stems, petiole, leaf rachis, pinna rachis and inflorescence peduncle and rachis glabrous or almost so.

Distribution. South Africa (Natal), Lesotho.

Habitat and ecology. In grassland.

var. *pubescens* (E. Phillips) S.A. O'Donnell & G.P. Lewis, comb. nov.
urn:lsid:ipni.org:names:77303577-1

Type. SOUTH AFRICA. Natal, Estcourt District, near Little Tugela, 1219 m alt., *J. Medley-Wood 2867* (holotype: NH [NH0002867-0]).

Basionym. *Elephantorrhiza woodii* E. Phillips var. *pubescens* E. Phillips, Bothalia 1: 193. 1923.

Description. Stems, petiole, leaf rachis, pinna rachis and inflorescence peduncle and rachis pubescent.

Distribution. South Africa (Natal), Lesotho.

Habitat and ecology. In grassland.

Note. Grobler (2012, p. 151) viewed stem pubescence in *E. woodii* as an unreliable basis for distinguishing these two varieties.

***Entada zeylanica* Kosterm., Misc. Pap. Landbouwhoogeschool 19: 226. 1980.**

Type. SRI LANKA. Southwest Sri Lanka, Sinharaja Forest, *A.J.G.H. Kostermans 26787* (holotype: G; isotypes: K, US [US00170433, US00170434]).

Description. Liana to 50 m long, stem to 50 cm diameter at base; bark greyish-brown, rough, peeling; slash red, fibrous, wood yellow with sparse red sap. **Leaves:** arranged spirally; rachis 8–15 cm long, terminating in a long, strong bifurcating tendril; pinnae 2 pairs per leaf, 5–15 cm long, with 2–4(–5) pairs of leaflets; leaflets 3.5–4.7 × 1.5–2.2 cm, obovate to obliquely oblong, apex obtuse, retuse to emarginate, base acute, lamina glabrous. **Inflorescence:** a spike, 20–22 cm long, axillary, solitary, axis pubescent. **Flowers:** red to dark brown, sessile; calyx reddish-brown, 1–1.5 mm long, glabrous; petals 2.5–3 mm long, green outside, white inside; stamen filaments 3.5 mm long, white. **Fruit:** a torulose, spirally twisted craspedium, 40 × 8 cm, with transverse septa between seeds dividing the fruit into one-seeded segments which, upon ripening, fall from the persistent replum; epicarp woody, endocarp chartaceous. **Seeds:** circular, laterally compressed, concave on both surfaces, 2–3.5 cm diameter, 1.5 cm thick, pleurogram lacking.

Distribution. Sri Lanka.

Habitat and ecology. Wet evergreen rainforest, up to 500 m alt.

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RESEARCH ARTICLE

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Disintegration of the genus *Prosopis* L. (Leguminosae, Caesalpinioideae, mimosoid clade)

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Abstract

Robust evidence from phylogenomic analyses of 997 nuclear genes has recently shown, beyond doubt, that the genus *Prosopis* is polyphyletic with three separate lineages, each with affinities to other genera of mimosoids: (i) *Prosopis africana* is an isolated lineage placed in the grade of *Plathymenia*, *Newtonia* and *Fillaeopsis* that subtends the core mimosoid clade; (ii) the remaining Old World species of *Prosopis* form a clade that is sister to the Indo-Nepalese monospecific genus *Indopiptadenia* and (iii) New World *Prosopis* has the Namibian / Namaqualand monospecific endemic genus *Xerocladia* nested within it. This means that it is now clear that maintaining the unity of the genus *Prosopis* sensu Burkart (1976) is no longer tenable. These three distinct lineages of *Prosopis* species correspond directly to Burkart's (1976) sectional classification of the genus, to previously recognised genera and to the differences in types of armature that underpin Burkart's sections. Here, we address this non-monophyly by resurrecting three segregate genera – *Anonychium*, *Neltuma* and *Strombocarpa* and provide 57 new name combinations where necessary, while maintaining the morphologically distinctive and geographically isolated genera *Xerocladia* and *Indopiptadenia*. The genus *Prosopis* itself is reduced to just three species and an emended description is presented. The impacts of these name changes for a genus of such high ecological and human use importance are discussed. These impacts are mitigated by clear differences in armature which facilitate identification and by potential benefits from the deeper biological understanding brought about

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by recognition of these divergent lineages at generic rank. We provide an identification key to genera and present a map showing the distributions of the segregate genera, as well as drawings and photos illustrating variation in armature and fruits.

Keywords
Anonychium, Fabaceae, generic delimitation, *Indopiptadenia*, monophyly, *Neltuma*, *Strombocarpa*, taxonomy, *Xerocladia*

Introduction

Burkart's (1976) worldwide taxonomic monograph of the genus *Prosopis* L. recognised 44 species placed in five sections. Since then, 13 additional species have been described (Schinini 1981; Earl and Lux 1991; Palacios 2006; Vásquez Núñez et al. 2009; De Mera et al. 2019) one of which, *P. bonplanda* P.R. Earl & Lux, was subsequently treated as a synonym by Palacios (2006). All of these additional species belong morphologically in section *Algarobia* DC., such that the generic unity and infrageneric classification, proposed by Burkart (1976), remain the current framework for understanding the genus. Following Bentham (1875), Burkart (1976) justified the generic unity of a widely delimited *Prosopis*, based on the broad uniformity of flowers and fruits across *Prosopis* s.l. Perhaps the most important uniting feature was the modified indehiscent cylindrical or thickened legume, with a more or less sugary, fleshy or fibrous mesocarp and an endocarp more or less hardened and segmented into one-seeded coriaceous to bony seed chambers, these closed or sometimes opening easily. Fruits of this type are eagerly consumed by herbivores, including all kinds of livestock, the seeds benefiting from scarification as they pass through the digestive tract and as a result being widely dispersed (see below), a seed dispersal syndrome that unites all species of *Prosopis* s.l. Moreover, Burkart (1976) explicitly downplayed vegetative characters and notably variation in armature, as of less significance for classification, stating that "the main differences between sections *Prosopis*, *Algarobia* and *Strombocarpa* Benth. are vegetative spine characters and are, therefore, only of subgeneric rank" (Burkart 1976: 227), even though he acknowledged that the variation in armature probably had phylogenetic significance (see below).

This long-held generic concept of *Prosopis* established by Bentham (1842, 1875) and followed by Burkart in his 1976 monograph, is no longer sustainable, because molecular phylogenies have demonstrated, beyond doubt, that *Prosopis* is polyphyletic. This non-monophyly was first revealed by Catalano et al. (2008) and confirmed by LPWG (2017) who showed that *P. africana* (Guill. & Perr.) Taub. forms an isolated monospecific lineage quite separate from the rest of *Prosopis* and that the monospecific Namibian/S. African endemic genus *Xerocladia* Harv. was potentially nested within *Prosopis*, but these analyses lacked robust support and sampling of critical taxa. Recent phylogenomic analyses of a much larger DNA sequence dataset, based on 997 nuclear genes (Koenen et al. 2020) that now includes all but five of the 152 genera of

Caesalpinioideae (Ringelberg et al. 2022), have confirmed this non-monophyly showing robust support for three separate lineages (Fig. 1): (i) a lineage comprising *P. africana*, which is placed in a grade made up of the genera *Plathymenia* Benth., *Fillaeopsis* Harms and *Newtonia* Baill., as found by Catalano et al. (2008); (ii) a lineage comprising the remaining Old World species of *Prosopis* which is robustly supported as sister to the monospecific genus *Indopiptadenia* Brenan from the Himalayan foothills of the Terai border region of Nepal and India (Bajpai et al. 2014); (iii) a lineage comprising the New World species of *Prosopis* plus the Namibian/South African endemic genus *Xerocladia*, which is nested within this clade, again confirming the preliminary results of Catalano et al. (2008). The DNA sequence dataset of Ringelberg et al. (2022), based as it is on a large number of nuclear genes, can also be used to quantify how many genes support a particular species tree topology and, thereby, how robust the phylogeny is (Fig. 1B) and also how many genes support alternative species tree topologies. These analyses show that just 69 gene trees support a sister group relationship between sections *Strombocarpa* (= *Strombocarpa*) and *Algarobia* + *Monilicarpa* Ruiz Leal & Burkart (= *Neltuma* Raf.), while 629 of the gene trees conflict with that topology (Fig. 1C) and none of the gene trees supports a monophyletic *Prosopis* s.l. (Fig. 1D), confirming that there is an overwhelming number of gene trees supporting the species tree topology in Fig. 1B. It is thus now clear that maintaining *Prosopis* in its current circumscription is untenable.

What is immediately striking from Fig. 1 and the earlier phylogeny of Catalano et al. (2008) with its denser sampling of species across New World *Prosopis*, is that these three separate lineages of *Prosopis* species correspond to and are congruent with Burkart's sections (apart from the inclusion of *Xerocladia*) and with the variation in armature upon which Burkart's sections were based (Figs 2–4): Section *Anonychium* Benth. = *P. africana*, is unarmed in common with the rest of the grade of lineages (*Plathymenia*, *Fillaeopsis* and *Newtonia*) that subtend the large core mimosoid clade of Koenen et al. (2020) (Fig. 1; Ringelberg et al. 2022); Section *Prosopis* = the rest of Old World *Prosopis*, comprising *P. cineraria* (L.) Druce, *P. farcta* (Banks & Sol.) J.F. Macbr. and *P. koelziana* Burkart (from Iran), all have straight internodal prickles (Figs 2C, M and 3C), which are also found in the sister genus of this clade, *Indopiptadenia*, including in the form of large, conical, hard, sharp-pointed spines on older stems and trunk (Fig. 3B; see also Bajpai et al. 2014: figs 2B–H and 11A); species of Section *Strombocarpa* plus the genus *Xerocladia* have stipular spines (Figs 2E, H, I, O and 3A, D); and species of sections *Monilicarpa* + *Algarobia* variously have spinescent shoots or uninodal axillary solitary or geminate spines (Figs 2A, B, D, F, G, J–L, N and 3E, F and 4), but never the internodal prickles of section *Prosopis*, nor the stipular spines of section *Strombocarpa* (see also Benson 1941). These three types of armature are non-homologous, even though they have evolved to meet similar plant defence functions and can look superficially similar. To explore the evolution of armature across the *Prosopis* s.l. grade, we scored these different types of armature across genera of subfamily Caesalpinioideae and optimised these on to the Ringelberg et al. (2022) phylogeny. This reconstruction shows independent derivations of stipular spines, internodal prickles and axillary nodal spines (Fig. 4), each providing diagnostic synapomorphies for

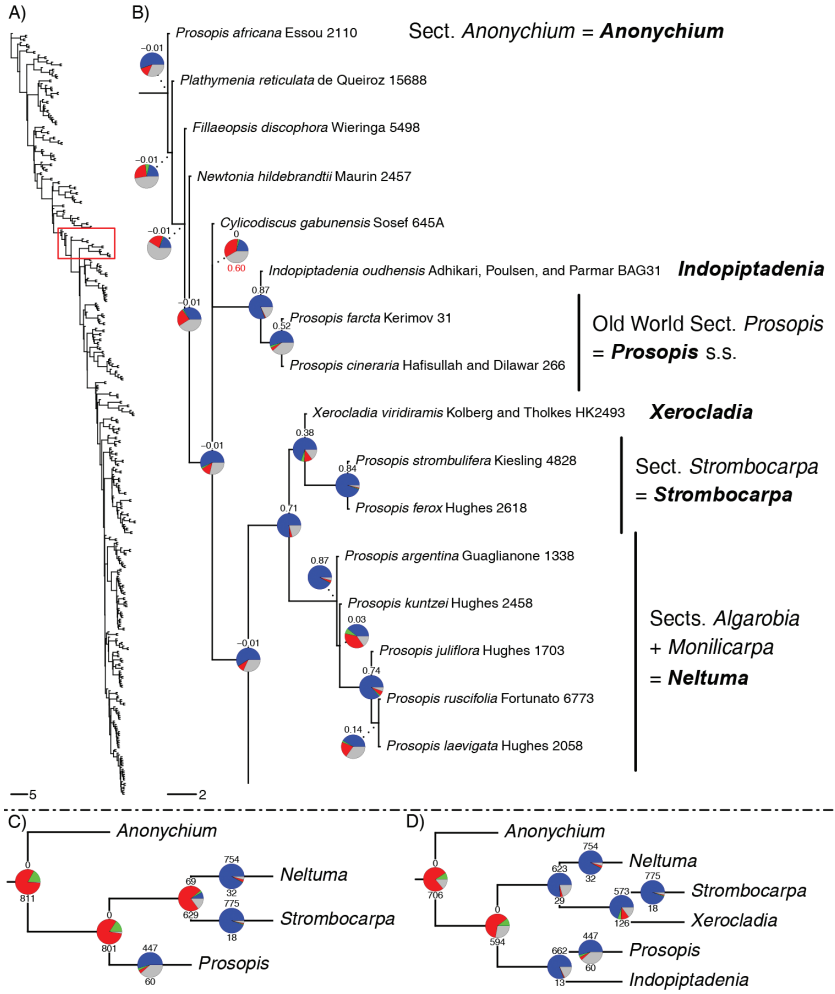

Figure 1. A Phylogeny of the Caesalpinioideae showing the placement of the *Prosopis* grade (boxed in red) within the subfamily, based on analyses of DNA sequences of 997 nuclear genes (Ringelberg et al. 2022) **B** the part of the phylogeny that includes all elements of *Prosopis* s.l. Genera recognised in the new generic system presented here are in **bold**. Pie charts show the fraction of gene trees supporting that bipartition in blue, the fraction of gene trees supporting the most likely alternative configuration in green, the fraction of gene trees supporting additional conflicting configurations in red and the fraction of uninformative gene trees in grey. Numbers above pie charts are Extended Quadripartition Internode Certainty (Zhou et al. 2020) scores. Branch lengths are expressed in coalescent units and terminal branches were assigned an arbitrary uniform length for visual clarity, see Ringelberg et al. (2022); the root is not drawn to scale **C, D** the two most likely alternative tree topologies which would allow for a monophyletic *Prosopis* s.l., either without (**C**) or with (**D**) *Xerocladia* and *Indopiptadenia*. In **C** and **D** numbers above pie charts = number of gene trees supporting the species tree, numbers below pie charts = number of gene trees conflicting with the species tree **C** lack of gene tree support (just 69 gene trees) for the alternative species tree topology where sections *Algarobia* + *Monilicarpa* (≡ *Neltuma*) are sister to section *Strombocarpa* (≡ *Strombocarpa*) vs. 573 genes supporting a sister group relationship between *Strombocarpa* and *Xerocladia* (as shown in **D**) **D** lack of gene trees (zero gene trees) supporting a monophyletic *Prosopis* s.l.

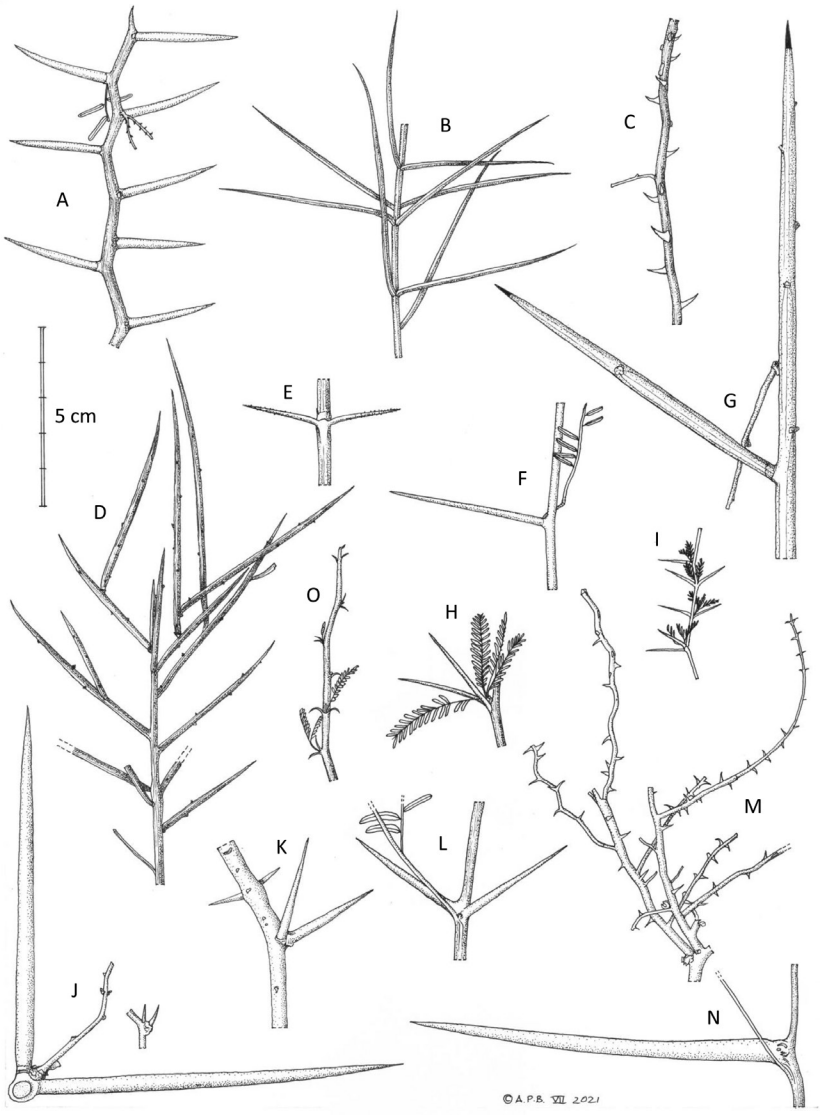

Figure 2. Variation in armature of *Prosopis*, *Strombocarpa*, *Neltuma* and *Xerocladia* **A** *Neltuma denudans* (nodal spines on a zig-zag stem) **B** *N. humilis* (paired striate spine-tipped branches) **C** *Prosopis cineraria* (scattered internodal prickles) **D** *Neltuma sericantha* (spine-tipped stems) **E** *Strombocarpa burkartii* (stipular spines) **F** *Neltuma argentina* (single nodal axillary spine) **G** *N. kuntzei* (spinescent shoots) **H** *Strombocarpa ferox* (stipular spines) **I** *S. strombulifera* (stipular spines) **J** *Neltuma elata* (variation in paired nodal spines on one specimen) **K** *N. alba* (paired nodal spines) **L** *N. velutina* (paired nodal spines) **M** *Prosopis farcta* (scattered internodal prickles) **N** *Neltuma ruscifolia* (single nodal axillary spine) **O** *Xerocladia viridiramis* (recurved, deflexed stipular spines) (5 cm scale bar). All specimens at K **A** drawn from *Seijo* 1489 **B** *Tweedie* s.n. **C** *Willcox* 299 **D** MERL 8792 **E** *Acosta & Rosas* 748 **F** *Guaglianone et al.* 1762 **G** *Nee & Coimbra* 35556 **H** *Atahuachi* et al. MA1147 **I** *Hunziker* 2036 **J** *Legname & Cuezzo* 10396 (large and small spines from same specimen) **K** *Hughes & Forrest* 2312 **L** *Harding & Balsinhas* 140 **M** *Guest et al.* 17463 **N** *Wood & Mamani* 14063 **O** *Kolberg & Tholkes* HK2493. Drawn by Andrew Brown, July 2021.

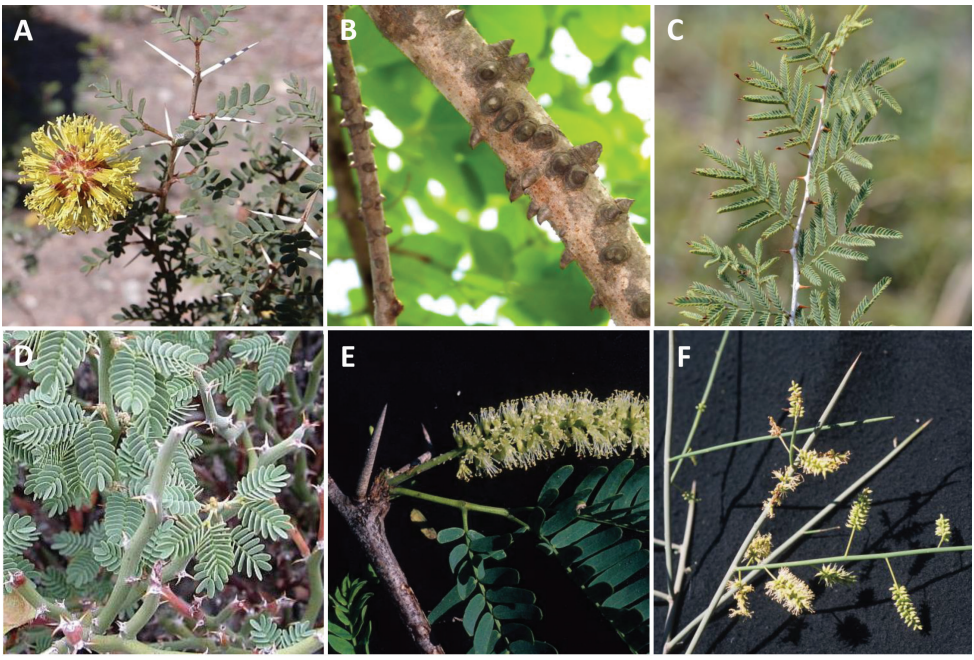

Figure 3. Variation in armature across *Prosopis* s.l. and allies **A** stipular spines of *Strombocarpa strombulifera* **B** internodal prickles on shoots and branches of *Indopiptadenia oudhensis* which it shares with its sister group, *Prosopis* s.s. illustrated in **C**; **C** internodal prickles of *Prosopis farcta* **D** stipular spines of *Xerocladia viridiramis* which it shares with its sister group, the genus *Strombocarpa* illustrated in **A**; **E** axillary nodal spines of *Neltuma juliflora* **F** spinescent straight cylindrical shoots of the subaphyllous *Neltuma kuntzei*. Photos courtesy of Guillermo Debandi (**A**) (see https//www.inaturalist.org/taxa/78750-Prosopis-strombulifera/browse_photos), Dr. Omesh Bajpai and Dr. Lal Babu Chaudhary (**B**), Zeynel Cebeci (**C**) (see https//commons.wikimedia.org/wiki/FileProsopis_farcta_-_Syrian_mesquite_01), N. Dreber (**D**) (see http//www.southernafricanplants.com/), Colin Hughes (**E, F**).

clades in the context of *Prosopis* s.l. (Fig. 4). Ironically, in his justification of the unity of *Prosopis*, Burkart (1976) pointed to *Acacia* Mill. s.l. as another group that also showed considerable diversity in types of armature and other vegetative traits, but which was considered (at that time) to comprise a single genus. Given that *Acacia* s.l. was later demonstrated to be polyphyletic (reviewed by Maslin et al. 2003) and has now been dismantled into seven segregate genera, several of which are distinguished primarily by differences in armature (e.g. the stipular spines that distinguish *Vachellia* Wight & Arn. from the cauline nodal and internodal prickles of *Senegalia* Raf.), Burkart's suggestion that a wide concept of *Acacia* chimed with his wide concept of *Prosopis* can now be seen with hindsight to have been misplaced.

The apparent phylogenetic significance of types of armature to distinguish important clades and genera across Caesalpinioideae, contrasts with the striking evolutionary lability of fruit types, as seen across *Prosopis* s.l. and allies (Figs 5–7). This is exemplified

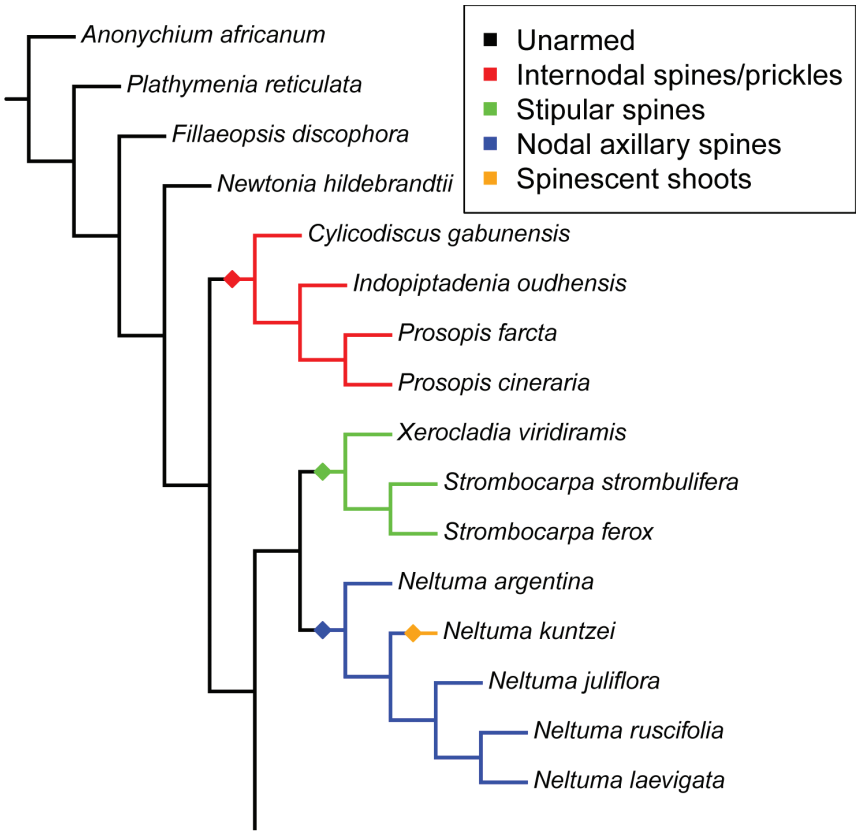

Figure 4. Independent evolutionary origins of stipular spines, axillary nodal spines and internodal spines across the segregate genera of the *Prosopis* s.l. grade. Diamonds indicate putative origins halfway along the branch subtending the clade with the character of interest. Note that, in the case of *Neltuma kuntzei*, a loss of axillary nodal spines, which are absent in that species, apparently coincides with an evolutionary gain of spinescent shoots (see also Fig. 3F) and with a shift to a largely aphyllous condition on the mature shoots. The reconstruction of armature characters shown here encompasses results of four independent optimisations of four types of armature, performed using the make.simmap option of R (R Core Team 2021) package phytools (Revell 2012), each with 500 simulations using the ARD model. Optimisations were performed on an ASTRAL phylogeny of the entire Caesalpinioideae, based on 821 single-copy genes (Ringelberg et al. 2022), but are here shown only for the *Prosopis* s.l. grade with standardised branch lengths.

by the contrast between the cylindrical or sub-cylindrical thickened indehiscent fruits of *Prosopis* s.l. (albeit varying considerably in the degree to which they are curved or coiled (see below)) and the very different plano-compressed fruits of *Indopiptadenia* (Figs 5M and 7B; see also Bajpai et al. 2014: Fig. 7), which is sister to section *Prosopis* and which lacks a thickened mesocarp and is dehiscent along one or both sutures. Similarly, *Xerocladia*, which is sister to section *Strombocarpa* (Fig. 1), has equally distinctive small reniform to flabellate, flattened, indehiscent, 1 (–2)-seeded, winged fruits,

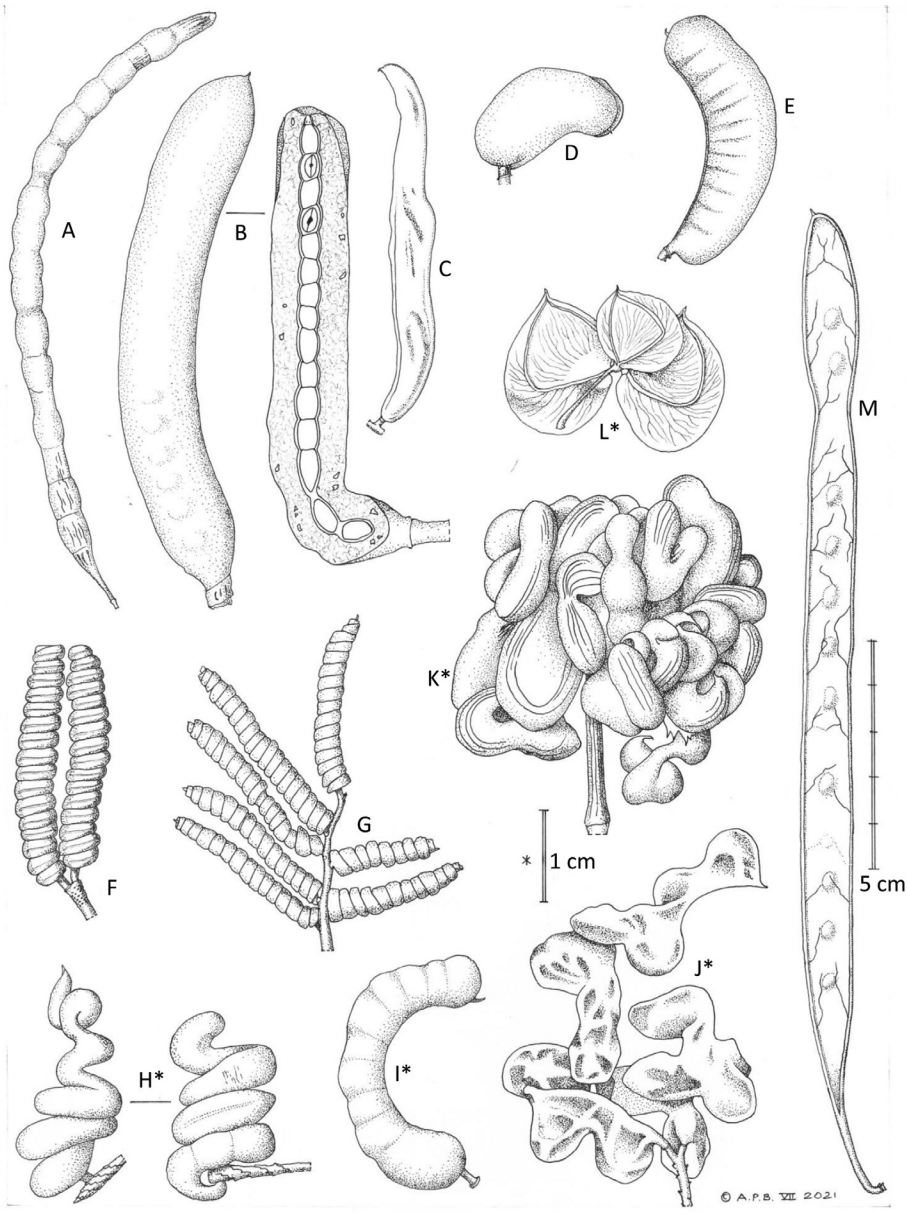

Figure 5. Fruits of *Prosopis*, *Strombocarpa*, *Xerocladia* and *Indopiptadenia* **A** *Prosopis cineraria* **B** *Anonychium africanum* **C** *Strombocarpa palmeri* **D** *Prosopis farcta* **E** *Strombocarpa ferox* **F** *S. strombulifera* **G** *S. pubescens* **H** *S. abbreviata* (2 examples) **I** *S. tamarugo* **J** *S. torquata* **K** *S. burkartii* **L** *Xerocladia viridiramis* **M** *Indopiptadenia oudhensis* **A-G, M** (5 cm scale bar) **H-L** (1 cm scale bar with asterisk). All specimens at K **A** drawn from *Gazanfar* SG4332 **B** *Dembele & Sanogo* ML-146 and longitudinal section of fruit from *Barter* 1193 **C** *Hughes et al.* 1552 **D** *van der Maesen* 1627 **E** *Atahuachi et al.* MA1147 **F** *Hunziker* 2036 **G** *Acocks* 1788 **H** *Tweedie* s.n. (from 2 type specimens) **I** *Aronson* 7742 **J** *Vuilleumier* 1019 **K** *Acosta & Rosas* 748 **L** *Kolberg & Tholkes* HK2493 **M** *Bajpai & Babu* 264498. Drawn by Andrew Brown, July 2021.

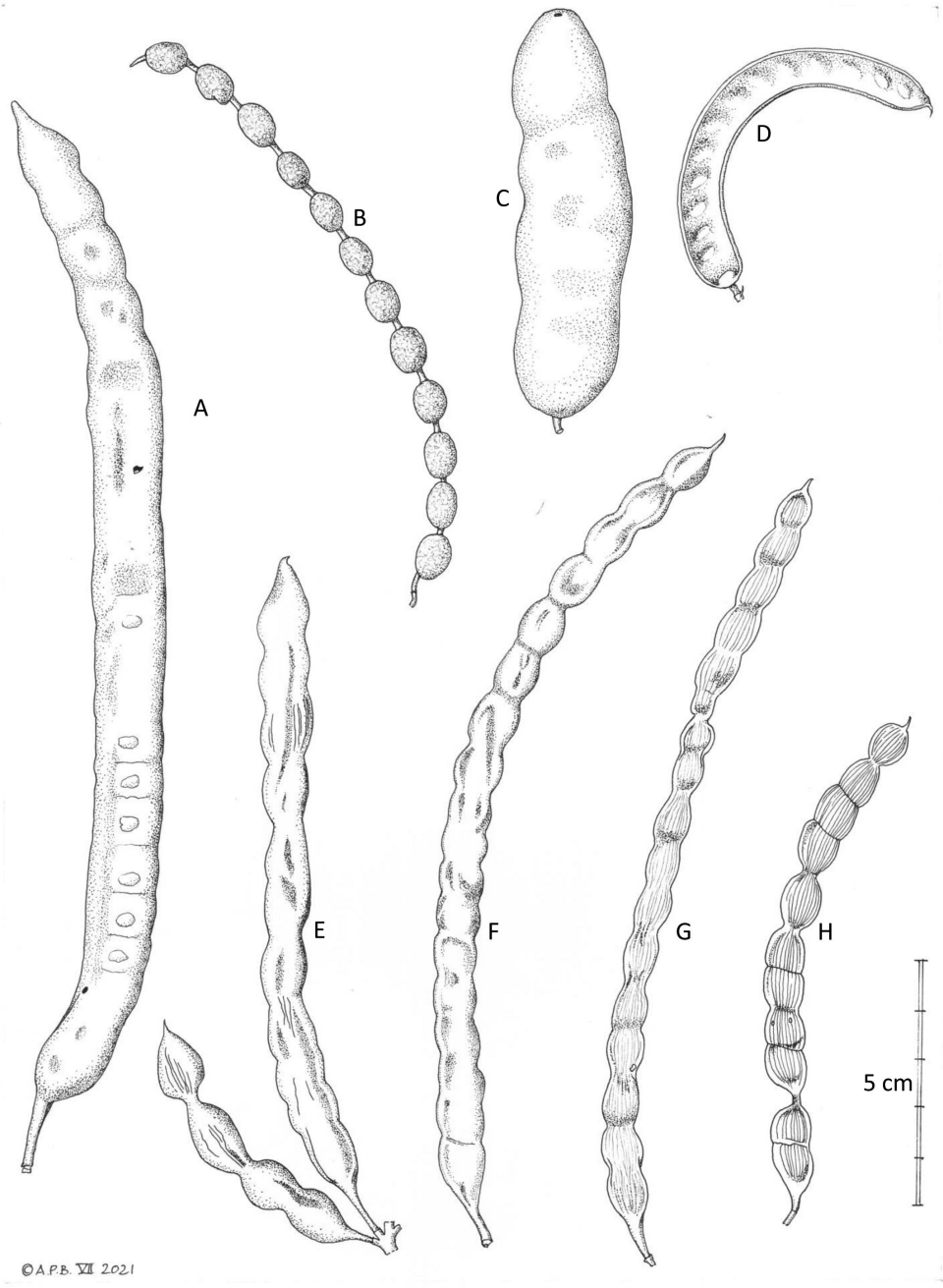

Figure 6. Fruits of *Neltuma* **A** *Neltuma alba* **B** *N. argentina* **C** *N. kuntzei* **D** *N. denudans* **E** *N. laevigata* **F** *N. nigra* **G** *N. articulata* **H** *N. ruscifolia*.(5 cm scale bar). All specimens at K **A** drawn from *Hughes & Forrest* 2312 **B** *Guaglianone et al.* 1762 **C** *Nee & Coimbra* 35556 **D** *Seijo* 1489 **E** *Manríquez & Tenorio* 6563 **F** *Arenas* 3123 **G** *Hughes et al.* 1559 **H** *Wood & Mamani* 14063. Drawn by Andrew Brown, July 2021.

Figure 7. Variation in fruits across *Prosopis* s.l. and allies **A** indehiscent pods of *Anonychium africanum* with thick pulpy mesocarp collected as fodder for livestock **B** plano-compressed pods of *Indopiptadenia oudhensis* lacking a thickened mesocarp and dehiscent along both sutures **C** indehiscent fruits of *Prosopis farcta* with a thick pulpy mesocarp **D** tightly coiled indehiscent screwbean fruits of *Strombocarpa strombulifera* **E** indehiscent pods of *Strombocarpa ferox* with a thick pulpy mesocarp **F** indehiscent fruits of *Strombocarpa palmeri* **G** small reniform to flabellate, flattened, indehiscent, 1 (–2)-seeded, winged fruits of *Xerocladia viridiramis* which are unique within mimosoid legumes **H** indehiscent fruits of *Neltuma articulata* with a thick mesocarp and a hard bony segmented endocarp which remains closed **I**. Unripe indehiscent pods of *Neltuma kuntzei* with a thick pulpy mesocarp, these turning dark blackish-brown when ripe, reminiscent in colour to fruits of *Anonychium*. Photos courtesy of Marco Schmidt (**A**) (see Dressler et al. 2014), Dr. Omesh Bajpai and Dr. Lal Babu Chaudhary (**B**), Zeynel Cebeci (**C**) (https//en.wikipedia.org/wiki/Prosopis_farcta), Dick Culbert (**D**) (see https//eol.org/pages/640506, Colin Hughes (**E, F, H, I**), and Herta Kolberg (**G**) (see Plants of Namibia https//herbaria.plants.ox.ac.uk/bol/namibia).

which are unique amongst mimosoid legumes as a whole (Figs 5L and 7G) and also lack the often-thick mesocarp of *Prosopis* s.l. fruits (Gunn 1984). Thus, it is now clear that the thickened, sub-cylindrical fruits of *P. africana* (section *Anonychium*), which are

superficially very similar (both are thick, woody, indehiscent and black when mature) to those of distantly related *P. kuntzei* Harms (section *Algarobia*) (Figs 5B, 6C, 7A, I), represent homoplasious evolutionary origins of similar endozoochorous seed dispersal syndromes, based on animal ingestion of highly palatable fruits and defecation of the seeds (Tybirk 1991; Weber et al. 2008) and, hence, are misleading as the basis for generic delimitation. In the light of phylogenetic data, it is now clear that Burkart's (1976) reliance on fruit morphology to unite his broad concept of *Prosopis* and demotion of armature as only useful at sub-generic rank and not for delimiting genera were misplaced.

It is notable that pollen exine structure also supports these groups. Pollen of the Old World species of section *Prosopis* is similar to that of its sister genus *Indopiptadenia*, showing a relatively thin (0.7–0.9 μm) tectum with irregularly areolate-verrucose raised sculpturing, whereas the New World species of *Prosopis*, and *Xerocladia* have a smooth (perforated) and even thinner (< 0.7 μm) tectum (Hernández and Guinet 1990: Fig. 5).

The type species of *Prosopis*, *P. spicigera* L. (a synonym of *P. cineraria* (L.) Druce), is from the Old World in section *Prosopis* of Burkart (1976), a clade that comprises just three of the 56 species currently recognised in the genus as a whole, implying that the remaining 53 species will require a name change to deal with the non-monophyly of *Prosopis* s.l. Segregation of the isolated monospecific lineage *P. africana* as a separate genus presents a straightforward and uncontroversial adjustment, here implemented by re-instatement of the genus *Anonychium* (Benth.) Schweinf. (see below). Generic re-delimitation of the New World species is less straightforward and is complicated by placement of the morphologically distinctive Namibian/Namaqualand monospecific genus *Xerocladia* nested within the New World *Prosopis* clade as sister to section *Strombocarpa* (Fig. 1). Despite its similar shrubby, multi-stemmed, branchy habit, green shoots, stipular spines (Fig. 3D) (shared with section *Strombocarpa*) and occurrence in arid succulent-rich vegetation, all of which are shared with New World *Prosopis*, the genus *Xerocladia* has been maintained as distinct from *Prosopis*, because it has highly distinctive reniform to flabellate, indehiscent, 1(–2)-seeded, winged fruits (Figs 5L and 7G), lacking a thickened mesocarp, which are very different from those of *Prosopis* s.l. and, indeed, from all other mimosoid legumes. Given this distinctive morphology, we retain *Xerocladia* as a separate genus. We also note that the material referred to under the name *Xerocladia pampeana* Speg. from Argentina, shows clear affinities to the genus *Prosopidastrum* Burkart, as suggested by Palacios and Hoc (2005). Even though Palacios and Hoc (2005) left *X. pampeana* as an excluded name in their treatment of Argentinian *Prosopidastrum*, examination of the material cited by them suggests that the fruits are not monospermous, but simply broken fragments of lomentiform fruits of *Prosopidastrum*.

Retention of the monospecific African *Xerocladia* at generic rank implies that the two subclades of New World *Prosopis* species, corresponding to Sections *Strombocarpa* and *Monilicarpa* + *Algarobia* of Burkart (1976) (Fig. 1), also need to be recognised as separate genera. Both of these groups have been previously ranked as genera. Bentham (1839), prior to uniting the various elements of *Prosopis* s.l. in a single genus in his

1875 treatment of Mimoseae, recognised section *Algarobia* at generic rank as the genus *Algarobia* Benth. (even though the name *Algarobia* is preceded by *Neltuma* Raf. published one year earlier in 1838). Similarly, section *Strombocarpa* was also afforded generic status as the genus *Strombocarpa* Englm. & A. Gray in 1845, a generic delimitation followed by Britton & Rose (1928) in their treatment for the North America Flora. The alternative to recognising these two New World clades as separate genera would be to transfer all New World species of *Prosopis* plus the African *Xerocladia* to the genus *Neltuma*. While it could be argued that this alternative would make generic-level identification in the New World easier, it would entail lumping *Xerocladia* with its highly unusual fruits which are unique within mimosoids and would detract from the overall ability to diagnose genera across mimosoids. We believe that upranking Burkart's sections *Strombocarpa* and *Algarobia* + *Monilicarpa* as the genera *Strombocarpa* and *Neltuma*, respectively, distinguished by the differences in armature that provided the basis for Burkart's sections, while retaining the African *Xerocladia* as a separate genus (Fig. 1), provides the best solution to render all genera monophyletic and ensure maximal ability to diagnose genera across mimosoids as a whole.

Finally, for completeness, we note that the genus *Sopropis* Britton & Rose, erected by Britton & Rose (1928) to accommodate the somewhat unusual species *Sopropis palmeri* (S. Watson) Britton & Rose (= *Prosopis palmeri* S. Watson) has the stipular spines of section *Strombocarpa*, but a straight (or only weakly falcate) fruit more typical of section *Algarobia* (Figs 5C and 7F), as noted by Benson (1941). In the phylogeny of Catalano et al. (2008), *P. palmeri* is placed in the clade corresponding to section *Strombocarpa* with robust support, vindicating the congruence of armature types across the phylogeny and we here treat *Sopropis* as a synonym of *Strombocarpa*. This is very much in line with Burkart's (1976) view that too much weight had been given by Britton and Rose (1928) to the curvature and coiling of the *Prosopis* fruit in the recognition of three distinct genera in their Flora of North America treatment. Indeed, it is clear that curvature of the pod across New World *Prosopis* s.l. shows a continuum from the tightly spirally coiled 'screwbean' pods of, for example, *P. strombulifera* (Lam.) Benth. and *P. pubescens* Benth. (Figs 5F, G and 7D), to fruits with fewer, larger and more open coils, annular fruits and those that are only weakly curved or completely straight, variation that is discordant with sectional boundaries (Figs 5B, C, E–K, 6 and 7D–F, H–I) and with the phylogeny (Fig. 1).

Taxonomic name changes are often unwelcome for many users, at least in the short term, especially for plant groups that are important ecologically and in terms of human uses. This is very much the case for *Prosopis* s.l. and especially so in the warm desert and dryland scrub ecosystems of the New World, where "few plant genera have received as much attention as *Prosopis*" (Simpson 1977: ix). Species of *Prosopis* are ecologically abundant in many parts of its New World range, dominating vast tracts of the Chaco in South America and the matorrales of the southern U.S.A. and parts of Mexico (Fig. 8) (Benson 1941). Trees of *Prosopis* s.l. also occupy a central place in silvo-pastoral systems more widely across the arid and semi-arid tropics from Rajasthan in NW India, through the Arabian Peninsula, across Sahelian Africa and

throughout the arid zones of the Neotropics (Leakey and Last 1980; Fagg and Stewart 1994; Pasiecznik et al. 2001; Weber et al. 2008), because of their dependable provision of abundant protein- and sugar-rich, non-toxic, highly palatable and nutritious fruits during the dry season that are eagerly consumed by diverse livestock (cattle, sheep, goats, camelids). Furthermore, *Prosopis* s.l. fruits, including the *mezquites* in North America (Felger 1977) and the *algorrobos* in South America (D'Antoni and Solbrig 1977), constituted one of the most important wild food sources for prehispanic cultures, with *P. velutina* Wooton, the velvet mesquite referred to as the 'tree of life' (Bell and Castetter 1937) and these uses potentially prompting long distance translocation of species by humans and their livestock within the Americas in pre-Colombian times (McRostie et al. 2017). In addition to livestock fodder and human food, the wood of *Prosopis* is dense and durable and widely used for firewood, charcoal and parquet flooring and the flowers provide high quality, reliable and abundant forage for honey bees. Moreover, such is the ability of some *Prosopis* species to disperse seeds, colonise and quickly form dense spiny impenetrable thickets, that some species of *Prosopis* are amongst the world's worst invasive weeds, both within and well beyond their native ranges. For example, several New World section *Algarobia* species are naturalised and invasive across many parts of Africa, the Middle East, the Indian subcontinent and Australia (e.g. Pasiecznik et al. 2001; Van Klinken and Campbell 2001; Ayanu et al. 2015) and have been recorded from 103 countries and considered to be invasives in 49 of those (Shackleton et al. 2014). Within their native distributions, *P. ruscifolia* Griseb. is a serious pest in the western Gran Chaco, referred to as a '*plaga nacional*' and *P. glandulosa* Torr. has prompted the so-called '*mesquite problem*' in Texas in the southern U.S.A. where that species is considered a serious rangeland weed (Fisher et al. 1959).

The impacts of name changes on a group of plants of such diverse importance cannot be denied and, inevitably, we anticipate resistance, in the short term, to the nomenclatural changes we propose here. Notwithstanding, we also expect that, ultimately, there will be benefits from aligning genera with monophyletic groups that more accurately reflect their evolutionary placements and provide a deeper biological understanding of these globally-important plants. In that light, it is notable that all the serious invasive and rangeland pest species fall into *Neltuma* (= section *Algarobia*), suggesting that a propensity for invasiveness is more problematic for species in that clade. Similarly, of 29 species of bruchid beetles known to predate seeds of New World *Prosopis*, only two span *Neltuma* (sections *Algarobia* + *Monilicarpa*) and *Strombocarpa*, such that each of the two New World clades has largely its own exclusive bruchid fauna, including, for example, the bruchid genus *Algarobius* Bridwell which is largely restricted to species of section *Algarobia* (Kingsolver et al. 1977). More generally, biocontrol programmes to mitigate invasions of New World species of *Neltuma* in Africa have focused on insects, such as the bruchid seed predator *Algorobius prosopis* (J.L. Leconte), that do not attack native African members of *Prosopis* s.l. including species of *Prosopis* s.s., *Anonychium* and *Xerocladia*, suggesting that many insects effectively distinguish amongst the genera proposed here (Kleinjan et al. 2021).

It is also notable that, while intra-sectional interspecific hybridisation has been reported to occur in both section *Strombocarpa* (e.g., the hybrid origin of *Prosopis burkartii* Muñoz, Contreras et al. 2020) and amongst a subset of species in the 'mesquite clade' of *Neltuma* (= sections *Algarobia* + *Monilicarpa*) (Hunziker et al. 1986; Castillo et al. 2021), there are no examples of inter-sectional hybrids between species belonging to *Neltuma* and *Strombocarpa* (Solbrig et al. 1977; Hunziker et al. 1986), despite their sympatry across many areas (Fig. 8). This lack of inter-sectional crossing prompted Hunziker et al. (1986) to suggest upranking sections *Algarobia* (= *Neltuma*) and *Strombocarpa* "at least to the level of subgenera", as also suggested by Saidman et al. (1996), based on genetic differences. Similarly, phylogenetic analysis of morphology and biochemical traits showed strong support for recognising *Strombocarpa* as a distinct clade (Burghardt and Espert 2007). These trait differences, alongside other ecological differences, are symptomatic of the deep (phylo)genetic split between these two clades which are estimated to have diverged 25 Myr (Ringelberg et al., in prep). All these differences in biology are of potential significance for genetic improvement, range management and biocontrol programmes (see Kleinjan et al. 2021), adding further justification to recognise Burkart's sections at generic rank.

Biogeography

One of the uniting features of *Prosopis* s.l. is the distribution of its various lineages, first and foremost, in seasonally dry and arid tropical and subtropical climates across the New and Old Worlds (Fig. 8), a distribution that spans, in large part, the transcontinental grass-poor succulent-rich, fire-free succulent biome sensu Schrire et al. (2005) and Ringelberg et al. (2020). However, in that sense, *Anonychium* (*P. africana*) is an outlier, just as it is phylogenetically, because it grows in savannahs across Sahelian Africa. The *Prosopis* s.s. + *Indopiptadenia* clade spans an interesting dry/monsoonal west-central Asian distribution which is unique amongst mimosoids. At first sight, the sister group relationship between *Strombocarpa* and *Xerocladia* spanning the Atlantic seems a surprising disjunction, but several other Caesalpinioid legumes show similar disjunct amphi-Atlantic distributions with most of their diversity in the Neotropics and outlying endemic species in Namibia and adjacent regions of southern Africa. These include the genera *Haematoxylum* L., *Parkinsonia* L. and *Pomaria* Cav., with *Haematoxylum dinteri* Harms, *Parkinsonia africana* Sond. and three species of *Pomaria* in Namibia and S. Africa. Two things are notable about these transatlantic disjunctions. First, they often show bicentric amphitropical ranges in the New World and disjunctions in SW Africa (the *Haematoxylum* + *Lophocarpinia* Burkart clade; *Pomaria* (Simpson et al. 2006); *Strombocarpa* - *Xerocladia*). Second, they share similar seasonally dry tropical, grass-poor, succulent-rich, fire-free ecologies across the transcontinental Succulent Biome (Schrire et al. 2005; Gagnon et al. 2019; Ringelberg et al. 2020).

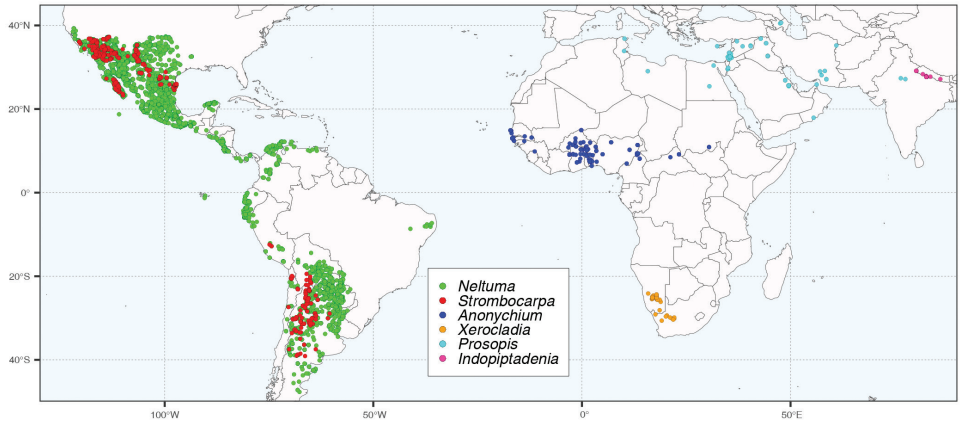

Figure 8. The distributions of *Indopiptadenia*, *Prosopis* s.s., *Anonychium*, *Xerocladia*, *Neltuma* and *Strombocarpa*, based on 6,469 quality-controlled species occurrences from GBIF (www.gbif.org), DryFlor (www.dryflor.info), SEINet (www.swbiodiversity.org/seinet) and several other data sources (Ringelberg et al., in prep.). Map created using R packages ggplot2 (Wickham 2016), sf (Pebesma 2018) and rnaturalearth (South 2017). The eight occurrence records, mapped in Bahia Brazil, are of *Neltuma ruscifolia* which is considered potentially native to that region (Burkart 1976 Oliveira & Queiroz 2020), while records of *N. juliflora* from Bahia, which is introduced and naturalised in that region, have been eliminated.

Key for the identification of the segregate genera of *Prosopis* and close allies (see Figs 2 and 3 for illustrations of armature characters used in the key)

1 Plants unarmed ..... ***Anonychium***
– Plants usually armed with stipular spines, axillary solitary or paired uninodal cauline spines, spinescent shoots or internodal prickles **2**
2 Plants armed with internodal prickles on shoots and/or stems, petals glabrous **3**
– Plants armed with stipular spines, axillary solitary or paired uninodal spines or spinescent shoots, petals villous or pilose **4**
3 Fruits indehiscent, cylindrical or subterete, with a pulpy or fibrous mesocarp, largest leaflets < 1.5 × 1 cm, mature stems with scattered prickles ... ***Prosopis***
– Fruits dehiscent, plano-compressed, coriaceous, lacking a thick mesocarp, larger leaflets > 3 × 3 cm, mature stems with spine-tipped woody protuberances ..... ***Indopiptadenia***
4 Fruits reniform to flabellate, indehiscent, 1–2-seeded and winged..... ..... ***Xerocladia***
– Fruits linear or oblong, always > 2-seeded **5**
5 Plants armed with stipular spines ..... ***Strombocarpa***
– Plants armed with axillary, uninodal, solitary or paired spines or spinescent shoots ..... ***Neltuma***

Taxonomy

We present a taxonomic synopsis of the four segregate genera, *Anonychium*, *Prosopis*, *Strombocarpa* and *Neltuma*, including 57 new nomenclatural combinations and associated synonymy. Type details are cited for accepted names, but not for heterotypic synonyms.

Anonychium (Benth.) Schweinf., Reliq. Kotschy.: 7. 1868.

Prosopis section *Anonychium*, Benth. Hook. J. Bot. 4: 347. 1842.

Type. *Prosopis oblonga* Benth. Benth., J. Bot. (Hooker) 4: 348. 1842, a synonym of *Anonychium africanum*.

Description. Unarmed trees 4–20 m high, branches lacking axillary brachyblasts. Stipules inconspicuous, long-lanceolate, pubescent, caducous as young leaves develop, absent from most herbarium sheets. Leaves somewhat pendulous, 1–4 pairs of pinnae, the petiole 3–5 cm long, the rachis 5–9 cm long, the pinnular rachises 6–15 cm long, with 4–13 pairs of opposite leaflets, these 1.3–3.5 × 0.4–1.5 cm, glabrous or finely pubescent, mid-vein subcentric. Inflorescences spicate, 5–9 cm long, axillary, solitary or in pairs, densely flowered; pedicels 0.5 mm. Flowers small, yellowish or greenish-white, sweetly scented; calyx ca. 1 mm long; corolla ca. 3.5 mm long, the petals linear, free, glabrous on both sides; anthers apically broadened with an unusual anther gland borne ventrally between the thecae and forming a triangular hood-shaped protrusion made up of papillate cells; pollen with costae on the pores and a smooth (perforated) tectum; ovary and style pilose or villous. Fruits indehiscent, straight or sub-falcate, dark reddish-brown to blackish, shiny, subterete, 10–20 × 1.5–3.3 cm, exocarp hard, 1–2 mm thick, mesocarp spongy, thick, dry, endocarp segments thin, longitudinal, in one row (Figs 5B and 7A). Seeds many, dark, shiny, ovate compressed, 8–10 × 4–9 mm, rattling within the pod when ripe.

Geographic distribution. Monospecific. Widespread across Sahelian Africa, from Senegal in the west to Sudan and Ethiopia in the east (Fig. 8).

Habitat and uses. *Anonychium africanum* is native across the whole Sahelian savannah belt. Trees are maintained and managed by farming and pastoralist communities in traditional silvo-pastoral systems throughout the African Sahel, providing essential products, including wood, fuel, food, livestock fodder and medicines and enhancing soil fertility (Weber et al. 2008). Seeds are widely dispersed by browsing animals, such as camels, cattle and goats at the end of the dry season (Tybirk 1991) and perhaps also by humans who collect the pods to feed to their animals, and cow dung (containing viable seeds) to fertilise their fields.

Etymology. *Anonychium* literally meaning the absence of nails or claws from the Latin or Greek 'onych' = 'ónyx' meaning nail or claw, refers to the lack of armature of this genus.

Affinities. *Prosopis africana* has long been considered anomalous within the genus and was placed in its own section *Anonychium* by Bentham (1842) and later this was upranked to its own genus, *Anonychium* by Schweinfurth (1868; under the name *A. lanceolatum* Schweinf.). Unlike almost all other species of *Prosopis* s.l., *P. africana* lacks armature, has internally glabrous petals, pollen with costae (Guinet 1969), V-shaped anthers with small stomia forming short pockets on the ventral surface of the anthers and anther glands that are apparently morphologically unique within mimosoids (Luckow and Grimes 1997). The anther glands of *Anonychium africanum* (as *P. africana*, Luckow and Grimes 1997: Figs 25–27) stand out as quite different from the typical mimosoid claviform anther glands of the remaining species of *Prosopis* s.l., being sessile, borne ventrally between the thecae, rather than stipitate borne apically or dorsally from the connective between the thecae as in most other mimosoids and forming triangular hood-shaped protrusions made up of papillate cells which are also unique amongst mimosoid anther glands (Luckow and Grimes 1997). Alongside the robust molecular evidence for placement of *P. africana* distantly related to the rest of *Prosopis* (Fig. 1), this suite of morphological differences amply justifies segregation of *P. africana* as a distinct monospecific genus.

Anonychium is a phylogenetically isolated lineage that subtends the grade of other unarmed, mainly species-poor genera, *Plathymenia*, *Fillaeopsis* and *Newtonia* which is paraphyletic with respect to the core mimosoid clade of Koenen et al. (2020) (Fig. 1; Ringelberg et al. 2022). This is in line with pollen of *Anonychium* which shows similarities to *Newtonia* (Guinet 1969).

***Anonychium africanum* (Guill. & Perr.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303578-1

Prosopis oblonga Benth., J. Bot. (Hooker) 4: 348. 1842.
Entada durissima Baill., Adansonia 6: 208. 1866.
Anonychium lanceolatum Schweinf., Reliq. Kotschy.: 7, pl. 7. 1868.
Prosopis africana (Guill. & Perr.) Taub. in H.G.A. Engler & K.A.E. Prantl, Nat. Pflanzenfam. 3(3): 119. 1892.
Entada coulteri Roberty, Bull. Inst. Fondam. Afrique Noire, Sér. A, Sci. Nat. 16: 346. 1954.

Basionym. *Coulteria africana* Guill. & Perr., Fl. Seneg. Tent.: 256, 1832.

Type material. Senegal. Kounoun, Presqu'île du Cap-Vert, *G.S. Perrottet 20* (holotype: P [P00418356]).

***Prosopis* L., Mantissa Pl. 68: 10. 1767. emend. C.E. Hughes & G.P. Lewis.**

Lagonychium M. Bieb., Fl. Taur.-Caucas. 3: 288. 1819.
Prosopis section *Adenopis* DC., Prodr. 2: 446. 1825.
Pleuromenes Raf., Sylva Tellur.: 144. 1838.

Type. *Prosopis spicigera* L., a synonym of *P. cineraria* (L.) Druce.

Description. Prickly subshrubs, shrubs, small trees or occasionally lianescent (*P. farcta*), 0.3–6.5 (–10) m high, deep-rooted and sometimes invading via root suckers, prickles internodal, scattered, straight, somewhat acroscopic, conical with broad bases, 3–5 mm long (Figs 2C, M and 3C), stipular or axillary spines absent. Stipules foliaceous, ovate-acute, caducous. Leaves with 1–6 (–7) pairs of pinnae, the petiole and rachis 0.5–4 cm, sometimes a prickle at the base of the petiole, the pinnular rachises 2–7 cm long, with 7–15 pairs of leaflets, these ovate or lanceolate, straight to sub-falcate or auriculate, mucronate, 2–15 × 2–4.5 mm, glabrous, puberulous or pubescent, mid-vein excentric. Inflorescences spicate, 4–13 cm long, axillary, solitary or in fascicles, peduncle sometimes with an amplexicaul bract, this caducous and leaving an oblique scar; pedicels 0.5–1.5 mm. Flowers small, yellow, yellowish-white, green or cream-green; calyx truncate, 0.8–1.2 mm long; corolla 3.5–4 mm long, the petals linear, nearly free, reflexed, glabrous on both sides; anthers with a minute caducous incurved claviform gland arising from the connective; pollen lacking costae on the pores, tectum irregularly areolate-verrucose. Fruits indehiscent, slender, elongate straight or sub-falcate, dark reddish-brown to blackish, shiny, cylindrical to sub-cylindrical, torulose, 1.5–19 × 0.4–2.5 cm, exocarp thin, brittle, shiny and smooth, orange-red becoming brown, red or black when ripe (Fig. 7C), mesocarp spongy, endocarp segments thin, little developed, seed chambers longitudinal or transverse. Seeds well separated, longitudinal, ovate to ovoid, compressed, 6–8.5 × 5–6 × 2.5–3 mm.

Geographic distribution. Reduced now to just three Old World species, these distributed across arid parts of North Africa (but apparently the genus rare at its western limits in Algeria and Tunisia), the Middle East and NW India (especially Punjab and Rajasthan) and reaching its northern limits in Afghanistan and Azerbaijan (Fig. 8).

Habitat and uses. Abundant in dry and arid parts of NW India, where it is sometimes the most common tree in parts of Punjab and Rajasthan and abundant in arid thorn scrub in parts of the Near East (where *P. farcta*, which can spread via root suckers, is sometimes considered weedy), tolerating saline soils. Highly valued as a source of high quality durable wood, pods for livestock feed and bee forage.

Etymology. Pasiecznick et al. (2001) suggested the name to be derived from *pros-* (Gk.: towards) and *Opis* (wife of Saturn, the Greek goddess of abundance and agriculture), hence 'towards agriculture' referring to the widespread utility of the genus.

Affinities. *Prosopis* s.s. is here reduced to three species and is sister to the monospecific genus *Indopiptadenia* (Fig. 1). These two genera share stem/internodal prickles and a W-C Asian distribution that is unique within mimosoids.

Prosopis cineraria (L.) Druce, Rep. Bot. Exch. Club Soc. Brit. Isles 3: 422. 1913. (publ. 1914).

Mimosa cinerea L., pro parte, Sp. Pl.: 517. 1753 (see note below).
Prosopis spicigera L., Mant. Pl.: 68. 1767.
Prosopis spicata Burm.f., Fl. Indica: 102. 1768.

Prosopis aculeata J. Koenig ex Roxb., Asiat. Res. 4: 405. 1795.
Adenanthera aculeata (J. Koenig ex Roxb.) W. Hunter, Asiat. Res. 6: 66. 1799.
Acacia cineraria (L.) Willd., Sp. Pl., ed. 4, 4: 1057. 1806.

Note. The name *Mimosa cineraria* L. (Syst. Nat., ed. 10: 1311. 1759), based on *M. cinerea* L. (Sp. Pl.: 517 [non 520]. 1753; see Art. 53 Ex. 19), was transferred to *Prosopis* L. by Druce (in Bot. Exch. Club Brit. Isles Rep. 3: 422. 1914) as *P. cineraria* (L.) Druce. However, the correct name in *Prosopis* would have been a combination based on *M. cinerea* (l.c.) had not that name been successfully proposed for rejection (see App. V). in ICN Art. 53.5, Note 4.

Type material. India.

***Prosopis farcta* (Banks & Sol.) J.F. Macbr., Contr. Gray Herb. 59: 17. 1919.**

Mimosa farcta Banks & Sol. in A. Russell, Nat. Hist. Aleppo, ed. 2, 2: 266. 1794.
Mimosa stephaniana M. Bieb., Tabl. Prov. Mer Casp.: 120. 1798.
Acacia stephaniana (M. Bieb.) Willd., Sp. Pl., ed. 4, 4: 1088. 1806.
Acacia heterocarpa Delile, Descr. Egypte, Hist. Nat.: 79. 1813.
Lagonychium stephanianum (M. Bieb.) M. Bieb., Fl. Taur.-Caucas. 3: 288. 1819.
Mimosa arvensis Sieber ex Steud., Nomencl. Bot. 1: 533. 1821, nom invalid.
Prosopis stephaniana (M. Bieb.) Kunth ex Spreng., Syst. Veg. 2: 326. 1825.
Mimosa agrestis Sieber ex Spreng., Syst. Veg. 2: 206. 1825.
Pleuromenes heterocarpa Raf., Sylva Tellur.: 145. 1838.
Acacia persica Sterler ex Steud., Nomencl. Bot., ed. 2, 1: 7. 1840.
Mimosa micrantha Vahl ex Walp., Repert. Bot. Syst. 5: 582. 1846.
Lagonychium farctum (Banks & Sol.) Bobrov in V.L. Komarov (ed.), Fl. URSS 11: 14. 1941.
Prosopis farcta var. *glabra* Burkart, J. Arnold Arbor. 57: 454. 1976.

Type material. Syria. Aleppo, without collector; no additional information in protologue.

***Prosopis koelziana* Burkart, J. Arnold Arbor. 57: 455. 1976.**

Prosopis koelziana var. *puberula* J. Léonard, Bull. Jard. Bot. Natl. Belg. 56: 485. 1986.

Type material. Iran. Madenu, Kirman, *Koelz 14246* (holotype: US [US00000985]).

***Strombocarpa* (Benth.) Engelm. & A. Gray, Boston J. Nat. Hist. 5: 243. 1845.**

Spirolobium A.D. Orb., Voy. Amér. Mér. 8 (Atlas, Bot): t. 13. 1839, nom. rej., non *Spirolobium* Baill. 1889. (Apocynaceae).
Prosopis sect. *Strombocarpa* Benth., J. Bot. (Hooker) 4: 351. 1841.

Sopropis Britton & Rose in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 182. 1928.

Type. *Prosopis strombulifera* (Lam.) Benth. [= *Strombocarpa strombulifera* (Lam.) A. Gray].

Description. Low spiny, sometimes creeping, shrubs or small trees, 0.15–3 (–18) m high, multi-stemmed from the base or sometimes with a short trunk to 10–30 (–45) cm diameter, usually densely and intricately much-branched, some species forming long underground, spreading, horizontal runners (gemmiferous roots or rhizomes), armed with strongly decurrent, straight, cinereous spiny stipules (Figs 2E, H, I and 3A), 0.1–3.5 (–5.5) cm long, brachyblasts congested, blackish. Leaves always unijugate, the petiole (0.5–) 2–15 mm, the pinnular rachises 1–4 cm long, with 3–30 pairs of well separated, alternate to opposite leaflets, these oblong or elliptic-oblong, obtuse to subacute, veins lacking or weakly 1–3-veined, 2–12 × 0.6–4 mm, glaucous, puberulous or glabrescent. Inflorescences axillary, solitary, globose, ovoid-elliptic heads to 1.5 cm diameter at anthesis or shortly cylindrical-spicate, 3–8 cm long. Flowers small, bright or lemon yellow, young filaments red; calyx, 1.5–2.3 mm long; corolla 3–4 (–6) mm long, the petals linear, partially united, villous within; stamens and style exserted, anthers with a minute, caducous, incurved claviform gland arising from the connective. Fruits densely clustered with 1–21 per flower head, indehiscent, lemon-yellow, straw-yellow or reddish-brown when ripe, slender, elongate, straight or falcate (in *S. palmeri* and *S. ferox*; Figs 5C, E and 7E–F), but usually more or less tightly spirally coiled (like corkscrews) with (1–) 8–19 (–24) regular coils, forming a cylindrical body 1.8–5.5 × 0.6–1.5 cm (Figs 5F, G and 7D) or irregularly and more openly coiled; exocarp crustaceous, mesocarp thin or more usually thick and pulpy, tannic, reddish, endocarp delicately segmented in longitudinal or transverse seed chambers which are easy to open or hard and closed. Seeds ovate or reniform ovoid, grey-green, 3–6 (–7) × 3–4 mm.

Geographic distribution. Ten species. Restricted to the New World and there occupying a markedly bicentric amphitropical distribution in arid and semi-arid regions of N. America (southern U.S.A., especially in the Sonoran Desert, Baja California and northern Mexico (Coahuila)) and S. America (south-central Peru to Argentina and Chile) (Fig. 8).

Habitat and uses. In cactus-rich semi-desert Monte vegetation, deserts and arid mesetas, dry river beds and washes and in the hyper-arid Pampa del Tamarugal in northern Chile (*S. tamarugo*), where it is the only tree present and dependent on moisture absorbed from fog. Fruits browsed by cattle and sheep and much valued in arid deserts for that purpose. Wood valued for fuel, and occasionally cultivated (*S. tamarugo*).

Etymology. *Strombo-* (Italian. = conch) and *-carpa* (Gk. = fruit), referring to the resemblance of the fruits to the spiral shells of tropical marine molluscs (see Figs 5F, G and 7D).

Affinities. *Strombocarpa* is robustly supported in recent molecular phylogenies as sister to the African monospecific genus *Xerocladia* (Fig. 1; Ringelberg et al. 2022). These two genera share the diagnostic synapomorphy of stipular spines which are not found elsewhere in *Prosopis* s.l.

***Strombocarpa abbreviata* (Benth.) Hutch., Gen. Fl. Pl. 1: 287. 1964.**

Prosopis abbreviata Benth., J. Bot. (Hooker) 4: 352. 1842.

Type material. ?Argentina. "San Jago", *Tweedie 168* (holotype: K [K000504799]).

***Strombocarpa burkartii* (Muñoz) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303579-1

Basionym. *Prosopis burkartii* Muñoz, Bol. Mus. Nac. Hist. Nat., Santiago de Chile 32: 364. 1971.

Type material. Chile. Prov. Tarapacá, Pampa del Tamarugal, El Gobierno, sector La Huaica, *C. Muñoz Pizarro 7370* (holotype: SGO [SGO000002436]).

***Strombocarpa cinerascens* A. Gray, Smithsonian Contr. Knowl. 3(5): 61. 1852.**

Prosopis cinerascens (A. Gray) Benth., Trans. Linn. Soc. London 30: 381. 1875.
Prosopis reptans var. *cinerascens* (A. Gray) Burkart, Darwiniana 4: 75. 1940.
Prosopis reptans subsp. *cinerascens* (A. Gray) A.E. Murray, Kalmia 13: 24. 1983.
Mimosa calcarea Buckley, Proc. Acad. Nat. Sci. Philadelphia 1861: 453. 1862.

Type material. Mexico. Nuevo León ("New Leon"), valley near Azufrosa, *Gregg 492* (holotype: GH [GH00003469]; isotypes: K [K000791013], MO [MO356342]).

***Strombocarpa ferox* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303580-1

Basionym. *Prosopis ferox* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 118. 1879.

Type material. Argentina. "in regione Puna pr. Humaguaca, pr S José de Tilcara", Jujuy, Humahuaca, *P.G. Lorentz* & *G.H.E.W. Hieronymus 776* (lectotype: GOET [GOET009646]; isolectotypes: CORD [CORD00004889], F [F0BN001461], SI [SI002480]).

***Strombocarpa palmeri* (S. Watson) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303581-1

Basionym. *Prosopis palmeri* S. Watson, Proc. Amer. Acad. Arts 24: 48. 1889.

Sopropis palmeri (S. Watson) Britton & Rose in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 183. 1928.

Type material. Mexico. Eastern Baja California, Mulegé, *E. Palmer 2* (isotypes: BM [BM000952298], GH [GH00003471], K [K000478262], NDG [NDG24111], NY [NY00005123], US [US00930830]).

***Strombocarpa pubescens* (Benth.) A. Gray, Smithsonian Contr. Knowl. 3(5): 60. 1852.**

Prosopis pubescens Benth., London J. Bot. 5: 82. 1846.
Prosopis emoryi Torr. In W.H. Emory, Not. Milit. Reconn. 2: 189. 1848.
Strombocarpa brevifolia Nutt. ex A. Gray, Smithsonian Contr. Knowl. 3(5): 60. 1852.

Type material. U.S.A. California: between San Miguel and Monterey, *Coulter s.n.*

***Strombocarpa reptans* (Benth.) A. Gray, U.S. Expl. Exped., Phan. 1: 475. 1854.**

Prosopis reptans Benth., J. Bot. (Hooker) 4: 352. 1842.
Prosopis abbreviata var. *argentina* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 133. 1874.

Type material. South America. with the label "Mortworta of Cordova, used as a cure for Dysentery" , *Tweedie s.n.* (K [K000504784]).

***Strombocarpa strombulifera* (Lam.) A. Gray, U.S. Expl. Exped., Phan. 1: 475. 1854.**

Mimosa strombulifera ("strumbulifera") Lam., Encycl. 1: 15. 1783.
Acacia strombulifera (Lam.) Willd., Sp. Pl., ed. 4, 4: 1055. 1806.
Prosopis strombulifera (Lam.) Benth., J. Bot. (Hooker) 4: 352. 1842.

Type material. Peru. no further details in protologue of *Mimosa strombulifera*.

***Strombocarpa strombulifera* var. *ruiziana* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303582-1

Basionym. *Prosopis strombulifera* var. *ruiziana* Burkart, J. Arnold Arbor. 57: 459. 1976.

Type material. Argentina. Mendoza: Dept. Junín, in aridis salsis inter Barrancas et Rodríguez Peña, *A. Ruiz Leal 3787* (holotype: SI [SI002507]).

Strombocarpa strombulifera* var. *strombulifera

Mimosa retortunium Lam., Encycl. 1: 15. 1783, nom. invalid pro syn.
Mimosa circinalis Cav., Icon. 6: 41. 1801, nom. illeg.
Spirolobium australe A.D. Orb., Voy. Amér. Mér. 8 (Atlas, Bot): t. 13. 1839.

***Strombocarpa tamarugo* (Phil.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303583-1

Basionym. *Prosopis tamarugo* Phil., Anales Mus. Nac. Santiago de Chile 1891: 21. 1891.

Type material. Chile. Prov. Tarapacá, Valle de Tamarugal, *F. Philippi 1840* (holotype: SGO [SGO000002445]; isotype: SI [SI002508]).

***Strombocarpa torquata* (Lag.) Hutch., Gen. Fl. Pl. 1: 287. 1964.**

Acacia torquata Lag., Gen. Sp. Pl.: 16, 206. 1816.
Prosopis torquata (Lag.) DC., Prodr. 2: 448. 1825.
Prosopis adesmioides Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 132. 1874.

Type material. probably t.36, ined., del Hortus de Cavanilles (fide Burkart in Darwiniana 4: 66. 1940).

***Neltuma* Raf., Sylva Tellur.: 119. 1838.**

Prosopis sect. *Algarobia* DC. Prodr. 2: 446. 1825.
Mitostax Raf., Sylva Tellur.: 120. 1838.
Algarobia (DC.) Benth., Pl. Hartw.: 13. 1839.
Prosopis sect. *Monilicarpa* Ruiz Leal ex Burkart, J. Arnold Arbor. 57(3): 230. 1976.

Type. *Neltuma juliflora* (Sw.) Raf. [= *Mimosa juliflora* Sw.].

Description. Spiny, erect to prostrate subshrubs, shrubs and small trees, (0.1–) 4–10 (–20) m high, usually with a short trunk to 40–60 (–>100) cm diameter, branching lax with a spreading rounded or flat-topped crown, twigs cylindrical, flexuous, often arched downwards, glabrous, green or reddish, often with rather long internodes, armed with uninodal axillary, solitary or paired, straight, strong, cylindrical, subulate spines (Figs 2 and 3E), these not necessarily at all nodes, 0.2–15 (–33) cm long × 0.2–1.4 cm in diameter and sometimes thicker than the subtending twig, or with spinescent rigid straight cylindrical branchlets 8–50 cm, brachyblasts congested, blackish. Stipules small, triangular and dry. Leaves with 1–3 (–8) pairs of pinnae, the petiole (0.2–) 2–7.5 cm long, the

pinnular rachises (0.2–) 4–19 (–24.5) cm long, with (1–) 2–30 (–50) pairs of opposite leaflets, these linear, ovate-oblong, oblong-linear or lance-ovate, more or less acute, palmately pinnativeined or almost without veins, (0.15–) 2.5–10 × 0.05–3.5 cm, puberulous to scarcely ciliolate or glabrous, or sometimes aphyllous or subaphyllous (*N. sericantha*, *N. kuntzei*), the leaves small and soon falling off the young developing shoots which become spinescent. Inflorescences axillary, solitary or fascicled, spicate, (1.5–) 3–15 cm long with 20–250 flowers on short 1.6 mm pedicels. Flowers white, yellow, greenish-yellow or occasionally red, often perfumed, sometimes some functionally male flowers; calyx 1–2 mm long; corolla 3–5 mm long, the petals almost free, pubescent, usually villous within; stamens and style exserted, anthers with a minute caducous incurved claviform gland arising from the connective. Fruits linear moniliform or compressed turgid (Figs 6 and 7H–I), straw yellow, sometimes tinged reddish-maroon or black, 1–several per infructescence, indehiscent, glabrous, mostly straight to subfalcate, S- or C-shaped or annular with 1–3 very lax open spirals, acuminate, (2–) 5–29 cm in length × 0.5–2.6 cm diameter, margins often thickened and undulate, valves striate corrugate or smooth, exocarp crustaceous, mesocarp thin or more usually thick and pulpy, mealy or spongy, dry, usually sweet, endocarp hard and bony or coriaceous, with convex faces and acute extremities, segmented in longitudinal or transverse subquadrate closed seed chambers. Seeds brown, compressed ovate, 5–10 × 3–6 mm. See also Johnston (1962).

Geographic distribution. Potentially up to 43 species, but probably somewhat fewer (see below). Widespread across seasonally dry tropical and arid regions of the Americas with a pseudo-amphitropical bicentric pattern of greatest species diversity in the Mexican-Texan and Argentinian-Chilean-Paraguayan regions, especially diverse and abundant in the Chaco, with an outlying disjunct occurrence of *Neltuma ruscifolia* of questionable nativity in the Caatinga in north-east Brazil (Burkart 1976; Oliveira & Queiroz 2020) and extending into warm and some colder temperate areas in Texas and Nevada in the north and Patagonia in the south, where *N. denudans* Benth. reaches 48 °S (Fig. 8).

Habitat and uses. Dominant across large tracts of the Gran Chaco in mixed sub-xerophyllous woodland, also in Monte vegetation, open desert forests in quebradas along seasonal rivers, in *Stipa*-dominated pampas and semi-desert shrub steppe with hot summers and cold winters in Patagonia as far as 48 °S, some species capable of surviving extreme drought; spanning a wide range of substrates and edaphic conditions including stony and sandy mesas, coastal and inland sand dunes and deep black seasonally inundated, sometimes saline, clay vertisols. Some species weedy and invasive, both within their native ranges and where introduced (see Introduction). The wood generally hard, dense, durable and flexible and widely used for fence posts, parquet flooring, barrels, firewood and charcoal and the fruits are eagerly consumed by all forms of livestock (see Introduction).

Etymology. Possibly derived from the common name *Mulla Thumma* in the Dravidian language Teluga in the Indian states of Andhra Pradesh and Telangana, where *Neltuma juliflora* is introduced.

Affinities. *Neltuma* is sister to, but deeply divergent from, the combined *Strombocarpa* + *Xerocladia* clade (Fig. 1).

Thirteen species of *Prosopis* have been described since the publication of Burkart's (1976) monograph. One of these, *Prosopis bonplanda* P.R. Earl & Lux, was already

placed in synonymy under *P. glandulosa* by Palacios (2006). All of the rest can be confidently placed in *Neltuma* (= *Prosopis* sect. *Algarobia* + *Prosopis* sect. *Monilicarpa*), based on morphological descriptions and illustrations from their respective protologues. We provide new combinations in *Neltuma* for all these names, listing potentially up to 43 species for the genus, but we suspect that some of these new species may be no more than regional variants of the widespread and taxonomically difficult *N. pallida* / *N. juliflora* species complex. Given the difficulties of species delimitation across parts of *Neltuma*, we suggest that a detailed molecular study with complete sampling of species and dense sampling of multiple accessions, representing intraspecific diversity, is needed to properly re-assess species boundaries and possible hybridisation. The *Mimobaits* gene set of Koenen et al. (2020) would be an ideal tool for such a study.

***Neltuma affinis* (Spreng.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303584-1

Prosopis algarobilla Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 131. 1874.
Prosopis nandubey Lorentz ex Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 117. 1879.
Prosopis algarobilla var. *nandubay* (Lorentz ex Griseb.) Hassl., Repert. Spec. Nov. Regni Veg. 16: 154. 1919.

Basionym. *Prosopis affinis* Spreng., Syst. Veg. 2: 326. 1825.

Type material. Uruguay. Montevideo, *F. Sello s.n.* (lectotype (designated by Burkart 1976: 491): MO [MO-954306]).

***Neltuma alba* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303585-1

Basionym. *Prosopis alba* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 131. 1874.

Type material. Argentina. Córdoba, Estancia Germania, *Lorentz 5* (isotypes: F [F0BN001457], M [M0218675], MPU [MPU016115], SI [SI002458]).

Neltuma alba* var. *alba

Prosopis siliquastrum var. *longisiliqua* Phil., Anales Mus. Nac. Santiago de Chile 1: 20. 1891.
Prosopis atacamensis Phil., Anales Univ. Chile 84: 444. 1893.

***Neltuma alba* var. *panta* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303586-1

Prosopis panta (Griseb.) Hieron., Bol. Acad. Nac. Ci. Republ. Argent. 4: 284. 1881.

Basionym. *Prosopis alba* var. *panta* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 118. 1879.

Type material. Argentina. Córdoba, *Lorentz s.n.*

***Neltuma alpataco* (Phil.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303587-1

Basionym. *Prosopis alpataco* Phil., Anales Univ. Chile 21(2): 394. 1862.

Type material. Argentina. nr Mendoza, *W. Diaz s.n.* (probable isotypes: SGO [SGO000002428], SI [SI002464]).

Neltuma alpataco* var. *alpataco

Prosopis stenoloba Phil., Anales Mus. Nac. Santiago de Chile 1: 20. 1891.

***Neltuma alpataco* var. *lamaro* (F.A. Roig) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303588-1

Basionym. *Prosopis alpataco* var. *lamaro* F.A. Roig, Parodiana 5: 56. 1987. (publ. 1988).

Type material. Argentina. *Roig 8946* (holotype: MERL).

***Neltuma alpataco* f. *rubra* (F.A. Roig) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303589-1

Basionym. *Prosopis alpataco* f. *rubra* F.A. Roig, Parodiana 5: 56. 1987. (publ. 1988).

Type material. Argentina. *Roig et al. 223* (holotype: MERL).

***Neltuma andicola* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303590-1

Prosopis andicola (Burkart) A. Galán, E. Linares, J. Montoya & Vicente Orell., Phytotaxa 414: 49. 2019.

Basionym. *Prosopis laevigata* var. *andicola* Burkart, J. Arnold Arbor. 57: 510. 1976.

Type material. Peru. Cuzco, Prov. Calca, Hacienda Urco, *J.C. Vargas-Calderón 709* (holotype: SI [SI002483]).

***Neltuma argentina* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303591-1

Basionym. *Prosopis argentina* Burkart, Revista Argent. Agron. 4: 39. 1937.

Type material. Argentina. Catamarca: Fiambalá, *A. Castellanos s.n.* (holotype: CTES [CTES0000667]; isotype: SI [SI002606]).

***Neltuma articulata* (S. Watson) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.**

Prosopis articulata S. Watson, Proc. Amer. Acad. Arts 24: 48. 1889.
Prosopis juliflora var. *articulata* (S. Watson) Wiggins, Contr. Dudley Herb. 4: 17. 1950.
Neltuma pazensis Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.
Prosopis pazensis (Britton & Rose) Wiggins, Contr. Dudley Herb. 4: 18. 1950.

Type material. Mexico. Sonora, Guaymas, *E. Palmer 197* (lectotype designated by Palacios (2006): GH [GH00003478]; isolectotypes: BM [BM000952297, BM000952297], K [K000478261], NY [NY00005127], US [US00000983, US00930831], YU [YU001419]).

***Neltuma caldenia* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303592-1

Prosopis dulcis Gillies ex Hook., Bot. Misc. 3: 203. 1833, nom. illeg.
Prosopis calden Monticelli, Lilloa 3: 348. 1939, nom. nud.

Basionym. *Prosopis caldenia* Burkart, Darwiniana 3: 111. 1939.

Type material. Argentina. San Luis: Sierra, El Volcán (cerca de la capital), *A.L. Pastore s.n., Herb Burkart 6629* (holotype: SI [SI002466]).

***Neltuma calderensis* (A. Galán, E. Linares, J. Montoya & Vicente Orell.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303593-1

Basionym. *Prosopis calderensis* A. Galán, E. Linares, J. Montoya & Vicente Orell., Phytotaxa 414: 50. 2019.

Type material. Peru. Arequipa: Mollebaya, *A. Galán et al. AG4633* (holotype: CPUN, isotypes: HUSA, MA, MO, USP).

Neltuma calingastana **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303594-1

Basionym. *Prosopis calingastana* Burkart, Bol. Soc. Argent. Bot. 6: 223. 1957.

Type material. Argentina. San Juan, Calingasta, Quebrada Las Leñas y Est. Las Hornillas, Valle de Los Patos, *Moreau & Perrone s.n.* (*BA55032*) (holotype: SI [SI002468]).

Neltuma campestris **(Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303595-1

Basionym. *Prosopis campestris* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 132. 1874.

Type material. Argentina. Córdoba, pr. Chañar, *P.G. Lorentz 2* (holotype: GOET [GOET009644]; isotypes: CORD [CORD00005674], F [F0BN001459], SI [SI002469]).

Neltuma castellanosii **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303728-1

Basionym. *Prosopis castellanosii* Burkart, Darwiniana 5: 66. 1941.

Type material. Argentina. Mendoza: Payún-Matrú, *A. Castellanos 14253* (*BA 36732*) (holotype: SI [SI002471]; isotypes: LIL [LIL000715], GH [GH00063863]).

Neltuma chilensis **(Molina) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303729-1

Prosopis chilensis (Molina) Stuntz, U.S.D.A. Bur. Pl. Industr. Invent. Seeds 31: 85. 1914.

Basionym. *Ceratonia chilensis* Molina, Sag. Stor. Nat. Chili: 172. 1782.

Type material. Chile. (no type details given in protologue to *Ceratonia chilensis*).

Neltuma chilensis **var.** ***catamarcana*** **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303730-1

Basionym. *Prosopis chilensis* var. *catamarcana* Burkart, J. Arnold Arbor. 57: 497. 1976.

Type material. Argentina. Prov. Catamarca, Dept. Belén, *Ulibarri 581* (holotype: SI [SI002472, SI002473]).

Neltuma chilensis **var.** ***chilensis***

Acacia siliquastrum Cav. ex Lag., Gen. Sp. Pl.: 16. 1816.

Prosopis siliquastrum (Cav. ex Lag.) DC., Prodr. 2: 447. 1825.
Prosopis siliquosa St.-Lag., Ann. Soc. Bot. Lyon 7: 132. 1880, orth. var.
Prosopis schinopoma Stuck., Bull. Acad. Int. Géogr. Bot. 13: 87. 1904.

***Neltuma chilensis* var. *riojana* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303731-1

Basionym. *Prosopis chilensis* var. *riojana* Burkart, Darwiniana 9: 75. 1949.

Type material. Argentina. Prov. de La Rioja: Quebrada de lka Troya, cerca de Jagüel, *A. Burkart 12355* (holotype: SI [SI002474]).

***Neltuma denudans* (Benth.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303732-1

Basionym. *Prosopis denudans* Benth., J. Bot. (Hooker) 4: 351. 1842.

Type material. Argentina. Patagonia, Santa Cruz, near Puerto Deseado ("Port Desire"), *Middleton s.n.* (holotype: K [K000504789]).

Neltuma denudans* var. *denudans

***Neltuma denudans* var. *patagonica* (Speg.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303733-1

Prosopis denudans var. *patagonica* (Speg.) Burkart, J. Arnold Arbor. 57: 480. 1976.

Basionym. *Prosopis patagonica* Speg., Revista Fac. Agron. Univ. Nac. La Plata 3: 510. 1897.

Type material. Argentina. Patagonia, "Golfo de San Jorge ", *C. Spegazzini s.n.*

***Neltuma denudans* var. *stenocarpa* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303734-1

Basionym. *Prosopis denudans* var. *stenocarpa* Burkart, Darwiniana 9: 75. 1949.

Type material. Argentina. Gob. del Chubut: Dept. Rawson, south of Trelew, *A. Krapovickas 4367* (isotypes: SI [SI002475, SI002476], BAB [BAB00000476]).

***Neltuma elata* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303735-1

Prosopis elata (Burkart) Burkart, Legum. Argent., ed. 2: 544. 1952.

Basionym. *Prosopis campestris* var. *elata* Burkart, Darwiniana 4: 112. 1940.

Type material. Paraguay. Chaco, Puesto Buenos Aires, en el sector Pilcomayo, *T. Rojas 8323* (holotype: SI [SI002477]).

***Neltuma fiebrigii* (Harms) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303736-1

Basionym. *Prosopis fiebrigii* Harms, Repert. Spec. Nov. Regni Veg. 13: 524. 1915.

Type material. Paraguay. Chaco, *Fiebrig 1254* (isotypes: F [F0BN001462, F0058760F, F0360901F], G [G00400139], K [K000504802], M [M0218669]).

***Neltuma flexuosa* (DC.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303737-1

Acacia flexuosa Lag., Gen. Sp. Pl.: 16 (1816), nom. illeg.

Basionym. *Prosopis flexuosa* DC., Prodr. 2: 447. 1825.

Type material. Chile.

***Neltuma flexuosa* var. *depressa* (F.A. Roig) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303738-1

Prosopis juliflora f. *fruticosa* Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 24: 391. 1913.
Prosopis alba f. *fruticosa* (Hauman) Monticelli, Lilloa 3: 347. 1938.

Basionym. *Prosopis flexuosa* var. *depressa* F.A. Roig, Parodiana 5: 53. 1987 (publ. 1988).

Type material. Argentina. Mendoza, Depto. Malargüe, Matancilla, *Roig et al. "coleción Sierra de Chachahuén 32"* (neotype: MERL).

Neltuma flexuosa* var. *flexuosa

Prosopis juliflora f. *arborea* Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 24: 391. 1913.

***Neltuma flexuosa* var. *fruticosa* (Meyen) C.E. Hughes & G.P. Lewis**

Prosopis flexuosa var. *fruticosa* (Meyen) F.A. Roig, Parodiana 5: 53. 1987. (publ. 1988).

Basionym. *Prosopis fruticosa* Meyen, Observ. Bot. 1: 376. 1834.
Type material. Chile. Prov. de Copiapó, *Roig 12536* (holotype: MERL).

***Neltuma flexuosa* f. *subinermis* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303739-1

Basionym. *Prosopis flexuosa* f. *subinermis* Burkart, J. Arnold Arbor. 57: 513. 1976.
Type material. Argentina. San Juan: Calingasta a Barreal, entre La Isla y Sorocayense, *J.H. Hunziker 6451* (holotype: SI).

***Neltuma glandulosa* (Torr.) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186 (1928).**

Prosopis glandulosa Torr., Ann. Lyceum Nat. Hist. New York 2: 192. 1827.
Dasiogyna glandulosa (Torr.) Raf., Atlantic J. 1: 146. 1832.
Algarobia glandulosa (Torr.) Torr. & A. Gray, Fl. N. Amer. 1: 399. 1840.
Prosopis juliflora var. *glandulosa* (Torr.) Cockerell, Bull. New Mexico Agric. Exp. Sta. 15: 58. 1895.
Prosopis chilensis var. *glandulosa* (Torr.) Standl., Contr. U.S. Natl. Herb. 23: 1658. 1926.

Type material. U.S.A. New Mexico, Union County, Major Long`s Creek (a tributary of the Canadian River ("on the Canadian"), *James s.n.* (holotype: NY [NY00005945]).

Neltuma glandulosa* var. *glandulosa

Prosopis juliflora var. *constricta* Sarg., Trees & Shrubs 2: 249. 1913.
Neltuma constricta (Sarg.) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186. 1928.
Neltuma neomexicana Britton, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186. 1928.
Prosopis bonplanda P.R. Earl & Lux. Publ. Biol. FCB/UANL. Mex. 5 (2): 38. 1991.

***Neltuma glandulosa* var. *prostrata* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303740-1

Basionym. *Prosopis glandulosa* var. *prostrata* Burkart, J. Arnold Arbor. 57: 516. 1976.
Type material. U.S.A. Texas: Kleberg County, western part of Laureles Division of King Ranch, *M.C. Johnston 54359* (holotype: COLO; isotype SI [SI015053]).

***Neltuma hassleri* (Harms) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303741-1

Basionym. *Prosopis hassleri* Harms, Repert. Spec. Nov. Regni Veg.13: 523. 1915.

Type material. Paraguay. river Pilcomayo, Puerto Tolderia, *T. Rojas 329* (isotypes: A [A00063864], BM [BM000545192], F [F0BN001463, F0360902F], GH, P).

Neltuma hassleri* var. *hassleri

***Neltuma hassleri* var. *nigroides* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303742-1

Basionym. *Prosopis hassleri* var. *nigroides* Burkart, J. Arnold Arbor. 57: 479. 1976.

Type material. Argentina. Prov. Santa Fe: Dept. General Obligado, Estancia Las Camelias, *A.E. Ragonese 2423* (holotype: SI [SI002481]).

***Neltuma humilis* (Gillies ex Hook.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303743-1

Basionym. *Prosopis humilis* Gillies ex Hook., Bot. Misc. 3: 204. 1833.

Type material. Argentina. in the Pampas of Buenos Aires ("Ayres"), *J. Gilles s.n.* (holotype: K [K000504787]; isotypes: E [E00158975, E00158976]).

***Neltuma juliflora* (Sw.) Raf., Sylva Tellur.: 119. 1838.**

Mimosa juliflora Sw., Prodr. Veg. Ind. Occ.: 85. 1788.
Acacia juliflora (Sw.) Willd., Sp. Pl., ed. 4, 4: 1076. 1806.
Prosopis juliflora (Sw.) DC., Prodr. 2: 447. 1825.
Algarobia juliflora (Sw.) Heynh., Alph. Aufz. Gew.: 18. 1846.
Entada juliflora (Sw.) Roberty, Bull. Inst. Fondam. Afrique Noire, Sér. A, Sci. Nat. 16: 346. 1954.

Type material. Jamaica. *O.P. Swartz s.n.* (S [S-R-3632, S06-5737]).

***Neltuma juliflora* var. *horrida* (Kunth) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303744-1

Prosopis juliflora var. *horrida* (Kunth) Burkart, J. Arnold Arbor. 57: 502. 1976.

Basionym. *Prosopis horrida* Kunth, Mimoses: 106. 1822.

Type material. Peru. "crescit ad radices Andium orientalium, juxta ripam fluminis Amazonum, inter Tomependa(m) et confluentem Chamaya; item prope litus Oceani Pacifici, in arenosis, inter Piura(m) et Lambayeque", *Humboldt & Bonpland 3603* (isotypes: P [P00679172, P02734496]).

Neltuma juliflora var. *juliflora*

Mimosa piliflora Sw., Fl. Ind. Occid. 2: 986. 1800.
Mimosa furcata Desf., Tabl. École Bot.: 180. 1804.
Acacia cumanensis Humb. & Bonpl. ex Willd., Sp. Pl., ed. 4, 4: 1058. 1806.
Mimosa salinarum Vahl, Eclog. Amer. 3: 35. 1807.
Acacia diptera Humb. & Bonpl. ex Willd., Enum. Pl.: 1051. 1809.
Mimosa algarrobo Azara, Voy. Amér. Mér. 2: 483. 1809.
Mimosa cumana Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 1: 65. 1810.
Mimosa levigata Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 1: 65. 1810.
Mimosa pallida Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 1: 65. 1810.
Acacia furcata (Desf.) Desv., J. Bot. Agric. 3: 67. 1814.
Acacia falcata Desf., Tabl. École Bot., ed. 2: 207. 1815, nom. illeg.
Mimosa diptera Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 5: 529. 1817.
Desmanthus salinarum (Vahl) Steud., Nomencl. Bot. 1: 269. 1821.
Prosopis cumanensis Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 6: 310. 1824.
Prosopis inermis Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 6: 307. 1824.
Acacia salinarum (Vahl) DC., Prodr. 2: 456. 1825.
Prosopis bracteolata DC., Prodr. 2: 447. 1825.
Prosopis domingensis DC., Prodr. 2: 447. 1825.
Mimosa pseudoschinus Terán & Berland., Mem. Comis. Limites: 11. 1832.
Algarobia dulcis Benth., Pl. Hartw.: 13. 1839.
Prosopis dulcis var. *domingensis* (DC.) Benth., J. Bot. (Hooker) 4: 350. 1842.
Mimosa laevigata Benth., Linnaea 22: 530. 1849, orth. var.
Prosopis vidaliana Náves, Descr. *Prosopsis vidaliana*: 15. 1877.
Neltuma bakeri Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.
Neltuma occidentalis Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.
Neltuma pallescens Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.
Prosopis juliflora var. *inermis* (Kunth) Burkart, J. Arnold Arbor. 57: 502. 1976.

Neltuma kuntzei (Harms ex C.E.O. Kuntze) C.E. Hughes & G.P. Lewis, comb. nov.

urn:lsid:ipni.org:names:77303745-1

Prosopis barba-tigridis Stuck., Comun. Mus. Nac. Buenos Aires 1: 66. 1899.
Prosopis casadensis Penz., Malpighia 12: 408. 1899.

Basionym. *Prosopis kuntzei* Harms ex C.E.O. Kuntze, Revis. Gen. Pl. 3(2): 71. 1898.

Type material. Bolivia. Sierra de Santa Cruz, *O. Kuntze s.n.* (isotypes: F [F0BN001465], NY [NY00003276], US [US00000986]).

***Neltuma laevigata* (Humb. & Bonpl. ex Willd.) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.**

Acacia laevigata Humb. & Bonpl. ex Willd., Sp. Pl., ed. 4, 4: 1059. 1806.
Prosopis laevigata (Humb. & Bonpl. ex Willd.) M.C. Johnst., Brittonia 14: 78. 1962.
Prosopis dulcis Kunth, Mimoses: 110. 1822.
Acacia tortuosa Billb. ex Beurl., Kongl. Svenska Vetensk. Acad. Handl., n.s., 2: 24. 1856, nom. illeg.
Mimosa rotundata Sessé & Moc., Pl. Nov. Hisp.: 178. 1890.
Neltuma michoacana Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.

Type material. Mexico. "in America meridionali", Morelos, between Huajintlán ("Guasintlan ") and Puente de Istla, fide Johnston (1962), *Humboldt & Bonpland* (holotype B, microfiche reproduction Herbarium Willdenow Cat. N. 19132 (MO), fide Palacios (2006).

***Neltuma limensis* (Benth.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303746-1

Basionym. *Prosopis limensis* Benth., J. Bot. (Hooker) 4: 350. 1842.

Type material. Peru. Lima, *H. Cuming 974* (lectotype designated by Perry 1998. Fl. Australia 12: 193; isolectotypes: BM [BM000952294], E [E00319916, E00319926], GH [GH00063865], K [K000821140], US).

***Neltuma mantaroensis* (L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303747-1

Basionym. *Prosopis mantaroensis* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 70. 2009.

Type material. Peru. Ayacucho, Prov. Huanta, Distr. Huanta, *L. Vásquez Núñez et al. 12845* (holotype: PRG; isotype: PRG).

***Neltuma mayana* (R.A. Palacios) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303748-1

Basionym. *Prosopis mayana* R.A. Palacios, Bol. Soc. Argent. Bot. 41: 115. 2006.

Type material. Mexico. Yucatán, entre Dzilam de Bravo y El Tajo, *R. Palacios 2362* (holotype: MEXU [MEXU01241933]; isotypes: BAFC, TEX [TEX00202236]).

***Neltuma mezcalana* (R.A. Palacios) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303749-1

Basionym. *Prosopis mezcalana* R.A. Palacios, Bol. Soc. Argent. Bot. 41: 105. 2006.

Type material. Mexico. Guerrero, entrada a Chacamerito y Tanganhuato, *R. Palacios 2402* (holotype: MEXU; isotypes: BAFC, TEX [TEX00202211]).

***Neltuma nigra* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303750-1

Prosopis nigra (Griseb.) Hieron., Bol. Acad. Nac. Ci. Republ. Argent. 4: 283. 1881.

Basionym. *Prosopis algarobilla* var. *nigra* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 118. 1879.

Type material. Argentina. Córdoba, prope urban Chacra de la Merced, *C. Galander s.n.* (?holotype: HBG [HBG519250].

***Neltuma nigra* var. *longispina* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303751-1

Basionym. *Prosopis nigra* var. *longispina* Burkart, J. Arnold Arbor. 57: 507. 1976.

Type material. Argentina. Prov. Corrientes, Dept. Capital, 2 km S of Paso Pessoa, *T.M. Pedersen 2808* (holotype: SI [SI002485]; isotypes: C [C10012323], CTES [CTES0000668], L [L0019214], MO [MO-954304], WAG [WAG0132133]).

Neltuma nigra* var. *nigra

Prosopis dulcis var. *australis* Benth., J. Bot. (Hooker) 4: 350. 1842.

***Neltuma nigra* var. *ragonesei* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303752-1

Basionym. *Prosopis nigra* var. *ragonesei* Burkart, Darwiniana 7: 518. 1947.

Type material. Argentina. Santa Fe: Videla, *A.E. Ragonese 2078* (holotype: SI [SI002490]).

***Neltuma nuda* (Schinini) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303753-1

Basionym. *Prosopis nuda* Schinini, Bonplandia (Corrientes) 5: 105. 1981.

Type material. Paraguay. Dep. Boquerón. Mariscal Estigarribia, *A. Schinini* & *E.E. Bordas 15222* (holotype: CTES [CTES0000670]; isotype: SI [SI002493]).

***Neltuma odorata* (Torr. & Frém.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303754-1

Strombocarpa odorata (Torr. & Frém.) A. Gray, U.S. Expl. Exped., Phan. 1: 475. 1854.
Prosopis juliflora var. *torreyana* L.D. Benson, Amer. J. Bot. 28: 751. 1941.
Prosopis glandulosa var. *torreyana* (L.D. Benson) M.C. Johnst., Brittonia 14: 82. 1962.
Prosopis glandulosa subsp. *torreyana* (L.D. Benson) A.E. Murray, Kalmia 12: 23. 1982.

Basionym. *Prosopis odorata* Torr. & Frém., in J.C. Frémont, Rep. Exped. Rocky Mts.: 313. Pl. 1. 1845. Pro parte, excluding the fruits, fide L. D. Benson Madroño 15: 53. 1959.

Type material. U.S.A. California, along Mohave and Virgin River, *Fremont s.n.* (lectotype designated Benson (1959): NY), excluding the fruits.

***Neltuma pallida* (Humb. & Bonpl. ex Willd.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303755-1

Prosopis pallida (Humb. & Bonpl. ex Willd.) Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 6: 309. 1824.
Mitostax pallida (Humb. & Bonpl. ex Willd.) Raf., Sylva Tellur.: 120. 1838.

Basionym. *Acacia pallida* Humb. & Bonpl. ex Willd., Sp. Pl., ed. 4, 4: 1059. 1806.

Type material. Peru. Prov. Jaén de Bracamoros, Passo de Matara, “in America meridionali”, ?Bonpland.

***Neltuma palmeri* Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.**

Prosopis tamaulipana Burkart, J. Arnold Arbor. 57: 494. 1976.

Type material. Mexico. Tamaulipas: vicinity of Victoria, *E. Palmer 400* (holotype: NY [NY00005077]; isotypes: CM [CM1060], GH, MO [MO-356247], US [US00000993]).

Although the nom. nov. *P. tamaulipana* Burkart was required when *Neltuma palmeri* Britton & Rose was transferred to *Prosopis* because the name *Prosopis palmeri* S. Watson (= *Strombocarpa palmeri* (S.Watson) C.E. Hughes & G.P. Lewis) was already occupied, the original *N. palmeri* provides a valid accepted name.

***Neltuma peruviana* (L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303756-1

Basionym. *Prosopis peruviana* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 74. 2009.

Type material. Peru. Apurímac, Prov. Andahuaylas, Distr. Sapichaca, *L. Vásquez Núñez et al. 12849* (holotype: PRG; isotype: PRG).

***Neltuma piurensis* (L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303757-1

Basionym. *Prosopis piurensis* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 76. 2009.

Type material. Peru. Piura, Prov. Sullana, borde de carretera panamericana cerca al Puente del rio Chira, *L. Vásquez Núñez et al. 13258* (holotype: PRG).

***Neltuma pugionata* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303758-1

Basionym. *Prosopis pugionata* Burkart, Darwiniana 9: 70. 1949.

Type material. Argentina. Prov. de Córdoba, extremo noroeste, bosques xerófilos a las Salinas Grandes, km 907, *A.E. Ragonese & B. Piccinini 6097* (holotype: BAB [BAB00000478]; isotype: SI [SI002497]).

***Neltuma purpurea* (L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303759-1

Basionym. *Prosopis purpurea* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 79. 2009.

Type material. Peru. Tumbes, Distr. Puerto Pizarro, *L. Vásquez Núñez et al. 12941* (holotype: PRG; isotype: PRG).

***Neltuma rojasiana* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303760-1

Basionym. *Prosopis rojasiana* Burkart, Darwiniana 5: 70. 1941.

Type material. Paraguay. Chaco paraguayo, Sector López de Filippis, *Rojas 8310* (holotype: SI [SI002500]).

***Neltuma rubriflora* (Hassl.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303761-1

Basionym. *Prosopis rubriflora* Hassl., Repert. Spec. Nov. Regni Veg. 8: 552. 1910.

Type material. Paraguay. Centurión, zwischen Apa und Aquidaban, *K. Fiebrig 5348* (isotypes: F [F0BN001468], GH [GH00063869], HBG [HBG519244], M [M0218666], P [P02436145], fragment SI [SI002502]).

***Neltuma ruizlealii* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303762-1

Basionym. *Prosopis ruizlealii* Burkart, Darwiniana 4: 328. 1942.

Type material. Argentina. Prov. Mendoza, Dep. San Rafael: Agua del Sapo, *Ruiz Leal 7358* (holotype: SI).

***Neltuma ruscifolia* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303763-1

Basionym. *Prosopis ruscifolia* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 130. 1874.

Type material. Argentina. Santiago del Estero, *P.G. Lorentz 21* (holotype: GOET [GOET009549]; isotypes: CORD [CORD00005670], SI [SI002504]).

***Neltuma sericantha* (Gillies ex Hook.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303764-1

Basionym. *Prosopis sericantha* Gillies ex Hook., Bot. Misc. 3: 204. 1833.
Type material. Argentina. Prov. San Luis, *J. Gilles s.n.* (holotype: K [K000504780]; isotypes: E [E00180081, E00180082], GH [GH00063870]).

***Neltuma tupayachensis* (L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303765-1

Basionym. *Prosopis tupayachensis* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 82. 2009.
Type material. Peru. Prov. Cuzco, Distr. Lucre, *L. Vásquez Núñez et al. 12846* (holotype: PRG; isotype: PRG).

***Neltuma velutina* (Wooton) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186. 1928.**

Prosopis velutina Wooton, Bull. Torrey Bot. Club 25: 456. 1898.
Prosopis juliflora var. *velutina* (Wooton) Sarg., Silva N. Amer. 13: 15. 1902.
Prosopis chilensis var. *velutina* (Wooton) Standl., Contr. U.S. Natl. Herb. 23: 1658. 1926.

Type material. U.S.A. Arizona, without further locality, *Pringle 13665* (lectotype NY [NY00003272] designated by Britton & Rose in N. Am. Fl. 23(3): 186. 1928; isolectotypes: A [A00003470], CM [CM1091], MO [MO-954307]).

***Neltuma* × *vinalillo* (Stuck.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303766-1

N. alba var. *panta* (as *P. panta*)× *N. ruscifolia*.

Basionym. *Prosopis* × *vinalillo* Stuck., Anales Mus. Nac. Buenos Aires 7 (ser. 2, t. 4): 73. 1902.
Type material. Argentina. Prov. Tucumán: Depto. De Burruyaco, ? Cañada Alegre.

***Neltuma yaquiana* (R.A. Palacios) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303767-1

Basionym. *Prosopis yaquiana* R.A. Palacios, Bol. Soc. Argent. Bot. 41: 117. 2006.

Type material. Mexico. Sinaloa, alrededores del Cementerio de Topolobampo, *R. Palacios 2417* (holotype: MEXU; isotypes: BAFC, TEX [TEX00202225]).

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Mezcala – a new segregate genus of mimosoid legume (Leguminosae, Caesalpinioideae, mimosoid clade) narrowly endemic to the Balsas Depression in Mexico

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Abstract

Recent results have demonstrated that the genus *Desmanthus* is non-monophyletic because the genus *Kanaloa* is nested within it, with a single species, *Desmanthus balsensis* placed as sister to the clade comprising *Kanaloa* plus the remaining species of *Desmanthus*. Here we transfer *D. balsensis* to a new segregate genus *Mezcala*, discuss the morphological features supporting this new genus, present a key to distinguish *Mezcala* from closely related genera in the Leucaena subclade, and provide a distribution map of *M. balsensis*.

Keywords

Desmanthus, Fabaceae, generic delimitation, *Kanaloa*, monophyly, taxonomy

Introduction

In the 35 years since *Desmanthus balsensis* J.L. Contr. was first described (Contreras 1986) and the more than 20 years since the monograph of the genus *Desmanthus* Willd. was published (Luckow 1993), discovery and description of the monospecific

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Hawaiian endemic genus *Kanaloa* Lorence and K.R. Wood (Lorence and Wood 1994) and assembly of molecular phylogenetic evidence (Luckow et al. 2003; Hughes et al. 2003; Luckow et al. 2005; Ringelberg et al. 2022), have demonstrated that the genus *Desmanthus* is non-monophyletic. To remedy this non-monophyly, we here segregate *D. balsensis* as a new genus, *Mezcala*, thereby rendering *Desmanthus* s.s. monophyletic.

The molecular evidence for the non-monophyly of *Desmanthus* with *Kanaloa* nested within the genus and *D. balsensis* as sister to the clade comprising *Kanaloa* and the rest of *Desmanthus*, presented by Ringelberg et al. (2022), is compelling as it is based on DNA sequences of 997 nuclear genes obtained via targeted enrichment (hybrid capture, or Hybseq) using a slightly modified version of the *Mimobaits* bait set of Koenen et al. (2020). This large phylogenomic dataset yields a phylogeny that receives maximal bootstrap and posterior probability support in concatenated phylogenetic analyses and shows a high fraction of gene trees supporting this species tree topology (Fig. 1; Ringelberg et al. 2022). Furthermore, analysis of accompanying plastome DNA sequence data obtained from off-target DNA sequence reads from the Hybseq data, confirms this non-monophyly of *Desmanthus* (Ringelberg et al. 2022). This non-monophyly was already hinted at in previous phylogenetic analyses based on small numbers of traditional DNA sequence loci (ITS, *trnL-trnF*, *trnK-matK*), which showed that *D. balsensis* is an outlier in the genus, but that the relationships between *D. balsensis*, *Kanaloa* and the rest of *Desmanthus* were either weakly supported or formed a polytomy (Hughes et al. 2003; Luckow et al. 2003; Luckow et al. 2005).

In her monograph of *Desmanthus*, Luckow (1993) pointed out that *D. balsensis* is morphologically unique within the genus. First, the fruits of *D. balsensis* are unusual within *Desmanthus*, being terete or sub-cylindrical in cross-section with thickened valves which are woody when ripe, held erect above the foliage (Fig. 2A–C), and tardily dehiscent along both sutures, the valves recurving from the apex as they open (Fig. 2B) and remaining attached at the base at least briefly after dehiscence. They are quite distinct from the dorsi-ventrally flattened fruits with chartaceous or coriaceous valves and passive dehiscence along one or both sutures which occur in the remaining species of *Desmanthus*. Second, the anthers of *D. balsensis* are capped by caducous terminal stipitate claviform glands (Fig. 2D; Luckow 1993: fig. 2F), which are lacking in the remainder of species in the genus and also absent in the genus *Kanaloa* (Lorence and Wood 1994). Third, the pollen of *D. balsensis* is also unique within the genus, being arranged in tetrahedral tetrads (Fig. 2E; Luckow 1993: fig. 3A), while the remaining species of *Desmanthus* and *Kanaloa* have eumonads. This suite of morphological character state differences resulted in placement of *D. balsensis* as sister to the rest of *Desmanthus* in cladistic analyses of morphological data (Luckow 1993: fig. 15), a set of analyses lacking the genus *Kanaloa* which had not been described at that time. These morphological differences, alongside the molecular evidence of non-monophyly, further support segregation of *D. balsensis* as a distinct genus.

An alternative generic delimitation to ensure generic monophyly would be to transfer *Kanaloa* to *Desmanthus*. However, *Kanaloa* itself has unique morphological features including tergeminately bipinnate leaves, a leaf formula not seen elsewhere

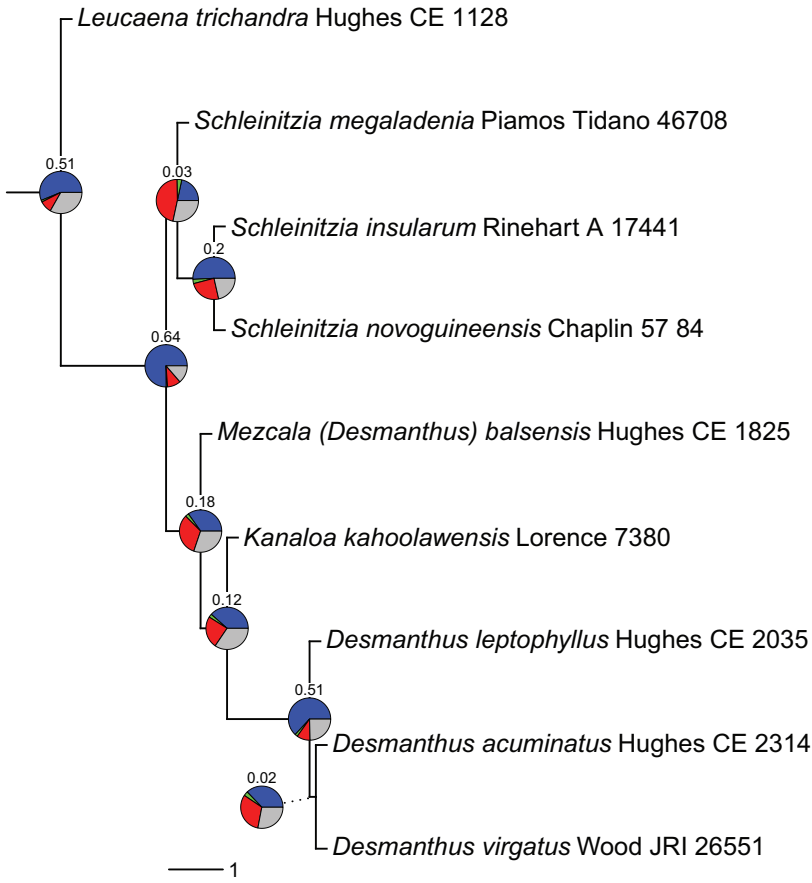

Figure 1. Phylogeny showing sister group relationships of the genera of the informal Leucaena group based on analysis of 997 nuclear gene sequences. The root of the phylogeny is indicated with an arbitrary branch length. Pie charts show the fraction of gene trees supporting that bipartition in blue, the fraction of gene trees supporting the most likely alternative configuration in green, the fraction of gene trees supporting additional conflicting configurations in red, and the fraction of uninformative gene trees in grey. Numbers above pie charts are Extended Quadripartition Internode Certainty scores. Branch lengths are expressed in coalescent units, and terminal branches were assigned an arbitrary uniform length for visual clarity, see Ringelberg et al. (2022).

in any genera of the informal Leucaena group (although not uncommon elsewhere in mimosoids); absence of an involucel of floral bracts subtending the capitula; a very broad funnelform anvil-shaped, flanged stigma on a style held below the anthers (Anna Palomino, pers. comm.), small, coriaceous, ovate or elliptic, monospermous fruits and unusual large cordiform seeds (Lorence and Wood 1994), a set of characters that clearly distinguish it from both *Desmanthus* and *Mezcala*, although the fruits of the unusual Baja California endemic *D. oligospermus* Brandegee are also monospermous and somewhat reminiscent of *Kanaloa* pods (Luckow 1993). Furthermore, this alternative

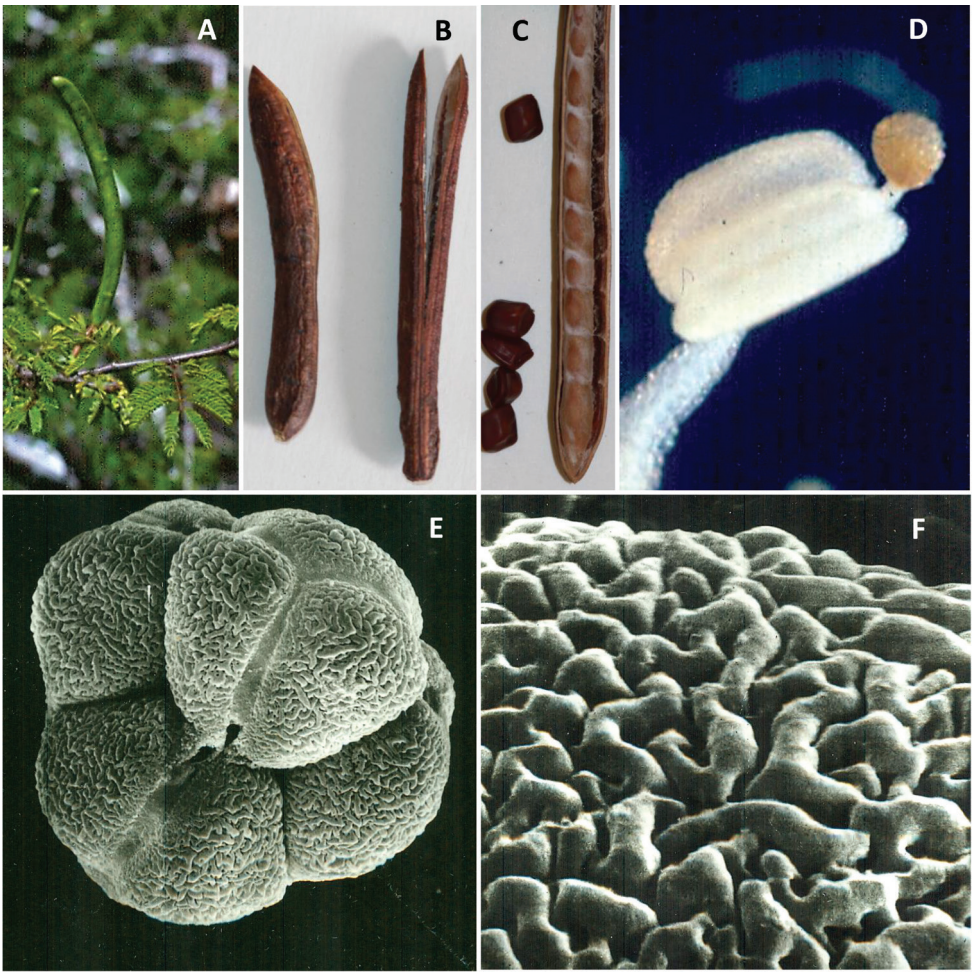

Figure 2. Morphology of *Mezcala balsensis* **A** unripe fruits held erect above branchlets **B, C** ripe fruits, tardily dehiscent from the apex, terete or sub-cylindrical in cross-section with thickened valves, and rhombic, four-angled seeds **D** claviform anther gland **E** tetrahedral tetrad of tricolporate pollen grains **F** exine of pollen showing striate ornamentation. Photos **A–C** José Luis Contreras Jiménez **D** Alejandro Martínez Mena, Facultad de Ciencias, Universidad Nacional Autónoma de México **E, F** Egon Köhler, Humboldt University, Berlin.

generic delimitation would not solve, but rather would accentuate the morphological heterogeneity within the genus *Desmanthus*, much of which is attributable to inclusion of *D. balsensis*. In addition, subsuming *Kanaloa* into *Desmanthus* would have the undesirable impact of detracting attention from the plight of *Kanaloa* and from the ongoing conservation battle to save this monospecific Hawaiian genus. When it was first described, *Kanaloa* was known from just a handful of individuals on a sea stack off the coast of the island of Kaho'olawe, the smallest of the main islands of the Hawaiian archipelago (Lorence and Wood 1994), and it is now thought to be extinct in the wild and is the focus of ongoing *ex-situ* conservation efforts at the Olinda Rare Plant Propagation Facility, Maui.

Mezcala is placed in the informal Leucaena group, a subclade now composed of five genera: *Leucaena* Benth., *Schleinitzia* Warb. ex Guinet, *Mezcala*, *Kanaloa* and *Desmanthus* (Fig. 1, Table 1; Ringelberg et al. 2022), placed within the wider Dichrostachys clade sensu Koenen et al. (2020). This wider Dichrostachys clade includes many taxa with heteromorphic inflorescences comprised of variable proportions of neuter (non-functional staminate), male and hermaphrodite flowers, sometimes with showy staminodia at the base of the inflorescences which are characteristic of the clade even though not universal within it (Koenen et al. 2020). This lability in flower types within an inflorescence is mirrored in *Mezcala* and *Kanaloa*. While inflorescences of both these genera lack showy basal staminodes, inflorescences of *Mezcala* frequently include a proportion of sterile basal flowers and have highly variable ratios of sterile, male and hermaphrodite flowers, including some inflorescences with entirely sterile or male flowers (Contreras 1986). The same apparently applies to *Kanaloa*, given that, when the genus was first described, only male flowers were found (Lorence and Wood 1994). This variation is also apparent in *Desmanthus* s.s., but here a number of species have long-exserted, flattened, fused and showy staminodes at the base of the inflorescence (Luckow 1993), while *Leucaena* and *Schleinitzia* apparently lack sterile flowers. Similar evolutionary lability is apparent in other morphological characters across the genera of the Leucaena subclade, and notably pollen and anther glands. As indicated above, the occurrence of pollen in tetrahedral tetrads (Fig. 2E) and the presence of anther glands (Fig. 2D) separate *Mezcala* from *Kanaloa* and *Desmanthus* s.s. which have eumonad pollen and lack anther glands. In fact, the pollen arranged in tetrahedral tetrads with striate exine ornamentation (Fig. 2E, F), and the stipitate claviform anther glands of *Mezcala* and *Schleinitzia* species are nearly identical (Nevling and Niezgoda 1978; Luckow 1993), reflecting the sister group relationship of *Schleinitzia* to the *Mezcala* + *Kanaloa* + *Desmanthus* s.s. clade (Fig. 1; Ringelberg et al. 2022). This close similarity of *Mezcala* and *Schleinitzia* may also be related to the likely allopolyploid origin of the genus *Schleinitzia* potentially involving the ancestor of *Mezcala* as one of the parents – see below (Ringelberg et al. unpubl. data), which is also reflected in the sister group relationship between these two genera in the plastome phylogeny of Ringelberg et al. (2022). Pollen also varies within the genus *Leucaena* which includes species with tricolporate eumonads as well as others with pollen in polyads (Hughes 1997), including distinctive acalymmate polyads made up of porate monad units that are quite different from the tetrahedral tetrads of *Schleinitzia* and *Mezcala*. While most species of *Leucaena* lack anther glands, a few have rounded or 'hooded' apiculae that have been equated as homologous with stipitate anther glands (Hughes 1997). Thus, these five genera display a mosaic of character state combinations that reflects extensive morphological homoplasy across this clade, as well as apparently complex and poorly understood variation in the reproductive biology of these species involving presence or absence of anther glands, presence or absence of pollen aggregated into polyads, and highly variable ratios of sterile, male and hermaphrodite flowers within an inflorescence (Table 1).

Reticulation may also have contributed to the morphological homoplasy across the genera of the Leucaena subclade, with independent whole genome duplications subtending two of the genera, *Schleinitzia* and *Leucaena*, which, in the case of *Schleinitzia*,

Table 1. Morphological differences among genera of the Leucaena subclade.

	Mezcala	*Desmanthus*	*Kanaloa*	*Schleinitzia*	*Leucaena*
Anthers	glabrous; stipitate, claviform, caducous anther glands	glabrous; anther glands absent	glabrous; anther glands absent	glabrous; stipitate, claviform, caducous anther glands	often hairy; anther glands mainly absent, some spp. with small pointed or hooded apiculae
Stigma	porate	porate	broad funnelform, anvil-shaped	porate	porate
Inflorescence	variable proportions of sterile, male and hermaphrodite flowers; showy staminodes absent	variable proportions of sterile, male and hermaphrodite flowers; most spp. with exserted flattened showy staminodes	variable proportions of sterile, male and hermaphrodite flowers; showy staminodes absent	sterile flowers and showy staminodes absent	sterile flowers and showy staminodes absent
Pollen	tetrahedral tetrads	monads	monads	tetrahedral tetrads	mainly monads, three spp. with polyads of two types
Fruits	terete / sub-cylindrical, linear, valves woody, apically dehiscent	plano-compressed, linear, valves chartaceous, inertly dehiscent along both sutures	plano-compressed, small, ovate / elliptic, valves chartaceous, inertly dehiscent, monospermous	plano-compressed, linear-oblong valves coriaceous, winged, functionally indehiscent	plano-compressed, linear, valves chartaceous or coriaceous, inertly dehiscent along one or both sutures
Polyploidy	not polyploid	not polyploid	not polyploid	likely paleo-allopolyploid	paleopolyploid & five neotetraploid spp.

is suggested to have involved an allopolyploid event most likely involving parental lineages from the *Mezcala* + *Kanaloa* + *Desmanthus* clade, one of which was likely the ancestor of *Mezcala* (Ringelberg et al. unpubl. data).

Mexico has been an important centre of legume diversity potentially throughout the Cenozoic (Centeno-González et al. 2021), and apparently had an especially rich Oligocene fossil legume flora that included many elements assigned to subfamily Caesalpinioideae and the mimosoid clade (Calvillo-Canadell and Cevallos-Ferriz 2005; Magallón-Puebla and Cevallos-Ferriz 1994), and Mexico remains an extremely important global centre of legume diversity today (Sousa and Delgado 1993). The segregation of *Mezcala* as a distinct genus adds to the tally of legume genera endemic to Mexico. This includes three other genera in subfamily Caesalpinioideae – *Heteroflorum* M. Sousa, *Conzattia* Rose and *Calliandropsis* H.M. Hern. and P. Guinet – which are also monospecific, and which also grow in similar seasonally dry tropical forest and scrubland habitats to *Mezcala* in south-central Mexico. Age estimates for the divergence times of these three monospecific genera and for *Mezcala* from their sister groups are strikingly congruent, all of them falling in the mid- to late-Miocene, 11–16 Myr (Ringelberg et al. in prep). This shows that these depauperon Mexican endemic dry habitat Caesalpinioid legume lineages are palaeoendemics and suggests they may be best viewed as potential relics of a formerly richer Oligocene / early Miocene Mexican seasonally dry tropical legume flora. All this further emphasizes the conservation importance of *Mezcala* and of the rich diversity of distinctive and deeply divergent legume lineages endemic to Mexico more generally (Sousa and Delgado 1993).

Key to the genera of the Leucaena subclade (see also Table 1)

1 Stipitate, terminal, claviform (orbicular on a filiform stalk) anther glands present **2**

– Anther glands lacking, or reduced to small protrusions (apiculae) on the apex of the anthers **3**

2 Fruits dorsi-ventrally flattened, functionally indehiscent, with slightly winged valves that split along both sutures but do not separate over the seed chambers; widespread across the western Pacific Basin (New Guinea, Melanesia, Micronesia, Polynesia) ..... ***Schleinitzia***

– Fruits sub-cylindrical, tardily dehiscent along both sutures from the apex; endemic to the Balsas Depression in south-central Mexico..... ***Mezcala***

3 Leaves tergeminately bipinnate, i.e. with a single pair of pinnae, each with three leaflets; endemic to Hawaii ..... ***Kanaloa***

– Leaves almost always with > 1 pair of pinnae, each pinna with ≥ 2 pairs of leaflets and generally > 5 pairs, and often many more, never tergeminate; widespread across the Americas **4**

4 Stipules simple, ovate or lanceolate, the mid vein visible with variably sized membranous wings on either side, sterile flowers generally lacking and flowers never with long-exserted staminodia, anthers often hairy ..... ***Leucaena***

– Stipules setiform with auriculate, erose, membranous, striately veined wings at the base, in some species the auricles developed into a tooth that curls under the petiole, capitula typically with a proportion of sterile flowers basally and these often with long-exserted, flattened, fused and sometimes showy staminodia, anthers glabrous ..... ***Desmanthus***

Taxonomy

Mezcala **C.E. Hughes & J.L. Contr., gen. nov.**
urn:lsid:ipni.org:names:77303768-1

Diagnosis. *Mezcala* is distinguished from *Desmanthus* s.s. and *Kanaloa* by the presence of a claviform anther gland with an orbicular head on a filiform stalk on the apex of the anthers, this best seen in bud and often caducous after anthesis, versus absence of anther glands; by the aggregation of pollen into tetrahedral tetrads as opposed to pollen shed as eumonads; and by its sub-cyclindrical, lignified fruits that are held erect above the shoots and which are tardily dehiscent along both sutures from the apex as opposed to the dorsi-ventrally flattened pods with chartaceous or coriaceous valves and passive dehiscence found in species of *Desmanthus* s.s and *Kanaloa*.

Type. *Mezcala balsensis* (J.L. Contr.) C.E. Hughes & J.L. Contr. = *Desmanthus balsensis* J.L. Contr.

Description. (modified from Luckow 1993: 59–60). Small multi-stemmed erect treelet or large shrub 1–3 m tall. Young shoots angled, woody, glabrous or with amorphous red glandular protrusions, reddish-brown when very young, soon exfoliating a waxy white cuticle; older stems terete, reddish-brown to grey, wrinkled, glabrous with conspicuous lenticels, branches geniculate; trunks with checkered grey bark. Stipules persistent, 1.5–3 mm long, setiform with striate, membranous wings, glabrous, red or green, the fused bases clothing short shoots on the older branches from which new leaves or side shoots arise. Leaves 2.5–4.5 cm long, petiole 5–9 mm long, rachis 11–18 mm long, red granular tissue scattered along the axes and concentrated at the junctions of the leaflets with the pinna, and pinnae with the rachis; pinnae 2–4 (–5) pairs, 9–20 mm long, the lowest pair bearing a stipitate nectary 0.4–0.7 mm in diameter on a 0.5–1 mm-long stipe, the tip orbicular, crateriform and flared; leaflets 8–14 pairs per pinna, inserted several millimeters above the base of the pinna, shortly petiolate, 2.5–3.5 × 0.8–1.2 mm, oblong, oblique to square basally, the apex acute, glabrous, finely ciliate along the margins, venation obscure except the nearly central midvein. Capitula 1–2 per leaf axil, borne on peduncles 1–3 cm long. Bracts subtending each flower 1–2.5 × 0.25–0.5 mm, deltate setiform, pale reddish or purple when dry, membranous with a single opaque midvein, peltate and short pedicellate at the centre of the capitulum, sessile at the base, persistent. Flower buds obovate, apically rounded. Capitula 0.5–1 cm long, containing 30–50 sterile, functionally male and hermaphrodite flowers, sterile or male flowers rarely absent, proportions of each flower type variable. Sterile flowers 0–5; calyx 1–1.75 × 0.5–1 mm, obconic, minutely 5-lobed; petals 2–2.5 × 0.2–0.4 mm, lanceolate, white or pale green; staminodia 10, 2.5–5 mm long, the same widths as the filaments of functional stamens, white. Male flowers 12–30, borne above the sterile flowers but with a perianth and androecium like that of the hermaphrodite flowers. Hermaphrodite flowers 5–25; calyx 1.4–2.7 mm long, obconic, the tube 1.3–2 mm long, 0.8–1.2 mm in diameter, rimmed with 5 free acute lobes 0.3–0.5 mm long; petals 2–3.5 × 0.3–0.5 mm, oblanceolate, pale green with white margins, glabrous; stamens 10; 3.5–5.5 mm long, anther apically with a minute orbicular gland borne on a filiform stalk, caducous; ovary 1–1.5 mm long, linear, glabrous, style 3.5–6 mm long, always more than three times the length of the ovary, exserted beyond the stamens. Fruiting peduncles 1–3 cm long, bearing 1 (–4) pods held erect above shoots and tardily dehiscent from the apex along both sutures, also splitting irregularly and transversely along valves, 3.2–5.5 (–10) × 3.3–5 × 0.25–5 mm, linear-oblong, straight to slightly arcuate, apex acute, valves initially fleshy, glabrous, bright emerald-green when unripe, becoming woody or sub-woody and turning dark brown when ripe. Seeds 5–13 per pod, 4.4–6 mm × 2.5–3.5 mm, longitudinally inserted, square to rhomboidal, 4-angled, deep reddish-brown; pleurogram 0.5–1 mm wide, 0.7–1.5 mm deep, deeply U-shaped, often asymmetric with unequal arms.

Geographic distribution. *Mezcala* is a narrowly restricted endemic genus, known from just a handful of localities in the central Balsas Depression in Guerrero, Mexico (Fig. 3). A large majority of the collections are from karst limestone ridges above the gorge of the Río Xochipala, a few km from the village of Xochipala in the Municipio Eduardo Neri, with two outlying localities to the east, close to Tlalcozotitlán, in Municipio Copalillo, and south-east of Olomatlán, in Municipio Tecomatlán, in

the extreme south-east of the State of Puebla. Given that *Mezcala* is undoubtedly globally rare, with an extremely restricted range, and is only known from a handful of populations, it is clear that the conservation status of the genus, although not formally assigned an IUCN threat category here, is likely to be vulnerable or potentially endangered.

Habitat. Locally common, or in places close to Xochipala even abundant, in typical succulent-rich, grass-poor, seasonally dry deciduous tropical forest (SDTF) and dry scrubland with *Bursera* Jacq. ex L. (Burseraceae), *Bourreria* P. Browne (Boraginaceae), *Neobuxbaumia mezcalaensis* (Bravo) Backeb. (Cactaceae), and *Bauhinia andrieuxii* Hemsl., *Conzattia multiflora* (B.L. Rob.) Standl., *Haematoxylum brasiletto* H. Karst., *Lysiloma tergeminum* Benth. and species of *Mimosa* L. (all Leguminosae), on dry karst limestone with shallow freely drained soils.

Etymology. *Mezcala* is named with reference to the indigenous Mezcala culture, which like the genus *Mezcala* itself, is little-known, elusive, distinctive and narrowly endemic to central Guerrero, and which blossomed in this area 700–200 BC. Vestiges of the Mezcala culture are found today along the Río Balsas and its tributaries (Reyna

Figure 3. Distribution of *Mezcala balsensis* in the central Balsas Depression in Guerrero, Mexico. Map based on 15 quality-controlled species occurrence records from GBIF (www.gbif.org), SEINet (www.swbiodiversity.org/seinet), and Contreras (1986), created using R packages ggplot2 (Wickham 2016), sf (Pebesma 2018), and rnaturalearth (South 2017), with data layers depicting Río Balsas and borders of Mexican states downloaded from the North American Environmental Atlas (www.cec.org/north-american-environmental-atlas).

Robles 2020), including an important archaeological site at Xochipala, the type locality of *M. balsensis*. This is the second mimosoid legume genus named after an indigenous Mexican cultural group following the earlier example of Hernández (1986) who coined the generic name *Zapoteca* H.M. Hern. Adding a second name of similar derivation recognizes the diversity and importance of, and threats to, both endemic legumes and indigenous cultures in Mexico.

***Mezcala balsensis* (J.L. Contr.) C.E. Hughes & J.L. Contr., comb. nov.**
urn:lsid:ipni.org:names:77303769-1

Basionym. *Desmanthus balsensis* J.L. Contr., Phytologia 60 (2): 89. (1986).

Type. Mexico, Guerrero, Mpio. Zumpango del Río, 4 km ENE of Xochipala, 7 Nov. 1985, *Contreras 1737* (holotype: FCME!; isotypes: MEXU – 2 sheets!, MO, TEX!).

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RESEARCH ARTICLE

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New segregates from the Neotropical genus *Stryphnodendron* (Leguminosae, Caesalpinioideae, mimosoid clade)

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Abstract

Non-monophyly is a prominent issue in mimosoid legumes, even in some of the less speciose genera such as the neotropical genus *Stryphnodendron*. This genus includes 35 species occurring from Nicaragua to Southern Brazil mostly in humid forests and savannas. Previous taxonomic studies of *Stryphnodendron*

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have highlighted morphologically distinct groups within the genus, recognized by differences on leaves (number of pinnae and size of leaflets), inflorescences (a simple or compound thyrse), and fruit types (legume, nucoid legume or follicle). Recent phylogenetic analyses have confirmed the non-monophyly of *Stryphnodendron*, supporting the recognition of three independent and morphologically well-delimited genera. Here we re-circumscribe *Stryphnodendron* and propose the two new genera *Gwilymia* and *Naiadendron*. In addition, we also provide an updated taxonomic account of the closely related genus *Microlobius*, including the proposal of a lectotype for the single species in the genus.

Keywords

Gwilymia, Leguminosae, *Microlobius*, *Naiadendron*, *Parapiptadenia*, Phylogeny, Piptadenia group, *Pityrocarpa*, *Pseudopiptadenia*

Introduction

Non-monophyly is an issue for several mimosoid legume genera, with relatively few, but significant exceptions as seems to be the case in the genera *Mimosa* L. (Simon et al. 2011) and *Inga* Mill. (Dexter et al. 2017). As well as questioning the characters that were traditionally used to circumscribe mimosoid genera, various molecular phylogenetic studies have revealed the need for new taxonomic circumscriptions of previously large (e.g., *Acacia* Mill.), medium sized (e.g., *Calliandra* Benth.; Souza et al. 2013; *Prosopis* L.; Hughes et al. 2022) and small genera (e.g., *Pseudopiptadenia* Rauschert; Simon et. al. 2016; Borges et al. 2022).

Stryphnodendron Mart. currently comprises 35 species mostly distributed in humid forests and savannas of tropical America (Occhioni 1990; Lima et al. 2020; Scalon et al. 2022). The genus has been traditionally distinguished from other genera with diplostemonous flowers (stamens twice the petal number per flower) in tribe Mimoseae (*sensu* Lewis and Elias 1981) by its juvenile spicate inflorescences covered by prophylls and by pinnae with alternate leaflets (Lewis and Elias 1981), as well as by its young shoots covered in reddish granular trichomes and its indehiscent fruits. However, these and other putative diagnostic characters are not exclusive to *Stryphnodendron*, and they vary within the genus (as traditionally circumscribed) as well as across the phylogeny in which the genus is placed (Occhioni-Martins 1981; Guinet and Caccavari 1992; Caccavari 2002; Simon et al. 2016), casting doubts on the genus circumscription.

The recognition of morphologically distinct groups of *Stryphnodendon*, based on the morphology of leaves (number of pinnae and size of leaflets), inflorescences, fruits (Occhioni-Martins 1981; Scalon et al. 2022) and pollen grains (Guinet and Caccavari 1992), has long been known. Phylogenetic studies based on a limited number of plastid and nuclear molecular markers, but including a comprehensive sampling of species, concurred with this view by demonstrating that *Stryphnodendron*, as currently circumscribed, is a polyphyletic assemblage containing three strongly

supported lineages (Simon et al. 2016). In addition, the relationships between these three lineages and the closely related genera *Parapiptadenia*, *Pseudopiptadenia* and *Microlobius* remain unresolved (Simon et al. 2016; Ribeiro et al. 2018). The polyphyly of *Stryphnodendron* was recently confirmed by phylogenomic studies, although with a sparser taxonomic sampling (Koenen et al. 2020; Ringelberg et al. 2022), but since these phylogenomic studies did not sample the monospecific *Microlobius*, its phylogenetic position was unclear.

Microlobius is here included in the phylogenomic framework depicted by Ringelberg et al. (2022) and this sheds light on its relationship to the different lineages that compose the genus *Stryphnodendron* in its current circumscription. In addition, we combine morphological and phylogenetic evidence to assess the taxonomic limits of *Stryphnodendron*. Based on our results, we propose a narrower circumscription for the genus *Stryphnodendron* by segregating two new genera. In addition, we provide an identification key to the seven genera now recognized within the Stryphnodendron clade, present an updated description of *Microlobius*, and designate a lectotype for the single species in that genus.

Materials and methods

Phylogenomic analyses

To test the placement of *Microlobius* in a phylogenomic context, we merged transcriptome data for three mimosoid species (*Albizia julibrissin* Durazz., *Entada abyssinica* Steud. ex A.Rich., and *Microlobius foetidus* (Jacq.) M. Sousa & G. Andrade) generated by Koenen et al. (2020) with a hybrid capture dataset now increased to 997 genes for 63 Caesalpinioid taxa, 33 from Koenen et al. (2020) and 30 from Ringelberg et al. (2022). The hybrid capture dataset contains ten taxa from the Stryphnodendron clade (sensu Koenen et al. (2020)), including three *Stryphnodendron* species, and abundant outgroup sampling across Caesalpinioideae, including 25 taxa from the Albizia clade and nine taxa from the Entada clade (Suppl. material 2: Table S1). As this method combines molecular data from different data sets (transcriptome and hybrid capture), the placement of the *Albizia julibrissin* and *Entada abyssinica* transcriptome samples in the final phylogeny serves as confidence tests for the placement of *Microlobius foetidus*: if the transcriptome samples of *A. julibrissin* and *E. abyssinica* are placed in the expected place in their correct clades, this suggests that *M. foetidus*, for which only transcriptome data are available, is also placed correctly.

We cleaned raw transcriptome reads using Trimmomatic v. 0.36 (Bolger et al. 2014) with the same settings as used by Nicholls et al. (2015): ILLUMINACLIP:TruSeq3-PE.fa: 2:30:10 LEADING:3 TRAILING:3 SLIDINGWINDOW:4:15 MINLEN:36. Gene assembly was performed with HybPiper (Johnson et al. 2016), using default settings and the updated 997 nuclear MimoBaits sequences (Koenen et al. 2020,

Ringelberg et al. 2022) as a target set. Assembled gene sequences of the three transcriptome samples were expressed as DNA sequences by HybPiper. We recovered 991, 956, and 988 genes with at least 75% of the target length for *A. julibrissin*, *E. abyssinica*, and *M. foetidus*, respectively. HybPiper recovers multiple sequences of at least 75% of the target length for a taxon-gene combination; these are flagged as 'potential paralogs'. Relatively few such potential paralogs (from now on referred to simply as paralogs) were found: 55, 46, and 45, respectively. All sequences, including paralogs, were used in the downstream analyses. At this point the transcriptome sequences (three taxa) and hybrid capture sequences (63 taxa, assembled by Ringelberg et al. 2022) were merged, i.e., transcriptome- and hybrid capture-derived sequences, both expressed as DNA, were pooled across all 66 taxa for each gene. This resulted in a combined dataset with sequences of 997 genes, including all paralogs of both transcriptome and hybrid capture data, which was used in downstream analyses.

We removed outlier sequences, i.e. strongly-divergent sequences placed on very long branches in preliminary gene trees due to orthology assessment or alignment errors, with two rounds of a modified version of the Yang and Smith (2014) pipeline: we aligned all the sequences for each gene with MACSE v. 2.01 (Ranwez et al. 2011), removed sites with a column occupancy < 0.3 with pxclsq (Brown et al. 2017), inferred gene trees using RAxML v. 8.2.12 (Stamatakis 2014) (with the GTRGAMMA model and 200 rapid bootstraps), and removed taxa on long branches with the trim_tips.py script of Yang and Smith (2014), with a relative cut-off of 0.1 and an absolute cut-off of 0.3. In the first round of this approach 181 sequences were removed, out of a total of 66,455 sequences across all genes, and in the second 26, indicating that most outliers, resulting from factors such as alignment errors, have been removed from the 997 gene trees.

We analysed the root-to-tip variance of each of the 997 gene trees with the dist. nodes function of the R (R Core Team 2022) package *ape* (Paradis and Schliep 2019). Four trees with a root-to-tip variance > 0.009 were removed, leaving 993 gene trees. These gene trees were used to generate a species tree with the multi-species coalescent approach using ASTRAL-Pro v. 1.1.6 (Zhang et al. 2020). ASTRAL-Pro was selected because it can use multi-labelled gene trees, i.e. gene trees in which individual taxa may be represented by multiple gene copies, thereby avoiding preliminary orthology assessment. Finally, we used PhyParts (Smith et al. 2015) to assess gene tree support and conflict for each node in the species tree, using the nodes with a bootstrap support of > 50% in the 993 gene trees.

Phylogenetic analysis and ancestral state inference

We complemented the phylogenomic analyses described above with the phylogenetic analysis of nuclear (ITS) and plastid (*matK/trnK*, *trnD-T*, *trnL-F*) fragments (White et al. 1990; Taberlet et al. 1991; Möller and Cronk 1997; Hu et al. 2000; Wojciechowski et al. 2004; Simon et al. 2009) for the broader taxon sampling of Simon et al. 2016. The

dataset included 96 terminals, of which 49 belonged to *Stryphnodendron* (23 species), two to *Microlobius* (one species), four to *Parapiptadenia* (four species), seven to *Pseudopiptadenia* (five species) and three to *Pityrocarpa* (Benth.) Britton & Rose (three species). Remaining terminals are external groups, and belong to *Anadenanthera* Speg., *Inga*, *Parkia* R. Br., *Piptadenia* Benth., *Mimosa*, *Senegalia* Raf., and *Vachellia* Wight & Arn.

Trees were inferred using a backbone constraint based on the results of the phylogenomic analyses, which included the following relationships: (*Lachesiodendron viridiflorum*, (((*Piptadenia adiantoides*, *Piptadenia gonoacantha*), (*Mimosa myriadenia*, (*Mimosaceratonia*,*Mimosapigra*))),(((*Stryphnodendronpaniculatum*,*Microlobiusfoetidus*), (*Stryphnodendron pulcherrimum*, *Stryphnodendron adstringens*)), ((*Pseudopiptadenia contorta*, *Pseudopiptadenia psilostachya*), (*Stryphnodendron duckeanum*, (*Pityrocarpa moniliformis*, (*Parapiptadenia excelsa*, *Parapiptadenia zehntneri*)))))).

Phylogenetic analyses were performed with both maximum parsimony and Bayesian methods. Search parameters for the parsimony analysis, all performed in PAUP* version 4 (Swofford 2003), included two rounds of heuristic search with 1000 replicates of random taxon addition and tree bisection-reconnection branch swap, saving 15 trees per replicate. We estimated branch support using 10000 iterations of bootstrap resampling using the same parameters mentioned above. We used the CIPRES Science Gateway (Miller et al. 2010) implementation of MrBayes version 3.2 (Ronquist et al. 2012) for Bayesian inference. We performed two runs of four chains using a GTR+I+G model for all partitions for 10^7 generations, sampling trees every 1000 generations. Sampled trees and branch posterior probabilities were summarized on a 50% majority rule tree after discarding the first 25% trees as burn-in.

To infer putative morphological synapomorphies, we optimized 17 morphological characters previously sampled for the group (Simon et al. 2016; http://morphobank.org/permalink/?P2220) onto the resulting Bayesian tree with Mesquite v. 3.70 (Maddison and Maddison 2021). All characters were mapped using parsimony and treated as unordered.

Taxonomic analysis

The taxonomic updates that we present here are based on taxon observations made during field expeditions and on examination of specimens from the following herbaria (acronyms according to Thiers 2018): ALCB, B, BHCB, BM, BOTU, BR, CEN, CEPEC, CESJ, CPAP, CVRD, E, ESA, F, G, GUA, HB, HEPH, HRB, HRCB, HTO, HUEFS, HUFU, IAC, IAN, IBGE, INPA, IPA, K, M, MBM, MG, MO, NY, OUPR, OXF, P, R, RB, RFA, SP, SPF, SPSF, U, UB, US, UEC, UFG, UFMS, VIC, W, WU.

We follow Scalon et al. (2022) and Harris and Harris (2001) for habit, indumentum, and leaf terminology; Weberling (1989) for inflorescence and flower terminology; and Barroso et al. (1999) for fruits. The geographical distribution maps were made using SimpleMappr (Shorthouse 2010).

Results and discussion

Placement of *Microlobius* and *Stryphnodendron* polyphyly

Our phylogenomic analysis places *Microlobius* in a clade together with all *Stryphnodendron* species, except for *Stryphnodendron duckeanum* (Fig. 1). While this placement is not supported by all gene trees, the most likely alternative topology is far less common among the gene trees (Fig. 1). This suggests that most gene tree conflict found across the phylogeny (Suppl. material 1: Fig. S1) most likely reflects a lack of signal for particular nodes among many of the gene trees, rather than strong support for alternative topologies (Koenen et al. 2020, Ringelberg et al. 2022).

The combination of transcriptome- and hybrid capture-based samples in a single phylogenetic analysis is validated by placing of the two outgroup transcriptome samples in the resulting phylogeny (Suppl. material 1: Fig. S1). *Entada abyssinica* is placed within *Entada* in the sister clade of *Elephantorrhiza* (Burch.) Skeels, matching the *matK* phylogeny of LPWG (2017). *Albizia julibrissin* is resolved as the sister to *A. umbellata* (Vahl) E.J.M. Koenen in *Albizia* s.s., in accordance with unpublished data of Koenen et al.

The constrained parsimony and Bayesian analyses match the phylogenomic data and expands the relationships by presenting a denser taxonomic sampling. *Stryphnodendron* was recovered as a polyphyletic assemblage and its species group in three highly supported lineages: (1) *S. duckeanum* appears isolated from the remainder of the genus in a clade with representatives of the genera *Parapiptadenia, Pityrocarpa* and

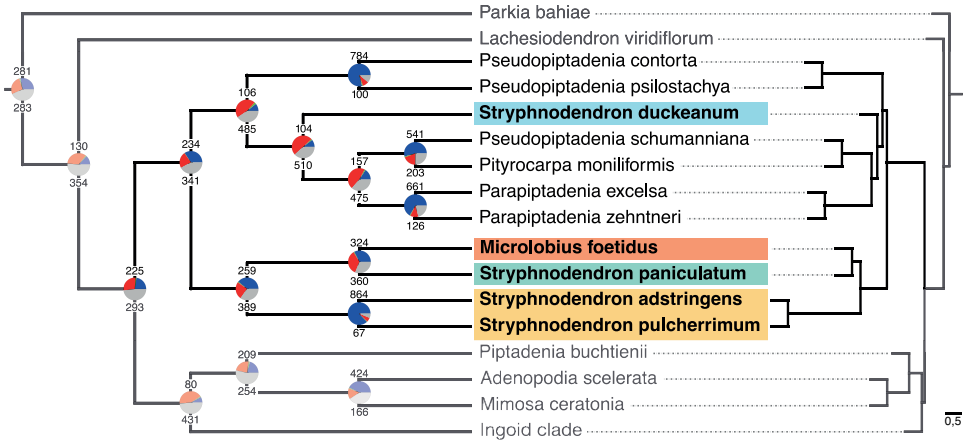

Figure 1. Phylogeny of the Stryphnodendron clade based on combined transcriptome and hybrid capture data. Left: Cladogram with pie charts depicting support and conflict per bipartition across 993 individual gene trees; blue sections indicate support, green sections support for the most common conflicting topology, red sections support for alternative conflicting topologies, and gray sections uninformative gene trees. Numbers above and below pie charts are numbers of supporting and conflicting gene trees, respectively. Right: Tree with internal branch lengths expressed in coalescent units, and terminal branches assigned an arbitrary uniform length.

Pseudopiptadenia (clade A); (2) *Microlobius foetidus* was supported as sister to a clade including seven species of *Stryphnodendron* (clade C); and (3) a main *Stryphnodendron* lineage (Clade D; Fig. 2).

Some of these relationships are supported by putative morphological synapomorphies (Fig. 2). Indehiscent fruits (nucoid legumes) and granular reddish trichomes support clade C, which includes *Microlobius* and the majority of *Stryphnodendron* sensu lato species (excluding *S. duckeanum*). Although changes from nucoid fruits to follicles occur (including in *Microlobius*), the nucoid legume is inferred as a synapomorphy for this group. Contrary to previous results (Simon et al. 2016), reddish granular trichomes are supported as having independent origins in *S. duckeanum* and the clade including *Microlobius* and the remaining *Stryphnodendron* species. Large leaflets are a synapomorphy for the *Stryphnodendron* lineage which is sister to *Microlobius* in clade C. Alternate leaflets and a tuft of trichomes at the base of the midrib, traits commonly associated with *Stryphnodendron*, support clade D that represents the main lineage of the genus. No studied morphological character was recovered as a synapomorphy of clade C, which includes *Microlobius* and *Gwilymia*. The remaining characters (Suppl. material 1: Figs S2–S18) are either too homoplastic or not informative in the context of *Stryphnodendron* polyphyly.

Given the phylogenetic evidence presented above and the morphological distinctiveness and diagnosability of the three *Stryphnodendron* lineages and *Microlobius*, we propose to split *Stryphnodendron* into three distinct genera: (1) the new genus *Gwilymia*, which includes mostly Amazonian species bearing leaves with few pinnae and large opposite leaflets, inflorescence usually a compound thyrse, and fruit a nucoid legume; (2) the new and monospecific Amazonian genus *Naiadendron* with long petiolar nectaries, opposite leaflets, and non-septate, papery legumes, more similar to the fruits of *Piptadenia* than to any other species of *Stryphnodendron* or *Gwilymia*; and (3) a re-circumscribed *Stryphnodendron s.str.*, which includes species with multipinnate leaves and small alternate leaflets (e.g., *S. adstringens* (Mart.) Coville, the type species of the genus), and the inflorescence a simple thyrse. In addition, we maintain *Microlobius*, which is sister to *Gwilymia*, as a monospecific genus with branches and leaves with a strong garlic odour, petiolar nectary absent, a few pairs of pinnae and opposite leaflets, and fruit a follicle.

An alternative to the circumscription proposed above would be not to describe a new genus and instead to merge *Microlobius* into *Stryphnodendron* (excluding *S. duckeanum*). Although this option would result in fewer taxonomic changes (a single species of *Microlobius* being transferred to *Stryphnodendron* vs. seven new combinations in *Gwilymia*), the marked morphological distinctiveness and easy diagnosability of the *Stryphnodendron* and *Gwilymia* lineages support their recognition as different genera (Figs 3–6; Table 1).

In addition, the circumscription adopted here preserves the morphological distinctiveness of *Microlobius* regarding both *Stryphnodendron* and *Gwilymia* (presence or absence of a garlic odour and petiolar nectary, number of pairs of pinnae, insertion of leaflets, type of inflorescence, type of fruit, and the color of the seeds) as well as the ecological identity of the groups since *Microlobius* is the only member of clade B inhabiting seasonally dry vegetation, whereas *Gwilymia* and *Stryphnodendron* are restricted to humid forests and savannas (Figs 3–6; Table 1).

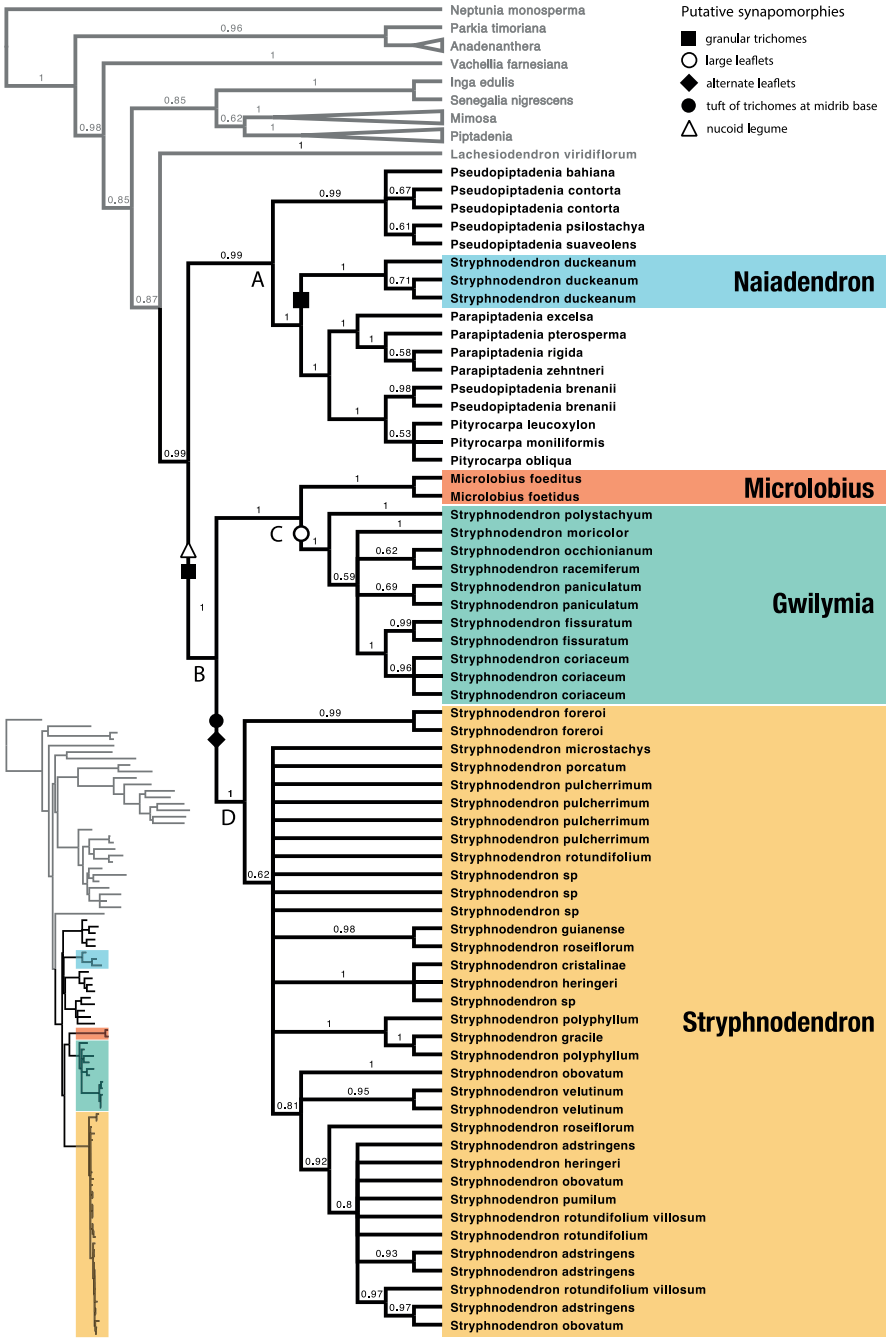

Figure 2. Relationships in the *Stryphnodendron* clade based on (*matK/trnK*, *trnD-trnT*, *trnL-trnF*) and nuclear (ITS) DNA data; constrained by a phylogenomic backbone. 50% majority-rule consensus tree and posterior probability values (above branches) from trees sampled in the posterior Bayesian analysis. Symbols indicate selected putative morphological synapomorphies. The inset tree depicts the Bayesian phylogram with inferred branch lengths.

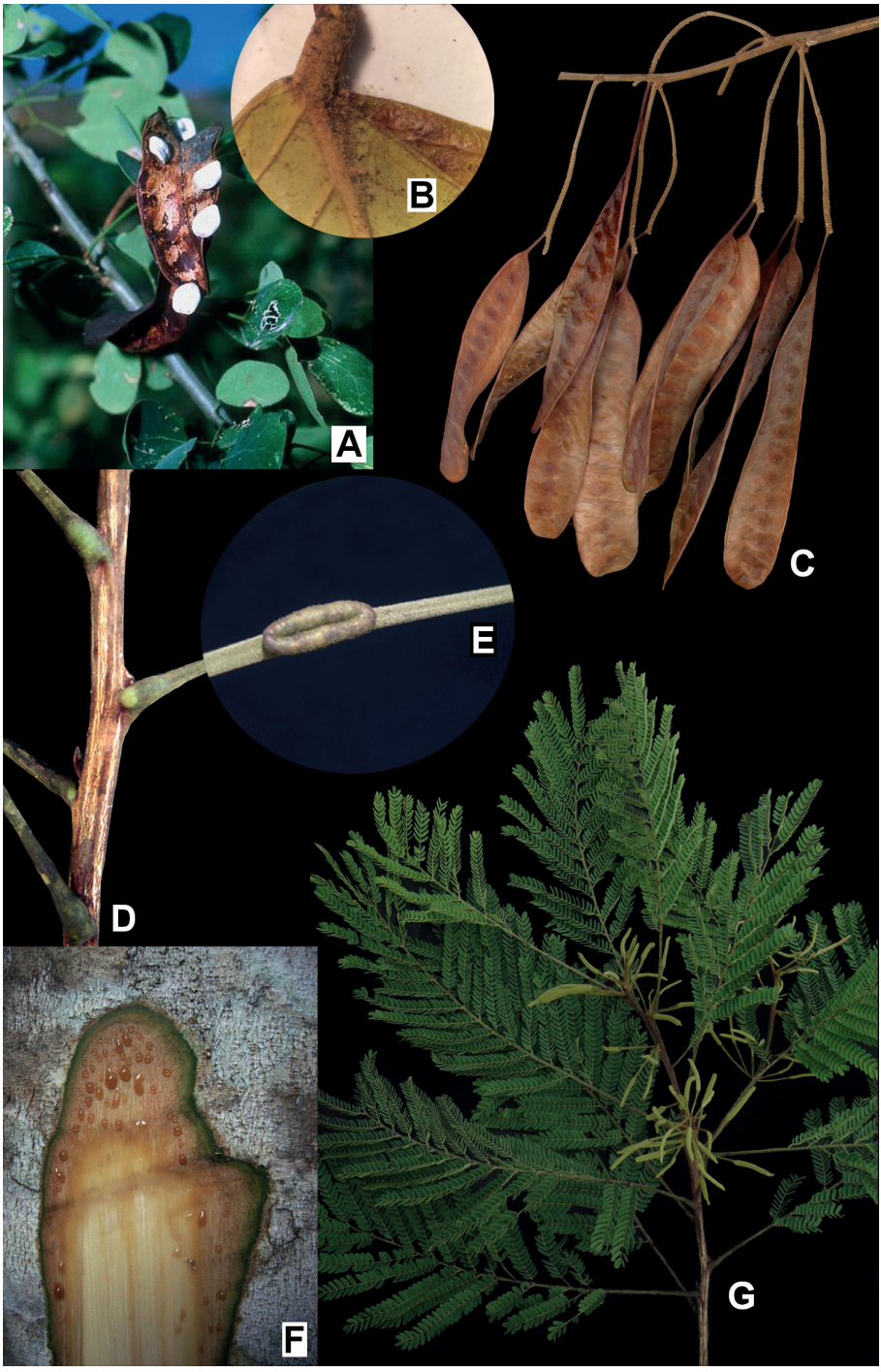

Figure 3. A, B *Microlobius foetidus*: **A** fruiting branch with white seeds exposed **B** detail of a leaflet showing the tuft of trichomes at the base of the midrib **C–G** *Naiadendron duckeanum*: **C** fruits **D** detail of the striated branch **E** detail of petiolar nectary (upper view, magnified) **F** bark slash showing reddish exudate **G** flowering branch. Photos: **A** Donovan Bailey **B** Alexandre Gibau de Lima **C–G** Marcelo Simon.

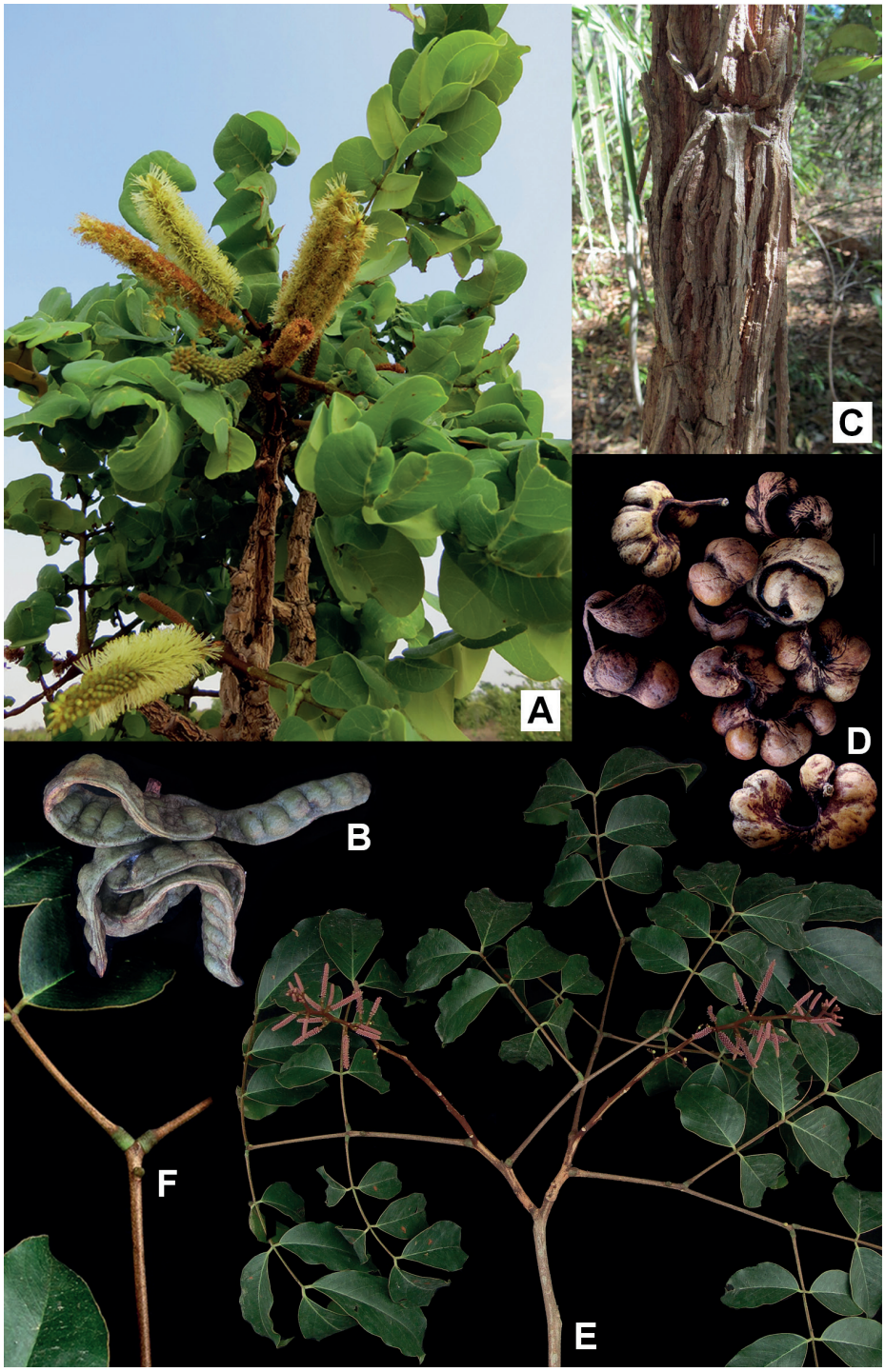

Figure 4. A, B *Gwilymia coriacea*: **A** flowering branch **B** fruit **C, D** *G. fissurata*: **C** detail of bark **D** fruit **E, F** *G. paniculata*: **E** flowering branch with young inflorescences **F** detail of the extrafloral nectary on the leaf rachis. Photos: Marcelo Simon.

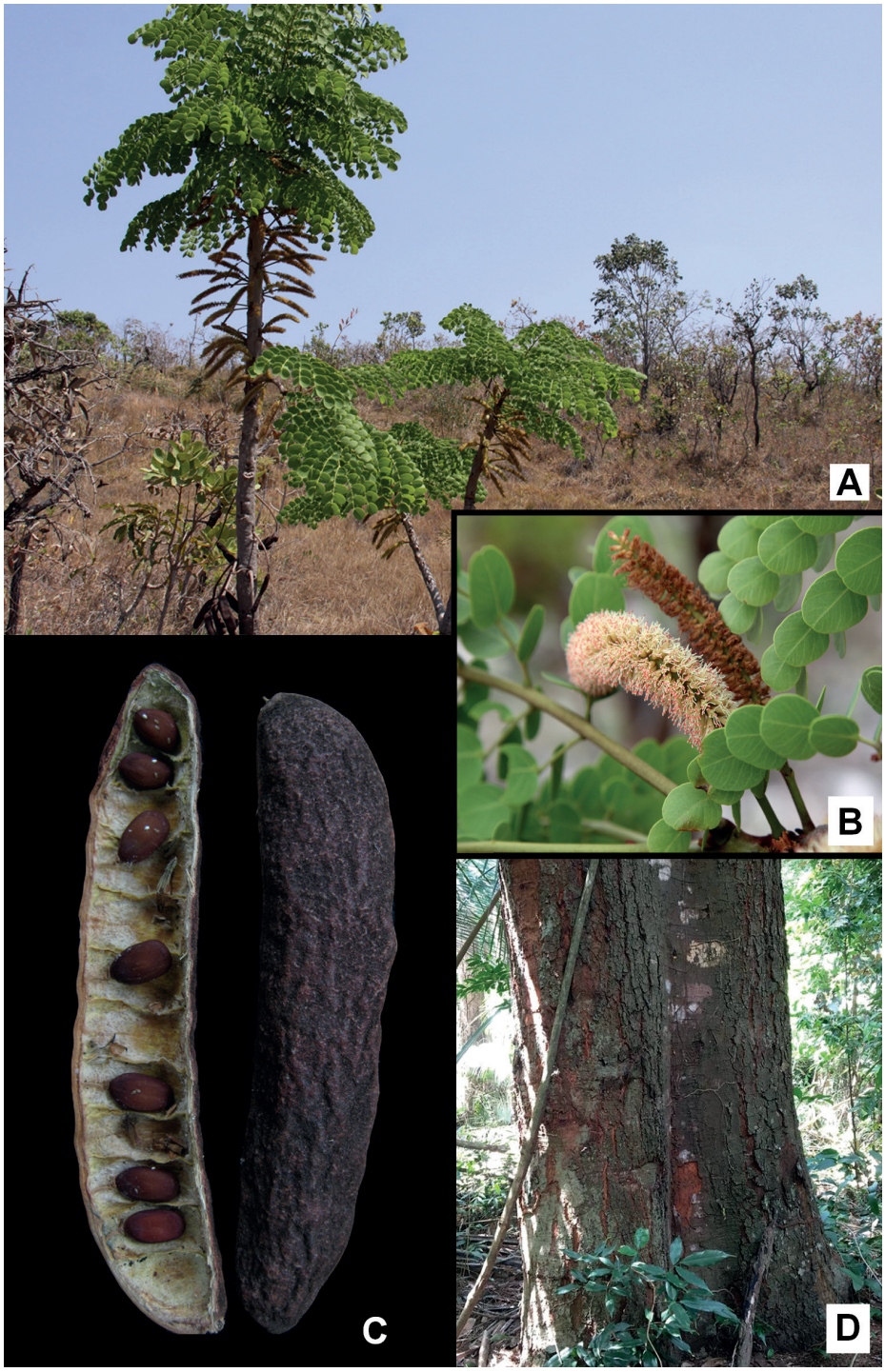

Figure 5. A, C *Stryphnodendron adstringens*: **A** habit **B** foliage and inflorescences **C** fruit (manually opened) and seeds **D** *S. flavotomentosum*: trunk and detail of bark. Photos: **A, B** Henrique Moreira **C** Marcelo Simon **D** Geovane Siqueira.

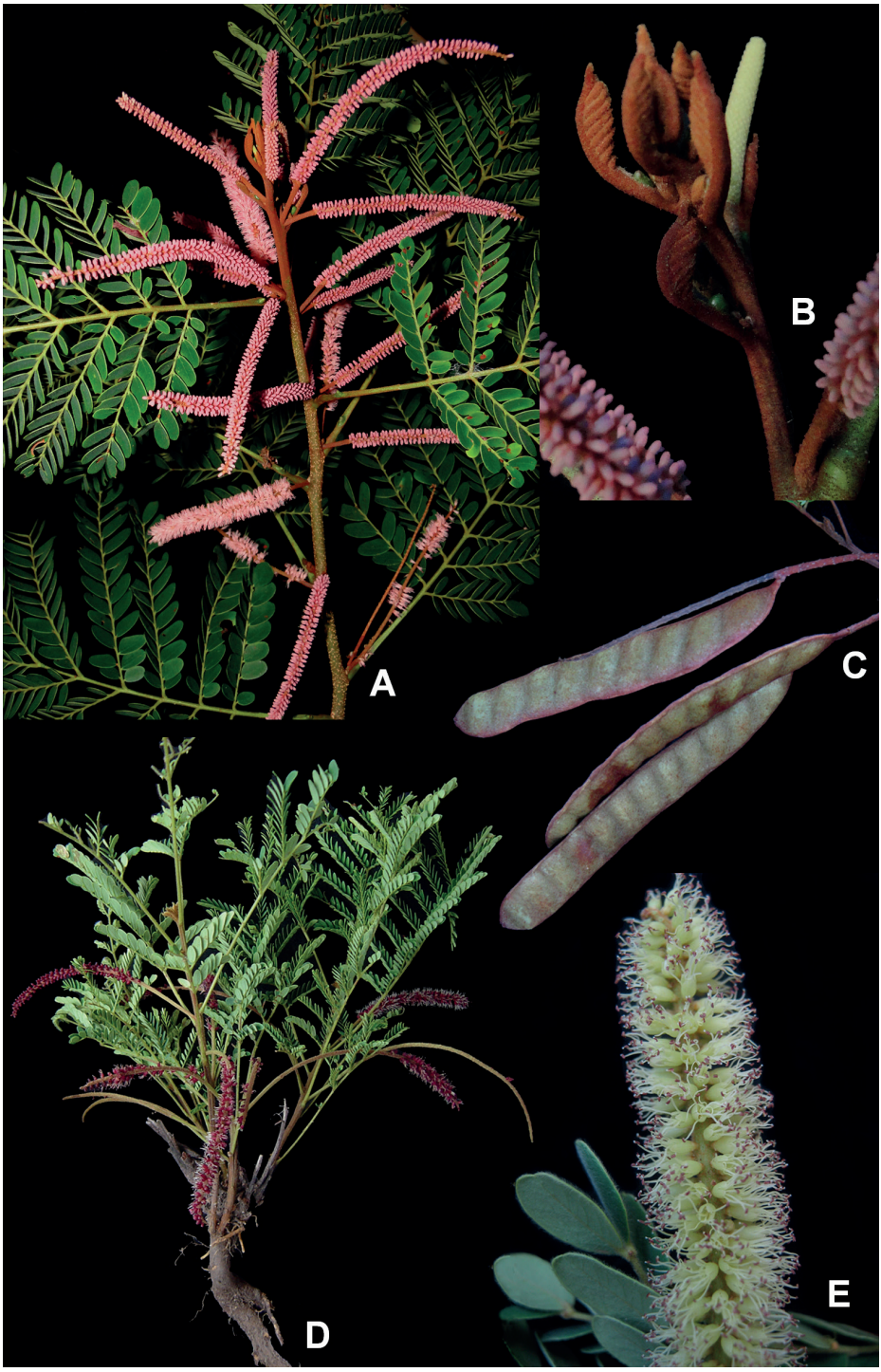

Figure 6. A, B *Styphnodendron forreroi*: **A** flowering branch **B** detail of young shoot covered by reddish granular trichomes **C, D** *S. heringeri*: **C** fruits **D** habit **E** *S. rotundifolium*: detail of inflorescence. Photos: Marcelo Simon.

Table 1. Diagnostic characters of the four Stryphnodendroid lineages. * *Microlobius* was not sampled in Guinet and Caccavari 1992; a description provided in a later work includes its single species (Caccavari 2002) which suggests that the genus might have its own distinct pollen type.

Character	*Microlobius*	*Gwilymia*	*Naiadendron*	*Stryphnodendron*
Garlic odour evident in branches and leaves	Present	Absent	Absent	Absent
Length of petiolar nectary (mm)	Nectary absent	0.5–2	8–12	0.5–2
Number of pairs of pinnae	1–2 (–3)	2–4 (–6)	10–22	(3–) 5–32
Insertion of leaflets	Opposite	Opposite	Opposite	Alternate
Size of leaflets (cm)	2–5 × 1–2.5	2.5–16 × 1.5–8	0.6–1.2 × 0.3–0.5	0.6–1.2 × 0.3–0.6
Tuft of trichomes on leaflets	Present or absent	Absent	Absent	Usually present
Type of Inflorescence	Simple thyrse	Compound thyrse (diplothyrsi or pleiothyrsi), except *G. coriacea* and *G. fissurata*	Simple thyrse	Simple thyrse
Fruit type	Follicle	Nucoid legume (indehiscent)	Legume (dehiscent along both margins)	Nucoid legume (indehiscent) or follicle
Fruit texture	Coriaceous	Coriaceous or woody	Chartaceous	Coriaceous or woody
Seed colour	White	Brown or ochre	Ochre	Brown or ochre
Pollen type (Guinet and Caccavari 1992)	*	*S.fissuratum*, *S.coriaceum* and *S.polystachyum* types	*S.adstringens* type	*S.adstringens*, *S.microstachyum* and *S.piptadenioides* types

Taxonomy

Key to the genera of the Stryphnodendron clade (sensu Koenen et al. 2020, Ringelberg et al. 2022, Borges et al. 2022)

1 Young branches and leaves lacking ferruginous granular trichomes **2**

– Young branches and leaves covered with ferruginous granular trichomes..... **4**

2 Fruit a legume, dehiscing along both margins; flowers with reddish petals and stamens..... ***Parapiptadenia***

– Fruit a follicle, dehiscing along one margin only; flowers with greenish petals and whitish stamens..... **3**

3 Extrafloral nectary between or just below the first pair of pinnae; spikes isolated in the axil of the coeval leaf; fruits moniliform, with deeply constricted margins, and with thick coriaceous and pubescent valves..... ***Pityrocarpa***

– Extrafloral nectary between the base and the middle of the petiole; spikes clustered in terminal efoliate pseudoracemes or below the coeval leaves; fruits with a linear or oblong body, straight or shallowly sinuous margins and thin to thick woody and glabrous valves..... ***Marlimorimia***

4 Branches and leaves with a strong garlic odour; leaves with 1–2 (–3) pairs of pinnae, each pinna comprising a single pair of leaflets, extrafloral nectary absent on the petiole and on the branches; inflorescence a spike, 3–6 cm long (peduncle and rachis); fruit 4–7 × 1–1.5 cm; seeds white..... ***Microlobius***

– Branches and leaves without a garlic smell; leaves always with more than one pair of pinnae, each pinnae comprising 3 or more pairs of leaflets, extrafloral nectary present on the petiole or, in *Gwilymia coriacea* and *G. fissurata*, on the branch directly below the insertion of the petiole; inflorescence a spike, 3.5–20 cm long (peduncle and rachis); fruit 8–14 × 2–3.5 cm; seeds brown or ochre **5**

5 Leaves with 2–4(–6) pairs of pinnae; leaflets 2.5–16 × 1.5–8 cm; inflorescence a compound thyrse (except in *Gwilymia coriacea* and *G. fissurata* which have a simple thyrse) ..... ***Gwilymia***

– Leaves with (3–)5–32 pairs of pinnae; leaflets 0.6–1.2 × 0.3–0.6 cm; inflorescence always a simple thyrsi **6**

6 Branches not striate; petiolar nectary 0.5–2 mm long; leaflets alternate, abaxial surface with a tuft of trichomes at the base of the midrib; petals cohered for at least ½ of their length; fruit coriaceous or woody and indehiscent (a nucoid legume) or splitting along a single margin (a follicle) ..... ***Stryphnodendron***

– Branches strongly striate; petiolar nectary ca. 10 mm long; leaflets opposite, without a tuft of trichomes on the abaxial surface; petals cohered for only ⅓ of their length; fruit chartaceous, dehiscent along both margins (a legume) .. .. ***Naiadendron***

1. *Microlobius* C. Presl, Abh. Königl. Böhm. Ges. Wiss. ser. 5, 3: 496. 1845.

Goldmania Rose, Mém. Soc. Phys. Genève 34: 274. 1903. Type. *Goldmania platycarpa* Rose [= *Microlobius foetidus* (Jacq.) M. Sousa & G. Andrade].

Type. *Microlobius mimosoides* C. Presl [= *Microlobius foetidus* (Jacq.) M. Sousa & G. Andrade]

Description. Trees or shrubs, 3–10 m tall; branches unarmed, smooth, lenticellate, glabrescent, sparsely covered with ferruginous granular trichomes, with a strong garlic odour (hence the epithet of its single species). **Stipules** caducous. **Leaves** bipinnate, petiole glabrescent, sparsely covered with ferruginous granular trichomes, petiolar nectary absent; rachis (0.2–) 3–7 cm long, glabrous or sparsely pubescent, sparsely covered with ferruginous granular trichomes, nectaries 1–3, 0.5–0.8 mm long, patelliform, inserted between the pairs of pinnae; pinnae in 1–2 (–3) opposite pairs, pinnae rachillae nectaries 1–2, 0.3 mm long, patelliform, positioned close to the pair of leaflets; leaflets in 1–2 opposite pairs, 2–5 × 1–2.5 cm, obovate or sometimes elliptic, a tuft of trichomes sometimes present at the base on the abaxial surface. **Inflorescence** a simple thyrse formed by cymules of 2–5 spikes, these 3–6 cm long (including the peduncle and rachis), covered with ferruginous granular trichomes, spike prophyll caducous, flower prophyll usually persistent during anthesis. **Flowers** monoclinous; calyx pentamerous, gamosepalous, 0.8–1 mm long, campanulate, pubescent; corolla pentamerous, gamopetalous, 3–4 mm long, cohered for at least ½ of its length, narrow-campanulate, pubescent; androecium with 10 stamens, anthers with a caducous apical gland. **Fruit** a follicle, sessile or subsessile, 4–7 × 1–1.5 cm, subfalcate, sparsely covered with ferruginous granular trichomes, valves coriaceous, dark brown. **Seeds** obovate, white. Fig. 3.

Geographic distribution and habitat. A monospecific genus distributed in seasonally dry forests of Mexico, Honduras, Venezuela, Brazil, Bolivia, Paraguay and Argentina (Fig. 7).

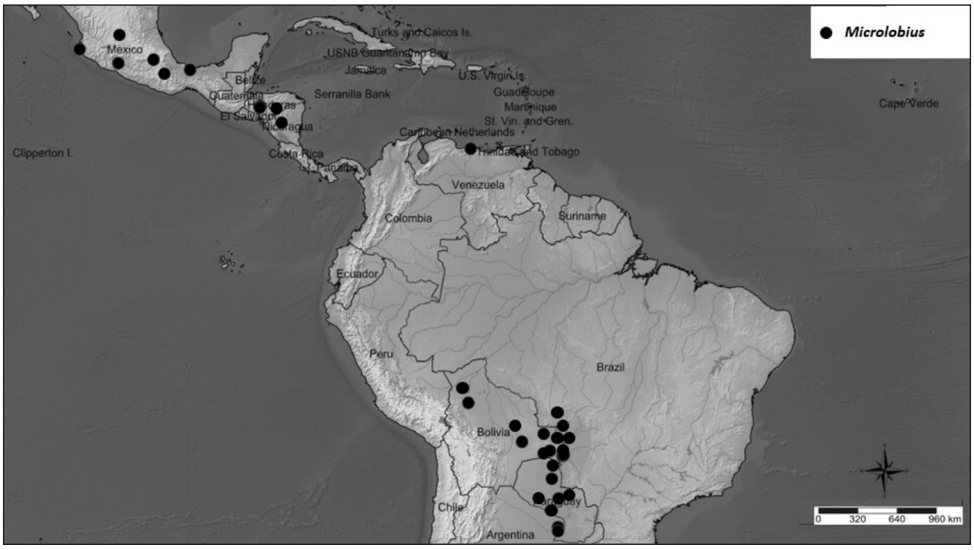

Figure 7. Distribution of *Microlobius foetidus*.

Etymology. From *micro-* (small) and *lobion-* (pods) in reference to the relatively small fruits, a noteworthy characteristic of *Microlobius* compared to closely related genera.

1.1 *Microlobius foetidus* (Jacq.) M. Sousa & G. Andrade, Anales Inst. Biol. Univ. Nac. Autón. México, Bot. 63(1): 104. 1992.

Mimosa foetida Jacq., Pl. Hort. Schoenbr. 3: 73. 1798. Type. [illustration] "*Mimosa fœtida* T. 390" in Jacquin, Pl. Hort. Schoenbr. 3, t. 390. 1798 (lectotype, designated here).
Inga foetida (Jacq.) Willd., Sp. Pl. Editio quarta 4(2): 1008. 1806.
Acacia foetida (Jacq.) Kunth, Nov. Gen. Sp. (quarto ed.) 6: 265. 1823.
Piptadenia foetida (Jacq.) Benth., Trans. Linn. Soc. London 30(3): 366. 1875.
Goldmania foetida (Jacq.) Standl., Contr. U.S. Natl. Herb. 23(2): 354. 1922.
Microlobius mimosoides C. Presl, Abh. Königl. Böhm. Ges. Wiss. ser. 5, 3: 497. 1845. Type. Mexico. *Habitat in Mexico*, 1791, *Haenke s.n.* (holotype: PRC 452782!).
Goldmania platycarpa Rose, Mém. Soc. Phys. Genève 4: 274. 1903. Type. Mexico, Culiacan, Sinaloa, 19 Mar 1899, *E.A. Goldman 371* (holotype: US360292! [catalog] US00001026! [barcode], isotype: GH00066208!).
Piptadenia platycarpa (Rose) J.F. Macbr., Contr. Gray Herb. 59: 18. 1919.

Notes. The protologue of *Mimosa foetida* ("*crescit in India Occidentali. In caldario floret Junio & Julio*") suggests that Jacquin had the plant growing in a heated greenhouse in the gardens of Schönbrunn Palace. However, it is not possible to know whether he based his description on a dried specimen from the Americas or on the

plant cultivated in Vienna. According to Stafleu and Cowan (1979), Jacquin "certainly made herbarium material of Austrian plants and plants in the gardens under his care" and they "are present in small numbers in a number of herbaria". His West Indies samples (which were acquired by Sir Joseph Banks), however, are very difficult to locate and it is not known if Jacquin made sizeable collections there; his specimens in the Banks herbarium (BM) are rare and consist of fragmentary specimens (Stafleu and Cowan 1979). The origin of the seeds that arrived in Vienna is also questionable, as there are currently no records of the species occurring in the Antilles, and the seeds were most probably gathered in eastern Mexico. We were unable to find any specimen that could be recognized as a type in the herbaria listed by Stafleu and Cowan (1979) and other collections, confirming Sousa and Andrade´s (1992) previous searches ("*holotipo W, no encontrado*"). For this reason, we select the colored plate accompanying the description of the species as the lectotype of *Mimosa foetida*.

Based on variable features and a very small sample of South American plants, Sousa and Andrade (1992) recognized the North/Central and South American disjunct populations of the genus as two subspecies (Fig. 7). It is not our objective to evaluate infraspecific taxa, so we opted to maintain the circumscription of *Microlobius foetidus* as currently accepted.

1.1.1 *Microlobius foetidus* (Jacq.) M. Sousa & G. Andrade subsp. *foetidus*.

1.1.2 *Microlobius foetidus* subsp. *paraguensis* (Benth.) M. Sousa & G. Andrade, Anales Inst. Biol. Univ. Nac. Autón. México, Bot. 63(1): 106. 1992.

Goldmania paraguensis (Benth.) Brenan, Kew Bull. 10(2): 178. 1955.

Piptadenia quadrifolia N.E. Br., 20: 53. 1894. Trans. & Proc. Bot. Soc. Edinburgh. Type. Paraguay. Rio Pilcomayo expedition, a small tree abundant in the isolated patches of monte around Fortin Page, 01 Sep 1890, *J.G. Kerr 1* (holotype: K000504735!).

Basionym. *Pithecellobium paraguense* Benth., Trans. Linn. Soc. London 30(3): 574. 1875.

Type. Paraguay. Monte Claro, 10 Jun 1858, *M. Gibert 39* (holotype: K000504734!).

Piptadenia paraguensis (Benth.) Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 24(3/7): 36. 1898.

Notes. Stafleu and Cowan (1976) mentioned that Gibert´s collections are distributed in several European, Argentine and Uruguayan herbaria, but we only found a single specimen of *M. Gibert 39*, housed at K. Since the Kew Herbarium includes that of Bentham, we indicate this specimen as the holotype of *Pithecellobium paraguense*. Many South American herbaria, which are still not digitized, may house Gibert's collections, including isotypes of *P. paraguense*.

2. *Gwilymia* A.G. Lima, Paula-Souza & Scalon, gen. nov.
urn:lsid:ipni.org:names:77303770-1

Type. *Gwilymia paniculata* (Poepp. & Endl.) A.G. Lima, Paula-Souza & Scalon ≡ *Stryphnodendron paniculatum* Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 81. 1845).

Diagnosis. *Gwilymia* is similar to *Microlobius*, but it differs in having branches and leaves without a garlic odour (*vs*. a strong garlic odour in *Microlobius*); leaves with 2–4 (–6) pairs of pinnae (*vs*. 1–2 pairs of pinnae); each pinna with at least 3 pairs of leaflets (*vs.* a single pair of leaflets); extrafloral nectary present on the petiole or, in *G. coriacea* and *G. fissurata*, on the branch directly below the insertion of the petiole (*vs.* extrafloral nectary absent on the petiole and on the branch); inflorescence usually a compound thyrse (*vs*. always a simple thyrse); spikes 4–20 cm long (*vs.* 3–6 cm long); fruit an indehiscent (nucoid) legume 12–14 × 2–2.5 cm (*vs.* a follicle 6–7 × 1–1.5 cm), and brown or ochre seeds (*vs*. white seeds). *Gwilymia* also resembles *Stryphnodendron*, but it differs in leaves with 2–4 (–6) pairs of pinnae (*vs.* (3–) 5–32 pairs of pinnae in *Stryphnodendron*), opposite leaflets, 2.5–16 × 1.5–8 cm (*vs*. alternate, 0.6–1.2 × 0.3–0.6 cm), inflorescence usually a compound thyrse (*vs.* always a simple thyrse).

Description. Trees 2.5–40 m tall. **Branches** unarmed, not odoriferous, smooth, usually lenticellate, young shoots and leaves glabrescent, pubescent, or tomentose and covered with reddish granular trichomes. **Stipules** caducous. **Leaves** bipinnate, petiolar nectary 1 (absent in *G. coriacea* and *G. fissurata*), 0.5–2 mm long, conical, lenticular or verruciform, positioned at the base or apex of the petiole; rachis 7–23 cm long, rachis nectaries 1–4, 0.5–2.5 mm long, conical, lenticular, patelliform or verruciform, inserted between the pairs of pinnae or just below them; pinnae in 2–4 (–6) opposite or subopposite pairs, rachillae nectaries 1–5, patelliform or verruciform, inserted between or just below the distal pairs of leaflets; leaflets in 3–5 opposite pairs, 2.5–16 × 1.5–8 cm, broadly-oblong, elliptic, ovate or obovate, not odoriferous, no tuft of trichomes at the midrib base. **Inflorescence** a compound thyrse (diplothyrsi or pleiothyrsi, a simple thyrse in *G. coriacea* and *G. fissurata*), cymules in 2–5 spikes, spike 4–20 cm long (including peduncle and rachis), covered with ferruginous granular trichomes, inflorescence prophyll persistent (caducous in *G. coriacea* and *G. fissurata*), floral bracts usually persistent. **Flowers** monoclinous; calyx pentamerous, gamosepalous, ca. 0.5–1 mm long, campanulate, cupuliform or tubular, puberulent or pubescent; corolla pentamerous, gamopetalous, 2–5 mm long, cohered for at least ½ of its length, campanulate or tubular, glabrous, pubescent, or tomentose; stamens 10, anthers with a caducous apical gland. **Fruit** an indehiscent, nucoid legume, sessile, 12–14 × 2–2.5 cm, curved, falcate or spiralled (straight to slightly curved in *G. moricolor* and *G. racemifera*), laterally-compressed or sub-turgid, sparsely covered with ferruginous granular trichomes, valves woody or coriaceous, brown. **Seeds** elliptic, obovate, or orbicular, brown or ochre. Fig. 4.

Geographic distribution and habitat. *Gwilymia* species occur in the Amazon rainforest, seasonal forests and savannas of Bolivia, Brazil, French Guiana, Guyana, Suriname and Venezuela (Fig. 8).

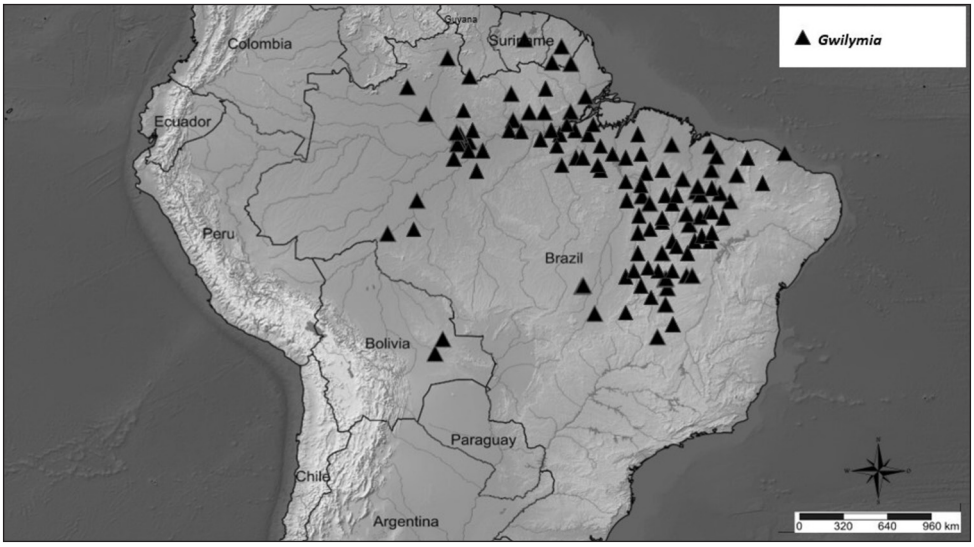

Figure 8. Distribution of *Gwilymia*.

Etymology. *Gwilymia* honors Dr. Gwilym Peter Lewis, one of the Royal Botanic Gardens Kew's most prominent botanists for his exceptional contributions to the advance of legume systematics.

Notes. *Gwilymia* comprises seven species formerly placed in *Stryphnodendron*, all of which have 2–4 (–6) pairs of pinnae, opposite leaflets, 2.5–16 × 1.5–8 cm, compound thyrses (except in *G. coriacea* and *G. fissurata*), and nucoid (indehiscent) legumes.

2.1 *Gwilymia coriacea* (Benth.) A.G. Lima, Paula-Souza & Scalon, comb. nov.

urn:lsid:ipni.org:names:77303771-1

Basionym. *Stryphnodendron coriaceum* Benth., Trans. Linn. Soc. London 30(3): 373. 1875.

Type. Brazil. Minas Gerais. "Fermoso provinciae Minas Geraes", s.d., *Martius 1820* (lectotype: M 0218783!, designated by Scalon et al. 2022; isolectotypes: F!, M!, MO!, NY!).

2.2 *Gwilymia fissurata* (E.M.O. Martins) A.G. Lima, Paula-Souza & Scalon, comb. nov.

urn:lsid:ipni.org:names:77303772-1

Basionym. *Stryphnodendron fissuratum* E.M.O. Martins, Revista Brasil. Biol. 40(4): 730. 1980.

Type. Brazil. Mato Grosso, "Habitat ad Município Barra do Garças, 265 km NNE de Xavantina, Serra do Roncador", s.d., *G. Eiten & L. Eiten 8956* (holotype: SP 129687!, isotypes: NY!, K!).

2.3 *Gwilymia moricolor* (Barneby & J.W. Grimes) A.G. Lima, Paula-Souza & Scalon, comb. nov.
urn:lsid:ipni.org:names:77303773-1

Basionym. *Stryphnodendron moricolor* Barneby & J.W. Grimes, Brittonia 36(1): 45. 1984.
Type. French Guiana. Saül, Monts La Fumée, 22 Nov 1982, *Mori & Boom 15236* (holotype: P 00077203! [transferred from CAY], isotypes: NY!, P 00710285!).

2.4 *Gwilymia occhioniana* (E.M.O. Martins) A.G. Lima, Paula-Souza & Scalon, comb. nov.
urn:lsid:ipni.org:names:77303774-1

Basionym. *Stryphnodendron occhionianum* E.M.O. Martins, Leandra 2(2): 121. 1972.
Type. Brazil. Pará, Rodovia Belém–Brasília km 306, 10 Mar 1960, *Oliveira 997* (holotype: IAN 106945!, isotypes: NY!, UB!).

2.5 *Gwilymia paniculata* (Poepp. & Endl.) A.G. Lima, Paula-Souza & Scalon, comb. nov.
urn:lsid:ipni.org:names:77303775-1

Piptadenia poeppigii Klotzsch ex Benth., Trans. Linn. Soc. London 30(3): 367. 1875.
Stryphnodendron rizzinianum E.M.O. Martins, Leandra 6(7): 92. 1975. Type. Brazil. Amazonas, Borba, "Habitat in silva ad flumen Madeira", 07 Nov 1935, *Ducke s.n.* (holotype: RB 29044!, isotypes: K!, OXF!, NY!, U!, *pro parte*, US!).

Basionym. *Stryphnodendron paniculatum* Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 81. 1845.
Type. Brazil. "Crescit in sylvis primaevis flumini Amazonum conterminis circum Ega [Tefé]", Nov 1834, *Poeppig 2783* (lectotype: W 0048790!, designated by Scalon et al. 2022; isolectotypes: G!, NY!, OXF!, P!, W 0048789!).

2.6 *Gwilymia polystachya* (Miq.) A.G. Lima, Paula-Souza & Scalon, comb. nov.
urn:lsid:ipni.org:names:77303776-1

Stryphnodendron polystachyum (Miq.) Kleinhoonte, Recueil Trav. Bot. Néerl. 22: 416. 1926.
Piptadenia tocantina Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 33. 1925. Type. Brazil. Pará, "Habitat in silva primaria non inundata infra stationen Arumateua viae ferreae Alcobacensis in regione fluminis Tocantins civitate Pará", 14 Jul 1916, *Ducke s.n.* (holotype: MG 16252!, isotypes: G!, K!, P!, RB!).

Basionym. *Piptadenia polystachya* Miq., Linnaea 18: 590. 1845.
Type. Suriname, "Crescit prope Bergendaal", September, *collector unknown s.n.* (holotype: U 52627–A!).

2.7 *Gwilymia racemifera* (Ducke) A.G. Lima, Paula-Souza & Scalon, comb. nov.
urn:lsid:ipni.org:names:77303779-1

Stryphnodendron racemiferum (Ducke) W.A. Rodrigues, Ciência e Cultura 21(2): 438. 1969.

Basionym. *Piptadenia racemifera* Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 124. 1930.

Type. Brazil. Amazonas, Maués, Rio Curuçá, 16 Dec 1927, *Ducke s.n.* (holotype: RB 20188!; isotypes: U!, US!).

3. *Naiadendron* A.G. Lima, Paula-Souza & Scalon, gen. nov.
urn:lsid:ipni.org:names:77303777-1

Type. *Naiadendron duckeanum* (Occhioni) A.G. Lima, Paula-Souza & Scalon ≡ *Stryphnodendron duckeanum* Occhioni f., Revista Brasil. Biol. 19: 209. 1959).

Diagnosis. *Naiadendron* is closely related to *Stryphnodendron*, but it differs in having strongly striate branches (*vs.* smooth or only slightly striate in *Stryphnodendron*), a petiolar nectary 8–12 mm long (*vs.* 0.5–2 mm long), leaflets inserted in opposite pairs (*vs.* alternate pairs), fruit a legume, valves dehiscing along both sutures (*vs.* fruit an indehiscent, nucoid legume or follicle). The genus differs from *Piptadenia* in having unarmed branches (*vs*. armed branches in *Piptadenia*) and ferruginous granular trichomes on branches and leaves (*vs*. ferruginous granular trichomes absent).

Description. Trees 8–30 m tall; branches unarmed, strongly striate, castaneous, apex yellow-tomentose and covered with ferruginous granular trichomes, not odoriferous. **Stipules** caducous. **Leaves** bipinnate, petiole yellow-puberulent or yellow-tomentulose, sparsely covered with ferruginous granular trichomes, petiolar nectary 1, 8–12 mm long, narrowly oblong, positioned at the base of the petiole; rachis 10–23 cm long, yellow-puberulent or yellow-tomentulose, sparsely covered with ferruginous granular trichomes, rachis nectary 1, ca. 2 mm long, oblong, inserted below the distal pair of pinnae; pinnae in 10–22 subopposite to opposite pairs, rachilla nectary 1, 1 × 0.4 mm, oblong, secretory, inserted below the distal pair of leaflets; leaflets in 15–23 opposite pairs, 0.6–1.2 × 0.3–0.5 cm, oblong, elliptic or sometimes obovate, no tuft of trichomes at the base on the abaxial surface, not odoriferous. **Inflorescence** a simple thyrse formed by cymules of 3–5 spikes, spike 4–7 cm long (peduncle plus rachis), covered with ferruginous granular trichomes, spike prophyll caducous, flower prophyll usually caducous. **Flowers** monoclinous; calyx pentamerous, gamosepalous, ca. 0.5 mm long, campanulate, puberulent; corolla pentamerous, gamopetalous, 1.8–2 mm long, cohered for ⅓ of its length, narrow-campanulate, yellow-tomentulose; androecium with 10 stamens, anthers with a caducous apical gland. **Fruit** a legume (dehiscent along both margins), peduncle 1.3–2 cm long, fruit body 12–15 × 2–2.5 cm, linear to narrow-oblong, laterally-compressed sparsely covered with ferruginous granular trichomes, chartaceous, brown. **Seeds** obovate to elliptic, ochre colored. Fig. 3.

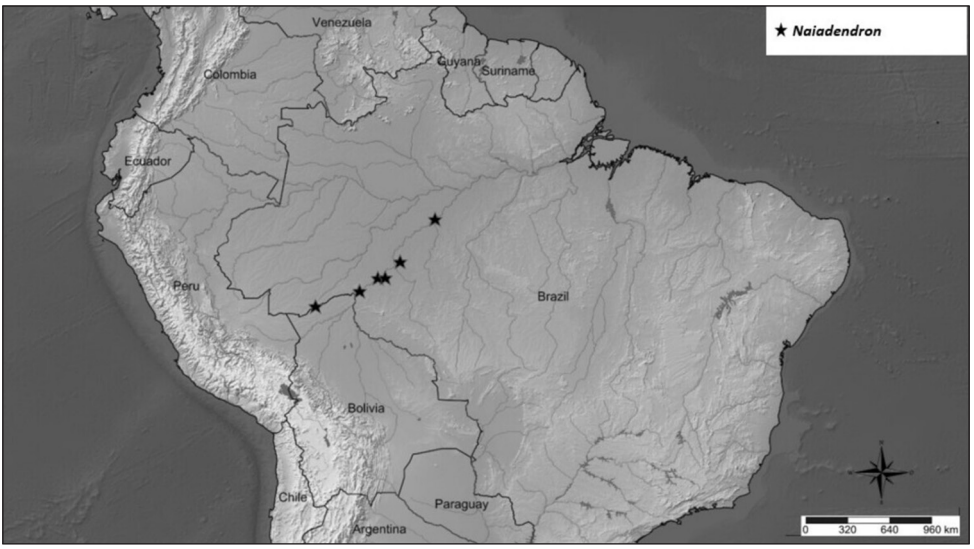

Figure 9. Distribution of *Naiadendron duckeanum*.

Geographic distribution and habitat. *Naiadendron* is endemic to the Amazon rainforest, being recorded from the Brazilian states of Acre, Amazonas and Rondônia. It grows on clay or sandy soil in ombrophilous and *terra firme* forests (Fig. 9).

Etymology. The name *Naiadendron* celebrates the Amazon rainforest and the legacy of Carl Friedrich Philipp von Martius (1794–1868), who named the Brazilian Amazon after the Naiads, Greek mythology's nymphs of freshwater.

Notes. Strongly striate branches, a petiolar nectary 8–12 mm long, and the fruit a legume (valves dehiscing along both margins) are the main diagnostic morphological characteristics of *Naiadendron*.

Occhioni (1959) described *Stryphnodendron duckeanum*, based only on flowering specimens, and pointed out its morphological similarity to *S. guianense*. However, both morphological (Scalon 2007; Lima et al. 2021; Scalon et al. 2022) and phylogenetic evidence (Simon et al. 2016; Ribeiro et al. 2018) have indicated that *S. duckeanum* should be recognized as an independent taxon, now named as the new genus *Naiadendron*.

3.1 *Naiadendron duckeanum* (Occhioni) A.G. Lima, Paula-Souza & Scalon, comb. nov.

urn:lsid:ipni.org:names:77303778-1

Basionym. *Stryphnodendron duckeanum* Occhioni f., Revista Brasil. Biol. 19: 209. 1959.

Type. Brazil. Rondônia, Porto Velho, Rio Madeira, Amazonas, 09 Jun 1936, *Ducke s.n.* (lectotype: RFA 11684!, designated by Scalon et al. 2022; isolectotype: US!).

4. *Stryphnodendron* Mart., Flora 20(2): Beibl. 117. 1837.

Folianthera Raf., Sylva Tellur.: 120. 1838. Type. *Folianthera guianensis* (Aubl.) Raf. [= *Stryphnodendron guianense* (Aubl.) Benth.].

Type. *Stryphnodendron barbadetiman* (Vell.) Mart. [= *Stryphnodendron adstringens* (Mart.) Coville].

Description. Trees, shrubs, or subshrubs, 0.25–45 m tall; branches unarmed, smooth or slightly striate, usually lenticellate, glabrescent, pubescent, tomentose, velutinous or villous, apex covered with ferruginous granular trichomes, not odoriferous. **Stipules** usually caducous **Leaves** bipinnate, petiole glabrescent, pubescent, tomentose, velutinous or villous, covered with ferruginous granular trichomes, petiolar nectary 1, 0.5–2 mm long, verruciform, conical, fusiform, lenticular or patelliform, positioned at the base or sometimes at the apex of the petiole; rachis 10–25 cm long, glabrescent, pubescent, tomentose, velutinous or villous, ferruginous-pulverulent, rachis nectaries 1–5, 0.5–3 mm long, conical, lenticular, patelliform or verruciform, inserted between the pairs of pinnae or just below them; pinnae in (3–) 5–32 subopposite, opposite or rarely alternate pairs, rachilla nectaries 1–5, conical, patelliform or verruciform, inserted between or just below the distal pairs of leaflets, leaflets in 8–20 alternate pairs, 0.6–1.2 × 0.3–0.6 cm, oblong, elliptic or sometimes obovate, a tuft of trichomes usually present at the base on the abaxial surface, not odoriferous. **Inflorescence** a simple thyrse formed by cymules of 2–6 spikes, spike 7–18 cm long (including peduncle and rachis), covered with ferruginous granular trichomes, spike prophyll caducous, flower prophyll usually caducous. **Flowers** monoclinous or rarely diclinous (only staminate flowers observed), calyx pentamerous, gamosepalous, 0.5–1 mm long, campanulate, cupuliform or tubular, glabrous, pubescent, puberulent, ciliate, tomentose, or villous; corolla pentamerous, gamopetalous 2.5–5 mm long, cohered for at least ½ of its length, campanulate, cupuliform or tubular, glabrous, pubescent, puberulent, tomentulose, tomentose, or villous; androecium with 10 stamens, anthers with apical gland caducous. **Fruit** a nucoid legume (indehiscent) or follicle, sessile, 8–14 × 2–3.5 cm, linear, oblong, or slightly curved, laterally compressed or turgid, sparsely covered with ferruginous granular trichomes, valves woody or coriaceous, brown. **Seeds** obovate to elliptic, black, brown, or ochre. Figs 5, 6.

Geographic distribution and habitat. *Stryphnodendron* is a neotropical genus with its northern limit in Nicaragua and southern limit in the Brazilian state of Paraná. *Stryphnodendron* species occur in several vegetation types, and are especially frequent in savannas and in the Amazonian forest (Fig. 10).

Etymology. The name *Stryphnodendron* comes from *stryphnos-* (adstringent) and *dendron-* (tree) and is a reference to the astringent properties of its tannin-rich bark.

Notes. *Stryphnodendron* was first described by Martius (1837) based on three species: *S. barbadetiman* (Vell.) Mart., *S. polyphyllum* Mart. and *S. rotundifolium* Mart.

Figure 10. Distribution of *Stryphnodendron*.

The genus subsequently received a more detailed description and a broader circumscription by Bentham (1841, 1875, 1876), and currently comprises 28 species.

The genus can be recognized by a suite of characters: unarmed branches, ferruginous granular trichomes on young shoots and leaves, caducous stipules, leaves with (3–)5–32 pairs of pinnae; leaflets 0.6–1.2 × 0.3–0.6 cm, inflorescence always a simple thyrse, and the fruit a nucoid (indehiscent) legume or follicle.

Stryphnodendron differs from *Microlobius* in having branches and leaves lacking a garlic odour (vs. branches and leaves with a strong garlic odour in *Microlobius*), leaves with (3–)5–32 pairs of pinnae (vs. leaves with 1–2 (–3) pairs of pinnae), alternate leaflets (vs. opposite leaflets), an extrafloral nectary present on the petiole (vs. extrafloral nectary absent on the petiole), brown or ochre seeds (vs. white seeds). The morphological distinctiveness and diagnosability among *Stryphnodendron*, *Gwilymia* and *Naiadendron* are addressed above.

4.1 *Stryphnodendron adstringens* (Mart.) Coville, Century Dict. 11: 111. 1910.

Mimosa barbadetiman Vell., Fl. Flumin. Icon. 11: 7. 29 Oct 1831. Type. [icon ined.] "Polyg. Monoec.: MIMOSA barbadetimao Tab. 7" (Manuscript Sect. of Torre do Tombo, Lisbon PT-TT-MSLIV-2780_m0021; icon ined. copy in Manuscript Sect., Bibliot. Nac., Rio de Janeiro No. I-17, 06, 001, mss1198660_011. Lectotype, designated by Scalon et al. 2022).

Stryphnodendron barbadetiman (Vell.) Mart., Flora 20(2): Beibl. 117. 1837 ("*barbatiman*").

Basionym. *Acacia adstringens* Mart., Reise Bras. 2: 548. 1828.

Type. Brazil. Minas Gerais. "Habitat in campus agrestibus, Minas Geraes, Serro Frio ad Tejuco et alibi parfim", May, *Martius s.n.* (holotype: M 0218791!).

4.2 *Stryphnodendron barbatulum* Rizzini & Heringer, Revista Brasil. Biol. 47(3): 449. 1987.

Stryphnodendron sallesianum Heringer & Rizzini, Revista Brasil. Biol. 47: 450. 1987. Type. Brazil. Distrito Federal, Brasília, Barragem do Torto, 11 Nov 1985, *Salles 388* (holotype: RB 288834!, isotype: RB!).

Type. Brazil. Distrito Federal, Brasília, Barragem do Torto, 14 Sep 1985, *Salles & Heringer 241* (holotype: RB 288833!).

4.3 *Stryphnodendron confertum* Heringer & Rizzini, Anais Acad. Brasil. Ci. 38(Suppl.): 104. 1966.

Type. Brazil. Distrito Federal. Brasília, Parque Nacional de Brasília, 10 Sep 1963, *Heringer 9178* (holotype: RB 118803!, isotypes: HB!, K!, M!, NY!, RFA!, UB!).

4.4 *Stryphnodendron conicum* Scalon, Phytotaxa 544(3): 237. 2022.

Type. Brazil. Pará, Oriximiná, Área de Mineração Rio Norte, 5 km da vila residencial, 1°28'S, 56°23'W, 11 Nov 1987, *C.A. Cid Ferreira 9548* (holotype: INPA 155605!, isotypes: F!, K!, MO!, NY!, RB!, US!).

4.5. *Stryphnodendron cristalinae* Heringer, Anais Acad. Brasil. Ci. 40: 234. 1968.

Stryphnodendron campestre Forero, Brittonia 24(2): 143. 1972. Type. Brazil. Goiás, "Serra dos Christaës", 1818, *Pohl 847* (holotype: NY00003371!, isotypes: F!, MO!, W!).

Type. Brazil. Goiás, Cristalina, elev. 1350 m, 15 Aug 1967, *E.P. Heringer 11182* (holotype: RB 132217!, isotypes: HB! K! MG! UB!).

4.6 *Stryphnodendron dryaticum* Scalon, Phytotaxa 544(3): 240. 2022.

Type. Brazil. Rio de Janeiro, Macaé, estrada para Glicério, ca. 2 km do Córrego do Ouro, 42°04'W, 22°13'S, 23 Jun 1987, *Lima et al. 2988* (holotype: RB 265629!, isotype: MBM!).

4.7 *Stryphnodendron excelsum* Harms, Repert. Spec. Nov. Regni Veg. 19(4–7): 64. 1923.

Type. Costa Rica. Atlant. Küste, Savannen und Wälder am Rio Hondo, elev. 150–300 m, Jun 1903, *Pittier 16997* (lectotype: G 00367833!, designated by Scalon et al. 2022; isolectotypes: US!, NY!).

4.8 *Stryphnodendron flavotomentosum* A.G. Lima & V.C. Souza, Syst. Bot. 46(1): 70. 2021.

Type. Brazil. Espírito Santo, Baixo Guandú, Fazenda Galiléia, no barranco do rio próximo a estrada do Mutum Preto em Baixo Guandu, lado esquerdo, 11 Dec 1991, *D.A. Folli 1519* (holotype: ESA 108191!, isotypes: CVRD!, VIES!).

4.9 *Stryphnodendron foreroi* E.M.O. Martins, Contr. Univ. Michigan Herb. 14: 83. 1980.

Type. Brazil. Rondônia, track from Mutumparaná to rio Madeira, 30 Nov 1968, *Prance et al. 8995* (holotype: MG 039652!, isotypes: F!, NY!, R!, S!, US!).

4.10 *Stryphnodendron glandulosum* (Forero) Scalon, Phytotaxa 544(3): 245. 2022.

Basionym. *Stryphnodendron guianense* (Aubl.) Benth. subsp. *glandulosum* Forero, Brittonia 24(2): 145. 1972.

Type. Brazil. Pará, "Museu Paraense, Cult. et Peruvia orientalis (Rio Huallaga J. Huber anno 1898)", Sep 1936, *A. Ducke 274* (holotype: NY 00003368!, isotypes: K!, R!, US!).

4.11 *Stryphnodendron gracile* Heringer & Rizzini, Anais Acad. Brasil. Ci. 38(Suppl.): 105. 1966.

Type. Brazil. Minas Gerais, Serra do Cipó, 12 Nov 1959, *Heringer 7361* (lectotype: RB00584092!, designated by Scalon et al. 2022; isolectotypes: NY!, UB!).

4.12 *Stryphnodendron guianense* (Aubl.) Benth., Trans. Linn. Soc. London 30(3): 374. 1875.

Acacia guianensis (Aubl.) Willd., Sp. Pl. 4(2): 1061. 1806.
Folianthera guianensis (Aubl.) Raf., Sylva Tellur. 120. 1838.

Piptadenia guianensis (Aubl.) Benth., J. Bot. (Hooker) 4(30): 335. 1841.
Stryphnodendron purpureum Ducke, Arch. Jard. Bot. Rio de Janeiro 1(1): 16. 1915. Type. Brazil. "Alcobaça ad fluvium Tocantins, in sylvis secundariis terrae argillosae rubrae valde frequens", 28 Dec 1914, *Ducke s.n.* (holotype: MG 15556!, isotypes: BM!, G!, S!, US!).

Basionym. *Mimosa guianensis* Aubl., Hist. Pl. Guiane 2: 938. 1775.
Type. French Guiana, "Habitat in sylvis Caïenna & Guiana", s.d., *Aublet s.n.* (holotype: BM001135589!).

4.13 *Stryphnodendron heringeri* Occhioni f., Bol. Mus. Bot. Kuhlmann 8(1): 63. 1985.

Type. Brazil. Goiás, Alto Paraíso de Goiás, a ca. 87 km ao N da cidade, 30 Oct 1979, Equipe IBGE ["*Heringer*"] *2636* (holotype: IBGE 15208!, isotypes: HB!, K!, MO!, NY!, RB!, UEC!).

4.14 *Stryphnodendron holosericeum* Scalon, Phytotaxa 544(3): 247. 2022.

Type. Brazil. Minas Gerais, Formoso, Parque Nacional Grande Sertão Veredas, margem esquerda do Rio Preto, 05 Nov 1989, *Walter et al. 510* (holotype: RB 375879!, isotypes: ESA! IBGE!, K!, RFA!).

4.15 *Stryphnodendron levelii* R.S. Cowan, Mem. New York Bot. Gard. 10(1): 144. 1958.

Type. Venezuela. Ter. Fed. Amazonas, Cano Guazuriapana, Rio Atabapo near San Fernando de Atabapo, 16 May 1954, *Level 104* (holotype: NY 3369!, isotype: F!, K!, US!, VEN).

4.16 *Stryphnodendron microstachyum* Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 82. 1845.

Type. Brazil. "Crescit in sylvis primaevis flumini Amazonum conterminis circum Ega [Tefé]", Oct 1831, *Poeppig 2738* (holotype: W 0002775!).

4.17 *Stryphnodendron orinocense* Scalon, Phytotaxa 544(3): 252. 2022.

Type. Venezuela. Território Amazonas, Rio Orinoco, along left bank of river just below mouth of Rio Ventuari, 125–150 m, 16 Jun 1959, *Wurdack & Adderley 42999* (holotype: IAN 114608!, isotypes: F!, K!, NY!, U!, US!).

4.18 *Stryphnodendron platycarpum* Scalon,Phytotaxa 544(3): 254. 2022.

Type. PERU. Loreto, Requena, bosque inundable, ca. 800 m de la Base Yarina, margen derecha del caño Yarina, en la Zona Reservada del río Pacaya, margen izquierda del Río Ucayali, 22 Mar 1977, *Encarnación E–1071* (holotype: G 0252076!, isotypes: K!, US!).

4.19 *Stryphnodendron platyspicum* Rizzini & Heringer, Anais Acad. Brasil. Ci. 38(Suppl.): 106. 1966.

Stryphnodendron pumilum Glaz., Bull. Soc. Bot. France 53 Mem. 3b: 177. 1906, *opus utiq. oppr.*

Type. Brazil. Distrito Federal, Brasília, "Crescit ad campos in Goiás", 5 Nov 1961, *Heringer 8733* (holotype: RB 113247!, isotypes: HB!, R!, UB!).

4.20 *Stryphnodendron polyphyllum* Mart., Flora 20(2): Beibl. 117. 1837.

Type. Brazil. Minas Gerais, "Minas", s.d., *Martius 1102* (lectotype: M 0218780!, designated by Scalon et al. 2022; isolectotypes: BR!, G!, K!, P!).

4.21 *Stryphnodendron porcatum* D.A. Neill. & Occhioni f., Ann. Missouri Bot. Gard. 76(1): 357. 1989.

Type. Ecuador. Napo, 1 km N of Coca, 00°25'S, 77°00'W, 15 Sep 1986, *Neill & Palacios 7359* (holotype: QCNE 233!, isotypes: G!, INPA!, K!, MO!, NY!, RFA!, US!).

4.22 *Stryphnodendron procerum* Scalon, Phytotaxa 544(3): 260. 2022.

Type. Brazil. Amazonas, Maraã, Rio Japurá, margem esquerda, Lago Maraã, 29 Oct 1982, *Amaral et al. 232* (holotype: INPA 106613!, isotypes: K!, MG!, MO!, NY!, UB!, US!).

4.23 *Stryphnodendron pulcherrimum* (Willd.) Hochr., Bull. New York Bot. Gard. 6(21): 274. 1910.

Mimosa pulcherrima (Willd.) Poir., Encycl., Suppl. 1(1): 66. 1810.
Piptadenia foliolosa Benth., J. Bot. (Hooker) 4(30): 336. 1841. Type. Brazil. Amazonas river, s.d., *Poeppig 2776* (lectotype: F0360538F!, designated by Scalon et al. 2022).

Stryphnodendron floribundum Benth., J. Bot. (Hooker) 4(31): 343. 1841. Type. Brazil. s.d., *Gardner 986* (lectotype: K 000090447!, designated by Scalon et al. 2022; isolectotypes: BM!, E!, G!, GH!, NY!, OXF!, P!).

Stryphnodendron angustum Benth., Trans. Linn. Soc. London 30(3): 375. 1875. Type. Brazil. Amazonas, "prope Barra do Rio Negro", s.d., *Martius Obs. 2758* / *Obs. 2578* (lectotype: M 0218774!, designated by Scalon et al. 2022; isolectotypes: M 0218773!, M 0218775!, M 0218776!).

Stryphnodendron melinonis Sagot, Ann. Sci. Nat., Bot., sér. 6, 13: 322. 1882. Type. Guiana Francesa, "in sylvis Maroni", s.d., *Mélinon s.n.* (lectotype: P 00199449!, designated by Scalon et al. 2022; isolectotypes: BM!, E!, F!, K!, P 00199447! P 00199448!).

Stryphnodendron guianense f. *floribundum* (Benth.) Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 250. 1925.

Piptadenia cobi Rizzini & A. Mattos, Anais Acad. Brasil. Ci. 40: 233. 1966. Type. Brazil. Bahia, Oct 1939, *Menezes* ["*Moisés*"] *135* (holotype: RB 55432!, isotype: K!).

Basionym. *Acacia pulcherrima* Willd., Sp. Pl. 4(2): 1061. 1806.

Type. Brazil. "Habitat in provincia Para Brasiliae", s.d., *Hoffmannsegg s.n.* (holotype: B-W 19136!).

4.24 *Stryphnodendron riparium* Scalon, Phytotaxa 544(3): 265. 2022.

Stryphnodendron inaequale Benth., Trans. Linn. Soc. London 30(3): 374. 1875, *pro syn.*

Type. Brazil. Amazonas, Rio Solimões, ca. 1 km ao sul da Vila Careiro, 23 Aug 1973, *C.C. Berg et al. 1971*1 (holotype: INPA 43195!, isotypes: F!, K!, MG!, MO!, NY!, R!, RFA!).

4.25 *Stryphnodendron roseiflorum* (Ducke) Ducke, Bol. Tecn. Inst. Agron. N. 2: 8. 1944.

Basionym. *Stryphnodendron guianense* (Aubl.) Benth. subsp. *guianense* var. *roseiflorum* Ducke, Arch. Jard. Bot. Rio de Janeiro 6: 15. 1933.

Type. Brazil. Amazonas, "Frequens in sylvis secundariis siccioribus circa Manaos", 22 Jun 1929, *Ducke s.n.* (lectotype: RB 10406/ 00540075!, designated by Occhioni-Martins 1981; isolectotypes: G!, K!, US!).

4.26 *Stryphnodendron rotundifolium* Mart., Flora 20(2): Beibl. 117. 1837.

Type. Brazil. Piauí, "Oeiras, Prov. Piauhy", s.d., *Martius s.n.* (holotype: M 0218772!).

4.26.1 *Stryphnodendron rotundifolium* Mart. var. *rotundifolium*.

Stryphnodendron discolor Benth., J. Bot. (Hooker) 4(31): 342. 1841. Type. Brazil. Piauí, "Serra de Araripe, near Caldas, Prov. Piauhy", 1838–1841, *Gardner 1945* (lectotype: BM 000884631!, designated by Scalon et al. 2022; isolectotypes: E!, F!, G!, K!, NY!, OXF!, P!, W!).

Stryphnodendron obovatum Benth., Trans. Linn. Soc. London 30(3): 374. 1875. Type. Brazil. "Habitat inter Natividade et Porto Imperial, provinciae Goyaz", May 1865, *Burchell 8343* (lectotype: K 000504730!, designated by Scalon et al. 2022; isolectotypes: F!, P!).

Stryphnodendron rotundifolium f. *retusa* Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 4(6): 559. 1904. Type. Paraguay. "In campis cerrados in regione cursus superioris fluminis Apa", Nov 1901–1902, *Hassler 7829* (lectotype: G 00400140!, designated by Scalon et al. 2022; isolectotypes: A, F!, G 00400103!, G 00400106!, G 00400108!, K!, MPU, NY!, P!, W!).

4.26.2 *Stryphnodendron rotundifolium* var. *villosum* (Benth.) Scalon, Phytotaxa 544(3): 269. 2022.

Stryphnodendron goyazense Taub., Bot. Jahrb. Syst. 21(4): 434. 1896. Type. Brazil. "Habitat in locis Cerrados dictis prope Meiaponte", Oct 1892, *Ule 2836* (lectotype: HBG 506635!, designated by Borges et al. 2018; isolectotype: P! [2], R!).

Stryphnodendron humile E.M.O. Martins, Leandra 6–7(7): 19. 1977. Type. Brazil. Minas Gerais, João Pinheiro, via Brasília-Minas, 30 Nov 1960, *Heringer 7783* (holotype: RFA 18438!; isotype: IAN!).

Basionym. *Stryphnodendron polyphyllum* var. *villosum* Benth., Fl. Bras. 15(2): 285. 1876. **Type.** Brazil. "Prov. Sao Paulo", s.d., *Burchell 5600* (lectotype: K 000504733!, designated by Scalon et al. 2022; isolectotypes: GH, P!).

4.27 *Stryphnodendron velutinum* Scalon, Phytotaxa 544(3): 269. 2022.

Type. Brazil. Minas Gerais, Unaí, fragmento de cerradão no km 11 da rodovia Unaí/Paracatú, elev. 650 m, 16°15'S, 46°45'W, 22 Oct 1995, *Pereira & Alvarenga 2943* (holotype: IBGE 36575!; isotypes: CEN!, NY!, RB!, RFA!).

4.28 *Stryphnodendron venosum* Scalon, Phytotaxa 544(3): 272. 2022.

Type. Bolivia. Santa Cruz: Ichilo, Reserva Florestal Choré, Rio Ibabo, Bosque Experimental "Elias Meneces", 180 m, 16°35'S, 64°31'W, 16–18 Aug 1990, fr., *D. Neill & R. Quevedo 9361* (holotype: MO 3807891!; isotypes: G!, NY!, U!).

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Appendix 1

Voucher information for sequence data used in the phylogenetic analyses, all of which come from Koenen et al. (2020), Ringelberg et al. (2022) and Simon et al. (2016).

Supplementary material 1

Figures S1–S18

Authors: Alexandre Gibau de Lima, Juliana de Paula-Souza, Jens Ringelberg, Marcelo Fragomeni Simon, Luciano Paganucci de Queiroz, Leonardo M. Borges, Vidal de Freitas Mansano, Vinicius Castro Souza, Viviane Renata Scalon

Data type: Phylogenetic

Explanation note: Figure S1. Phylogeny of mimosoid legumes based on combined transcriptome and hybrid capture data. Figures S2–S18. Optimization of characters 1–17 of Simon et al. (2016) over the 50% majority-rule consensus tree obtained in Bayesian analysis of molecular data.

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Supplementary material 2

Table S1

Authors: Alexandre Gibau de Lima, Juliana de Paula-Souza, Jens Ringelberg, Marcelo Fragomeni Simon, Luciano Paganucci de Queiroz, Leonardo M. Borges, Vidal de Freitas Mansano, Vinicius Castro Souza, Viviane Renata Scalon

Data type: Phylogenetic

Explanation note: List of taxa and voucher information used in the phylogenomic analyses.

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Misleading fruits: The non-monophyly of *Pseudopiptadenia* and *Pityrocarpa* supports generic re-circumscriptions and a new genus within mimosoid legumes

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Abstract

Generic delimitation in *Piptadenia* and allies (mimosoid legumes) has been in a state of flux, particularly caused by over-reliance on fruit and seed morphology to segregate species out of *Piptadenia* into the genera *Parapiptadenia*, *Pityrocarpa* and *Pseudopiptadenia*. Although supporting their segregation from *Piptadenia*, previous phylogenetic analyses suggested that some of these segregated genera are not monophyletic. Here, we test the monophyly of *Parapiptadenia*, *Pityrocarpa* and *Pseudopiptadenia* with dense taxon sampling across these genera, including the type species of each genus. Our analysis recovers *Parapitadenia* as monophyletic, but places *Pseudopiptadenia* species in two distinct lineages, one of which includes all three species of *Pityrocarpa*. Given that the type species of both *Pseudopiptadenia* and *Pityrocarpa* are nested in the same clade, we subsume *Pseudopiptadenia* under the older name *Pityrocarpa*. The remaining *Pseudopiptadenia* species are assigned to the new genus *Marlimorimia*. Alongside high molecular phylogenetic support, recognition of *Parapiptadenia*, *Pityrocarpa* and *Marlimorimia* as distinct genera is also supported by combinations of morphological traits, several of which were previously overlooked.

Keywords

Caesalpinioideae, Fabaceae, Leguminosae, *Parapiptadenia*, Stryphnodendron clade, tropical America

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Introduction

Generic delimitation in the mimosoid legumes is being continually revised, notably across the informal Piptadenia group sensu Lewis and Elias (1981), which included *Anadenanthera* Speg., *Microlobius* C. Presl, *Mimosa* L., *Parapiptadenia* Brenan, *Piptadenia* Benth., *Pityrocarpa* (Benth.) Britton & Rose, *Pseudopiptadenia* Rauschert and *Stryphnodendron* Mart. Most of the proposed generic re-circumscriptions within the Piptadenia group have involved segregating species out of *Piptadenia*, which was morphologically poorly-defined (Brenan 1955) and is known to be polyphyletic (Luckow et al. 2003; Jobson and Luckow 2007; Simon et al. 2016; Ribeiro et al. 2018). While previous phylogenetic and phylogenomic analyses confirm the segregation of *Parapiptadenia*, *Pityrocarpa* and *Pseudopiptadenia* and place them together with *Stryphnodendron* and *Microlobius* in the Stryphnodendron clade sensu Koenen et al. (2020), the monophyly of these three genera is still uncertain because of incomplete taxon sampling in previous analyses (Simon et al. 2016; Koenen et al. 2020; Ringelberg et al. 2022).

Species of *Parapiptadenia*, *Pityrocarpa* and *Pseudopiptadenia* are trees inhabiting Neotropical rain forests and seasonally dry tropical forests and woodlands (SDTFWs sensu Queiroz et al. 2017), with the majority of species in South America and just two taxa in North America (*Pi. obliqua* (Pers.) Brenan var. *obliqua* and *Ps. psilostachya* (DC.) G.P. Lewis & M.P. Lima) (Brenan 1955, 1963; Rauschert 1982; Lima and Lima 1984; Lewis and Lima 1991; Queiroz 2009). Their bipinnate leaves vary widely in the number of pinnae, as well as leaflet number, size and shape. Flowers are pentamerous, dialipetalous or gamopetalous and arranged in elongated spikes. The diverse fruits and seeds have been the most prominent traits used to define each genus (Brenan 1955; Lewis and Elias 1981). *Parapiptadenia* includes six species with plano-compressed fruits opening along both sutures (typical legumes) and flat, compressed, narrowly-winged seeds lacking a pleurogram. Eleven species with similar seeds, but with follicles (fruits splitting along the upper suture only) were placed in *Pseudopiptadenia* (Rauschert 1982; Lewis and Lima 1991). The three species in *Pityrocarpa*, which was first proposed as a section of *Piptadenia* (Bentham 1842), differ from the other two genera by their regularly constricted moniliform legumes and lentiform whitish seeds with an U-shaped pleurogram (Jobson and Luckow 2007).

The first phylogenetic analysis including these three genera recovered each as monophyletic, with *Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima and *Ps. psilostachya* forming a clade sister to *Pityrocarpa* (three species sampled), while the relationship of *Parapiptadenia* (three species sampled) to other genera was uncertain (Fig. 1; Jobson and Luckow 2007). The relationships amongst these genera and the putative monophyly of *Pseudopiptadenia* were later questioned by analyses with larger DNA sequence datasets and increased taxon sampling (Simon et al. 2016; Ribeiro et al. 2018). In these analyses, *Parapiptadenia* (four species sampled) emerged as sister to a clade including all sampled species of *Pseudopiptadenia* (five species, including *Ps. contorta* and *Ps. psilostachya*), except *Ps. brenanii* G.P. Lewis & M.P. Lima, which

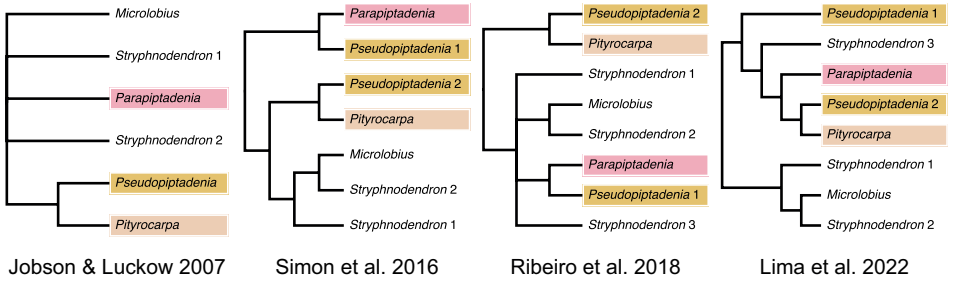

Figure 1. Topological differences amongst phylogenetic analyses of the Stryphnodendron clade.

was sister to *Pityrocarpa* (Fig. 1). This latter clade appeared more closely related to *Stryphnodendron* and *Microlobius* than to the group formed by *Parapiptadenia* and *Pseudopiptadenia.* Phylogenomic analyses with sparse taxonomic sampling recovered slightly different relationships between these three genera (Fig. 1), but reinforced the non-monophyly of *Pseudopiptadenia* (Lima et al. 2022; Ringelberg et al. 2022).

While it is clear that the non-monophyly of *Pseudopiptadenia* means that taxonomic adjustments are needed, the type species of the genus, *Ps. leptostachya*, has not been included in any previous phylogenetic analyses, raising doubts about its placement and, hence, about which generic name should be applied to the clade containing that species. In this study, we infer the phylogenetic relationships between *Parapiptadenia*, *Pityrocarpa* and *Pseudopiptadenia* using near-complete taxon sampling, including the type species of all three genera, and re-evaluate the circumscriptions of these genera, based on the resulting phylogenetic hypothesis.

Materials and methods

Phylogenetic inference

To further test the polyphyly of *Pseudopiptadenia* indicated by previous studies (Simon et al. 2016; Ribeiro et al. 2018; Ringelberg et al. 2022) and further investigate sister group relationships across the Stryphnodendron clade, we carried out phylogenetic analyses including near-complete sampling of species of *Parapiptadenia*, *Pityrocarpa*, *Pseudopiptadenia* and allies. Phylogenetic analyses were based on the nuclear ribosomal 5.8S subunit and internal transcribed spacer region (nrITS) and plastid regions *matK* and *trnD-trnT*. We generated 60 new sequences (21 nrITS, 23 *matK*, 16 *trnD-trnT*), including two accessions of *Ps. leptostachya*, the type species of *Pseudopiptadenia*, sampled here for the first time. Published sequences of other members of the Stryphnodendron clade and other genera were obtained from GenBank (Hughes et al. 2003; Simon et al. 2009; Simon et al. 2016; LPWG 2017; Ribeiro et al. 2018). Sampling comprised 60 accessions, including nine species (18 accessions) of *Pseudopiptadenia* (only

the poorly known *Ps. colombiana* and *Ps. pittieri* were not sampled), all three species of *Pityrocarpa* (six accessions), all six known species of *Parapipitadenia* (11 accessions), plus representatives of the allied genera *Microlobius* (monospecific; two accessions) and *Stryphnodendron* (14 accessions, including members of the three major lineages of this non-monophyletic genus; see Lima et al. 2022). A selection of mimosoid lineages closely related to the Stryphnodendron clade (Jobson and Luckow 2007; Simon et al. 2016; Ribeiro et al. 2018; Ringelberg et al. 2022) were included as outgroups. Voucher details and GenBank accession numbers are provided in Table 1 and in the Suppl. material 1.

Total DNA was extracted from about 20 mg of silica gel-dried leaf material using a modified CTAB-based protocol (Inglis et al. 2018a). We checked DNA quality and integrity using agarose gel electrophoresis and DNA quantity and purity estimated by Nanodrop spectrophotometry (Thermo Scientific). Laboratory procedures, primer sequences and amplification protocols followed Inglis et al. (2018b) for nrITS and Simon et al. (2016) for *matK* and *trnD-trnT*. PCR products were prepared for direct Sanger sequencing using ExoSAP (ThermoFisher) and both DNA strands were sequenced using the Big Dye v.3.1 kit (Applied Biosystems), using the amplification primers. We obtained further sequences included in the analysis from GenBank (Table 1).

We assembled contigs using Geneious Prime 2021 (https://www.geneious.com) and aligned matrices with MAFFT v.7 (Katoh and Standley 2013). Maximum Likelihood (ML) phylogenetic analysis was performed using IQ-TREE (Nguyen et al. 2015), using 1000 ultrafast bootstrap replicates to estimate branch support (Hoang et al. 2018) and models estimated with ModelFinder (Kalyaanamoorthy et al. 2017). Trees were drawn with FigTree (http://tree.bio.ed.ac.uk/software/figtree/) and rooted using *Lachesiodendron viridiflorum* (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow, following Ringelberg et al. (2022). Analyses of individual loci produced similar topologies, although the plastid trees were substantially less well-resolved compared to the nrITS phylogeny. In the absence of major incongruence between individual gene trees, we inferred phylogenetic relationships with a concatenated dataset (nrITS, *matK*, *trnD-trnT*) containing 3280 bp and 13% of missing data and used it as the basis for proposing taxonomic rearrangements.

Data Resources

The data underpinning the analysis reported in this paper are deposited in GitHub at https://doi.org/10.5281/zenodo.6611789

Results and discussion

Our densely sampled phylogenetic analysis recovers *Parapitadenia* as monophyletic, reinforces the non-monophyly of *Pseudopiptadenia* and shows that *Pityrocarpa* is also non-monophyletic (Fig. 2). Although the backbone of the phylogeny remains weakly-

Table 1. Voucher information and GenBank accession numbers for taxa used in this study. Newly-generated sequences are in bold. See the Suppl. material 1 for a digital version.

Taxon	Voucher	Herbarium	nrITS	*matK*	*trnD-trnT*
Inga edulis Mart.	*Queiroz 13797*; *Pennington 13282*	HUEFS; K	JX870764	AF523078	JQ417383
Lachesiodendron viridiflorum (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow	*Queiroz 13090*	HUEFS	MG001274	MG001286	MG001305
Microlobius foetidus (Jacq.) M. Sousa & G. Andrade	*Hughes 2150*	FHO	KT364047	KT364172	FJ981976
Microlobius foetidus (Jacq.) M. Sousa & G. Andrade	*Macqueen 432*	FHO	AF458783	AF523095	(No data)
Mimosa palmeri Rose	*Simon 823*	FHO	KT364059	KT364212	FJ982142
Mimosa pigra L.	*Hughes 2414*	FHO	KT364060	KT364213	FJ982148
Mimosa ursina Mart.	*Simon 704*	CEN	KT364061	KT364210	FJ982217
Parapiptadenia blanchetii (Benth.) Vaz & M.P. Lima	*Queiroz 15358*	HUEFS	**OM575100**	**ON409904**	**ON409927**
Parapiptadenia blanchetii (Benth.) Vaz & M.P. Lima	*Thomas 12372*	NY	**OM575099**	**ON409905**	(No data)
Parapiptadenia excelsa (Griseb.) Burkart	*Hughes 2425*	FHO	KT364062	KT364160	FJ982235
Parapiptadenia ilheusana G.P. Lewis	*Neves 1659*	RB	**OM575101**	KY046081	**ON409928**
Parapiptadenia pterosperma (Benth.) Brenan	*Cardoso 2359*	HUEFS	**OM575102**	**ON409906**	**ON409929**
Parapiptadenia pterosperma (Benth.) Brenan	*Ribeiro 902*	HUEFS	MG001260	**ON409910**	MG001292
Parapiptadenia rigida (Benth.) Brenan	*Marestoni 26*	HUEFS	MG001261	**ON409909**	(No data)
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima	*Cotarelli 2029*	HUEFS	**OM575104**	**ON409907**	(No data)
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima	*Pereira-Silva 3102*	CEN	KT364063	KT364063	KT364108
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima	*Queiroz 10974*	HUEFS	**OM575105**	**ON409908**	(No data)
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima	*Queiroz 15692*	HUEFS	**OM575106**	KX302341	(No data)
Piptadenia gonoacantha (Mart.) J.F. Macbr.	*Simon 735*	FHO	KT364065	DQ790620	FJ982238
Piptadenia stipulacea (Benth.) Ducke	*Simon 702*; *Queiroz 3115*	CEN; HUEFS	KT386296	DQ790634	FJ982239
Pityrocarpa leucoxylon (Barneby & J.W. Grimes) Luckow & R.W. Jobson	*Fernandez 2909*	NY	(No data)	DQ790622	(No data)
Pityrocarpa moniliformis (Benth.) Luckow & R.W. Jobson	*Melo 7518*	HUEFS	(No data)	**ON409911**	**ON409936**
Pityrocarpa moniliformis (Benth.) Luckow & R.W. Jobson	*Queiroz 9084*	HUEFS	ON191501	**ON409912**	(No data)
Pityrocarpa moniliformis (Benth.) Luckow & R.W. Jobson	*Way 2449*	K	KT364067	KT364162	FJ982242
Pityrocarpa obliqua (Pers.) Brenan subsp. *brasiliensis* (G.P. Lewis) Luckow & R.W. Jobson	*Queiroz 12903*	HUEFS	**ON191500**	**ON409920**	(No data)
Pityrocarpa obliqua (Pers.) Brenan subsp. *obliqua*	*Macqueen 439*	FHO	KT364068	KT364206	FJ982243
Pseudopiptadenia bahiana G.P. Lewis & M.P. Lima	*Melo 138*	HUEFS	**OM575115**	**ON409916**	**ON409930**
Pseudopiptadenia bahiana G.P. Lewis & M.P. Lima	*Queiroz 15381*	HUEFS	MG001277	MG001290	**ON409931**
Pseudopiptadenia bahiana G.P. Lewis & M.P. Lima	*Queiroz 15504*	HUEFS	**OM575114**	**ON409917**	**ON409932**
Pseudopiptadenia brenanii G.P. Lewis & M.P. Lima	*Borges 680*	SPF	KT364069	(No data)	KT364111
Pseudopiptadenia brenanii G.P. Lewis & M.P. Lima	*Cardoso 2807*	HUEFS	**OM575108**	**ON409914**	**ON409937**
Pseudopiptadenia brenanii G.P. Lewis & M.P. Lima	*Harley 56005*	HUEFS	**OM575109**	**ON409915**	(No data)
Pseudopiptadenia brenanii G.P. Lewis & M.P. Lima	*Queiroz 15585*	HUEFS	MG001278	**ON409913**	**ON409938**
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima	*Queiroz 15507*	HUEFS	(No data)	KT364155	KT364113
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima	*Queiroz 15582*	HUEFS	MG001279	KX302348	MG001308
Pseudopiptadenia inaequalis (Benth.) Rauschert	*Lima 7790*	RB	**OM575111**	**ON409921**	**ON409939**
Pseudopiptadenia leptostachya (Benth.) Rauschert	*Lima 8231*	RB	**OM575113**	**ON409922**	**ON409940**
Pseudopiptadenia leptostachya (Benth.) Rauschert	*Lima 8326*	RB	**OM575112**	**ON409923**	**ON409941**
Pseudopiptadenia psilostachya (DC.) G.P. Lewis & M.P. Lima	*Simon 1245*	CEN	KT364070	KT364170	KT364114
Pseudopiptadenia schumanniana (Taub.) G.P. Lewis & M.P. Lima	*Lima 7938*	RB	**OM575110**	**ON409924**	**ON409942**
Pseudopiptadenia sp.	*Neves 1675*	RB	**OM575116**	**ON409918**	**ON409933**
Pseudopiptadenia sp.	*Ribeiro 351*	HUEFS	**OM575117**	**ON409919**	(No data)
Pseudopiptadenia suaveolens (Miq.) J.W. Grimes = *P. psilostachya*	*Moacir & Clovis sn*	IAN	**OM575119**	**ON409925**	**ON409934**
Pseudopiptadenia warmingii (Benth.) G.P. Lewis & M.P. Lima	*Queiroz 12761*	HUEFS	**OM575118**	**ON409926**	**ON409935**
Senegalia macrostachya (Rchb. ex DC.) Kyal. & Boatwr.	*Miller 1322*	CANB	KY688790	KY688920	(No data)
Senegalia nigrescens (Oliv.) P.J.H. Hurter	*Maurin 255*	JRAL	JQ265858	GQ872237	(No data)
Stryphnodendron adstringens (Mart.) Coville	*Souza 29702*	ESA	KT364072	KT364198	KT364116
Stryphnodendron coriaceum Benth.	*Scalon 718*	ESA	(No data)	KT364200	KT364120
Stryphnodendron duckeanum Occhioni	*Simon 1343*	CEN	KT364076	(No data)	KT364122
Stryphnodendron fissuratum E.M.O. Martins	*Ivanauskas sn*	ESA	KT364077	KT364175	KT364124
Stryphnodendron foreroi E.M.O. Martins	*Assis 1143*	SPF	KT364079	KT364201	KT364126
Stryphnodendron gracile Rizzini & Heringer	*Scalon 458*	ESA	KT364080	KT364177	KT364127
Stryphnodendron obovatum Benth.	*Scalon 712*	ESA	KT364081	KT364182	KT364130
Stryphnodendron occhionianum E.M.O. Martins	*Simon 1597*	CEN	KT364083	(No data)	KT364132

Taxon	Voucher	Herbarium	nrITS	*matK*	*trnD-trnT*
Stryphnodendron paniculatum Poepp.	*Simon 1058*	CEN	KT364084	(No data)	KT364133
Stryphnodendron polyphyllum Mart.	*Mello-Silva 2659*	SPF	KT364086	KT364184	KT364136
Stryphnodendron pulcherrimum (Willd.) Hochr.	*Simon 980*	CEN	KT364087	(No data)	KT364137
Stryphnodendron roseiflorum (Ducke) Ducke	*Scalon 728*	ESA	KT364090	KT364193	KT364143
Stryphnodendron rotundifolium Mart.	*Scalon 715*	ESA	KT364094	KT364194	KT364147
Stryphnodendron velutinum Scalon	*Scalon 719*	ESA	KT364101	KT364187	KT364153

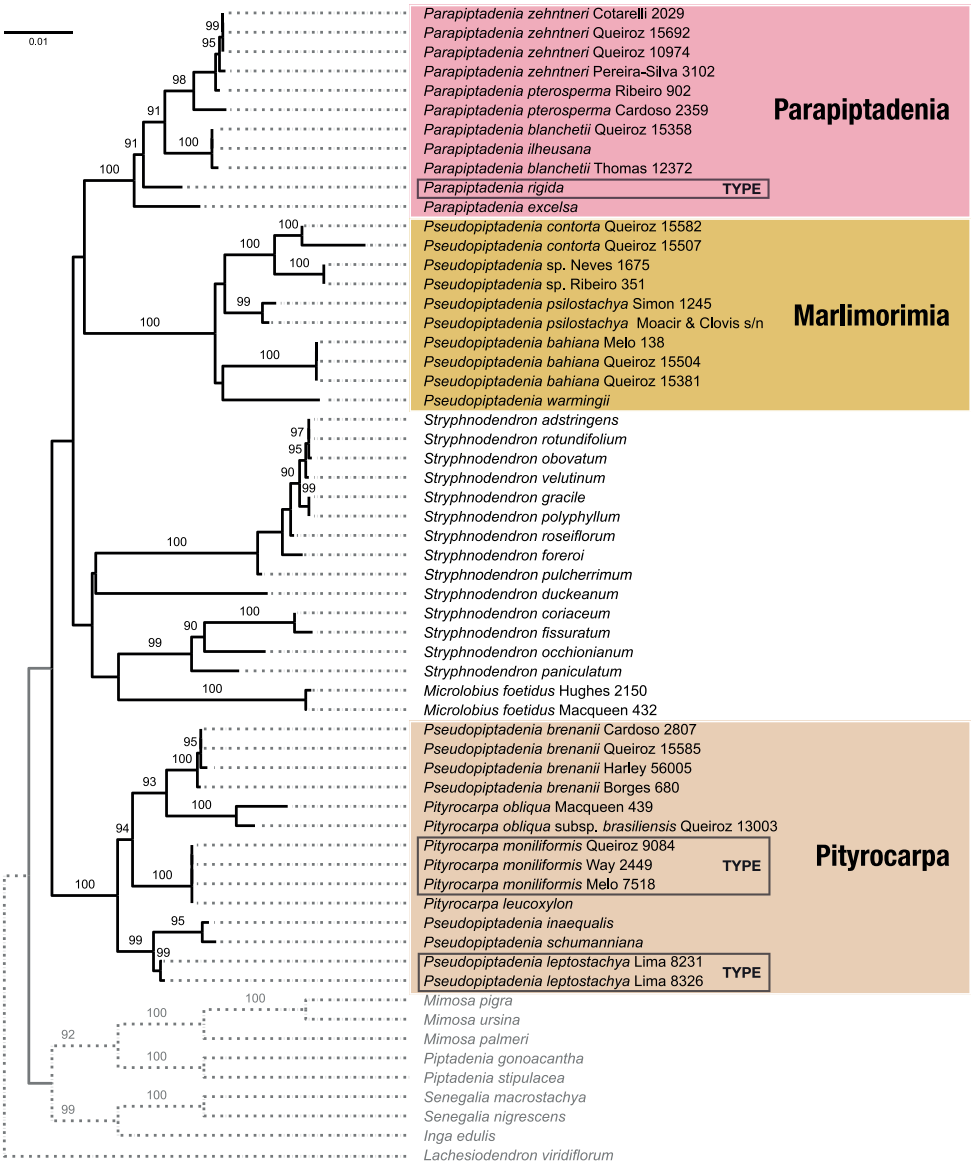

Figure 2. Phylogeny of the Stryphnodendron clade, based on Maximum Likelihood analysis of the concatenated nrITS, *matK* and *trnD-trnT* data. Significant ultrafast bootstrap values (> 90%) are given above branches. The tree was rooted using *Lachesiodendron viridiflorum*. Scale bar: expected number of changes per site; dotted branches not to scale.

supported, the three main clades relevant to the delimitation of genera and the taxonomic decisions proposed here have full (100%) bootstrap support.

The first clade, hereafter referred to as *Pseudopiptadenia pro parte*, includes *Ps. bahiana* G.P. Lewis & M.P. Lima, *Ps. contorta*, *Ps. psilostachya*, *Ps. warmingii* (Benth.) G.P. Lewis & M.P. Lima and a putative new species yet to be described. The second clade, hereafter referred to as the *Pityrocarpa* clade, encompasses the remaining *Pseudopiptadenia* species, including the type species of the genus, *Ps. leptostachya*, intermixed with accessions of the three species of *Pityrocarpa*, including *Pi. moniliformis* (Benth.) Luckow & R.W. Jobson, the type species of *Pityrocarpa*.

The placement of *Parapiptadenia*, *Pityrocarpa*, and *Pseudopiptadenia* species in three distinct lineages and the robustly supported monophyly of *Parapiptadenia* agree with previous phylogenetic analyses (Fig. 1; Simon et al. 2016; Ribeiro et al. 2018; Lima et al. 2022; Ringelberg et al. 2022). However, the relationships amongst these three clades and other members of the Stryphnodendron clade remain unclear, because of the lack of support across the backbone of the clade (Figs 1 and 2) and disagreement with previous analyses. For example, although analyses of nuclear and plastid data (Simon et al. 2016; Ribeiro et al. 2018) also placed *Pseudopiptadenia p.p.* and *Parapiptadenia* in the same clade, this group could be sister to the remainder of the Stryphnodendron clade (Simon et al. 2016) or sister to the clade comprising *Stryphnodendron* and *Microlobius* (Ribeiro et al. 2018). Phylogenomic analyses based on 997 nuclear genes (Lima et al. 2022; Ringelberg et al. 2022) placed *Pseudopiptadenia p.p.* as sister to a group including *Stryphnodendron duckeanum* Occhioni f. plus a clade formed by *Parapiptadenia* and the *Pityrocarpa* clade. Furthermore, these nodes across the backbone of the Stryphnodendron clade show high gene tree conflict (Ringelberg et al. 2022) coinciding with very short branches and weak support in both conventional and phylogenomic analyses, highlighting the difficulties of inferring relationships across this part of the mimosoid phylogeny.

Despite uncertainties regarding generic relationships, our results provide an additional example of how over-reliance on particular traits, in this case fruits and seeds (Brenan 1955; 1963; Lewis and Elias 1981), may lead to unnatural taxonomies. Presence of follicles and of flat and winged seeds, which were used to diagnose *Pseudopiptadenia*, are respectively shared by most lineages within the Stryphnodendron clade or homoplastic between *Pseudopiptadenia p.p.* and members of the *Pityrocarpa* clade. All this is not to say that fruits have no taxonomic significance, as the vast majority of *Parapiptadenia* species have distinctive legumes with valves plicate above the seeds, not seen in any other member of the Stryphnodendron clade. Nonetheless, most species in the *Pityrocarpa* clade, even though variable in seed morphology (flat and winged vs. lentiform and wingless), share a number of similarities, including the position of the extrafloral nectaries between or just below the first pair of pinnae; few pinnae pairs; inflorescence spikes in general solitary and axillary to coeval leaves; and bifoliolate seedlings (Fig. 3). These features are not shared with most *Pseudopiptadenia p.p.* species, which have extrafloral nectaries on the lower half of the petiole; many pairs of pinnae; inflorescence spikes arranged in complex efoliate synflorescences; and pinnate or bipinnate seedlings (see Table 2). Although fairly homogeneous within the *Pityrocarpa* clade and *Pseudopiptadenia p.p.*, the characters

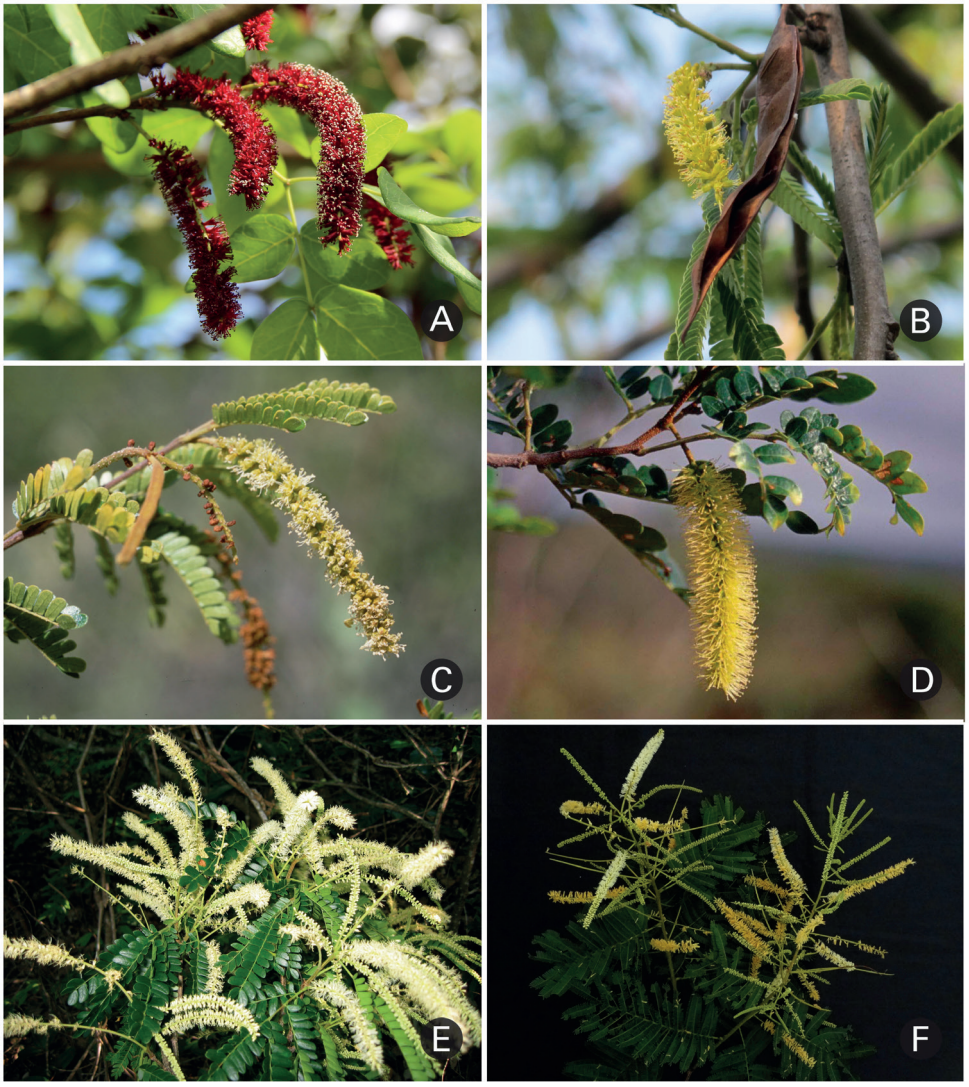

Figure 3. Inflorescences of *Parapiptadenia*, *Pityrocarpa* and *Marlimorimia* **A** *Parapiptadenia pterosperma* (Benth.) Brenan showing reddish inflorescences in the axils of coeval leaves **B** *Pa. rigida* (Benth.) Brenan showing yellowish inflorescences and fruits with valves plicate above the seeds **C** *Pityrocarpa brenanii* showing whitish, solitary spikes in the axils of coeval leaves **D** *Pi. moniliformis* showing yellowish, solitary spikes in the axil of a coeval leaf **E** *Marlimorimia bahiana* (G.P. Lewis & M.P. Lima) L.P. Queiroz & L.M. Borges, showing whitish spikes clustered in efoliate terminal pseudoracemes **F** *Marlimorimia sp*. showing yellowish spikes clustered in efoliate terminal pseudoracemes (Photos: **A** PG Ribeiro; **B** RT de Queiroz **C–E** LP Queiroz; **F** G Siqueira).

highlighted above sometimes vary amongst and within species, particularly in a context including *Parapiptadenia*. For example, solitary inflorescences occur in species of both *Parapiptadenia* and the *Pityrocarpa* clade, while *Pseudopiptadenia p.p.* species

Table 2. Morphological comparison amongst *Parapiptadenia*, *Pityrocarpa* and *Marlimorimia*. Traits in bold highlight diagnostic features separating *Pityrocarpa* and *Marlimorimia*. EFN - Extrafloral nectary.

	Parapiptadenia	***Pityrocarpa***	***Marlimorimia***
Pinnae number	1–8	1–4 (rarely to 5 in *Pi. brenanii*)	5–10 or more (2–5 in *M. bahiana* and *M. colombiana*)
Petiolar EFN position	Variable across species	**Between or just below the first pair of pinnae**	**Between the base and the middle of the petiole**
Spike arrangement	Solitary, axillary or supra-axillary to coeval leaves	**Solitary (very rarely up to 2 in *Pi. moniliformis*), axillary to coeval leaves**	**2–many fasciculate and further arranged in efoliate terminal pseudoracemes or on efoliate nodes below mature leaves**
Petals	Reddish (yellowish in *Pa. excelsa* and *Pa. rigida*); united at the base (free in *Pa. rigida*)	**White to yellowish or greenish; free and glabrous (united in *Pi. leucoxylon*)**	**White to yellowish or greenish; united and pubescent**
Fruit type (dehiscence)	Legume	Follicle	Follicle
Fruit shape	Flat compressed, valves plicate above the seeds (except in Pa. excelsa)	Flat compressed, valves not plicate above the seeds	Flat compressed, valves not plicate above the seeds
Fruit margins	Straight to shallowly sinuous	**Deeply constricted (moniliform) (sinuous in *P. brenanii*).**	**Straight, (shallowly and irregularly sinuous in *M. bahiana*, *M. colombiana* and *M. warmingii*), sometimes constricted where seeds abort**
Valve consistency and indumentum	Thin, chartaceous, glabrous	**Thick, coriaceous, mostly pubescent**	**Thin, coriaceous (thicker and harder in *M. warmingii*), glabrous**
Embryo plumule	Developed and multifid	**Rudimentary (developed and multifid in *P. brenanii*)**	**Developed and multifid**
Seedling eophylls	Pinnate	**Bifoliolate**	**Pinnate or bipinnate**

sometimes do not have spikes arranged in complex synflorescences (e.g. particular specimens of *Ps. bahiana* and *Ps. contorta*). Nonetheless, taken together, the traits highlighted here provide better recognition of these lineages as distinct genera than fruit morphology alone.

These results from phylogenetic and morphological analyses provide robust support for re-circumscription of *Pseudopiptadenia* as it was traditionally conceived and also *Pityrocarpa*. Given that the type species of these two genera are nested in the same clade and that no morphological traits support the recognition of a narrow circumscription of *Pseudopiptadenia*, we subsume the name *Pseudopiptadenia* under *Pityrocarpa*, the oldest validly published generic name (Britton and Rose 1928; Lewis and Lima 1991; Turland et al. 2018). We assign the remaining *Pseudopiptadenia* species to the new genus *Marlimorimia*.

Key to the genera Parapiptadenia, Pityrocarpa, and Marlimorimia. See Lima et al. (2022) for a key to all genera of the Stryphnodendron clade

1 Petals reddish (yellowish in *Pa. excelsa* and *Pa. rigida*); fruit a legume (dehiscing along both sutures), the valves plicate above the seeds (except in *Pa. excelsa*) . ..... ***Parapiptadenia***

– Petals white to yellowish or greenish; fruit a follicle (splitting along one suture only), the valves not plicate above the seeds **2**

2 Petiolar nectary just below or between the first pair of pinnae; spikes solitary in axils of coevally developing leaves; petals free (united in *Pi. leucoxylon*) and

glabrous; fruit margins deeply constricted (sinuous in *Pi. brenanii*)..... .....***Pityrocarpa***

– Petiolar nectary between the base and the middle of the petiole; spikes 2-many-fasciculate, the fascicles usually arranged in efoliate terminal pseudoracemes or on efoliate nodes below the leaves; petals united and pubescent; fruit margins straight or shallowly and irregularly sinuous, sometimes constricted where seeds abort..... ***Marlimorimia***

Taxonomy

1. *Pityrocarpa* (Benth.) Britton & Rose, N. Amer. Fl. 23(3): 190. 1928.

Monoschisma Brenan, *Kew Bull.* 10(2): 179. 1955, *nom. inval.*, non *Monoschisma* Duby, Mém. Soc. Phys. Genève 19: 294. 1868. Type. *Monoschisma leptostachyum* (Benth.) Brenan, syn. nov.

Pseudopiptadenia Rauschert, Taxon 31(3): 559. 1982. Type. *Pseudopiptadenia leptostachya* (Benth.) Rauschert, syn. nov.

Basionym. *Piptadenia* sect. *Pityrocarpa* Benth., J. Bot. (Hooker) 4: 339. 1842.

Type. *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson [≡ *Piptadenia moniliformis* Benth., designated by Britton and Rose 1928].

Description. Unarmed trees or shrubs. *Leaves* bipinnate; petiole with an extrafloral nectary between or shortly below the first pair of pinnae; pinnae 1–4 (5) pairs, exceptionally to 10 pairs in *Pi. leptostachya*; leaflets 1–10 pairs per pinna, rarely to 20 pairs (*Pi. brenanii* and *Pi. leptostachya*), mostly rhomboid sometimes also asymmetrically elliptical or lanceolate. *Inflorescences* spikes, solitary in the axils of coeval leaves, commonly pendulous. *Flowers* pentamerous; petals free (except possibly *Pi. leucoxylon*), glabrous; stamens 10, anther gland present; ovary shortly stipitate and included within or exserted from the corolla. *Fruit* a follicle, dehiscing along the lower suture, flat compressed, mostly moniliform, the margins deeply and regularly constricted, rarely sinuous margins and shallowly constricted (*Pi. brenanii* and occasionally in *Pi. leucoxylon*); valves stiffly coriaceous. *Seeds* mostly flat compressed with a coriaceous testa and a narrow marginal wing, lacking a pleurogram or, less frequently, ovoid or discoid with a hard, whitish testa, wingless and with a 'U'-shaped pleurogram (*Pi. leucoxylon*, *Pi. moniliformis* and *Pi. obliqua*); embryo with a rudimentary plumule (except *Pi. brenanii*). *Seedlings* with bifoliolate eophylls.

Distribution. *Pityrocarpa* is distributed in tropical America, from Mexico to southern Brazil and Paraguay. Most species occur in the Brazilian Atlantic rainforests (*Pi. inaequalis*, *Pi. leptostachya*, *Pi. schumanniana*), in the northern Amazonian rainforests (*Pi. leucoxylon*), in seasonally dry tropical forests and woodlands in the north-eastern Brazilian Caatinga (*Pi. brenanii*, *Pi. moniliformis*, *Pi. obliqua* subsp. *brasiliensis*), western Mexico (*Pi. obliqua* subsp. *obliqua*) or in Venezuelan savannas and Paraguayan Chaco (*Pi. moniliformis*).

Notes. As circumscribed here, *Pityrocarpa* includes seven species, all with a moniliform fruit, with the margins deeply constricted between the seeds (Fig. 4). This

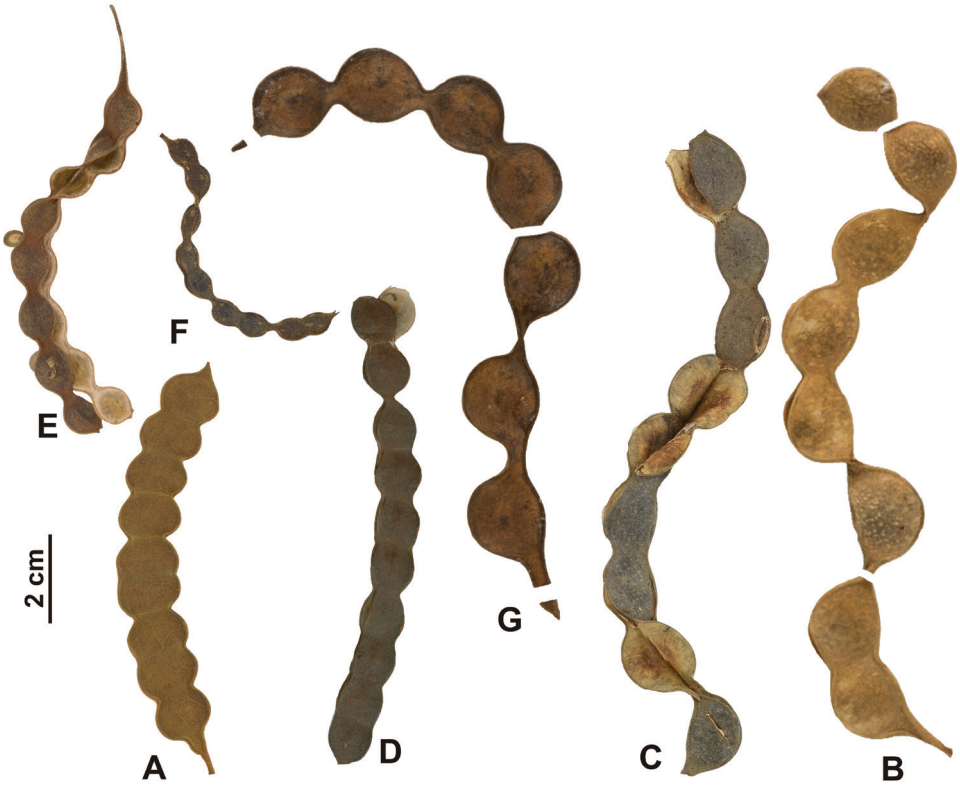

Figure 4. Fruits of *Pityrocarpa* species **A** *Pi. brenanii* (from *Lewis et al. 1899*, NY) **B** *Pi. inaequalis* (from *Moreira et al. 3*, F) **C** *Pi. leptostachya* (from *Baez et al. 1174*, NY) **D** *Pi. leucoxylon* (from *de Bruijn 1750*, NY) **E** *Pi. moniliformis* (from *Nunes 597*, HUEFS) **F** *Pi. obliqua* subsp. *brasiliensis* (from *Mori 11837*, NY) **G** *Pi. schumanniana* (from *Lima 2994*, RB).

trait is shared by species formerly included in *Pityrocarpa* (sensu Jobson and Luckow 2007) and some species previously placed in the genus *Pseudopiptadenia* (sensu Lewis and Lima 1991). These two genera had been separated based on seed morphology, *Pityrocarpa* characterised by ovoid or discoid seeds with a hard, whitish seed coat and a 'U'-shaped pleurogram, while *Pseudopiptadenia* included species with flat compressed and narrowly winged seeds with a coriaceous testa lacking a pleurogram. *Pityrocarpa brenanii* and *Pi. leucoxylon* have fruits with only shallowly sinuous margins, more similar to species of the genus *Marlimorimia*.

Besides sharing these fruit traits, *Pityrocarpa* species also have leaves with few pinnae (1 to 4 [5] pairs, rarely up to 10 pairs in *Pi. leptostachya*) and relatively large rhomboid leaflets compared to species of *Marlimorimia*. One exception are the leaves of *Pi. brenanii*, which are similar to those of *M. bahiana*. All species of *Pityrocarpa* present an extrafloral nectary between or shortly below the first pair of pinnae, in contrast to species of *Marlimorimia* that have the nectary below mid-petiole, frequently close to the pulvinus.

Floral traits, although previously disregarded as being generically diagnostic in the group, provide further evidence for the distinction between *Pityrocarpa* and *Marlimorimia*. The solitary inflorescence spikes in the axils of coevally developing leaves in *Pityrocarpa* contrast with the more complex synflorescences of *Marlimorimia* (Fig. 3; see notes under *Marlimorimia*). All species of *Pityrocarpa* have free and glabrous petals, except for *Pi. leucoxylon*, in which the petals are connate for a little over 1 mm (Barneby and Grimes 1984).

Lima (1985) and Lewis and Lima (1991) provided additional information on embryos and seedlings that are potentially useful for distinguishing *Pityrocarpa* from *Marlimorimia*. Embryos of *Pityrocarpa* species have a rudimentary plumule, while in *Marlimorimia*, the plumule is developed and multifid. This seems to be correlated with seedling morphology as the studied species of *Pityrocarpa* have bifoliolate eophylls and those of *Marlimorimia* species have pinnate or bipinnate eophylls (Lewis and Lima 1991). *Pityrocarpa brenanii*, however, has embryo morphology more similar to that reported for species of *Marlimorimia* (Lewis and Lima 1991).

1.1. *Pityrocarpa brenanii* (G.P. Lewis & M.P. Lima) L.P. Queiroz & L.M. Borges, comb. nov.

urn:lsid:ipni.org:names:77303780-1

Basionym. *Pseudopiptadenia brenanii* G.P. Lewis & M.P. Lima, Arch. Jard. Bot. Rio de Janeiro 30: 50–51. 1991.

Type. Brasil, Bahia, *Harley et al. 21346* (holotype CEPEC; isotypes BR, K, M, MBM, MEXU, NY, RB, US).

1.2. *Pityrocarpa inaequalis* (Benth.) L.P. Queiroz & Marc.F. Simon, comb. nov.

urn:lsid:ipni.org:names:77303781-1

Monoschisma inaequale (Benth.) Brenan, Kew Bull. 10(2): 179. 1955.
Pseudopiptadenia inaequalis (Benth.) Rauschert, Taxon 31(3): 559. 1982.

Basionym. *Piptadenia inaequalis* Benth., J. Bot. (Hooker) 4: 339. 1842.

Type. Brazil, Rio de Janeiro, *Pohl 1386* (lectotype K 000504704, designated here; isolectotype K 000504706).

1.3. *Pityrocarpa leptostachya* (Benth.) L.P. Queiroz & P.G. Ribeiro, comb. nov.

urn:lsid:ipni.org:names:77303782-1

Monoschisma leptostachyum (Benth.) Brenan, Kew Bull. 10(2): 179. 1955.
Pseudopiptadenia leptostachya (Benth.) Rauschert, Taxon 31(3): 559. 1982.

Basionym. *Piptadenia leptostachya* Benth., J. Bot. (Hooker) 4: 339. 1842.

Type. Brasil, *Sellow s.n.* (Lectotype K 000504709, designated here; isolectoypes F 0360957F [fragment], K 000504710, TUB 009699).

Note. Lewis and Lima (1991) unintentionally lectotypified this name by indicating the holotype to be at B and the isotype to be at K. However, the B specimen was destroyed and, hence, cannot serve as a lectotype. Moreover, K holds two duplicates of an un-numbered Sellow collection. Here, we chose the one previously belonging to Bentham's herbarium as the lectotype.

1.4. *Pityrocarpa leucoxylon* (Barneby & J.W. Grimes) Luckow & R.W. Jobson, Syst. Bot. 32(3): 573. 2007.

Basionym. *Piptadenia leucoxylon* Barneby & J.W. Grimes, Brittonia 36(3): 236–238. 1984.

Type. Venezuela: Bolivar, *de Bruijn 1750* (holotype NY; isotypes MO, VEN, US).

1.5. *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson, Syst. Bot. 32(3): 573. 2007.

Stryphnodendron piptadenioides E.M.O. Martins, Leandra 5(6): 90. 1975. Type. Brazil. Pernambuco, "lectum in silva pluviali ad S. José Belmonte", Mata da Mina, 29 Oct 1971, *Ramalho 52* (holotype RFA 17173) .

Stryphnodendron consimile E.M.O. Martins, Leandra 5(6): 92. 1975. Type. Brazil. Piauí, "habitat in caatinga ad Paulistana", Fazenda Altamira, 04 Nov 1974, *Lima 1330* (holotype RFA 17172).

Basionym. *Piptadenia moniliformis* Benth., *J. Bot.* (Hooker) 4: 339. 1842.

Type. Brazil, Bahia, Serra de Jacobina, *Blanchet 2701* (lectotype K 000090193, designated here; isolectotypes F, K 000205897, MO, NY 00003233).

1.6. *Pityrocarpa obliqua* (Pers.) Brenan, Kew Bull. 10(2): 176. 1955.

Acacia thibaudiana DC., Prodr. 2: 456. 1825.

Piptadenia obliqua (Pers.) J.F. Macbr., Contr. Gray Herb. 59: 17. 1919.

Basionym. *Sophora obliqua* Pers., Syn. P*l.* 1: 452. 1805.

Type. "Amer. australi?", Herb. D. Thibaud. (not located).

1.6.1. *Pityrocarpa obliqua* subsp. *obliqua*

1.6.2. *Pityrocarpa obliqua* subsp. *brasiliensis* (G.P. Lewis) Luckow & R.W. Jobson, Syst. Bot. 32(3): 573. 2007.

Basionym. *Piptadenia obliqua* subsp. *brasiliensis* G.P. Lewis, *Kew Bull.* 46(1): 160–162. 1991.

Type. Brazil, Bahia, *Mori et al. 9519* (holotype CEPEC; isotypes HUEFS, K, NY).

1.7. *Pityrocarpa schumanniana* (Taub.) L.P. Queiroz & L.M. Borges, comb. nov.
urn:lsid:ipni.org:names:77303784-1

Pseudopiptadenia schumanniana (Taub.) G.P. Lewis & M.P. Lima, Arch. Jard. Bot. Rio de Janeiro 30: 53. 1991.

Basionym. *Piptadenia schumanniana* Taub., *Flora* 75: 75. 1892.

Type. Brazil, "Brasilia austro-orientale", Rio de Janeiro, *Glaziou 13774* (lectotype R 00008369, designated here; isolectotypes A 00064056, F 0058675F, K 000504703, MPU 016109, NY 00003244, NY 00003245, US 00001018, US 00997081).

2. *Marlimorimia* L.P. Queiroz, L.M. Borges, Marc.F. Simon & P.G. Ribeiro, gen. nov.
urn:lsid:ipni.org:names:77303785-1

Newtonia sect. *Neonewtonia* Burkart, Fl. Il. Catarin. fasc. LEGU: 285. 1979, syn. nov. Type. *Newtonia nitida* (Benth.) Brenan (= *Marlimorimia contorta* (DC.) L.P. Queiroz & P.G. Ribeiro).

Diagnosis. *Marlimorimia* shares with *Pityrocarpa* the follicle, a fruit dehiscing along the lower suture only, and flat, compressed winged seeds, which lack a pleurogram. It can be differentiated from *Pityrocarpa* by the position of the extrafloral nectary on the petiole (from the base to the mid-petiole in *Marlimorimia* vs. between or just below the first pair of pinnae in *Pityrocarpa*); inflorescence spikes clustered in terminal pseudoracemes or in fascicles at efoliate nodes, surpassed by mature leaves (vs. solitary spikes in the axils of coeval leaves); petals united and joined into a gamopetalous corolla (vs. petals free and glabrous); and fruits with margins straight to shallowly sinuous (vs. margins deeply constricted).

Type. *Marlimorimia contorta* (DC.) L.P. Queiroz & P.G. Ribeiro

Description. Unarmed trees. *Leaves* bipinnate; petiole with an extrafloral nectary well below the first pair of pinnae, close to the pulvinus, always below mid-petiole; pinnae 5–10 to many pairs per leaf (2–3 pairs in *M. colombiana* and 3–5 in *M. bahiana*); leaflets mostly > 10 pairs per pinna, (6–8 in *M. colombiana*), mostly oblong to linear from an asymmetrical base, rarely rhomboid (*M. bahiana*). *Inflorescences* spikes, grouped in fascicles, these being arranged in terminal pseudoracemes or forming clusters below the coeval leaves. *Flowers* pentamerous; petals united into a gamopetalous corolla, pubescent; stamens 10, anther gland present; ovary shortly stipitate and included

or exserted from the corolla. *Fruit* a follicle, dehiscing along the lower suture, flat compressed, straight, curved or longitudinally twisted, the margins usually straight, rarely irregularly sinuous and only becoming constricted where the seeds fail to develop (*M. bahiana* and *M. warmingii*), valves coriaceous, thin or thick. *Seeds* flat compressed with a coriaceous testa, presenting a narrow or somewhat wider marginal wing, pleurogram lacking; embryo with a developed, multifid plumule (unknown in *M. colombiana* and *M. pittieri*). *Seedlings* with pinnate or bipinnate eophylls (unknown in *M. bahiana*, *M. colombiana* and *M. pittieri*).

Distribution. *Marlimorimia* comprises six species with a bicentric distribution in the two main areas of tropical humid forests in South America. Three species occur in eastern Brazil, two of which are restricted to the Atlantic wet forests (*Marlimorima bahiana* and *M. warmingii*) and *M. contorta*, which extends to inland semi-deciduous forests. The three other species are distributed in northern South America. *Marlimorimia psilostachya* is widely distributed across Amazonia, sparsely extending to Central America (Costa Rica) and *M. colombiana* and *M. pittieri* have restricted ranges in Colombia and Venezuela, respectively.

Etymology. The genus *Marlimorimia* is named in honour of Dr. Marli Pires Morim, taxonomist at the Rio de Janeiro Botanical Garden, for her outstanding contribution to our knowledge of the diversity and taxonomy of Brazilian mimosoid legumes.

Notes. The new genus *Marlimorimia* is proposed to accommodate a monophyletic group of species, previously classified in *Pseudopiptadenia* (sensu Lewis and Lima 1991; Luckow 2005), but which could not retain the genus name, because its type species is now included in *Pityrocarpa*.

Besides the molecular phylogenetic evidence, morphology also supports recognition of *Marlimorimia* as distinct from *Pityrocarpa*. *Marlimorimia* brings together most of the species formerly placed in *Pseudopiptadenia* which have multipinnate leaves, small oblong to linear leaflets and fruits with straight (or shallowly sinuous) margins. *Marlimorimia bahiana* and *M. colombiana*, however, have leaves with few pinnae and rhomboid leaflets.

Species of *Marlimorimia* have more complex inflorescences than those of *Pityrocarpa*. While the spikes of *Pityrocarpa* are solitary in the axils of coevally developing leaves, *Marlimorimia* species have spikes in fascicles of 2–3, which are arranged in terminal efoliate pseudoracemes or clustered on nodes below mature leaves (Fig. 3). Sometimes, as leaves expand, *Marlimorimia* synflorescences may resemble those of *Pityrocarpa* and *Parapiptadenia* (e.g. particular specimens of *M. contorta* such as *Hatschbach 50149* [NY]). Nonetheless, flowers of *Marlimorimia* have pubescent petals united into a gamopetalous corolla (vs. free glabrous petals in the majority of *Pityrocarpa* species).

Two types of fruits are found in *Marlimorimia* (Fig. 5). Some species have long linear fruits, frequently curved or longitudinally twisted with straight margins (*M. colombiana*, *M. contorta*, *M. pittieri* and *M. psilostachya*), while *M. bahiana* and *M. warmingii* have oblong fruits with shallowly sinuous margins. The valves of the fruits are woody, although usually thin, becoming thicker and harder in *M. warmingii*.

The seeds of *Marlimorimia*, although superficially similar to those of most species of *Pityrocarpa*, have embryos with multifid plumules that result in seedlings with pinnate or bipinnate eophylls (Lima 1985; Lewis and Lima 1991).

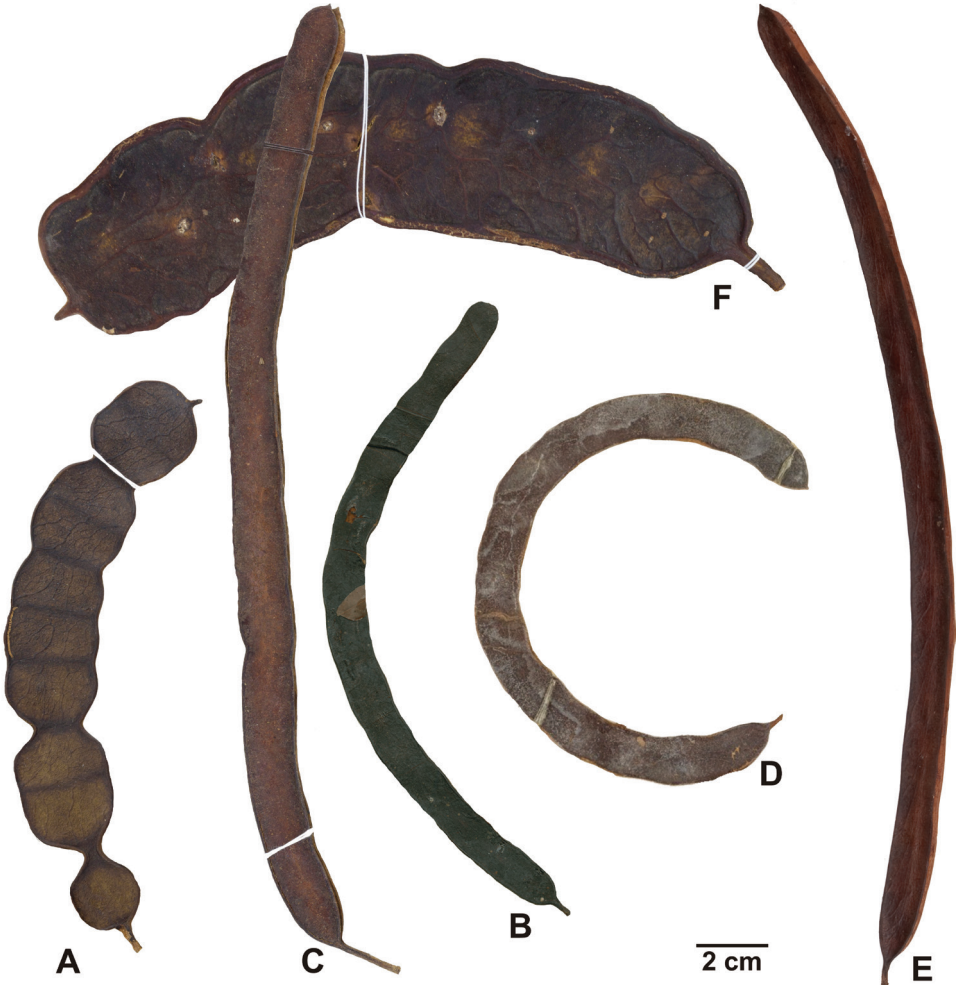

Figure 5. Fruits of *Marlimorimia* species **A** *Marlimorimia bahiana* (from *Amorim 1009*, NY) **B** *Marlimorimia colombiana* (from *Killip 16268*, NY) **C** *Marlimorimia contorta* (from *Gomes 257*, NY) **D** *Marlimorimia pittieri* (from *Guevara 1264*, F) **E** *Marlimorimia psilostachya* (from *Rabelo 2753*, NY) **F** *Marlimorimia warmingii* (from *Nunes et al. 2*, NY).

2.1. *Marlimorimia bahiana* (G.P. Lewis & M.P. Lima) L.P. Queiroz & L.M. Borges, comb. nov.

urn:lsid:ipni.org:names:77303786-1

Basionym. *Pseudopiptadenia bahiana* G.P. Lewis & M.P. Lima, Arch. Jard. Bot. Rio de Janeiro 30: 54–55. 1991.

Type. Brasil, Bahia, *Mori & King 12223* (holotype CEPEC; isotypes HUEFS, K, NY, RB).

2.2. *Marlimorimia colombiana* (Britton & Killip) L.P. Queiroz & Marc.F. Simon, comb. nov.
urn:lsid:ipni.org:names:77303787-1

Pseudopiptadenia colombiana (Britton & Killip) G.P. Lewis

Basionym. *Stryphnodendron colombianum* Britton & Killip, Ann. New York Acad. Sci. 35(3): 155. 1936.

Type. Colombia, Santander, *Killip & Smith 16268* (holotype NY 00003356; isotypes A, GH, US).

Notes. In the absence of phylogenetic evidence, the petiolar extrafloral nectaries located at mid-petiole and fruits with straight to shallowly sinuous margins support the transfer of *Pseudopiptadenia colombiana* to *Marlimorimia*.

2.3. *Marlimorimia contorta* (DC.) L.P. Queiroz & P.G. Ribeiro, comb. nov.
urn:lsid:ipni.org:names:77303788-1

Piptadenia nitida Benth., J. Bot. (Hooker) 4: 336. 1842.
Piptadenia contorta (DC.) Benth., Trans. Linn. Soc. Lond. 30: 368. 1875.
Newtonia nitida (Benth.) Brenan, Kew. Bull. 10 (2): 182. 1955.
Newtonia contorta (DC.) Burkart, Fl. Il. Catarin. fasc. LEGU: 289. 1979.
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima, Arch. Jard. Bot. Rio de Janeiro 30: 57. 1991.

Basionym. *Acacia contorta* DC., Prodr. 2: 470. 1825.

Type. Brasil, Rio de Janeiro, *Raddi s.n.* (lectotype FI, designated here).

2.4. *Marlimorimia pittieri* (Harms) L.P. Queiroz & L.M. Borges, comb. nov.
urn:lsid:ipni.org:names:77303789-1

Piptadenia similis Britton & Killip, Ann. New York Acad. Sci. 35(3): 156. 1936. Holotype Colombia, Barranquilla, *Elias 263* (US).
Pseudopiptadenia pittieri (Harms) G.P. Lewis, Kew Bull. 46(1): 118. 1991.

Basionym. *Piptadenia pittieri* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 8(71): 51–52. 1921.

Type. Venezuela, Carabobo, *Pittier 8859* (lectotype US 00001013, designated here; isolectotypes GH 00064052, NY 00003236).

Notes. Although *Pseudopiptadenia pittieri* was not included in the phylogenetic analyses, the presence of extrafloral nectaries at the base of the petiole, spikes arranged in pseudoracemes and fruits with straight margins support its transfer to *Marlimorimia*.

2.5. *Marlimorimia psilostachya* (DC.) L.P. Queiroz & Marc.F. Simon, comb. nov.

urn:lsid:ipni.org:names:77303790-1

Piptadenia psilostachya (DC.) Benth., J. Bot. (Hooker) 4: 336. 1842.
Piptadenia suaveolens Miq., Linnaea 18: 589–590. 1845. Type Surinam, Bergendaal, *Focke 936* (holotype U).
Newtonia psilostachya (DC.) Brenan, Kew. Bull. 10 (2): 182. 1955.
Newtonia suaveolens (Miq.) Brenan, Kew. Bull. 10 (2): 182. 1955.
Pseudopiptadenia psilostachya (DC.) G.P. Lewis & M.P. Lima, Arch. Jard. Bot. Rio de Janeiro 30: 55. 1991.
Pseudopiptadenia suaveolens (Miq.) J.W. Grimes, Brittonia 45(1): 27. 1993.

Basionym. *Acacia psilostachya* DC., Prodr. 2: 457. 1825.

Type. French Guiana, Cayenne, *Martin 2* (lectotype K 000504699, designated by Lewis & Lima 1991; isolectotype P 02930999).

Notes. Contrary to Grimes (1993), who recognised *Pseudopiptadenia psilostachya* and *Ps. suaveolens* as distinct species, we agree with Lewis and Lima (1991) on the synonymisation of *Ps. suaveolens* under *M. psilostachya*. These plants grow sympatrically and the traits used by Grimes (1993) to support recognition of two species are too variable to be diagnostic.

2.6. *Marlimorimia warmingii* (Benth.) L.P. Queiroz & P.G. Ribeiro, comb. nov.

urn:lsid:ipni.org:names:77303791-1

Piptadenia glaziovii Harms, Repert. Spec. Nov. Regni Veg. 17: 203. 1921. Type. Brasil, Rio de Janeiro, Serra da Estrela, *Glaziou 8440* (lectotype K, designated by Lewis and Lima 1991).
Newtonia glaziovii (Harms) Burkart ex Barth & Yoneshigue, Mem. Inst. Oswaldo Cruz 64: 102. 1966.
Newtonia warmingii (Benth.) G.P. Lewis, Legumes of Bahia p. 111. 1987.
Pseudopiptadenia warmingii (Benth.) G.P. Lewis & M.P. Lima, Arch. Jard. Bot. Rio de Janeiro 30: 54. 1991.

Basionym. *Mimosa warmingii* Benth., Trans. Linn. Soc. London 30(3): 413. 1875.

Type. Brasil, Minas Gerais, Lagoa Santa, *Warming s.n.* (lectotype K 000504702, designated by Lewis and Lima 1991).

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Supplementary material 1

Voucher information and GenBank accession numbers (internal transcribed spacer-ITS sequences) for taxa used in this study

Authors: Leonardo M. Borges, Peter W. Inglis, Marcelo F. Simon, Pétala Gomes Ribeiro, Luciano P. de Queiroz

Data type: excel file

Explanation note: Voucher information and GenBank accession numbers for taxa used in this study.

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Dilemmas in generic delimitation of *Senegalia* and allies (Caesalpinioideae, mimosoid clade): how to reconcile phylogenomic evidence with morphology and taxonomy?

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Abstract

Senegalia comprises 219 species distributed in tropical and subtropical regions of North and South America, Africa, Asia and Australia. Two sections are currently recognised within *Senegalia* and these are most readily distinguished by the differences in disposition of their cauline prickles, i.e. sect. *Senegalia* with prickles at or near leaf nodes and sect. *Monacanthea* with mostly internodal prickles. Previous phylogenetic studies, based primarily on small numbers of plastid DNA loci, found *Senegalia* to be monophyletic with two large subclades corresponding to the sections. Here, we present new phylogenomic evidence from 997 single-copy nuclear gene sequences for a small, but representative set of species. These new analyses show that *Senegalia* is non-monophyletic, but instead, forms a grade that is paraphyletic with respect to the remainder of the ingoid clade (i.e. Ingeae + *Acacia* s.s. + *Acaciella*), comprising two well-supported subclades most likely representing the same clades as found in previous phylogenetic studies of the genus

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and, interspersed between these, a third, moderately supported clade, comprising the genera *Mariosousa*, *Pseudosenegalia* and *Parasenegalia*. In marked contrast to the nuclear phylogeny, the two *Senegalia* clades are sister groups in the plastid phylogeny, based on analyses of 72 chloroplast genes, rendering the genus monophyletic, based on plastid data alone. We discuss this new evidence that *Senegalia* is non-monophyletic in relation to the marked cytonuclear discordance, high gene tree conflict and lack of resolution across this senegalioid grade and review the consistency of the key morphological characters distinguishing the two sections of *Senegalia*. We conclude that it is likely that *Senegalia* will need to be split into two (or possibly more) genera: a re-circumscribed *Senegalia* s.s. that corresponds to the existing *Senegalia* sect. *Senegalia* plus the *S. ataxacantha* group (*Senegalia* sect. *Monacanthea* s.s.; future studies may show that this group warrants generic status) and a new genus corresponding to the remainder of sect. *Monacanthea* (here designated as *Senegalia* sect. *Monacanthea* p.p.). However, re-delimiting *Senegalia* now would be premature given that the key morphological characters are not fully congruent with the two sections and pending denser phylogenetic sampling of taxa. A judiciously selected list of critical taxa is presented to facilitate future phylogenomic studies. Finally, we discuss the identity of *Albizia leonardii*, which is also placed in this senegalioid grade in these new phylogenomic analyses and place it in synonymy with *Parasenegalia vogeliana*.

Keywords
Cytonuclear discordance, Fabaceae, Leguminosae, *Mariosousa*, Mimosoideae, *Parasenegalia*, *Pseudosenegalia*

Introduction

Senegalia Raf. was segregated from *Acacia* Mill. by Rafinesque (1838) with a very brief description. However, the genus was subsequently overlooked or ignored for almost 100 years, until it was resurrected by Britton and Rose (1928), alongside the newly-segregated genus *Acaciella* Britton & Rose, in their treatment of *Acacia* for the *Flora of North America*. However, despite this recognition by Britton and Rose (1928), *Senegalia* was subsequently ignored (Pedley 1987) and Bentham's (1875) delimitation of *Acacia* sensu lato (s.l.) as a broadly circumscribed pantropical genus persisted until the reclassification of *Acacia* by Pedley (1986).

Pedley (1986) divided *Acacia* into three genera: *Acacia* sensu stricto (s.s.), *Senegalia* and *Racosperma* Mart. These genera corresponded to the three subgenera of *Acacia* s.l. recognised by Vassal (1972), namely subg. *Acacia* (now *Vachellia* Wight & Arn.), subg. *Aculeiferum* Vassal (now *Senegalia* and allied genera) and subg. *Phyllodineae* DC. (syn. subg. *Heterophyllum* Vassal and *Racosperma*, now *Acacia* s.s.), respectively. Although Pedley's classification was not immediately adopted, over the following two decades, a series of molecular and morphological phylogenetic analyses demonstrated that *Acacia* s.l. was polyphyletic and could not be sustained as a single genus (e.g. Luckow et al. 2003; Miller and Seigler 2012). While these analyses confirmed the monophyly of *Vachellia* and *Acacia* s.s., Vassal's subg. *Aculeiferum* formed a paraphyletic grade. Thus, while *Senegalia* was again resurrected, its delimitation remained problematic. Subsequently, more densely sampled phylogenetic analyses of molecular and morphological data led to the segregation (or resurrection) of

four small New World genera, namely *Acaciella* (Rico-Arce and Bachman 2006), *Mariosousa* Seigler & Ebinger (Seigler et al. 2006), *Parasenegalia* Seigler & Ebinger (Seigler et al. 2017) and *Pseudosenegalia* Seigler & Ebinger (Seigler et al. 2017). These four genera all differ from *Senegalia* in lacking cauline and foliar prickles (Miller et al. 2017). Recent phylogenomic analyses (Koenen et al. 2020; Ringelberg et al. 2022) have shown that *Senegalia*, *Mariosousa*, *Parasenegalia* and *Pseudosenegalia* together form a poorly-resolved paraphyletic grade (see below), while *Acaciella* is placed in the *Calliandra* clade sensu Koenen et al. (2020) where it is sister to a clade comprising *Calliandra* Benth. and *Afrocalliandra* E.R. Souza & L.P. Queiroz and is not discussed further in this paper.

Senegalia today comprises 219 species (235 taxa) distributed pantropically (Fig. 1) with 99 species in the Americas, 68 species in Africa plus Madagascar, 57 species in Asia [i.e. Arabian Peninsula to East and Southeast Asia (including Papua New Guinea)] and two species in Australia and with particular hotspots of species richness in Brazil (63 species), Mexico (30 species), East Asia (China, 22 species) and east Africa (e.g. Somalia, 21 species; Mozambique, 20 species) (Fig. 1).

Two sections are currently recognised within *Senegalia* (fide Maslin et al. 2019), sect. *Senegalia* (armed with cauline prickles at or near leaf nodes) and sect. *Monacanthea* (Vassal) Maslin (prickles mostly internodal). The monophyly of *Senegalia* was supported by recent phylogenetic analyses of plastid DNA sequences (Bouchenak-Khelladi et al. 2010; Kyalangalilwa et al. 2013; Boatwright et al. 2015), consistently recovering two well-supported clades that are sister to each other. These two clades were also recovered in an analysis of plastid loci combined with nrDNA ITS sequences by Terra et al. (2017). A more recent phylogenomic study using genome-scale nuclear sequence data (Koenen et al. 2020) also robustly supported the same two clades, but revealed that these are not sister to each other, rejecting the monophyly of *Senegalia*.

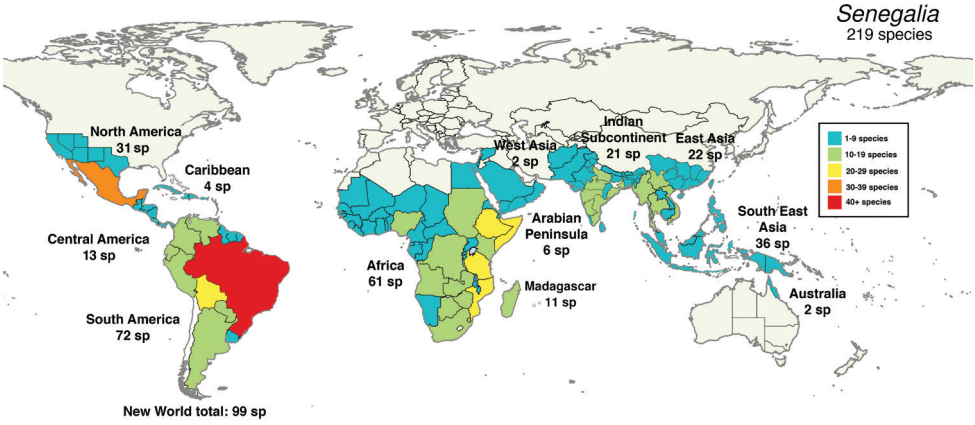

Figure 1. Global distribution of *Senegalia*. Species numbers derived from Maslin and Wilson (2021) at WorldWideWattle website (http://worldwidewattle.com).

New phylogenomic evidence

In this paper, we review new phylogenomic evidence derived from analyses of sequences of 997 nuclear and 72 plastid genes for 422 taxa of subfamily Caesalpinioideae that sampled all but one of the 90 genera in the mimosoid clade (Ringelberg et al. 2022). These analyses are based on a slightly modified set of the same *Mimobaits* genes used by Koenen et al. (2020), but sampled four more species of *Senegalia*, plus representatives of *Mariosousa*, *Parasenegalia* and *Pseudosenegalia* (Fig. 2) which were not included by Koenen et al. (2020). Taxon sampling across the nuclear and plastid phylogenies of Ringelberg et al. (2022) is not identical (Fig. 2), because off-target plastid data were not recovered for all taxa. While taxon sampling is limited (six species of *Senegalia* and one each of *Mariosousa*, *Parasenegalia* and *Pseudosenegalia*), it does represent a reasonable geo-taxonomic sampling of the group. The wider phylogeny showing the relationships of this senegalioid grade within the mimosoid clade (Fig. 2A, C) is presented in detail by Ringelberg et al. (2022). Here, we examine this new phylogenomic evidence presented by Ringelberg et al. (2022), re-visit the key morphological characters underpinning the two sections of *Senegalia* to see how they correspond to the new phylogeny and discuss the implications of these results for generic delimitation and taxonomy.

The two clades of *Senegalia* in this new phylogeny (Fig. 2B) are congruent with the two main *Senegalia* clades found by Bouchenak-Khelladi et al. (2010), Kyalangalilwa et al. (2013), Boatwright et al. (2015) and Terra et al. (2017) that had more comprehensive taxon sampling. In the nuclear phylogeny (Koenen et al. 2020; Ringelberg et al. 2022), the two well-supported clades correspond to: (1) a clade combining *Senegalia* sect. *Senegalia*, represented by *S. nigrescens* (Oliv.) P.J.H. Hurter and *Senegalia* sect. *Monacanthea* s.s. represented by *S. ataxacantha* (DC.) Kyal. & Boatwr. on the one hand (clade A in Terra et al. 2017); and (2) *Senegalia* sect. *Monacanthea* pro parte (p.p.) represented by *S. bahiensis* (Benth.) Seigler & Ebinger, *S. sakalava* (Drake) Boatwr., *S. borneensis* (I.C. Nielsen) Maslin, Seigler & Ebinger and *S. pentagona* (Schumach. & Thonn.) Kyal. & Boatwr. on the other hand (clade B in Terra et al. 2017). Furthermore, a third, moderately supported clade is shown that includes *Mariosousa sericea* (M. Martens & Galeotii) Seigler & Ebinger, *Parasenegalia visco* (Lorentz ex Griseb.) Seigler & Ebinger and *Pseudosenegalia feddeana* (Harms) Seigler & Ebinger (Fig. 2B), interspersed between the two *Senegalia* clades. These three clades form a paraphyletic grade together with an accession that was included by Barneby and Grimes (1996) in *Albizia leonardii* Britton & Rose ex Barneby & J.W. Grimes (discussed below) and form successive sister groups to the remainder of the ingoid clade sensu Koenen et al. (2020). Thus, as shown by Koenen et al. (2020), the new analyses presented here (Ringelberg et al. 2022) show that, in the nuclear gene phylogeny, *Senegalia* is not monophyletic (Fig. 2B).

In marked contrast to the nuclear phylogeny, the two *Senegalia* sections are sister clades in the plastid phylogeny presented by Ringelberg et al. (2022), that supported the genus as monophyletic, based on plastid data alone (Fig. 2D). This cytonuclear conflict was also shown by Koenen et al. (2020) and probably explains why previous phylogenetic studies found *Senegalia* to be monophyletic because these

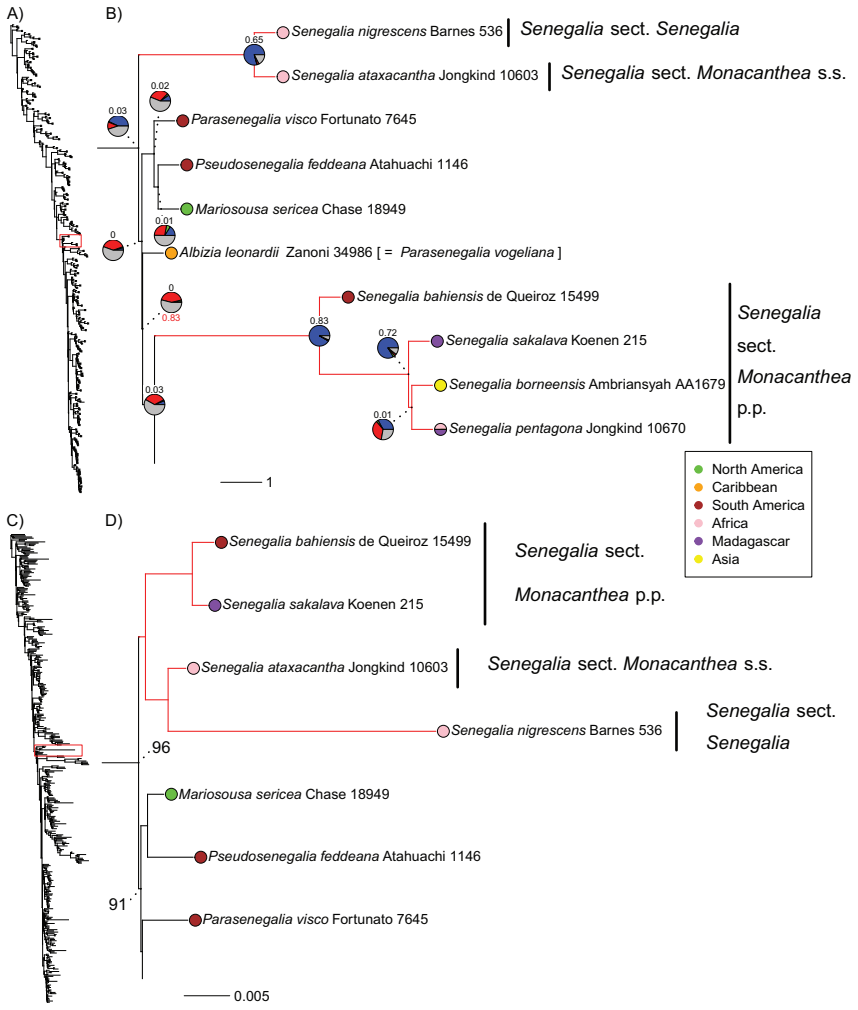

Figure 2. Cytonuclear discordance in *Senegalia* and allies **A** phylogeny of Caesalpinioideae, showing the placement of *Senegalia* and closely related genera (boxed in red) within the subfamily (Ringelberg et al. 2022). The phylogeny contains 420 taxa (excluding outgroups) and is based on 997 nuclear genes analysed using ASTRAL (Mirarab 2019) **B** phylogeny of *Senegalia* and allies (details from **A**). Pie charts at nodes show the fraction of gene trees supporting that bipartition in blue, the fraction of gene trees supporting the most likely alternative configuration in green, the fraction of gene trees supporting additional conflicting configurations in red and the fraction of uninformative gene trees in grey. Numbers above pie charts show quartet-based Extended Quadripartition Internode Certainty scores (Zhou et al. 2020), numbers below pie charts the outcome of ASTRAL's polytomy test, which tests the null hypothesis that a branch should be replaced by a polytomy (only values > 0.05 are shown). In both **A** and **B**, branch lengths are expressed in coalescent units and terminal branches were assigned an arbitrary uniform length for visual clarity **C** plastid gene tree of Caesalpinioideae showing the placement of *Senegalia* and closely-related genera (boxed in red) within the subfamily (Ringelberg et al. 2022). The phylogeny contains 381 taxa (excluding outgroups) and is based on 72 concatenated plastid genes analysed using RAxML (Stamatakis 2014) **D** plastid phylogeny of *Senegalia* and allies (details from **C**). Numbers at nodes show bootstrap support values for nodes that are not fully supported. In both **C** and **D**, branch lengths reflect nucleotide substitutions. In both **B** and **D**, the root is not drawn to scale.

studies either exclusively relied on plastid DNA sequences (Bouchenak-Khelladi et al. 2010; Kyalangalilwa et al. 2013; Boatwright et al. 2015) or primarily plastid genes in combination with limited taxon sampling outside *Senegalia* (Terra et al. 2017).

The analyses of Koenen et al. (2020) and Ringelberg et al. (2022) are based on DNA sequence data derived from 964 or 997 targeted nuclear genes, respectively, plus 72 plastid genes, datasets that are an order of magnitude larger than previous phylogenetic datasets. These large nuclear datasets provide robust support for the non-monophyly of *Senegalia*, with the two separate clades of *Senegalia* subtended by long, well-supported branches (Fig. 2B). However, notwithstanding the large number of genes underlying the analyses of Ringelberg et al. (2022), the backbone of this senegalioid grade is still characterised by extremely short branches (Fig. 2). Having data for many genes also means that conflict amongst individual gene trees can be examined and quantified, revealing high levels of gene tree conflict across the backbone of this senegalioid grade, but very high proportions of gene trees supporting each of the two *Senegalia* clades (Fig. 2B). These short branches across the senegalioid grade, combined with high levels of gene tree conflict across these nodes, plus the marked cytonuclear discordance suggest that alongside a rapid radiation characterised by incomplete lineage sorting, there may also be a history of reticulation, i.e. chloroplast capture or hybridisation. This is also evident from the unstable placements of *Albizia leonardii* and the *Parasenegalia*, *Pseudosenegalia* and *Mariosousa* clade across the different topologies presented by Ringelberg et al. (2022), where they swap places in the ASTRAL and amino acid RAxML phylogenies compared with the nucleotide RAxML phylogenies. This suggests that the branch subtending *Albizia leonardii* should be collapsed into a polytomy, as indicated by ASTRAL's polytomy test (Fig. 2B) and the PhyloBayes consensus tree of Ringelberg et al. (2022), at least pending further phylogenomic evidence.

Given that the incongruence observed amongst the lineages of *Senegalia* and allies is likely caused by evolutionary processes, such as incomplete lineage sorting and introgression or chloroplast capture, this raises a number of fundamental questions about how to interpret these patterns: (1) how to define paraphyly vs. monophyly when there is pronounced cytonuclear discordance indicative of incomplete lineage sorting or reticulation and (2) is it justified to divide a genus into multiple segregate genera when the relationships amongst the constituent lineages are unresolved (i.e. form a potential hard polytomy)? With respect to the first question, we suggest that, given the propensity for plastid capture or introgression in plants (Larson et al. 2021; Rose et al. 2021) and the fact that the plastid genome is uniparentally inherited and represents a single largely non-recombining locus, relationships determined by a large set of nuclear genes provide a better basis for assessing monophyly and for delimiting taxa (Wei et al. 2021). With regard to the second question, lack of molecular resolution means that we should rely even more than usual on morphological diagnosability as the key criterion for delimiting lineages across a polytomy as separate genera. Thus, careful re-examination and evaluation of morphological variation across this grade of *Senegalia* and allies are needed to ascertain to what extent morphological data support the complex phylogenomic patterns revealed and provide the basis for an improved generic classification.

Morphology and taxonomic implications

The phylogenomic evidence, discussed here, shows that *Senegalia* is non-monophyletic and suggests that the two clades of *Senegalia* species (some of which are illustrated in Figs 3, 4) could potentially be treated as two (or possibly three) separate genera. Here, we evaluate the consistency of the morphological characters supporting the currently recognised sections, which largely correspond to the two recovered clades, except for the small *S. ataxacantha* group (sect. *Monacanthea* s.s.).

The disposition of cauline prickles (at or close to the leaf nodes in sect. *Senegalia* – Fig. 3A, C; vs. mostly internodal in sect. *Monacanthea* – Fig. 4A, B) and, to a lesser extent, inflorescence shape (usually spicate in sect. *Senegalia* – Fig. 3C, D, vs. globose, subglobose/oblongoid or sometimes spicate in sect. *Monacanthea* – Fig. 4C–F) and also plant growth form (always trees and shrubs in sect. *Senegalia* – Fig. 3F, G, vs. lianas, trees and shrubs in sect. *Monacanthea* – Fig. 4G–L) are the most informative characters for distinguishing the two sections. However, there are some exceptions (discussed below) and, furthermore, the practical utility of branchlet armature is somewhat diminished because cauline prickles are not infrequently absent from individual plants or herbarium specimens in species where they are otherwise known to exist. Nevertheless, what is clear is that prickles are present in all species of *Senegalia*, while they are absent in the three allied genera in the New World, namely *Mariosousa*, *Parasenegalia* and *Pseudosenegalia* (fide Miller et al. 2017).

The Afro-Asian sect. *Senegalia* contains 51 species distributed in Africa, the Arabian Peninsula, West Asia and the Indian Subcontinent to Myanmar and Laos in Southeast Asia, with the greatest diversity of species in Somalia in the Horn of Africa (Fig. 5A, Table 1). Morphologically, the species of this section appear to be relatively invariable. Importantly, most possess between one and three prickles at or near the leaf nodes (Fig. 3A, C) and invariably lack internodal prickles. The only exceptions known to us are two African species documented by Ross (1979) in his conspectus of what was then African *Acacia*. First, *Senegalia pseudonigrescens* (Brenan & J.H. Ross) Kyal. & Boatwr. was described as unarmed, but this species was known only from the type, which could be anomalous and examination of additional material is needed to verify this observation. Second, *Senegalia caffra* (Thubb.) P.H. Hurter & Mabb. was described as rarely having a few scattered prickles on the internodes, in addition to the pair located at the nodes. Flowers in 95% of species of sect. *Senegalia* are aggregated in spikes (containing sessile flowers) or occasionally spiciform racemes (i.e. spikes with pedicellate flowers), while globose or sometimes oblongoid heads occur in only two African taxa, *S. densispina* (Thulin) Kyal. & Boatwr. and *S. mellifera* subsp. *detinens* (Burch.) Kyal. & Boatwr. In the majority of species of sect. *Senegalia*, the inflorescences are axillary, but occasionally they are arranged in racemes or panicles, e.g. *S. burkei* (Benth.) Kyal. & Boatwr. and *S. caffra* from Africa. Unlike many species of sect. *Monacanthea*, lianas are never found amongst the species of sect. *Senegalia* (which are either shrubs or trees, Fig. 3F, G).

The much larger pantropical sect. *Monacanthea* p.p. contains 164 species (excluding the four species of sect. *Monacanthea* s.s., see below) distributed in the Americas (especially Brazil with 63 species), Africa, Asia and Australia (Fig. 5C, Table 1).

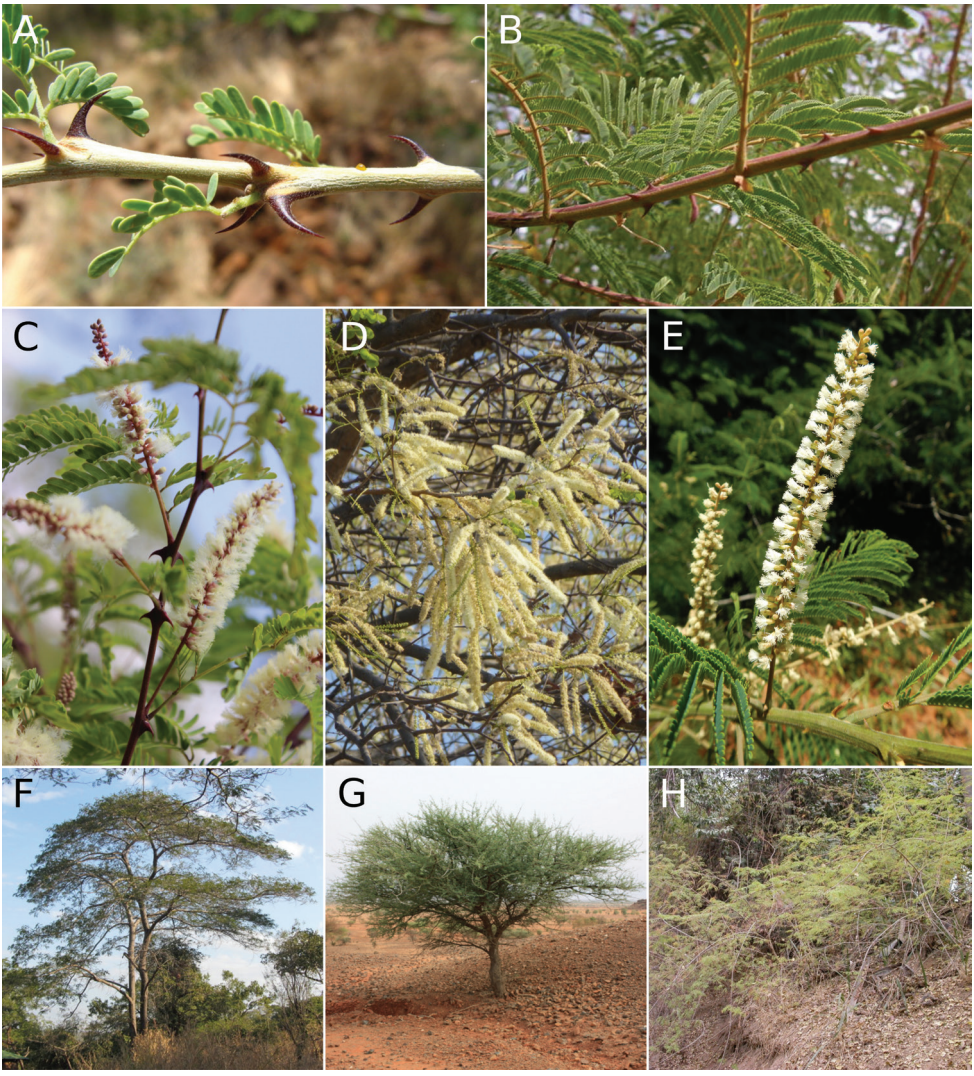

Figure 3. Key morphological features of the clade composed of *Senegalia* sect. *Senegalia* (**A, C, D, F, G**) and sect. *Monacanthea* s.s. (**B, E**, **H**). **A** prickles clustered at the nodes in *Senegalia senegal* Britton **B** internodal prickles in *S. ataxacantha* **C** paired prickles at the nodes and axillary, spicate inflorescences of *Senegalia goetzei* (Harms) Kyal. & Boatwr. **D** spicate inflorescence in racemes of *Senegalia nigrescens* (Oliv.) P.J.H. Hurter **E** spicate inflorescences of *S. ataxacantha* **F** tree habit of *Senegalia polyacantha* (Willd.) Seigler & Ebinger **G** treelet habit of *Senegalia laeta* (R. Br. ex Benth.) Seigler & Ebinger **H** lianescent shrub habit of *S. ataxacantha*. Photo credits: **A** Alex Dreyer **B** Sylvain Piry **C, D** Claude Boucher Chisale **E** Erik Koenen **F** Elke Faust **G** Marco Schmidt **H** Philippe Birnbaum **A–D, F–H** from African plants – A Photo Guide (www.africanplants.senckenberg.de) **E** from living collection Pretoria National Botanical Garden, South Africa.

Section *Monacanthea* p.p. is not only more speciose and geographically widespread than sect. *Senegalia*, but also morphologically more variable, especially in the New World. The best morphological feature for distinguishing sect. *Monacanthea* p.p. from sect. *Senegalia* appears to be cauline prickle distribution, mostly internodal in sect. *Monacanthea* p.p. (Fig. 4A, B) and nodal in sect. *Senegalia* (Fig. 3A, C). However, in the New World (where sect. *Senegalia* is not known to occur), there is some variation in armature that appears to reduce the discriminating value of this character in that region and which warrants further investigation. Of the 99 species New World species of *Senegalia* sect. *Monacanthea* p.p. there are 28 species that possess nodal prickles, at least some of the time. For example, it is not uncommon to find specimens, especially amongst species in the informal *S. berlandieri* species-group and *S. monacantha* (Willd.) Seigler & Ebinger from the informal *S. monacantha* species-group, which have 1–3 prickles associated with some or most nodes, in addition to those on the internodes. Furthermore, the following three species have one or two prickles associated with some nodes, but none on the internodes, namely, *S. emilioana* (Fortunato & Ciald.) Seigler & Ebinger, *S. gilliesii* (Steud.) Seigler & Ebinger (Fig. 4C) and *S. subsessilis* Britton & Rose from the informal *S. greggii* (A. Gray) Britton & Rose species-group.

Inflorescence shape (i.e. globose or occasionally subglobose/oblongoid heads vs. cylindrical spikes) is a useful character for distinguishing sect. *Monacanthea* p.p. from sect. *Senegalia*, but again, some New World species differ somewhat from those elsewhere. In the Afro-Asian region where the two sections co-occur, 92% of sect. *Monacanthea* p.p. species possess globose/oblongoid heads (Fig. 4D), contrasting with sect. *Senegalia* where almost all species possess cylindrical spikes (see above). Of the five sect. *Monacanthea* p.p. species from this region that possess spikes, three are from Madagascar [*S. hildebrandtii* (Vatke) Boatwr., *S. menabeensis* (Villiers & Du Puy) Boatwr. and *S. pervillei* (Benth.) Boatwr.] and two are from Southeast and East Asia [*S. donnaiensis* (Gagnep.) Maslin et al. and *S. yunnanensis* (Franch.) Maslin et al., respectively]. In the New World (where sect. *Senegalia* is not known to occur), there is a stronger bias towards spicate inflorescences within sect. *Monacanthea* p.p. where 26 species (representing 27% of the species from the region) possess spikes (Fig. 4E), while 70 species (71%) possess globose or sometimes subglobose heads (Fig. 4C, F). It is noted that several other mimosoid genera that are known to be monophyletic are polymorphic with regards to these inflorescence shapes (e.g. *Inga* Mill., *Zygia* P. Browne., *Mimosa* L., *Acacia*, *Parkia* R. Br.). Globally, a higher percentage of sect. *Monacanthea* p.p. species also has inflorescences arranged in terminal racemes or panicles than those with inflorescences arising from the axils of leaves, contrasting with sect. *Senegalia* where most species have axillary inflorescences. In sect. *Monacanthea* p.p., lianas are relatively common (Fig. 4G–I), whereas in sect. *Senegalia*, they never occur. However, sect. *Monacanthea* p.p. also includes trees and shrubs (Fig. 4J–L), especially in the New World.

Senegalia ataxacantha and its three relatives, *S. macrostachya* (Rchb. ex DC.) Kyal. & Boatwr., *S. chariessa* (Milne-Redh.) Kyal. & Boatwr. and *S. eriocarpa* (Brenan) Kyal. & Boatwr. have consistently been placed in the same clade as sect. *Senegalia* in

Figure 4. Key morphological features of the *Senegalia* sect. *Monacanthea* p.p. clade. **A** internodal prickles of *Senegalia pennata* subsp. *insuavis* (Lace) Maslin, Seigler & Ebinger **B** internodal prickles of *Senegalia serra* (Benth.) Seigler & Ebinger **C** paired forked spines at the nodes and capitate inflorescences of *S. gilliesii* **D** paniculately compound inflorescence consisting of racemes of heads of *Senegalia clandestina* Maslin, B.C. Ho, H. Sun & L. Bai **E** spikes in racemes of *Senegalia bonariensis* (Gillies) Seigler & Ebinger **F** capitate inflorescence of *Senegalia polyphylla* (DC.) Britton & Rose **G** tendril with prickles of *Senegalia kunmingensis* (C. Chen & H. Sun) Maslin, B.C. Ho, H. Sun & L. Bai **H, I** liana habit of *Senegalia megaladena* (Desv.) Maslin, Seigler & Ebinger **J** tree habit of *Senegalia picachensis* Britton & Rose **K** shrub habit of *Senegalia teniana* (Harms) Maslin, Seigler & Ebinger **L** shrub habit of *S. gilliesii*. Photo credits: **A, D, G, H** Lin Bai B **F** Ítalo A.C. Coutinho **C** Guy Atchison **E** Vanessa Terra **I** Bruce Maslin **J, L** Colin Hughes **K** Hang Sun. Vouchers: **A** *B.R. Maslin 11043* **B** *V. Terra & Í.A.C. Coutinho 701* **C** *G. Atchison 12*. **D** *B.R. Maslin 11032* **E** *V. Terra & D.M.P. Pena 679* **F** *V. Terra & Í.A.C. Coutinho 683* **G** *L. Bai 2*, H, **I** *B.R. Maslin 11040* **J** *C.E. Hughes 1416* **K** unvouchered **L** *C.E. Hughes 2306*.

all phylogenetic studies that included one or other of these species (i.e. Bouchenak-Khelladi et al. 2010; Kyalangalilwa et al. 2013; Boatwright et al. 2015; Terra et al. 2017; Koenen et al. 2020; Ringelberg et al. 2022), as well as in the morphological cladistic study of Chappill and Maslin (1995). This group is referred to herein as sect. *Monacanthea* s.s., because it includes the type of the section (*S. ataxacantha*), while the remainder of the section is referred to as sect. *Monacanthea* p.p. However, unlike species of sect. *Senegalia* that have prickles located at or near the leaf nodes, these four African species (Fig. 5C) possess internodal cauline prickles (Fig. 3B; although sometimes in *S. chariessa*, a few prickles may also be grouped irregularly in pairs near the nodes), similar to the majority of species of sect. *Monacanthea* p.p. Indeed, Vassal (1972) united the species with scattered internodal prickles in this section and treated *Acacia ataxacantha* (≡ *Senegalia ataxacantha*) as the type of the section (which has potential nomenclatural implications, depending upon how *Senegalia* is classified in the future). These four species have flowers arranged in spikes (Fig. 3E), a character almost ubiquitous for sect. *Senegalia*, but rare in other Afro-Asian species of sect. *Monacanthea* p.p. Finally, these species have a lianescent or scrambling shrubby habit (Fig. 3H) that is not seen in sect. *Senegalia*, while a liana or lianescent habit is relatively common in species of sect. *Monacanthea* p.p. (as discussed above). These intermediate characteristics of sect. *Monacanthea* s.s. are in line with their phylogenetic placement as either sister to sect. *Senegalia* or sister to the rest of sect. *Senegalia* minus *S. catechu* (L.f.) P.J.H. Hurter & Mabb. (Kyalangalilwa et al. 2013; Boatwright et al. 2015; Terra et al. 2017). Given the phylogenetic position and morphological characteristics of sect. *Monacanthea* s.s., this group could either be regarded as a distinct genus or remain classified within the genus *Senegalia* alongside sect. *Senegalia*; these matters require further investigation. It also appears that the large majority of *Senegalia* species currently placed in sect. *Monacanthea* p.p. will need to be reclassified as a separate genus, pending further phylogenomic studies with increased taxon sampling (as outlined below). The name *Manganaroa* Spegazzini (1923) is available for this genus, but its type species, the South American *S. monacantha*, while placed in sect. *Monacanthea* p.p., has not so far been included in any phylogenetic study. In any case, it is clear that this discordant combination of internodal prickles and spicate inflorescences undermines the potential of these two characters to straightforwardly diagnose the two major clades of *Senegalia* (Figs 3, 4).

Albizia leonardii

The phylogenetic placement of *Albizia leonardii* amongst *Senegalia* and allies (Fig. 2B) raises questions about its identity and the identity of the material used in the Ringelberg et al. (2022) analysis under this name. This species was described by Barneby and Grimes (1996) who acknowledged that, in the absence of having adequate flowering material, even the generic placement of their new entity was uncertain. Our examination of online images of *Leonard 7490*, the holotype of *A. leonardii* at the US Herbarium, a fragment of the isotype at NY and a paratype (*Zanoni 34986*, NY, material that was used in the present phylogenomic studies), reveals that these collections show a suite of

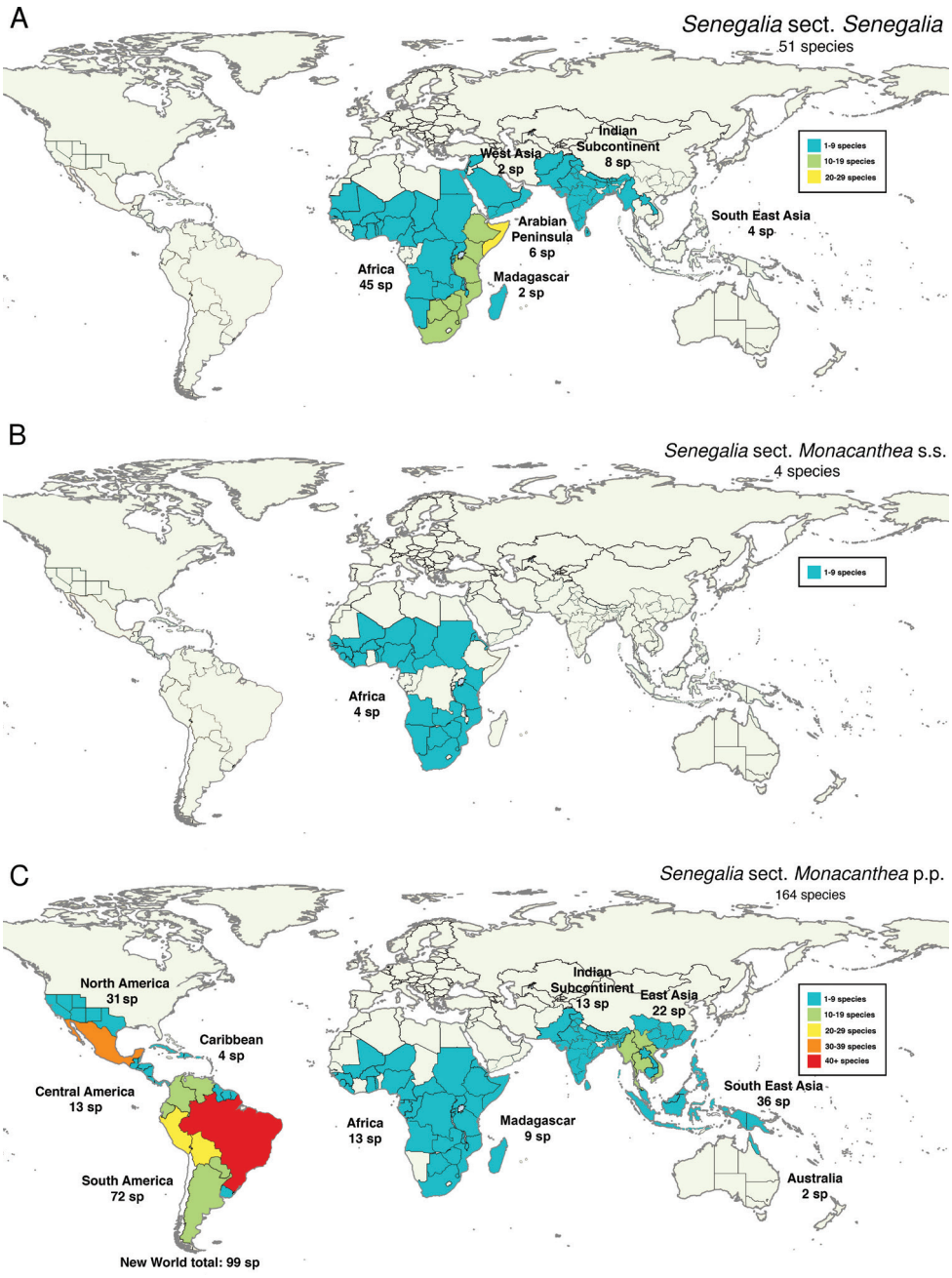

Figure 5. Distribution of the main groups of *Senegalia* **A** *Senegalia* sect. *Senegalia*. **B** *Senegalia* sect. *Monacanthea* s.s. **C** *Senegalia* sect. *Monacanthea* p.p. Species numbers derived from Maslin and Wilson (2021) at WorldWideWattle website (http://worldwidewattle.com).

Table 1. Major groups of the senegalioid grade showing species numbers and regional distribution derived from Maslin and Wilson (2021) at WorldWideWattle website (http://worldwidewattle.com). Note: As used here, North America includes Mexico and the U.S.A. and Asia includes New Guinea.

Name	Total species number	Distribution (species number)
Senegalia	219	**Pantropical**
Sect. *Senegalia*	51	**Old World only. African region**: Africa (45 spp.), Madagascar (2 spp.), Arabian Peninsula (6 spp.); **Asian region**: West Asia (2 spp.), Indian subcontinent (8 spp.), Southeast Asia (4 spp.)
Sect. *Monacanthea* p.p.	164	**Pantropical: New World**: Caribbean (4 spp.), Central America (13 spp.), North America (31 spp.), South America (72 spp.); **African region**: Africa (13 spp.), Madagascar (9 spp.); **Asian region**: Indian subcontinent (13 spp.), East Asia (22 spp.), Southeast Asia (36 spp.); **Australia** (2 spp.)
Sect. *Monacanthea* s.s	4	**Africa** (4 spp.)
Mariosousa	14	**New World**: Central America (3 spp.), North America (13 sp.)
Parasenegalia	11	**New World**: Caribbean (3 spp.), Central America (1 sp.), South America (7 spp.)
Pseudosenegalia	2	**New World**: South America – endemic to Bolivia (2 spp.)

vegetative characters that are consistent with those of *Parasenegalia vogeliana* (Steud.) Seigler & Ebinger: there are no prickles on the branches; the petiolar nectary has the same position and shape; similar leaflet shape, size, apex, base and veins; number of pinnae pairs (about 4) and number of leaflets per pinna (about 10). This is in line with the determination of the US holotype as *Lysiloma vogelianum* (Steud.) Stehlé, which is a homotypic synonym of *Parasenegalia vogeliana* (Seigler et al. 2017) and with the close geographical proximity of the type localities of *A. leonardii* and *P. vogeliana* in Haiti. Despite the lack of flowers on any of the material of *A. leonardii* referred to above, the combined morphological similarities coinciding with geographical proximity of type localities and the phylogenetic placement of *A. leonardii* (Fig. 2B), support treatment of *A. leonardii* as a synonym of *P. vogeliana*. This result implies that *Parasenegalia* is also potentially non-monophyletic, adding further to the difficulties of delimiting genera across *Senegalia* and allies. Given such a significant consequence, it is recommended that sequencing of additional *Parasenegalia* species, preferably using the *Mimobaits* gene set of Koenen et al. (2020), is needed to further assess the potential non-monophyly of *Parasenegalia*. This is especially relevant, given the lack of support for the genus and the extremely short branch subtending *Parasenegalia visco* (which is also morphologically somewhat anomalous) in the phylogenetic analysis of Miller et al. (2017).

***Parasenegalia vogeliana* (Steud.) Seigler & Ebinger in Seigler et al., Novon 25(2): 197–199, fig. 9. 2017.**

Acacia ambigua Vogel, Linnaea 10: 600–601. 1836, nom. illeg., non *Acacia ambigua* Hoffmanns., Zweit. & Dritt. Nacht. Verz. Pfl.-Kult., [3rd addendum] 15. 1826. Type: B†.

Acacia vogeliana Steud., Nomencl. Bot. [Steudel], ed. 2,1: 9. [Aug.] 1840, replacement name for *Acacia ambigua* Vogel, Type: Based on *Acacia ambigua* Vogel.

Senegalia vogeliana (Steud.) Britton & Rose, N. Amer. Fl. 23(2): 116. [25 Sep.] 1928. Type: Based on *Acacia ambigua* Vogel.

Lysiloma vogelianum (Steud.) Stehle, Bull. Mus. Natl. Hist. Nat., sér. 2, 18(2): 193–194. 1946. Type: Based on *Acacia ambigua* Vogel.

Type material. Haiti. Santo Domingo: Plaine prés de Port-au-Prince, Ramuli partem cl. Ehrenberg misit tantum summam; 1828–1839, *C.A. Ehrenberg 274* (lectotype, designated by Seigler et al. 2006, pg 79: HAL [HAL0040798] [fr.], HAL photo at K; isolectotypes, B fragm. at US [US000000564], B photo at K; NY [NY00001533].

=*Albizia leonardii* Britton & Rose ex Barneby & J. W. Grimes. syn. nov. 1996. Silk Tree, Guanacaste, Monkey's Earring, Memoirs of the New York Botanical Garden, Volume 74, Part 1, p 216.

Type materials. Haiti. Dept. du Nord; Habilitation Baille n of Atalaye Plantation, S. Michel de l'Atalaye, in dry thicket; 350 m alt.; 26 Nov 1925. *E. C. Leonard 7490*. Holotype: US; isotype (fragment of holotype) + photo of holotype, NY. Paratype: Haiti. Dept. Artibonite: Dubedou (de Gonaives), 20 km al N. de Gonaives en la carretera a Port-de Paix, zona arida; 130 m alt.; 8 Jun 1985; [young bud]; *T. Zanoni et al. 34986* (JBSD, NY).

Conclusions

All phylogenetic studies have shown that *Senegalia* comprises two, robustly supported clades, which largely correspond to sect. *Senegalia* and sect. *Monacanthea*, but with the exception of the *S. ataxacantha* group (sect. *Monacanthea* s.s.) which aligns with sect. *Senegalia*. The recent phylogenomic analyses, discussed here, show that these two clades are not sister groups and that *Senegalia* is non-monophyletic supporting the possible recognition of these clades as separate genera, based on nuclear data. We anticipate that *Senegalia* will indeed need to be re-classified to reflect this non-monophyly. However, it is also clear that the key morphological traits distinguishing these two clades, namely, armature and, to a lesser extent, inflorescence shape, are not totally consistent across the majority of species within these clades. The most notable inconsistency presently known is the small African *S. ataxacantha* group that is morphologically discordant with the phylogenetic evidence and whether this group is most appropriately treated as a separate genus or retained within the genus *Senegalia* remains to be decided. Given that only about 75 of the total 219 species of *Senegalia* have so far been included in phylogenies (with only six in the recent phylogenomic studies) and that a number of morphologically anomalous species have not yet been sampled for molecular data, it is clear that splitting *Senegalia* at this point would be premature, especially given the nomenclatural repercussions involving name changes for 164 species on four continents. More species of the two clades of *Senegalia* and the allied genera *Mariosousa*, *Parasenegalia* and *Pseudosenegalia* need to be sequenced

and an in-depth investigation of possible reticulate patterns, including with the use of phylogenetic network analysis, should be carried out before any decisions regarding formal taxonomic rearrangements are made. Consequently, below we provide a list of critical taxa for future sequencing, ideally to be carried out using the *Mimobaits* nuclear gene set of Koenen et al. (2020).

Critical taxa for inclusion in future phylogenomic studies

The following species are suggested for inclusion in future phylogenomic studies to achieve taxon sampling that is geographically, morphologically and taxonomically representative of *Senegalia*. In addition, denser sampling of taxa across the allied genera *Mariosousa*, *Parasenegalia* and *Pseudosenegalia* is needed.

1. *Mariosousa* species: *M. centralis* (Britton & Rose) Seigler & Ebinger, *M. coulteri* (Benth.) Seigler & Ebinger.
2. *Parasenegalia* species: *P. miersii* (Benth.) Seigler & Ebinger, *P. muricata* (L.) Seigler & Ebinger, *P. rurrenabaqueana* (Rusby) Seigler & Ebinger, *P. vogeliana* (Steud.) Seigler & Ebinger.
3. *Pseudosenegalia riograndensis* (Atahuachi & L. Rico) Seigler & Ebinger.
4. *Senegalia* species:

- Africa (sect. *Monacanthea* p.p. species with globose or oblongoid heads): *S. brevispica* subsp. *brevispica* (Harms) Seigler & Ebinger, *S. schweinfurthii* (Brenan & Exell) Seigler & Ebinger (either variety).
- Africa (sect. *Monacanthea* s.s.): **Ataxacantha species-group:** *S. eriocarpa*, *S. chariessa*, *S. macrostachya*.
- Africa (sect. *Senegalia*): *S. burkei* or *S. caffra* (inflorescences racemes or panicles), *S. densispina* (heads globose), *S. erubescens* (Welw. ex Oliv.) Kyal. & Boatwr., *S. laeta* (R. Br. ex Benth.) Seigler & Ebinger or *S. rovumae* (Oliv.) Kyal. & Boatwr. (inflorescence, a spiciform raceme), *S. senegal* (L.) Britton (any variety), *S. mellifera* (Vahl) Seigler & Ebinger.
- Americas (sect. *Monacanthea* p.p.): **Amazonica species-group**: *S. amazonica* (Benth.) Seigler & Ebinger, *S. serra* (Benth.) Seigler & Ebinger; **Berlandieri species-group**: *S. berlandieri* (Benth.) Britton & Rose, *S. bonariensis* (Gillies ex Hook. & Arn.) Seigler & Ebinger, *S. gaumeri* (S.F. Blake) Britton & Rose or *S. langsdorffii* (Benth.) Seigler & Ebinger, *S. kelloggiana* (A.M. Carter & Rudd) C.E. Glass & Seigler, *S. paganuccii* Seigler, Ebinger & P.G. Ribeiro, *S. picachensis* (Brandegee) Britton & Rose or *S. interior* Britton & Rose; **Greggii species-group**: *S. emilioana*, *S. gilliesii*, *S. greggii*, *S. occidentalis* (Rose) Britton & Rose, *S. subsessilis*; **Martiusiana species-group**: *S. martiusiana* (Steud.) Seigler & Ebinger; **Monacantha species-group:** *S. monacantha*; **Pedicellata species-group**: *S. pedicellata* (Benth.) Seigler & Ebinger; **Polyphylla species-group**: *S. polyphylla* (DC.) Britton & Rose; **Riparia species-group**: *S. riparia* (Kunth) Britton & Rose;

Tamarindifolia species-group: *S. tamarindifolia* (L.) Britton & Rose; **Tenuifolia species-group**: S. *mirandae* (L. Rico) Seigler & Ebinger, *S. tenuifolia* (L.) Britton & Rose. **Unplaced in any group**: *S. kallunkiae* (J.W. Grimes & Barneby) Seigler & Ebinger, *S. piptadenioides* (G.P. Lewis) Seigler & Ebinger, *S. ricoae* (Bocage & Miotto) L.P. Queiroz , *S. weberbaueri* (Harms) Seigler & Ebinger.

- Asia (sect. *Monacanthea* p.p.): **Caesia species-group**: *S. caesia* (L.) Maslin, Seigler & Ebinger; **Hainanensis species-group**: *S. hainanensis* (Hayata) H. Sun and/or *S. pluricapitata* (Steud. ex Benth.) Maslin, Seigler & Ebinger; **Pennata species-group**: *S. kerrii* (I.C. Nielsen) Maslin, B.C. Ho, H. Sun & L. Bai, *S. pennata* (L.) Maslin (either or both subspecies) or *S. megaladena* (Desv.) Maslin, Seigler & Ebinger (either subspecies); **Rugata species-group**: *S. rugata* (Lam.) Britton & Rose; **Teniana species-group**: *S. kunmingensis* (C. Chen & H. Sun) Maslin, B.C.Ho, H.Sun & L.Bai or *S. prominens* Maslin, B.C. Ho, H. Sun & L. Bai, *S. yunnanensis*; **Unplaced in any group**: *S. donnaiensis*, *S. kostermansii* (I.C. Nielsen) Maslin, Seigler & Ebinger, *S. kekapur* (I.C. Nielsen) Maslin, Seigler & Ebinger, *S. thailandica* (I.C. Nielsen) Maslin, Seigler & Ebinger.
- Asia: (sect. *Senegalia*)*: S. catechu*, *S. modesta* (Wall.) P.J.H. Hurter.
- Madagascar (sect. *Monacanthea* p.p. species with spikes): *S. menabeensis.*

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RESEARCH ARTICLE

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Revisiting the phylogeny and taxonomy of the Pithecellobium clade (Leguminosae, Caesalpinioideae) with new generic circumscriptions

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Abstract

We present the most complete molecular phylogeny to date of the Pithecellobium clade of subfamily Caesalpinioideae. This neotropical group was informally recognised (as the Pithecellobium alliance) at the end of the 20th century by Barneby and Grimes (1996) and includes five genera and 33 species distributed from the southern United States and Caribbean Islands to north-eastern South America. Our aims were to further test the monophyly of the group and its genera and to identify sister group relationships within and amongst the genera. A phylogenetic analysis of nuclear ribosomal DNA sequences (ITS and ETS) was performed. The results provide further support for the monophyly of the Pithecellobium clade. The genera *Ebenopsis*, *Pithecellobium* and *Sphinga* were strongly supported as monophyletic. *Havardia* and *Painteria* were found to be non-monophyletic, prompting their re-circumscriptions and the description of two new genera: *Gretheria* and *Ricoa*. New combinations are made for the three species transferred to the new genera.

Keywords

Fabaceae, Ingeae, Ingoid clade, mimosoid, New World, phylogenetic systematic, taxonomy

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Introduction

In their seminal monographic treatment of the American synandrous mimosoid legumes, Barneby and Grimes (1996, 1997) significantly altered generic circumscriptions within Leguminosae tribe Ingeae (subfamily Caesalpinioideae; see LPWG 2017; Koenen et al. 2020), which, as traditionally defined, is clearly non-monophyletic, with part of tribe Acacieae nested within it (Luckow et al. 2003; Miller et al. 2003; Brown et al. 2008; LPWG 2017; Koenen et al. 2020). They also presented preliminary hypotheses on phylogenetic relationships amongst and within the treated genera. Most of the American species of the tribe were assigned to five informal alliances, each named for its most prominent genus (i.e. *Abarema* Pittier, *Chloroleucon* (Benth.) Britton & Rose, *Inga* Mill., *Pithecellobium* Mart. and *Samanea* (Benth.) Merr., respectively). Of these, only the so-called Pithecellobium alliance (henceforth called the Pithecellobium clade) has been consistently supported as monophyletic in subsequent molecular phylogenies (e.g. Brown et al. 2008; de Souza et al. 2013; Iganci et al. 2015; LPWG 2017; Koenen et al. 2020; Soares et al. 2021), albeit with limited taxonomic sampling. In a recent large-scale phylogenetic study of the mimosoid legumes by Koenen et al. (2020), the Pithecellobium clade was resolved within the so-called "ingoid clade", where it belongs to a large clade comprising the majority of the genera formerly placed in tribe Ingeae plus *Acacia* (sensu Orchard and Maslin 2003).

The Pithecellobium clade consists of five genera: *Pithecellobium*, with 19 species, is the largest genus, followed by *Havardia* Small, with five species and *Ebenopsis* Britton & Rose, *Painteria* Britton & Rose and *Sphinga* Barneby & J.W. Grimes, each with three species. It is restricted to the tropics and subtropics of the New World, with species distributed from the southern United States and the Caribbean Islands to Peru and north-eastern Brazil. Its centre of species diversity lies in Mexico, which harbours all five genera and 18 species. The Antilles and South America each harbour eight species. Habitats include subtropical and tropical deciduous and semi-deciduous forests, thorny scrub, chaparral, desert grasslands and other xeromorphic vegetation, as well as coastal scrub and swamp forests, including mangroves. Amongst the American synandrous mimosoids, the clade is defined morphologically by sympodial growth, proleptic, dimorphic branches forming vegetative and/or reproductive short-shoots; spinescent stipules; buds protected by the adaxial side of the petiole; coeval or late-suppressed leaves; inflorescences with monomorphic flowers; and colporate non-equatorial pollen apertures (Barneby and Grimes 1996).

The five genera differ from each other most obviously in pod and seed characters (Barneby and Grimes 1996). In *Pithecellobium*, the pods are oblong to linear and recurved or coiled; following dehiscence, the seeds are suspended from the often-twisting valves by the funicle and the distal end of the funicle forms a red, pink or white fleshy aril cupping the lower third to half of the seed. The other four genera have non-arillate seeds. In *Ebenopsis*, the fruit is subterete, woody and internally septate between the overgrown (obese) seeds. In *Havardia* and *Sphinga*, the fruit is more strongly compressed

and chartaceous to coriaceous, with the cavity continuous, the seeds not overgrown and the funicle sigmoid or contorted. In *Painteria*, the fruit is like in *Ebenopsis*, woody and subterete, but it is not internally septate between the plump lentiform seeds and the funicle is straight or sinuous. Another notable generic character is the presence of flask-shaped mature flower buds in *Sphinga* (vs. obovoid-pyriform in other genera).

Barneby and Grimes (1996, 1997) undertook morphologically based phylogenetic analyses that included all taxa of the Pithecellobium clade. In their analyses, all five genera were recovered as monophyletic. *Sphinga* and *Havardia* formed a clade, which was, in turn, placed as sister to a clade containing the remaining three genera, within which *Painteria* and *Pithecellobium* were resolved as sister genera (Fig. 1). Hypothetical relationships (and morphological character state transformations) amongst and within the five genera were depicted in their fig. 12 of the first volume of their monograph (Barneby and Grimes 1996) and Fig.1 of the second volume (Barneby and Grimes 1997).

To date, most molecular phylogenetic analyses that included species of the Pithecellobium clade have sampled single species of *Ebenopsis*, *Havardia*, *Pithecellobium* and *Sphinga* and no species of *Painteria* (e.g. Brown et al. 2008; de Sousa et al. 2013; Iganci et al. 2015; Koenen et al. 2020; Soares et al. 2021). Although each of these studies supported the monophyly of the group, with respect to relation-

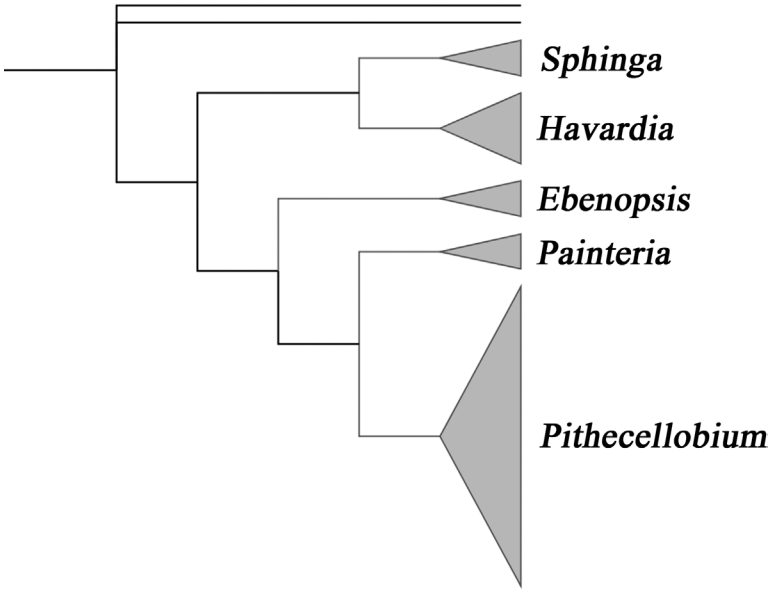

Figure 1. Summary cladogram based on maximum parsimony analyses of 29 morphological characters of the Pithecellobium clade (one of two trees resulting, the second involves differences in the internal topology of *Painteria*) from Barneby and Grimes (1996). Five genera were then recognised: Ebenopsis Britton & Rose (3 species), *Havardia* Small (5), *Painteria* Britton & Rose (3), *Pithecellobium* Mart. (19) and *Sphinga* Barneby & J. W. Grimes (3).

ships amongst the sampled genera, the analyses yielded mostly unresolved or poorly supported topologies (i.e. < 70% bootstrap support in parsimony analyses and/or < 0.95 posterior probabilities in Bayesian analyses). Three of these studies (Iganci et al. 2015; Koenen et al. 2020; Soares et al. 2021) strongly supported *Havardia* as the sister group of *Pithecellobium*.

Two molecular phylogenetic studies had substantially greater sampling of species of the Pithecellobium clade. The first, published as an electronic supplement to LPWG (2017), comprised an analysis of chloroplast *matK* sequences from a large and phylogenetically broad sample of species of Leguminosae (LPWG 2017), amongst which were two species of *Ebenopsis*, three of *Havardia*, one of *Painteria*, seven of *Pithecellobium* and two of *Sphinga*. Although the fine-scale details of the phylogenetic results were not discussed in the article, the analysis also recovered the Pithecellobium clade as monophyletic and resolved three well-supported clades, respectively grouping the two sampled species of *Sphinga*, the three sampled species of *Havardia* and six of the sampled species of *Pithecellobium*; the seventh *Pithecellobium* species, *P. keyense* was placed in an unresolved position and relationships amongst the genera were also unresolved.

The second study (Ringelberg et al. 2022, published in this special issue) is a phylogenomic analysis of subfamily Caesalpinioideae that produced an ASTRAL species tree, based on 821 single– or low-copy nuclear gene trees. It sampled all five genera and 11 species of the Pithecellobium clade, including the previously unsampled *Havardia campylacantha* and *Painteria elachistophylla*. The topology obtained is better resolved than that of LPWG (2017). It supports the monophyly of *Pithecellobium*, while rendering both *Havardia* and *Painteria* non-monophyletic.

Nevertheless, over half of the species of the Pithecellobium clade remain unsampled in these phylogenetic studies and, thus, knowledge of relationships within the group is still incomplete. Filling the sampling gaps is needed to establish a more robust phylogenetic framework for revising the classification of the group and, ultimately, for reconstructing its evolutionary history.

Here, we present the most comprehensively sampled molecular phylogenetic study of the Pithecellobium clade to date, based on analysis of sequences from nuclear ribosomal DNA regions. The following questions are addressed: 1) Are the Pithecellobium clade and its constituent genera monophyletic? 2) Does analysis of molecular data support the relationships amongst and within the genera recovered by previous analysis of morphology (Barneby and Grimes 1996, 1997)?

Material and methods

Taxon sampling and molecular markers

The ingroup sample included multiple representative species of all five genera of the Pithecellobium clade, for a total of 20 of the 33 species (61%) of the group (Table 1).

Table 1. Voucher information and GenBank accession numbers for the DNA sequences used in the present study.

	ETS	ITS
outgroup		
Calliandra eriophylla	MN755770.1	-
Calliandra haematocephala	MN755769.1	JX870694.1
Cojoba arborea	MW849552.1	JX870758.1
Cojoba graciliflora	MW849557.1	MZ015531.1
Faidherbia albida	EF638163.1	JF270778.1
Hesperalbizia occidentalis	MN755774.1	MW699959.1
Lysiloma divaricatum	MN755783	MN755826
Lysiloma latisiliquum	MN755785	MN755827
Mariosousa dolichostachya	EF638084.1	EF638199.1
Vachellia farnesiana	EF638128.1	EF638219.1
Zapoteca formosa	MN755771	AY125854.1
Zapoteca tehuana	MZ327390 *A. Campos 4108* (MEXU)	OM634641 *A. Campos 4108* (MEXU)
Ingroup		
Ebenopsis confinis	MZ327411 *A.L. Reina 696* (FCME)	KF921650.1
Ebenopsis ebano	MZ327410 *W. Torres et al. 84* (CICY)	EF638101.1
Havardia albicans	MZ327403 *R. Duno 1945* (CICY)	OM634648 *R. Duno 1945* (CICY)
Havardia campylacantha (***Gretheria campylacantha***)	MZ327405 *E. Soto Núñez et al. 8036* (FCME)	OM634650 *E. Soto Núñez et al. 8036* (FCME)
Havardia mexicana	MZ327397 *T. R. van Devender 2005-1085* (MEXU)	JX870762.1
Havardia pallens	KF921656.1	EF638194.1
Havardia sonorae (***Gretheria sonorae***)	MZ327404 *A. Flores 4875* (FCME)	OM634649 *A. Flores 4875* (FCME)
Painteria elachistophylla	MZ327409 *García y Lorence 708* (FCME)	-
Painteria leptophylla (***Ricoa leptophylla***)	MZ327407 *R. Cruz Durán 224* (MEXU)	OM634651 *R. Cruz Durán 224* (MEXU)
Painteria leptophylla 2 (***Ricoa leptophylla***)	MZ327406 *J. Calónico 3751* (FCME)	*C.E. Hughes 1539* (FCME)
Painteria revoluta	MZ327408 *E. López 1107* (CICY)	-
Pithecellobium diversifolium	MZ327399 *A. Laurenio 71* (MO)	JX870768.1
Pithecellobium excelsum	MZ327400 *Tropical house Bot. Garden Aarhus* 2013	EF638208.1
Pithecellobium dulce	OM674458 *E. López* 1146 (CICY)	MZ015540.1
Pithecellobium keyense	MZ327394 *R. Duno et al. 2216* (CICY)	OM634645 *R. Duno et al. 2216* (CICY)
Pithecellobium lanceolatum	MZ327398 *E. Endañú 1310* (CICY)	-
Pithecellobium winzerlingii	MZ327393 *R. Duno 2434* (CICY)	OM634644 *R. Duno 2434* (CICY)
Pithecellobium oblongum	MZ327396 *I. Coronado & R.M. Rueda 5064* (MO)	OM634647 *I. Coronado & R.M. Rueda 5064* (MO)
Pithecellobium unguis-cati	MZ327395 *H. M. Burdet & M. Burdet 02* (MO)	OM634646 *H. M. Burdet & M. Burdet 02* (MO)
Sphinga acatlensis	MZ327391 *E. López 1004* (CICY)	OM634642 *E. López & E. Endañu 1020* (CICY)
Sphinga platyloba	MZ327392 *R. Duno et al. 2471 (*CICY)	OM634643 *R. Duno et al. 2471 (*CICY)

Species were sampled from across the geographical range of the Pithecellobium clade. The number of species sampled per genus relative to total diversity was as follows: *Ebenopsis* (2/3), *Havardia* (5/5), *Painteria* (3/3) *Pithecellobium* (8/18) and *Sphinga* (2/3). Although less than half of the species of *Pithecellobium* were sampled, these included species of the three most basal lineages of the genus, as identified in the morphological analysis of Barneby and Grimes (1997). We were unable to sample the en-

demic Antillean species of *Pithecellobium* (e.g. *P. circinale* (L.) Benth., *P. cynodonticum* Barneby & J.W. Grimes and *P. histrix* (A. Rich.) Benth.), as well as some species from Central America (e.g. *P. furcatum* Benth. and *P. peckii* Blake). Based on the results of previous phylogenetic studies, the outgroup was composed of representative species of nine more distantly related mimosoid genera (Table 1; Brown et al. 2008; Kyalangalilwa et al. 2013; Iganci et al. 2015; Koenen et al. 2020). *Vachellia farnesiana* (L.) Wight & Arn was used to root the analyses.

DNA sequences were gathered from two nuclear ribosomal regions, ETS and ITS

Thirty-two sequences were newly generated for this study, while 31 sequences were obtained from GenBank (www.ncbi.nlm.nih.gov/genbank); most of the latter were generated for the studies of Miller and Bayer (2001), Miller et al. (2003), Brown et al. (2008) and Duno de Stefano et al. (2021). The ETS dataset consisted of 34 sequences (21 new) from 33 species; the ITS dataset consisted of 29 (11 new) sequences from 30 species. GenBank accession numbers for all sequences are given in Table 1.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from fresh leaves collected from the living collection in the Roger Orellana Regional Botanical Garden of the Centro de Investigación Científica de Yucatán, A. C., from leaflet tissue collected in the field and dried with silica gel or from herbarium specimens deposited in the following Herbaria: CICY, FCME, MA, MEXU, MO, UCOL and ZEA (acronyms as in Thiers (2020[and onwards]). Total DNA (from fresh or herbarium material) was obtained with DNeasy Plant Mini Kits (QIAGEN Inc., Valencia, California), following the manufacturer's specifications. Concentration and relative quality of DNA was evaluated using the protocol in Duno de Stefano et al. (2021).

Amplifications were performed in an Applied Biosytems Veriti 96 Well Thermal Cycler (Applied Biosystems, Foster City, USA). Volumes of reagents in PCR reactions (all reactions were brought to final volume by adding ultrapure water) and cycling conditions were as follows for the two DNA regions: 1) ETS: 30 µl of mix containing 3 µl 10X Buffer, 2.5 µl $MgCl_2$, 0.6 µl (~ 10 ng) each of primers, 4 µl Q solution, 1 µl 1.25 mM l-1 dNTP, 0.2 µl (1 U) TAQ polymerase, 2 µl (~ 10 ng) DNA; 94 °C for 3 min + 30 cycles (94 °C for 1 min + 60.5 °C for 1 min + 72 °C for 2 min) + 72 °C for 7 min; primers were 18S-IGS and 26S-IGS (Baldwin and Markos 1998) 2) ITS: 25 µl mix containing 2.5 µl 10X Buffer, 2.5 µl $MgCl_2$, 0.6 µl (~ 10 ng) each of primers, 4 µl Q solution, 1 µl 1.25 mM l-1 dNTP, 0.2 µl (1 U) TAQ polymerase, 2 µl (~ 10 ng) DNA; 94 °C for 3 min + 30 cycles (94 °C for 1 min + 60.5 °C for 1 min + 72 °C for 2 min) + 72 °C for 7 min; primers were Ac 12F and Ac 1290R from Miller and Bayer (2001). PCR products (and the primers used for amplifications) were sent to Macrogen Korea, Seoul, South Korea for sequencing.

Figure 2. Morphological diversity of the genera of the Pithecellobium clade as circumscribed here. *Ebenopsis ebano* (Berland.) Barneby & J.W. Grimes **A** inflorescence **B** pod. *Gretheria campylacantha* (L. Rico & M. Sousa) Duno & Torke **C** bark. *Pithecellobium excelsum* (Kunth) Mart. **D** bark. *Havardia albicans* (Kunth) Britton & Rose **E** inflorescence. *Painteria elachistophylla* (A. Gray ex S. Watson) Britton & Rose **F** pod **G** seed. *Pithecellobium dulce* (Roxb.) Benth. **H** leaves. *Pithecellobium winzerlingii* Britton & Rose **I** inflorescence. *Pithecellobium keyense* Britton **J** inflorescence. *Pithecellobium lanceolatum* (Humb. & Bonpl. ex Willd.) Benth. **K** inflorescence. *Pithecellobium unguis-cati* (L.) Benth. **L** pod and seed. *Pithecellobium lanceolatum* (Humb. & Bonpl. ex Willd.) Benth. **M** pod and seed. *Sphinga acatlensis* (Benth.) Barneby & J.W. Grimes **N** branch, leaves and inflorescences **O** pod. *Sphinga platyloba* (Bertero ex DC.) Barneby & J.W. Grimes **P** leaves and inflorescence. Photos: **A, B, I–K, P** German Carnevali **C, D, N, O** Colin E. Hughes **E, L** Gustavo A. Romero **F, G** Pedro Najéra Quezada, https://www.naturalista.mx) **H** Peter Pedersen **M** Rodrigo Duno.

Sequence assembly, alignment and molecular phylogenetic analyses

Assembly and editing of sequences were carried out in BioEdit v.7.0.9 (Hall 1999). Each of the two partitions was aligned independently in the online version of MAFFT (Katoh et al. 2002, 2017; https://mafft.cbrc.jp/alignment/server/) using the default settings (gap opening penalty = 1.53 and offset value = 0.00). Following exploratory phylogenetic analyses employing maximum parsimony, the concatenated alignment matrix was analysed using Bayesian Inference as implemented in MrBayes v. 3.2.7 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), with each partition (ETS and ITS) treated as independent and associated with its own nucleotide substitution model. The best fitting model for each partition was selected in jModelTest v. 2.1.7 (Darriba et al. 2012), based on the Akaike Information Criterion (AIC). The following substitution models were selected: ETS = TIM3+I+G and ITS = GTR+I+G. Bayesian analyses consisted of two independent Metropolis-coupled Markov Chain Monte Carlo (MCMC) runs, each starting from a randomly chosen tree and run for five million generations, with one tree sampled every 2000 generations. Twenty percent of the sampled trees were discarded as burn-in after evaluation of the output parameters generated by the Bayesian analysis in Tracer v.1.6 (Rambaut et al. 2014). The remaining sampled trees were summarised in a 50% majority-rule consensus tree, with clade posterior probabilities (PP, i.e. the proportion of trees containing particular clades) used to measure clade support.

Posterior Probabilities of < 0.95 were considered weakly supported, whereas PP of 0.95–1.0 were deemed to be well supported. The convergence of MCMC runs was assessed with Tracer v. 1.7.1 (Rambaut et al. 2014) verifying that the effective sample size (ESS) for all parameters was > 200 (Nascimento et al. 2017).

Results

The Bayesian analysis of ETS and ITS strongly supported the monophyly of the Pithecellobium clade (clade A in Fig. 3, PP = 1.0) and yielded a largely resolved topology within the group, with most nodes being well supported (Fig. 3). The genera *Ebenopsis*, *Pithecellobium* and *Sphinga* were each recovered as monophyletic with robust support values (clades L, G and F, respectively, PP = 0.98–1.0), but *Havardia* and *Painteria* were both resolved as non-monophyletic. Immediately above the base of the Pithecellobium clade, a marginally supported node (clade C, PP = 0.94) grouped a clade (E; PP = 1.0) comprised of three species of *Havardia* (*H. albicans*, *H. mexicana* and *H. pallens*) with *Pithecellobium* and *Sphinga*; the latter two genera were, in turn, well-supported as sister taxa (clade D; PP = 0.98). Within *Pithecellobium*, a well-supported clade (PP = 0.98), comprising *P. unguis-cati* and *P. oblongum*, was placed as the sister group to a poorly supported clade (PP = 0.86) containing the other sampled species of the genus. Two members of *Pithecellobium* section *Spicata*, *P. winzerlingii* and *P. lanceolatum*, were placed sister to each other (PP = 1.0) in this last clade. Another well-supported clade grouped the species *P. keyense* and *P. dulce* (as sister taxa) with *P. diversifolium* and *P. excelsum* (as sister taxa).

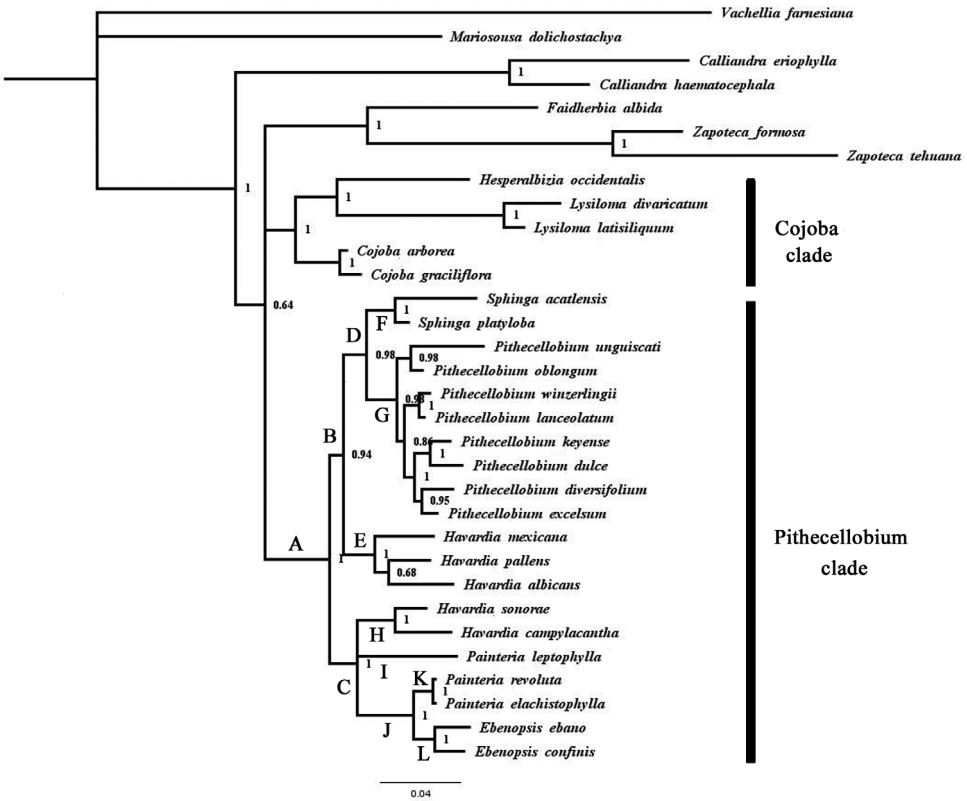

Figure 3. Results of majority rule consensus tree of the Bayesian analysis of the nuclear ribosomal ETS and ITS regions the clade Pithecellobium.

The other half of the basal dichotomy in the Pithecellobium clade was strongly supported (clade C, PP = 1.0) and grouped a clade (H, P = 1.0) containing two other species of *Havardia* (*H. campylacantha* and *H. sonorae*) with *Painteria* and *Ebenopsis*. Two of the three species of *Painteria* (*P. elachistophylla* and *P. revoluta*) formed a strongly-supported clade (K, PP = 1.0) that was placed as the sister group (clade J, P = 0.1) to *Ebenopsis*; the exclusion of *Painteria leptophylla* from this clade rendered *Painteria* paraphyletic.

Discussion

Comparison with previous studies

Our study shows both agreement and disagreement with well-supported results (PP ≥ 0.95 and/or likelihood or parsimony bootstrap ≥ 80%) of previous (Brown et al. 2008; Iganci et al. 2015; LPWG 2017; Koenen et al. 2020; Soares et al. 2021) and concurrent (Ringelberg et al. 2022) molecular phylogenetic studies. Our study is in

agreement with all of these studies in strongly supporting the monophyly of the Pithecellobium clade. It also agrees with LPWG (2017) in supporting the monophyly of *Sphinga* and in the recovery of a clade grouping *Havardia albicans*, *H. mexicana* and *H. pallens*. With Ringelberg et al. (2022), which unlike the other studies sampled the key taxa *Havardia campylacantha* and *Painteria elachistophylla*, our study agrees in demonstrating the non-monophyly of both *Havardia* and *Painteria*, the latter due to the nesting of *Ebenopsis* within it and also agrees in supporting the monophyly of *Pithecellobium*.

Our results conflict with those of several studies by placing *Pithecellobium* as the sister taxon to *Sphinga* (Fig. 3). For example, the study of Iganci et al. (2015), although it sampled only single species of each genus (and none of *Painteria*), placed *Havardia pallens* sister to *Pithecellobium dulce* (PP = 0.99), to the exclusion of *Sphinga acatlensis*. The same result, but even more strongly supported (100% likelihood bootstrap), was obtained by Koenen et al. (2020), while Ringelberg et al. (2022) had *H. pallens* sister to *Pithecellobium*, but with more species sampled for the later genus. Interestingly, Koenen et al. (2020) recovered a clade within which *Ebenopsis confinis* was sister to *H. pallens* plus *P. dulce* (likelihood = 0.93, PP = 0.81), a result not recovered by any other analysis. The resolution of relationships within *Pithecellobium* is also somewhat conflicting between our study and those of LPWG (2017) and Ringelberg et al. (2022), although the overlap in sampling of species of the genus was limited between studies. For example, LPWG (2017) placed *P. keyense* in an unresolved position outside a clade comprising the other sampled species of the genus and Ringelberg et al. (2022) placed it sister to that clade, while in our phylogeny, *P. keyense* occupies a more nested position within *Pithecellobium*.

The causes of such conflict are unknown. Unlinked DNA regions used in the different studies may reflect different evolutionary histories, each with the potential to be differently impacted by evolutionary phenomena that cause phylogenetic conflict, such as gene duplication, hybridization and incomplete lineage sorting (Schrempf and Szöllősi 2020). Conversely, conflict may be attributable to statistical error, resulting from large differences in taxonomic sampling, the choice of sequence alignment criteria and/or the phylogenetic methods used, some of which may be more or less prone to phenomena, such as long branch attraction (Bergsten 2005). With respect to the present comparisons, we suspect that the latter is more prevalent since the other molecular phylogenetic studies of the Pithecellobium clade have less taxonomic sampling than our study. Moreover, we surmise that, in cases of conflict, our results are more compatible with previous taxonomic hypotheses, based on morphology.

Indeed, our study exhibits considerable agreement with the phylogenetic analysis of morphological data in Barneby and Grimes (1996, 1997), especially if the comparison is restricted to the clades from the morphological analyses that were supported by three or more putative morphological synapomorphies. For example, the monophyly of the alliance and the genera *Ebenopsis*, *Pithecellobium* and *Sphinga*, which were each strongly supported in our study, were also each supported by four to seven morphological synapomorphies in the analysis of Barneby and Grimes (1996, their fig. 12). Conversely, the two genera that were resolved as non-monophyletic in our phylogeny in conflict with Barneby and Grimes (1996), *Painteria* and *Havardia*, were respectively supported by only one and two putative morphological synapomorphies in the latter study. Within

Pithecellobium, internal nodes supported by one or two morphological characters in Barneby and Grimes (1997, their Fig. 1) were not recovered by our analysis, whereas a node supported by seven morphological characters was resolved in our phylogeny (but with fewer sampled taxa) by the grouping of *P. lanceolatum* and *P. winzerlingii*. Even some clades supported by only one or two morphological characters in Barneby and Grimes (1996), such as a clade grouping *Havardia sonorae* and *H. campylacantha* and another clade grouping *H. albicans*, *H. mexicana* and *H. pallens*, were recovered in our analysis. However, one significant area of conflict involved the strongly supported sister relationship (PP = 1.0) between *Pithecellobium* and *Sphinga* in our study. In contrast, *Painteria* was resolved as the sister genus to *Pithecellobium* in Barneby and Grimes (1996), with four morphological characters supporting the result.

In cases of conflict between our molecular results and the morphological analyses of Barneby and Grimes (1996, 1997), we favour the former results for several reasons. First, although they mapped character state transitions on their phylogenies, Barneby and Grimes (1996) did not provide bootstrap values or other statistical measures of branch support in their phylogenies. Second, the morphological characters that were included in their phylogenetic studies included features, such as degree of pod compression, pod texture, pod curvature, valve reflection and coiling and degree development of an ovary stipe, which show continuous (or near continuous) variation when viewed across the entire Pithecellobium clade; thus, the division of the features into discrete states is subjective. Third, relative to molecular sequence data, suites of morphological characters may be more prone to homoplasy caused by shared selection pressures and/or developmental constraints (Scotland et al. 2003; Wiens 2004). Finally, relative to the phylogenies of Barneby and Grimes (1996), the well-supported phylogenetic results of our analyses show a greater degree of congruence with the results of previous molecular phylogenetic studies, including those based on analysis of other DNA regions (e.g. Brown et al. 2008; LPWG 2017; Koenen et al. 2020; Soares et al. 2021).

Other phylogenetic analysis in relation to the Pithecellobium clade sampled 15 species for *matK* (LPGW 2017) and 11 species for 997 nuclear genes (Ringelberg et al. 2022). They show different topologies for the Pithecellobium clade as well as the current topology (Fig. 3). The reasons for these differences could be due to the difference in the number of terminals, the number of nucleotides, alignment and analysis methods. Although the LPGW (2017) analysis has a few more terminals than Ringelberg et al. (2022), the latter has more key species (e.g. more taxa of *Havardia* and *Painteria*) and although this last study supports different generic relationships, it is congruent with the results presented here in demonstrating the non-monophyletic nature of *Havardia* and *Painteria*.

Implications for the generic taxonomy of the *Pithecellobium* clade

Our results further substantiate that three of the five genera of the Pithecellobium clade, *Ebenopsis*, *Pithecellobium* and *Sphinga*, are monophyletic, whereas *Havardia* and *Painteria* are not. While there exist multiple taxonomic solutions that would yield a classification consisting of only monophyletic genera (see Backlund and Bremer 1998; Humphreys and Linder 2009), we strongly favour an option that preserves the first three genera. Be-

Table 2. Morphological comparison between the genera of the Pithecellobium clade as circumscribed here (modified from Barneby and Grimes 1996, 1997).

	Ebenopsis	***Gretheria***	***Havardia***	***Painteria***	***Pithecellobium***	***Ricoa***	***Sphinga***
Habit	Tree or shrub	Shrub or tree	Tree	Shrub	Tree or shrub	Shrub	Shrub or tree
Leaflets, size	Microphyllous	Microphyllous	Microphyllous	Microphyllous	Micro- to Macrophyllous	Microphyllous	Macrophyllous
Branching, pattern	Proleptically	Sylleptically and proleptically	Sylleptically and proleptically	Proleptically	Proleptically	Proleptically	Proleptically
Extrafloral gland, position	Interpinal	Near midpetiole,	Interpinal but the first below proximal pinna-pair or near midpetiole	Between proximal pinna-pair, rarely between 2 pairs, not on petiole proper	Interpinal	between the first pinnae pair	Near midpetiole, rarely at tip of petiole
Leaflet, venation	Palmate	Pinnate	Pinnate, weakly pinnate, simple, weakly palmate-pinnate	Palmate or simple weakly developed superficially	Pinnate and usually also reticulate	Weakly developed, nearly simple or 1-branched	Pinnate or subpalmate
Inflorescence	Capitula or shortly spiciform	Capituliform racemes	Capitula or spiciform	Capitula or shortly spiciform	Capitula or spikes	Capitula	Capitula
Flower, anthesis	Diurnal	Vespertine	Diurnal	Diurnal	Diurnal	Vespertine	Vespertine
Corolla, lobes	Erect	Erect	Recurved	Erect	Erect	Recurved	Erect
Disc (ovary)	Absent	Simple callosities or 5-lobed	Absent, obsolete callosities, rarely lobed disc	Callosities obsolete or absent	Callosities obsolete, rarely developed into a lobed disc	Callosties developed or sometimes subobsolete (staminate flowers)	Developed, clasping the stipe
Funiculus, shape	Straight (not sigmoid)	dilated, sigmoid	Sigmoid	Straight or sinuous (not sigmoid)	Spongy arilliform	Straight or sinuous (nor sigmoid)	Contorted or sigmoid
Fruit, shape	massive, compressed, sausage-like	Oblong plano-compressed	Oblong or broad-linear straight, plano-compressed	Compressed but turgid, retrofalcate, falcately or subcircinnately broad-linear	oblong or linear in profile, backwardly recurved or coiled and sometimes also twisted	Falcately or subcircinnately broad-linear	Broad-linear plano-compressed
Fruit, consistence	Woody	Stiff	Chartaceous or thinly coriaceous	Leathery	Leathery or woody	Stiffly leathery	Papery
Fruit, septation	Yes	No	No	No	No or incipient	No	No
Seed	Plumply obese	disciform to orbicular	Lentiform, orbicular or oblong-elliptic	Plumby lentiform	plumply	Compressed but plumb	Lentiform

yond minimising nomenclatural changes, such a solution is desirable since the first three genera are each morphologically distinctive and easily diagnosed.

There are two other nomenclatural options, which, in our opinion, are less appropriate. The first one would be to include all members of clade C (Fig. 3) - *Havardia p.p.* (excluding the type), *Ebenopsis* and *Painteria* - in a single genus named *Ebenopsis*, which

has nomenclatural priority. However, this would result is a heterogeneous genus with respect to fruit morphology (Figs. 2b, f and n), habit and ecology. The second option would be to recognise members of clade H (Fig. 3) as a new genus (as we do here) to transfer *Painteria elachistophylla* and *P. revoluta* to *Ebenopsis*. This new circumscription of *Ebenopsis* reduces morphological variation, but retains notable differences in habit and ecology. While *Ebenopsis*, although less expansive than in the first option, nevertheless encompasses trees growing in lowlands, *Painteria* comprises shrubs growing in highlands of up 2600 m elevation.

As for *Havardia* and *Painteria*, the preferred option retains these generic names for the clades that include the generic type species, *H. pallens* and *P. revoluta*, respectively. It thus requires the erection of two new genera: one for the clade comprised of *H. sonorae* and *H. campylacantha*, another for the species *P. leptophylla*. These four genera (the re-defined *Havardia s.s*. and *Painteria s.s.* and the proposed new genera) are individually diagnoseable by morphology.

Havardia, as here circumscribed, can be diagnosed within the complex for having both sylleptical and proleptical shoots, inflorescences arising from long shoots, leaves with one pair of pinnae and flowers with recurved corolla lobes. The new genus that we name *Gretheria* (containing *H. sonorae* and *H. campylacantha*) also has both sylleptical and proleptical shoots and inflorescences arising from long shoots, but the pinnae are distally accrescent and the corolla lobes are erect-ascending.

Painteria as redefined here, could be diagnosed by the combination of the valves of the pod elastically reflexed with age, the leaves with just one pair of pinnae and the corolla lobes erect-ascending, whereas the new monotypic genus *Ricoa* (comprising *P. leptophylla*), while also having the valves elastically reflexed with age, has leaves with the pinnae decrescent at each end and the corolla lobes recurved.

In the taxonomic treatment that follows, we provide descriptions (drawing heavily from data in Barneby and Grimes 1996) for the two new genera and make the necessary new combinations for the three species contained within them. Table 2 summarises the diagnostic characters of the seven recognized genera of the Pithecellobium clade.

Taxonomy

Key to the genera of the *Pithecellobium* clade (modified from Barneby and Grimes 1996)

1 Trees or shrubs, generally sarmentous; petiolar gland in the mid-petiole; flower bud flask-shaped, flowers opening at night; androecium up to 9 cm long . ..... ***Sphinga***

– Trees or shrubs, erect never sarmentous; petiolar gland at the point of origin of the first (or only) pair of pinnae or in the mid-petiole; flower bud ovoid-pyriform, flowers opening during day; androecium usually less than 3 cm long, very rarely up to 7 cm long **2**

2 Petiolar gland below the first pair of pinnae; fruits flattened, papery and straight **3**
– Petiolar gland between the first pair of pinnae; fruits never flattened, never papery and occasionally straight (then woody or sub-woody)..... **4**
3 Flowers with calyx 1.0–2.0 mm long, teeth 0.25–1.5 mm long, shallowly campanulate; corolla lobes recurved in anthesis; ovary disc absent ..... ***Havardia***
– Flowers with calyx 2.8–3.4 mm long, teeth 0.3–0.8 mm long, deeply campanulate; corolla lobes erect in anthesis; ovary disc present (sometimes poorly developed) ..... ***Gretheria***
4 Leaves with one pair of pinnae and leaflets one pair per pinna or leaves with more than two pairs of pinnae and leaflets two to many pairs per pinna; seeds with fleshy, often brightly coloured arils..... ***Pithecellobium***
– Leaves with two or more pairs of pinnae, never one, leaflets 2–30 pairs per pinna; seeds without aril **5**
5 Pod cylindrical, woody, straight or slightly curved, deeply internally septate; seeds globose; growing in lowlands of Mexico and the United States (Texas). ..... ***Ebenopsis***
– Pod flattened or slightly subterete, sub-woody and curved, without internal septa; seeds lentiform; growing in highlands of Mexico..... **6**
6 Leaves with one or two pairs of pinnae; leaflets 3 to 10 per pinna, rarely 12; blades suborbicular, broadly oblong or elliptic (then revolute); corolla lobes ascending..... ***Painteria***
– Leaves with 3–7(9) pairs of pinnae; leaflets 10 to 25 per pinna; blades narrowly oblong, linear-oblong or lanceolate; corolla lobes recurved ..... ***Ricoa***

Gretheria Duno & Torke, gen. nov.

urn:lsid:ipni.org:names:77303792-1

Diagnosis. Similar to *Havardia* in arboreal or shrubby habit, vegetative branches arising both proleptically and sylleptically, leaves microphyllous, inflorescence arising on long shoots, pod flattened-compressed and seed plumply disciform to orbicular, but differing in the pinnae distally accrescent (vs. decrescent at each end in *Havardia*), the calyx longer and deeply campanulate (vs. shorter, and shallowly campanulate), and the corolla lobes erect-ascending at anthesis (vs. recurved).

Type. *Gretheria sonorae* (S. Watson) Duno & Torke.

Description. Xerophytic, microphyllous arborescent shrubs and small trees, 2–14 m tall, commonly armed with stout recurved, lignescent stipules on the trunk and at each node of long-shoots, indumented with minute whitish trichomes on new growth. ***Leaves*** bipinnate, with 1–6 (13) pairs of pinnae; leaflets 10–31 per pinna; principal leaf axis typically 2–15 cm long, with the petiole 2–24 mm long, bearing a nectary at or below the mid-point of the petiole, the nectary sessile, shallow-

cupular, thick-rimmed or plane and dimpled, pinnae axes sometimes with similar but smaller nectaries between 1–2 (3) distal-most pinna pairs and a minute one at the tip of some pinna-rachises; leaflets opposite, the blade oblong-elliptic to linear-oblong, subcordate at base, obtuse or shortly apiculate at apex; pilosulous or glabrous and marginally ciliolate; venation pinnate, immersed above, prominulous beneath, the mid-rib slightly displaced, giving rise on each side to 2–5 weak secondary veins expiring submarginally or faintly brochidodromous. ***Inflorescence*** capituliform racemes arising from leaf axils of long shoots and coeval with or preceding the leaf and/or arising from brachyblasts; peduncles (1.3) 2 cm long; capitula 10–37-flowered, receptacle clavate, 1.5–2.5 mm diameter; bracts ovate, minute, less than 1 mm long, sessile, persistent into anthesis. ***Flowers*** sessile, homomorphic, the perianth 5-merous; calyx deeply campanulate, glabrous, teeth deltate-ovate, ciliolate and sometimes distally puberulent or strigose; corolla subcylindrical, lobes erect, white-silky strigose dorsally; androecium 40–52-merous, 9–13 mm long, tube 3.6–5 mm long, nectar disc simple callosities or 5-lobed, 0.2 – 0.35 mm tall; ovary subsessile, slenderly ellipsoid, stipe 0.1–0.25 mm long; style about as long as stamens, the stigma poriform. ***Pods*** 1–3 per capitulum, oblong in profile, contracted at base into a pseudostipe ± 5–14 mm long and abruptly so at apex into an erect cusp 1.5–8 mm long; body straight or almost straight, 6.5–13 × (1.3) 1.2–2.4 (2.6) cm, plano-compressed, the valves bluntly framed by longitudinally 3-ridged sutures ±1.5–2 mm wide, stiff, somewhat brittle, brownish-green, externally veinless, glabrous, red-granular or both granular and puberulent outside, the cavity continuous; funicle dilated, sigmoid. ***Seeds*** transverse, 8–13, plumply disciform to orbicular in outline, 9–12 × 7–10 mm, the pleurogram U-shaped.

Geographic distribution. *Gretheria* comprises two species in United States (Texas), Mexico and Central America (Honduras and Nicaragua).

Habitat. *Gretheria* grows in tropical deciduous dry forests, thorn scrubs and brush-woodlands, between sea level and 400 m elevation, occasionally ascending to 700 m.

Etymology. The generic name honours Rosaura Grether González, an extraordinary and prolific Mexican botanist, with whom we had the pleasure of sharing her experience as a botanist and colleague. Her profound dedication and perseverant commitment to botanical research over decades has contributed importantly to our knowledge and understanding of Leguminosae, especially of the genus *Mimosa* L.

Key to the species of *Gretheria* (modified from Barneby and Grimes 1996)

1 Petiole 8–24 mm long; leaves with (5) 6–11 (13) pairs of pinnae, leaflets (17) 19–31 per pinna; leaflets linear or linear-oblong, 3.3–6.5 × 0.8–2 mm; capitula 12–37-flowered ..... ***Gretheria campylacantha***

– Petiole 2–7.5 mm long; leaves with 1–5 pairs of pinnae, leaflets (10) 13–21 per pinna; leaflets narrowly oblong or oblong-elliptic, 2.2–5.5 × 0.8–1.3 mm; capitula 10–17-flowered ..... ***Gretheria sonorae***

1.1. *Gretheria campylacantha* (L. Rico & M. Sousa) Duno & Torke, comb. nov.

urn:lsid:ipni.org:names:77303793-1

Basionym. *Pithecellobium campylacanthum* L. Rico & M. Sousa (as "*campylacanthus*"), Ann. Missouri Bot. Gard. 73: 722–724. 1986[1987]. *Havardia campylacantha* (L. Rico & M. Sousa) Barneby & J.M. Grimes (as "*campylacanthus*"), Mem. New York Bot. Gard. 74(1): 167. 1996.

Type. México. Oaxaca, distrito de Tehuantepec, 7 km al O-NO de Tehuantepec, 17 March 1981, *M. Sousa et al. 11938* (holotype: MEXU! 410015; isotypes: BM, CAS accession 0004063 [image!], F accession 2064374 [image!], MEXU accessions 41011 [image!], 410013 [image!], 410016 [image!], MO accession 3481860 [!]).

Geographic distribution. *Gretheria campylacantha* occurs discontinuously in the Pacific lowlands of south-eastern Mexico (Guerrero, Michoacán and Oaxaca) and in the interior and Pacific lowlands of Central America (from Comayagua Department in Honduras to Boaco Department in Nicaragua).

Habitat. It grows in tropical deciduous brush-woodlands, along intermittent streams, between sea level and 200 m elevation, occasionally ascending to 700 m.

1.2. *Gretheria sonorae* (S. Watson) Duno & Torke, comb. nov.

urn:lsid:ipni.org:names:77303794-1

Basionym. *Pithecellobium sonorae* S. Watson, Proc. Amer. Acad. Arts 24: 49. 1889. *Havardia sonorae* (S. Watson) Britton & Rose, N. Amer. Fl. 23: 42. 1928.

Type. México. Sonora, common at Guaymas 1887, *E. Palmer 58* (holotype: GH accession 00064044 [image!]; isotypes: K accession 000082458 [image!], NDG 46766 [image!], NY accessions 00329628, 00329629 [images!], UC accession 84451 [image!], US accessions 00918587, 00918589 [image!], YU accession 001418 [image!]).

Geographic distribution. Coastal plain of Baja California Sur, Sonora and Sinaloa in Mexico.

Habitat. Plains and foothills below 400 m in deciduous dry forest and thorn scrub and along washes in mesquite grassland along the coastal plain.

Ricoa Duno & Torke, gen. nov.

urn:lsid:ipni.org:names:77303795-1

Type. *Ricoa leptophylla* (DC.) Duno & Torke.

Diagnosis. Similar to *Painteria* in shrubby habit with pronounced growth dimorphism into long- and short-shoots, deciduous microphyllous leaves and recurved pods with the fruit valves coriaceous to lignescent and elastically reflexed with age, but differing in the leaves with 3–7(9) pairs of pinnae (vs. 1–2 in *Painteria*), the leaflets 10–25 per pinna (vs. 3–12), the floral bracts 0.8–2.1 mm long (vs. 0.4–0.7 mm), the flowers shortly pedicellate (vs. sessile) and the corolla lobes recurved (vs. erect-ascending).

Description. Low xerophytic stiffly branched microphyllous shrubs 2–1.5 m tall, often growing in patches several metres in diameter, armed at each node of flexuous long shots with a pair of lignescent stipules, young growth indumented with minute whitish hairs. ***Stipules*** converted with straight to recurved spines with a thickened base, the spines 3–10 mm long. ***Leaves*** bipinnate with 3–7 (9) pairs of pinnae; leaflets 8–25 pairs per pinna, the primary leaf axis 0.5–5 cm long, with the petiole 2.5–10 (18) mm long and a subsessile circular nectary between the first pinnae pair (sometimes also between the second pair), nectaries absent on pinna-rachises; leaflets opposite, narrowly- or linear-oblong or lanceolate, semi-cordate at base, obtuse to weakly apiculate at apex, puberulous abaxially, marginally ciliate, the venation weakly developed, nearly simple or 1-branched, the mid-rib prominulous only dorsally, subcentric. ***Inflorescence*** of capitula arising from brachyblasts, peduncle 1–18 mm long; receptable clavate, 1.5–2.5 mm long, capitula globose, 1–1.5 cm in diameter, 16–35-flowered; bracts linear-oblanceolate or spatulate, 0.8–2.1 mm long, persistent into anthesis. ***Flowers*** externally homomorphic, but some functionally staminate, pedicellate, perianth 5-merous; pedicel 0.2–0.6 mm long; calyx campanulate, contracted at base, 1.3–3.2 mm long, minutely puberulent (or just on teeth), teeth ovate or deltate, 0.2–0.9 mm long; corolla reddish or greenish, tubular, 3.5–5 mm long, lobes ovate, recurving. 1.2–1.9 mm long, puberulous and densely fimbriolate on lobes; androecium 40–76-merous, 5–10.5 mm long, tube 2–4 mm long; ovary slenderly ellipsoid, compressed, glabrous, on a short stipe 1–1.4 mm long, style in bisexual flowers often longer and more robust than stamens. ***Pods*** l–2 (4) per capitulum, falcately or subcircinnately broadly linear in profile, attenuate into an erect cusp 2–6 mm long, the body 7–11.5 × 1.1–1.9 cm, 8–10-seeded, the valves stiffly leathery, at first plano-compressed, becoming turgid and low-convex (on both faces of pod) over each seed, densely grey puberulent, becoming glabrescent and dark castaneous, indistinctly venulose, the cavity continuous, dehiscence inert through both sutures; funicle straight or sinuous (but not sigmoid), seeds obliquely descending, 8–10, plumply lentiform, 7.5–11 × 3–4 mm, the testa smooth, hard, moderately lustrous, dark castaneous, the pleurogram incomplete.

Distribution. *Ricoa* is found scattered over the Mexican Central Plane, in the States of Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tlaxcala and Zacatecas.

Habitat. It grows in grasslands, scrubs and at the lower edge of the pine-oak belt, on both basaltic and calcareous substrates, at 1600–2800 m elev. Plants flower between March and August.

Common names. The common name is Huisache. This name is also given to *Vachellia farnesiana* (L.) Wight & Arn. and other related species (Barneby and Grimes 1996). Other common names are charrasquillo, gatuña and tehuixtle (Calderón de Rzedowski 2007).

Etymology. The generic name honours María Lourdes Rico, whose profound dedication and perseverant commitment to botanical research over decades has deeply enhanced knowledge and understanding of the Leguminosae, especially tribe Ingeae.

2.1. *Ricoa leptophylla* (DC.) Duno & Torke, comb. nov.

urn:lsid:ipni.org:names:77303796-1

Basionym. *Acacia leptophylla* DC., Cat. PI. Horti Monsp. 74. 1813. *Mimosa leptophilla* [sic] Cavanilles, Elench. PI. Horti Matr. 24. 1803, *nom. nud*. *Pithecolobium leptophyllum* (DC.) Daveau, Bull. Soc. Bot. France 59: 635, t. XVI. 1912. *Painteria leptophylla* (DC.) Britton & Rose, N. Amer. Fl. 23: 36. 1928.

Type. Mexico. verosimiliter in Hispanorum territorio Americano, *P. M. A. Broussonet s.n.* [870]. (holotype: M; isotypes: G-DEL [image!], photo, MO [image!]).

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Phylogeny and classification of the Australasian and Indomalayan mimosoid legumes *Archidendron* and *Archidendropsis* (Leguminosae, subfamily Caesalpinioideae, mimosoid clade)

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Abstract

The morphologically variable genus *Archidendron* is the second largest mimosoid legume genus from the Indomalayan-Australasian region, yet it has not been well represented in phylogenetic studies. Phylogenies that have included multiple representatives of *Archidendron* suggest it may not be monophyletic, and the same applies to *Archidendropsis*, another understudied genus of the Archidendron clade. The most comprehensive phylogeny of *Archidendron* and *Archidendropsis* to date is presented, based on four nuclear markers (ITS, ETS, SHMT and RBPCO). Exemplars from all genera of the wider Archidendron clade are sampled, including representatives of all series within *Archidendron* and the two subgenera of *Archidendropsis*. Our results confirm that *Archidendron* and *Archidendropsis* are not monophyletic. Within *Archidendron*, only one series (ser. *Ptenopae*) is resolved as monophyletic and species of *Archidendron* are divided into two primarily geographic lineages. One clade is distributed in western Malesia and mainland Asia and includes most representatives of series *Clypeariae*, while the other is mostly restricted to eastern Malesia and Australia and includes representatives of the seven other series plus two samples of series *Clypeariae*. No taxonomic changes are made for *Archidendron* due to the high level of topological uncertainty and the lack of discrete macromorphological characters separating these two lineages. Each of the two subgenera of *Archidendropsis* is monophyletic but they are not closely related. A new genus endemic to Queensland (Australia), *Heliodendron* Gill.K. Br. & Bayly, **gen. nov.**, is described for the former *Archidendropsis* subg.

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Basaltica, and combinations for its three species are proposed: *Heliodendron basalticum* (F. Muell.) Gill.K. Br. & Bayly, **comb. nov.**, *Heliodendron thozetianum* (F. Muell.) Gill.K. Br. & Bayly, **comb. nov.**, and *Heliodendron xanthoxylon* (C.T. White & W.D. Francis) Gill.K. Br. & Bayly, **comb. nov.**

Keywords
Fabaceae, ingoid clade, legumes, low copy nuclear gene, Malesia, phylogeny, targeted amplicon sequencing

Introduction

The classification of mimosoid legumes has been significantly transformed in the past 20 years since the first comprehensive molecular phylogeny of the then subfamily Mimosoideae (Luckow et al. 2003). Understanding of relationships within the mimosoid legumes has improved through studies at generic, regional, alliance, subfamilial and familial levels (see references in Legume Phylogeny Working Group 2017; Koenen et al. 2020; Ringelberg et al. 2022). In the comprehensive phylogeny and revision of the legume family (Leguminosae or Fabaceae), the mimosoid legumes formed a clade nested within the re-circumscribed subfamily Caesalpinioideae (Legume Phylogeny Working Group 2017). Recent phylogenomic data have sufficiently enhanced resolution to enable recognition of several clades within subfamily Caesalpinioideae, including the mimosoid, core mimosoid and ingoid clades (Koenen et al. 2020; Ringelberg et al. 2022). However, within these clades some large genera, such as *Archidendron* F. Muell. and allies have remained under-studied relative to *Acacia* Mill. s.l. and many Neotropical ingoid genera and groups (e.g. Murphy et al. 2010; de Souza et al. 2013; Iganci et al. 2016; Miller et al. 2017; Ferm et al. 2019; Comben et al. 2020).

The two largest mimosoid genera from the Indomalayan-Australasian region are *Acacia* and *Archidendron*. These are placed in the Archidendron clade (sensu Koenen et al. 2020), along with *Archidendropsis* I.C. Nielsen, *Falcataria* (I.C. Nielsen) Barneby & J.W. Grimes, *Pararchidendron* I.C. Nielsen, *Paraserianthes* I.C. Nielsen, *Serianthes* Benth. and *Wallaceodendron* Koord. The Archidendron clade is biogeographically distinct within the mimosoid legumes, being primarily restricted to the Indomalayan and Australasian regions, and has been given several names over the years to reflect this: the Australian & SE Asian Ingeae clade (Brown et al. 2008) and the Australo-Malesian mimosoids (Brown et al. 2011). Within the Archidendron clade, *Pararchidendron*, *Paraserianthes* and *Wallaceodendron* are monotypic, and three of the other five genera (*Acacia* s.s., *Falcataria*, and *Serianthes*) are well documented as monophyletic based on morphological and genetic data (Chappill and Maslin 1995; Miller and Bayer 2001; Luckow et al. 2003; Brown et al. 2008, 2011; Murphy et al. 2010; Demeulenaere et al. 2022; Ringelberg et al. 2022). However, *Archidendron* has been suggested to be paraphyletic (Brown et al. 2008, 2011; Iganci et al. 2016; Demeulenaere et al. 2022; Ringelberg et al. 2022), as has *Archidendropsis* (Demeulenaere et al. 2022; Ringelberg et al. 2022).

Archidendron is the second largest genus in this clade after *Acacia*, with 99 described species and an additional 20 putative species that are poorly known due

to limited collections or destroyed types (Nielsen et al. 1984b; Cowan 1998; Wu and Nielsen 2010; Dash and Sanjappa 2011). They are small to medium-sized trees found in lowland and montane tropical and subtropical rainforests of the Australo-Malesian and Pacific regions, distributed from Kerala (southern India) and Sri Lanka in the west, to the Solomon Islands in the east; and from Taiwan and the Ryukyu Islands in the north, to Australia in the south (Fig. 1; Nielsen et al. 1984b, 1984a). In the 1970s and 1980s, an extensive revision of the Australo-Malesian and Pacific Ingeae was undertaken (Nielsen 1979, 1981, 1982; Nielsen et al. 1983b, 1983a, 1984b) and *Archidendron* was expanded based on evidence from wood, pollen, seed and inflorescence characteristics to include species previously referred by Kostermans (1954) to the genera *Abarema* Pittier, *Cylindrokelupha* Kosterm., *Morolobium* Kosterm., *Paralbizzia* Kosterm., *Zygia* P. Browne, and by Bentham (1875) to *Pithecellobium* sect. *Clypearia* sensu Benth. (Baretta-Kuipers 1981; Nielsen et al. 1984b; Nielsen 1992). *Archidendron* now includes unarmed trees or shrubs with bipinnate leaves, mostly opposite leaflets, extrafloral nectaries, and wood anatomy of strictly uniseriate rays and abundant parenchyma with a banded distribution (Nielsen et al. 1984b).

Archidendron is morphologically variable especially in leaf, inflorescence, flower, and pod characteristics, and has been divided into eight series (Nielsen et al. 1984b): *Clypeariae* (Benth.) I.C. Nielsen, *Archidendron*, *Calycinae* I.C. Nielsen, *Bellae* I.C. Nielsen, *Ptenopae* I.C. Nielsen, *Pendulosae* (Mohlenbr.) I.C. Nielsen, *Stipulatae* (Mohlenbr.) I.C. Nielsen and *Morolobiae* (Kosterm.) I.C. Nielsen. The largest series, *Clypeariae* (ca. 51 species) is distributed in mainland southeast Asia, western Malesia, and the Philippines, with only a few species found further east (Fig. 1A). This series is well defined by the absence of stipules and flowers that generally have one carpel per ovary that is often stipitate (Nielsen et al. 1984b). The second largest series, *Archidendron* (ca. 15 species), is found in eastern Malesia and Australia and is defined by the presence of stipules and stipular glands. Four of the series are largely confined to the island of New Guinea (Nielsen et al. 1984b): series *Calycinae* (3 species) with strongly ribbed inflated calyces, cauliflorous racemes and sessile ovaries; series *Bellae* (4 species) with large woody pods without overgrown seeds and cauliflorous paniculate inflorescences; series *Ptenopae* (2 species), which is defined by the presence of two-winged rachises and pinnae; series *Pendulosae* (3 species) have inflorescences with lax racemes (Nielsen et al. 1984a). Series *Stipulatae* (ca. 14 species) are found in New Guinea, the Moluccas, and Queensland (Australia) and have floral bracts with extra floral nectaries, stipular glands and cauliflorous branched racemes (Nielsen et al. 1984b). The three species of series *Morolobiae* have unifoliolate pinnae, and racemose inflorescences with flowers with single, sessile ovaries, and are disjunctly distributed: *A. monopterum* (Kosterm.) I.C. Nielsen in Halmahera (North Maluku Islands, Indonesia), *A. whitei* I.C. Nielsen in northern Queensland (Australia) and *A. muellerianum* (Maiden & R.T. Baker) I.C. Nielsen in northern New South Wales (Australia) (Nielsen et al. 1984b).

Prior to resolution of the Archidendron clade, the genus *Archidendron* was suggested to be related to taxa of the Inga-alliance (Barneby and Grimes 1996; Lewis and Rico Arce 2005) or to other Old World genera, such as *Archidendropsis*, *Falcataria*, *Pararchidendron*,

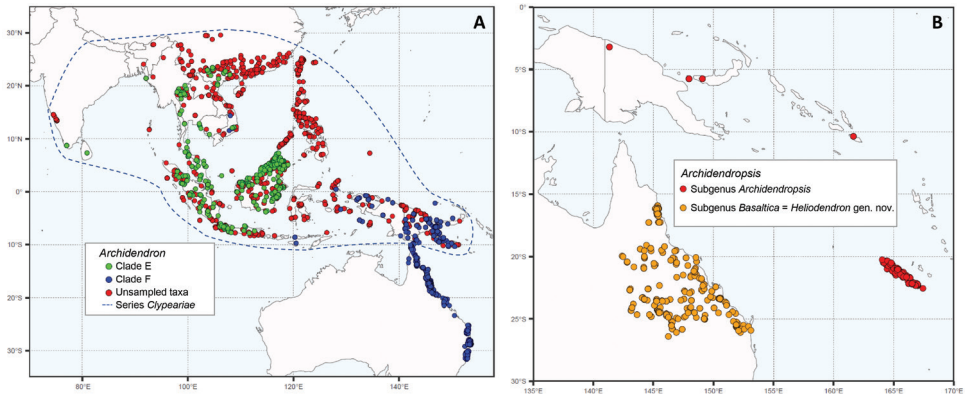

Figure 1. Distribution maps of the genera *Archidendron* and *Archidendropsis*. The maps are based on quality-controlled species-level digitised herbarium specimens from GBIF (www.gbif.org) (Ringelberg et al. 2022). Maps were created using R packages ggplot2 (Wickham 2016), sf (Pebesma 2018), and rnaturalearth (South 2017) **A** *Archidendron*. Species distributions are coloured according to the ncDNA phylogeny clades (Fig. 2) except for *A. clypearia:* Clade E (Clypeariae clade) = green dots; clade F (Archidendron s.s. clade) = blue dots; species not sampled for the phylogeny = red dots. *Archidendron clypearia* is widespread and falls in both clades E and F, so for this species locations of samples in the ncDNA phylogeny are coloured according to their clade and all other records of this species are coloured red. The overall distribution of series *Clypeariae* is shown by a blue dashed line **B** *Archidendropsis*. All species that belong to subg. *Archidendropsis* are coloured red and those in subg. *Basaltica* (= *Heliodendron* gen. nov.) are coloured orange.

Paraserianthes and *Serianthes* (Baretta-Kuipers 1981; Nielsen et al. 1984a; Nielsen 1992). *Archidendron* has not been well represented in molecular phylogenies to date with only ten of the 99 species and four of the eight series (*Archidendron*, *Clypeariae*, *Morolobiae* and *Ptenopae*) included in any one study. In all studies, samples of series *Clypeariae* are placed distantly from the other series (Brown et al. 2008, 2011; Iganci et al. 2016; Koenen et al. 2020; Demeulenaere et al. 2022; Ringelberg et al. 2022).

The genus *Archidendropsis* includes 14 species from New Caledonia, the Solomon Islands, New Britain, Papua New Guinea and Australia (Fig. 1B), with all species endemic to their respective region (Nielsen et al. 1983a). Species of *Archidendropsis* have winged, thin-walled seeds lacking a pleurogram (a mark or depression on both sides of the seed coat; Rodrigues-Junior et al. 2021) and are placed in two subgenera based on pollen and inflorescence characteristics. Species of subgenus *Basaltica* I.C. Nielsen are restricted to Australia, have smaller polyads (55–60 µm) and globular inflorescences, while species of subgenus *Archidendropsis* are not found in Australia, have larger polyads (80–120 µm) and flowers arranged in spicate racemes. Like *Archidendron*, *Archidendropsis* has been poorly represented in molecular phylogenies with only one or two of the 14 species included in any one study (Brown et al. 2008, 2011; Ferm et al. 2019; Koenen et al. 2020; Demeulenaere et al. 2022; Ringelberg et al. 2022). Only two studies have included representatives of each of the subgenera and in both, *Archidendropsis* is not resolved as monophyletic (Demeulenaere et al. 2022; Ringelberg et al. 2022).

This study aims to test the monophyly of the genera *Archidendron* and *Archidendropsis* and investigate phylogenetic relationships within the large genus *Archidendron* to test the monophyly of its infrageneric series.

Materials and methods

Taxon sampling and DNA isolation

A total of 87 accessions were sampled, representing 43 species of *Archidendron* (68 accessions), five species of *Archidendropsis* (six accessions) and nine species (11 accessions) of the other genera in the Archidendron clade; two species of Old World *Albizia* Durazz. were included as outgroups (Table 1). In total 43% of the species of *Archidendron* were sampled including representatives of all eight series. Both subgenera of *Archidendropsis* were sampled covering 36% of species in the genus. Samples were collected in the field and from herbarium specimens sourced from AAU, BISH, BRI, CANB, CNS, KEP, KUN, L, NY, MEL and MELU (herbarium codes as per Thiers, updated continuously).

Total genomic DNA (gDNA) was extracted following the CTAB method of Doyle and Doyle (1987) with modifications as per Shepherd and McLay (2011). Isolated gDNA was quantified with a NanoDrop 2000 (ThermoScientific) spectrophotometer and cleaned with a 2.4 M sodium acetate wash. Recalcitrant herbarium material that failed using the CTAB method was extracted using the AccuPrep Stool genomic DNA extraction kit (Bioneer) using the manufacturer's protocol with some modifications suggested by Schuster (pers. comm.). Only 30 mg of leaf material was used instead of the recommended 100–200 mg. A total of 600 µl of stool lysis buffer (SL) was added to the extraction tube instead of 400 µl, the incubation step was increased to one hour in total, centrifugation was done for 10 minutes at step five, and to maintain equal volumes, 600 µl of binding buffer was added. Two consecutive washes were performed using buffer 1 (W1). The final elution was done by adding 160 µl total elution buffer in two steps (first 60 µl, and then 100 µl) instead of a single elution with 200 µl.

Marker selection, primer design and library preparation

Eight nuclear markers (low copy genes: AIGP, CYB6, Eif3E, SHMT, RBPCO, UDPG; nrDNA: ITS, ETS) and four chloroplast DNA intergenic spacer regions (*trn*K-*mat*K, *trn*V-*ndh*C, *psb*D-*trn*T, *trn*L-*rpl*32) were assessed for variability between nine individuals spanning the series of *Archidendron* using Sanger sequencing.

PCR reagents, primers and cycling conditions are described in Suppl. material 1 (Johnson and Soltis 1994; Sun et al. 1994; Käss and Wink 1997; Baldwin and Markos 1998; Miller and Bayer 2001; Ariati et al. 2006; Choi et al. 2006; Shaw et al. 2007; Li et al. 2008). PCR products were visualised on a 1.5% agarose gel with Easy ladder I (Bioline) and cleaned with ExoSAP-IT (USB) as per the manufacturer's protocol. The purified amplicons were sequenced on an AB3730xl sequencer (Thermo Scientific) at

Table 1. Linked data table of specimens sampled for phylogeny. Specimen accession number linking herbarium specimen to sample ID, taxon name with authorities, locality information and geocode (where available) as provided on the specimen/database. GenBank numbers are provided for each marker and where multiple alleles were identified for a specimen, the two GenBank numbers are separated by a semi colon. If the marker was not successfully sequenced for a particular specimen, then the GenBank field is left blank.

Preserved specimen	Associated sequences							Taxon name/MOTU	Sample ID	Location	
Specimen code (InstCode and/or CollCode + Catalogue #)	SHMT	RBPCO	ITS	ETS	tmK	tmV	psbD			Geolocation name / locality	GPS Coordinates
MEL 2294706A			OM286906	OM286992	ON013654			*Acacia bauerii* Benth.	*Z176*	Great Sandy National Park, Fraser Island, Woralie track to Moon Point. Queensland, Australia	153°11'55"E, 25°11'38"S
MELU GB309b	OM984488	OM390190; OM390191	OM286907	OM286993	ON013655	ON101510	OM984574	*Acacia myrtifolia* (Sm.) Willd.	*JA150*	0.7km north of Playford Highway on Snug Bay Rd, Kangaroo Island, South Australia	136°52'51.8"E, 35°46'30.2"S
CANB 864530.1	OM984489		OM286908	OM286994	ON013656	ON101511	OM984575	*Albizia lebbeck* (L.) Benth.	*JA137*	Alva, NE of Ayr, Queensland, Australia	147°28'52"E, 19°27'11"S
MEL 2391890A	OM984490		OM286909	OM286995	ON013657	ON101512	OM984576	*Albizia retusa* Benth.	*Z106*	Atherton Arboretum. Tag #96. Queensland, Australia	145°29'8.6"E, 17°15'31.4"S
KUN0599506	OM984491		OM286910	OM286996	ON013658	ON101513	OM984577	*Archidendron alternifoliolatum* (T.L.Wu) I.C.Nielsen	*JA25*	China	100.85°E, 24.5667°N
BRI AQ0380081	OM984492; OM984493		OM286911	OM286997	ON013659	ON101514		*Archidendron arborescens* (Kosterm.) I.C.Nielsen	*JA36*	Papua New Guinea, Western Fly; Kwinja Lakes area of the Middle Fly River	141°41'33.987"E, 7°45'24.772S
KUN0599551	OM984494; OM984495		OM286912	OM286998	ON013660	ON101515		*Archidendron balansae* (Oliv.) I.C.Nielsen	*JA26*	China	
AAU D.McKey92-9	OM984496; OM984497	OM390192	OM286913	OM286999	ON013661	ON101516	OM984578	*Archidendron bigeminum* (L.) I.C.Nielsen	*JA14*	Sinharaja Forest, SW Sri Lanka	80°35'23"E, 6°21'17"N
AAU Balgooy6063	OM984498; OM984499	OM390193	OM286914	OM287000	ON013662	ON101517	OM984579	*Archidendron borneense* (Benth.) I.C.Nielsen	*JA70*	Tanah Merah, Kalimantan Timur	117°E, 1°S
KEP FRI53789	OM984500; OM984501		OM286915	OM287001	ON013663	ON101518	OM984580	*Archidendron bubalinum* (Jack) I.C.Nielsen	*JA22*	Pahang, Temerloh, Tasik Bera, Kg. Patihir, Malaysia	102.4167°E, 3.8167°N
CANB 730419.1		OM390194; OM390195	OM286916	OM287002	ON013664	ON101519		*Archidendron calliandrum* de Wit	*JA109*	Ambunti District, Waskut Hills, spur ridge NW of Musapien bivouac. East Sepik, PNG	142°43'55"E, 4°10'36"S
CANB 211609.1	OM984502		OM286917	OM287003	ON013665	ON101520	OM984581	*Archidendron calycinum* Pulle	*JA129*	Saw Mountains, near junction of Tauri and Kapau Rivers. Gulf Province, PNG	146°8'E, 7°47'S
AAU L.Averyanov4481	OM984503		OM286918	OM287004	ON013666	ON101521	OM984582	*Archidendron chevalieri* (Kosterm.) I.C.Nielsen	*JA71*	Bi Dup ridge, Vietnam	108°39'E, 12°6'N
AAU I.Nielsen26	OM984504		OM286919	OM287005	ON013667	ON101522	OM984583	*Archidendron clypearia* (Jack) I.C.Nielsen	*JA16*	Gunung Mulu National Park, Sarawak	114°55'E, 4°05'N
AAU H.M.Christensen38	OM984505		OM286920	OM287006	ON013668	ON101523	OM984584	*Archidendron clypearia* (Jack) I.C.Nielsen	*JA05*	Pa Dalih area, Sarawak	115°50'E, 3°40'N

Preserved specimen	Associated sequences							Taxon name/MOTU	Sample ID	Location	
Specimen code (InstCode and/or CollCode + Catalogue #)	SHMT	RBPCO	ITS	ETS	tmK	tmV	psbD			Geolocation name / locality	GPS Coordinates
AAU L.AveryanovVH3188	OM984506		OM286921	OM287007	ON013669	ON101524	OM984585	*Archidendron clypearia* (Jack) I.C.Nielsen	*JA15*	Bi Dup mountain system, Vietnam	108°39'E, 12°8'N
CANB 525617.1	OM984507	OM390196; OM390197	OM286922	OM287008	ON013670	ON101525	OM984586	*Archidendron clypearia* (Jack) I.C.Nielsen	*JA95*	East branch of the Avi Avi River. Gulf Province, PNG	146°30'E, 7°44'S
AAU AmbriW838			OM286923	OM287009	ON013671	ON101526	OM984587	*Archidendron cockburnii* I.C.Nielsen	*JA17*	Wanariset research area, Kalimantan Timur	117°E, 1°S
NY03986843		OM390198	OM286924	OM287010	ON013672	ON101527	OM984588	*Archidendron contortum* (Mart.) I.C.Nielsen	*T97*	Near Kuala Lumpur, Malaysia	
BRI AQ0380332			OM286925	OM287011				*Archidendron forbesii* Baker f.	*JA38*	Papua New Guinea, Central; Subitana, Sogeri sub-dist., Central, Papua	147°31'E, 9°25'S
BISH752370	OM984509	OM390199	OM286926	OM287012	ON013673	ON101528	OM984589	*Archidendron glabrum* (K.Schum.) Lauterb. & K.Schum.	*JA04*	Siboma, Sayama, track along the ridgeline S from Camp 1. PNG	147.298°E, 7.52857°S
BISH763497	OM984510	OM390200	OM286927	OM287013	ON013674	ON101529	OM984590	*Archidendron glabrum* (K.Schum.) Lauterb. & K.Schum.	*JA115*	Morobe Province; Oomsis, behind PNG Forestry station.	146.821°E, 6.71325°S
BRI AQ0380375			OM286928	OM287014	ON013675	ON101530	OM984591	*Archidendron glandulosum* Mohlenbr. ex Verdc.	*JA39*	Brown River F.R. Central Province, PNG	147°10'33.78"E, 9°30'24.60"S
AAU J.F.Maxwell82-141	OM984511		OM286929	OM287015	ON013676	ON101531	OM984592	*Archidendron globosum* (Blume) I.C.Nielsen	*JA20*	Near Bukit Kallang, Singapore	
AAU Bjornland445	OM984512		OM286930	OM287016		ON101532	OM984593	*Archidendron glomeriflorum* (Kurz) I.C.Nielsen	*JA10*	Chiang Mai: Amphoe Muang, Mae Rim, Thailand	
CANB 544379.1	OM984516		OM286933	OM287018	ON013679	ON101535	OM984596	*Archidendron grandiflorum* (Sol. ex Benth.) I.C.Nielsen	*JA100*	Gabba Island, Torres Strait. Queensland, Australia	142°38'22"E, 9°46'8"S
BRI AQ0814833	OM984513; OM984514		OM286931	OM287017	ON013677	ON101533	OM984594	*Archidendron grandiflorum* (Sol. ex Benth.) I.C.Nielsen	*JA42*	Curramore Sanctuary Nature Reserve, 14km NW of Maleny. Queensland, Australia	152°4'05"E, 26°41'43"S
CNS 131336.1	OM984515		OM286932		ON013678	ON101534	OM984595	*Archidendron grandiflorum* (Sol. ex Benth.) I.C.Nielsen	*JA43*	Mt Lewis, Carbine Tableland. Queensland, Australia	145°16'E, 16°31'S
MEL 2391892A	OM984517; OM984518	OM390201	OM286934	OM287019	ON013680	ON101536	OM984597	*Archidendron grandiflorum* (Sol. ex Benth.) I.C.Nielsen	*Z109*	Atherton Arboretum. Tag #846. Queensland, Australia	145°29'8.6"E, 17°15'31.4"S
AAU Kostermans22121			OM286935	OM287020	ON013681	ON101537		*Archidendron harmsii* Malm	*JA74*	Mbengen, West Flores	
AAU H.M.Christensen279	OM984519	OM390202; OM390203	OM286936	OM287021	ON013682	ON101538	OM984598	*Archidendron havilandii* (Ridl.) I.C.Nielsen	*JA75*	Pa Dalih area, Sarawak	115°50'E, 3°40'N
CANB 596487.1	OM984521	OM390206	OM286939	OM287024	ON013685	ON101541	OM984600	*Archidendron hendersonii* (F.Muell.) I.C.Nielsen	*JA103*	Greenfield Road, Lennox Head. New South Wales, Australia	153°36'E, 28°49''S
MEL 2293327A	OM984520	OM390204; OM390205	OM286937	OM287022	ON013683	ON101539	OM984599	*Archidendron hendersonii* (F.Muell.) I.C.Nielsen	*JA44*	Brandy Creek Road, 9 km S of Airlie Beach. Queensland, Australia	148°43'15"E, 20°21'2"S

Preserved specimen	Associated sequences							Taxon name/MOTU	Sample ID	Location	
Specimen code (InstCode and/or CollCode + Catalogue #)	SHMT	RBPCO	ITS	ETS	tmK	tmV	psbD			Geolocation name / locality	GPS Coordinates
QRS 18805.2			OM286938	OM287023	ON013684	ON101540		*Archidendron hendersonii* (F.Muell.) I.C.Nielsen	*JA45*	Between Starcke homestead and Starcke River. Queensland, Australia	145°5'E, 14°55'S
MEL 2391969A	OM984522	OM390207; OM390208	OM286940	OM287025	ON013686	ON101542	OM984601	*Archidendron hendersonii* (F.Muell.) I.C.Nielsen	*Z114*	Cairns, cultivated in garden. Queensland, Australia	145°46'15"E, 16°55'13"S
QRS 117169.1	OM984523	OM390209	OM286941	OM287026	ON013687	ON101543	OM984602	*Archidendron hirsutum* I.C.Nielsen	*JA46*	Claudie River. Queensland, Australia	143°15'E, 12°44'S
CNS 142441.1	OM984524	OM390210	OM286942	OM287027	ON013688	ON101544	OM984603	*Archidendron hirsutum* I.C.Nielsen	*JA86*	Umagico, Cape York. Queensland, Australia	142°21'E, 10°53'19"S
MEL 2391887A	OM984525	OM390211	OM286943	OM287028	ON013689	ON101545	OM984604	*Archidendron hirsutum* I.C.Nielsen	*Z113*	Atherton Arboretum. Tag #482. Queensland, Australia	145°29'8.6"E, 17°15'31.4"S
BISH760310	OM984526	OM390212	OM286944	OM287029	ON013690	ON101546	OM984605	*Archidendron hispidum* (Mohlenbr.) Verdc.	*JA02*	Northern Province; Sibium Mountains; W of Akupe Camp, along Afase River. PNG	148.269°E, 9.28974°S
AAU R.Geesink7254	OM984527		OM286945	OM287030	ON013691	ON101547	OM984606	*Archidendron jiringa* (Jack) I.C.Nielsen	*JA12*	Kao Chong Botanical Garden, Thailand	99°45'E, 7°40'N
BRI AQ0738090	OM984528; OM984529	OM390213	OM286946	OM287031	ON013692	ON101548	OM984607	*Archidendron kanisii* R.S.Cowan	*JA47*	Oliver Creek. Queensland, Australia	145°26'E, 16°8'S
MELUD113392a	OM984530		OM286947	OM287032	ON013693	ON101549	OM984608	*Archidendron kanisii* R.S.Cowan	*JA65*	Shore of creek, end of Stonewood Road, Queensland, Australia	145.40497°E, 16.16685°S
MELUD113385a	OM984531	OM390214	OM286948	OM287033	ON013694	ON101550	OM984609	*Archidendron kanisii* R.S.Cowan	*JA66*	Shore of creek, end of Stonewood Road, Queensland, Australia	145.40497°E, 16.16685°S
BRI AQ0733240	OM984532							*Archidendron kanisii* R.S.Cowan	*Z49*	NPR133, Daintree, Oliver Creek, Queensland, Australia	145°26'29.997"E, 16°8'11.708"S
AAU I.Cowley110			OM286949	OM287034	ON013695	ON101551	OM984610	*Archidendron kinabaluense* (Kosterm.) I.C.Nielsen	*JA76*	Melilas. Ulu Belait, Brunei	
AAU H.M.Christensen1719			OM286950	OM287035	ON013696	ON101552	OM984611	*Archidendron kunstleri* (Prain) I.C.Nielsen	*JA07*	near Nanga Sumpa, Sarawak	112°10'E, 1°20'N
KUN 0599659	OM984533; OM984534	OM390215	OM286951	OM287036	ON013697	ON101553	OM984612	*Archidendron laoticum* (Gagnep.) I.C.Nielsen	*JA77*		
BRI AQ0835639	OM984535		OM286952	OM287037	ON013698	ON101554		*Archidendron lovelliae* (F.M.Bailey) I.C.Nielsen	*JA48*	Great Sandy National Park; Cooloola Section, Freshwater Road. Queensland, Australia.	153°6'52"E, 25°57'01S
BRI AQ0636343		OM390216; OM390217	OM286953	OM287038	ON013699	ON101555	OM984613	*Archidendron lovelliae* (F.M.Bailey) I.C.Nielsen	*Z112*	Harry's Hut Road, Cooloola National Park.Queensland, Australia	153°03'E, 25°26'S
MEL 2034578A	OM984536	OM390218; OM390219	OM286954	OM287039	ON013700	ON101556	OM984614	*Archidendron lucyi* F.Muell.	*JA49*	Indooroopilly, cultivated. Queensland, Australia	
MELUD113387a	OM984537		OM286955	OM287040	ON013701	ON101557	OM984615	*Archidendron lucyi* F.Muell.	*JA62*	Lake Road near Cairns, Queensland, Australia	145.6693°E, 16.875165°S

Preserved specimen	Associated sequences							Taxon name/MOTU	Sample ID	Location	
Specimen code (InstCode and/or CollCode + Catalogue #)	SHMT	RBPCO	ITS	ETS	tmK	tmV	psbD			Geolocation name / locality	GPS Coordinates
MELUD113393a	OM984538		OM286956	OM287041	ON013702	ON101558	OM984616	*Archidendron lucyi* F.Muell.	*JA63*	Lake Road near Cairns, Queensland, Australia	145.6693°E, 16.875165°S
MELUD113391a	OM984539		OM286957	OM287042	ON013703	ON101559	OM984617	*Archidendron lucyi* F.Muell.	*JA68*	Cape Tribulation Road, adjacent to Coconut Beach resort, Queensland, Australia	145.45726°E, 16.11345°S
MEL 2391968A	OM984540	OM390220	OM286958	OM287043	ON013704	ON101560	OM984618	*Archidendron lucyi* F.Muell.	*Z108*	Cairns, cultivated in garden. Queensland, Australia	145°46'15"E, 16°55'13"S
BISH760584	OM984541		OM286959	OM287044	ON013705	ON101561	OM984619	*Archidendron megaphyllum* Merr. & L.M.Perry	*JA03*	Central Province; Mt Gerebu, trail towards summit ridge. PNG	147.646°E, 9.46595°S
AAU H.M.Christensen1282			OM286960	OM287045		ON101562	OM984620	*Archidendron microcarpum* (Benth.) I.C.Nielsen	*JA06*	Near Sumpa, Sarawak.	112°10'E, 1°20'N
BRI AQ0499073	OM984544	OM390221; OM390222	OM286962	OM287047	ON013707	ON101564	OM984622	*Archidendron muellerianum* (Maiden & R.T.Baker) I.C.Nielsen	*JA112*	Big Scrub Flora Reserve, NNE of Lismore, New South Wales, Australia	153°19'44.880"E, 28°38'18.228"S
BRI AQ0763292	OM984542; OM984543		OM286961	OM287046	ON013706	ON101563	OM984621	*Archidendron muellerianum* (Maiden & R.T.Baker) I.C.Nielsen	*JA50*	Tallebudgera Creek Road, reveg site. Queensland, Australia	153°21'57"E, 28°10'37"S
BISH752405	OM984545; OM984546	OM390223	OM286963	OM287048	ON013708	ON101565	OM984623	*Archidendron parviflorum* Pulle	*JA01*	Morobe Province; Siboma, Sayama, above Sayama Creek, to E Camp 1. PNG	147.302°E, 7.52557°S
MEL 2074350A			OM286964	OM287049	ON013709			*Archidendron pellitum* (Gagnep.) I.C.Nielsen	*JA34*	N. de Dalat, prov. Ht. Donnai. Indochina: Annam. Vietnam	108°27'E, 11°57'N
Bell Museum 913425 (WP-3A0575)	OM984547; OM984548	OM390224	OM286965	OM287050	ON013710	ON101566	OM984624	*Archidendron ptenopum* Verdc.	*JA116*	Wanang village, Madang, PNG	145°10.631'E, 5°14.238'S
AAU C.Charoenphol5025	OM984549; OM984550		OM286966	OM287051	ON013711	ON101567	OM984625	*Archidendron quocense* (Pierre) I.C.Nielsen	*JA13*	Ko Rang Yai, Thailand	102°23'E, 11°48'N
MEL 2391884A	OM984557	OM390228	OM286969	OM287053	ON013717	ON101573	OM984630	*Archidendron ramiflorum* (F.Muell) Kosterm.	*Z111*	Atherton Arboretum. Tag #1652. Queensland, Australia	145°29'8.6"E, 17°15'31.4"S
MELUD113388a	OM984551		OM286967	OM287052	ON013712	ON101568	OM984626	*Archidendron ramiflorum* (F.Muell) Kosterm.	*JA67*	Regeneration plot, Daintree Rainforest Observatory, Queensland, Australia	145.45004°E, 16.10268°S
BRI AQ0485087		OM390225	OM286968					*Archidendron ramiflorum* (F.Muell) Kosterm.	*Z110*	Shiptons Flat. Queensland, Australia	145°14'E, 15°47'S
AAU Balgooy6769	OM984552	OM390226	OM286970	OM287054	ON013713	ON101569		*Archidendron sp. nov. in obs.*	*JA85*	Pulan Baun, Aru Island Indonesia	134°35'E, 6°30'S
BRI AQ0052837	OM984553; OM984554		OM286971	OM287055	ON013714	ON101570	OM984627	*Archidendron syringifolium* (Kosterm.) I.C.Nielsen	*JA41*	Agu River branch of the middle Fly River, PNG	141.166667°E, 6.966667°S
MEL 2041191A	OM984555	OM390227	OM286972	OM287056	ON013715	ON101571	OM984628	*Archidendron vaillantii* (F.Muell) F.Muell.	*JA51*	Cape Tribulation, Queensland, Australia	145°27'E, 16°6'15"S
BRI AQ0558405	OM984556		OM286973	OM287057	ON013716	ON101572	OM984629	*Archidendron vaillantii* (F.Muell) F.Muell.	*JA52*	Along Paluma Dam Road, Ethel Creek, Queensland, Australia	146°10'40.222"E, 19°0'7.863"S

Preserved specimen	Associated sequences							Taxon name/MOTU	Sample ID	Location	
Specimen code (InstCode and/or CollCode + Catalogue #)	SHMT	RBPCO	ITS	ETS	tmK	tmV	psbD			Geolocation name / locality	GPS Coordinates
MEL 2196304A	OM984558		OM286974	OM287058	ON013718	ON101574	OM984631	*Archidendron whitei* I.C.Nielsen	*JA53*	State Forest 310 Gadgarra. Queensland, Australia	145°43'26"E, 17°18'13"S
BRI AQ0824396		OM390229	OM286975	OM287059	ON013719	ON101575	OM984632	*Archidendron whitei* I.C.Nielsen	*JA54*	7km W of Babinda, Queensland, Australia.	145°54'30"E, 17°20'30"S
KUN 0599686	OM984559; OM984560		OM286976	OM287060	ON013720	ON101576	OM984633	*Archidendron xichouense* (C.Chen & H.Sun) X.Y.Zhu	*JA84*	China	
BRI AQ0611431			OM286978	OM287062	ON013723			*Archidendropsis basaltica* (F.Muell.) I.C.Nielsen	*Z218*	On Isaac River and Hill Creek. 25km S of Glenden, Queensland, Australia	148°7'E, 21°33'01"S
MEL 0290000A			OM286977	OM287061				*Archidendropsis basaltica* (F.Muell.) I.C.Nielsen	*Z44*	Bladensburg National Park, S of Winton, Poison Paddock. Queensland, Australia	143°2'23"E, 22°41'9"S
MEL 2333247A	OM984561; OM984562		OM286979	OM287063	ON013721	ON101577	OM984634	*Archidendropsis granulosa* (Labill.) I.C.Nielsen	*Z362*	Prov. Sud, near Yate, north side of Yate River. New Caledonia	166°56'0"E, 22°9'29"S
BRI AQ0430532			OM286980	OM287064	ON013724			*Archidendropsis lentiscifolia* (Benth.) I.C.Nielsen	*Z122*	c. 5km north of Kone, south of Kafeate. New Caledonia.	164.78333°E, 21.05°S
MEL 2095888A			OM286981	OM287065	ON013725	ON101578	OM984635	*Archidendropsis thozetiana* (F.Muell.) I.C.Nielsen	*JA144*	Palmgrove National Park, 5km W of Daydream Hill, Queensland, Australia	149°13'29"E, 24°59'3"S
BRI AQ0771148			OM286982	OM287066	ON013722			*Archidendropsis xanthoxylon* (C.T.White & W.D.Francis) I.C.Nielsen	*Z121*	Daintree, narrow ridge above Cassowary Creek, off Stewart Creek road, site 69. Queensland, Australia	145°17'46"E, 16°17'56"S
L.1958248	OM984563	OM390230	OM286983	OM287067	ON013726	ON101579	OM984636	*Falcataria moluccana* (Miq.) Barneby & J.W.Grimes	*JA134*	KPC area, Sebongkok Utara, East Kalimantan, Indonesia.	117°31'59"E, 0°48'0"N
CANB 367091.1	OM984564	OM390231	OM286984	OM287068	ON013727	ON101580	OM984637	*Falcataria toona* (F.M.Bailey) Gill.K.Br., D.J.Murphy & Ladiges	*JA149*	Near Earlando, 27 km N of Proserpine. Queensland, Australia	148°33'E, 20°10'S
MEL 1615244A	OM984567	OM390234; OM390235	OM286987	OM287071	ON013730		OM984640	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen	*Z50*	Palm Tree Creek, W of Mt Whitestone township, Queensland, Australia	152°4'E, 27°39'S
CNS 134531.1	OM984565	OM390232	OM286985	OM287069	ON013728	ON101581	OM984638	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen	*JA55*	CSIRO Arboretum, Queensland, Australia	145°29'6"E, 17°15'28"S
QRS 121813.1	OM984566	OM390233	OM286986	OM287070	ON013729	ON101582	OM984639	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen	*JA56*	Clarke Range, Queensland, Australia	148°31'E, 21°16'S,
MEL 2183015A	OM984568; OM984569	OM390236	OM286988	OM287072	ON013731	ON101583	OM984641	*Paraserianthes lophantha* (Willd.) I.C.Nielsen	*Z43*	Merrimu Reservoir, Victoria, Australia	144°29'23"E, 37°38'3"S
BRI AQ0408829	OM984570; OM984571	OM390237	OM286989	OM287073	ON013732	ON101584	OM984642	*Serianthes nelsonii* Merr.	*JA143*	Atop Sailigai Hulo, Rota. Northern Mariana Islands.	145°12'53"E, 14°09'03"N
MEL 2333248A	OM984572	OM390238	OM286990	OM287074	ON013733	ON101585	OM984643	*Serianthes petitiana* Guillaumin	*Z361*	Prov. Sud, near Prony, New Caledonia	166°49'52"E, 22°19'4"S
MELU SRA051	OM984573	OM390239	OM286991	OM287075	ON013734	ON101586	OM984644	*Wallaceodendron cellebicum* Koord.	*Z48*	Bogor Botanic Gardens collection Accession: B19610136	

the Australian Genome Research Facility, Melbourne. Sequences were aligned in Geneious v.8.1.4 (Biomatters Ltd.) and assessed for variability between the samples. The most variable loci were then used in a targeted amplicon sequencing (TAS) approach (McLay et al. 2021), sequencing pooled amplicons on an Illumina MiSeq. For this, additional internal primers were designed for the five loci that had a total amplicon length greater than 500 bp, in order to produce shorter amplicons that could be fully sequenced using a 500-cycle sequencing kit. These primers were designed using Primer 3 v.2.3.4 (Rozen and Skaletsky 2000) implemented in Geneious v.8.1.4 (Biomatters Ltd.), selecting priming sites in conserved regions across the nine sequenced individuals.

Library preparation followed the two-step PCR process outlined in McLay et al. (2021). The first step used the region-specific primers to amplify each locus individually for each sample. Initial PCR reactions included 1 × MyTaq Buffer (Bioline), 1.2 µl of $MgCl_2$ 2.5 M (Bioline, 100 mg mL), 1.2 µl of dimethyl sulfoxide (DMSO, 99.5%; Sigma-Aldrich), 3 µl of each "tailed" primer (10 µM), 0.375 U of MyTaq (Bioline), 100 ng of gDNA, and ultra-pure water to make up for 16 µl volume. Variations in these reactions are noted in Suppl. material 1 for specific loci. Conditions for PCR were based on those of Choi et al. (2006), Shaw et al. (2007), and Ariati et al. (2006) with modifications as required to obtain successful amplifications (Suppl. material 1). To estimate amplicon concentration to decide the volume of PCR product for amplicon pooling, 2.2 µl of PCR product and 2.5 µl of molecular ladder (Easyladder I, Bioline) were run on 1.5% agarose. A total of 120 ng of each nuclear DNA (ncDNA) region PCR product and 20 ng of each chloroplast region PCR product were pooled in the same well of a 96-well plate. The ncDNA were pooled in a higher concentration to account for the possible presence of different alleles. Pooled samples were cleaned with 1.5 × Serapure beads (Rohland and Reich 2012).

The second step used qPCR to add unique Illumina indexing barcodes to each sample for the pooled amplicons. Indexing PCR reactions consisted of 5 µM of each of index primer (McLay et al. 2021), 3 µl of pooled amplicons, 1 × Kapa HiFi ReadyMix (Biosystems) and ultra-pure water to make up a total of 25 µl reaction. Conditions for PCR were 95 °C for 1 min, followed by 13 cycles of 98 °C for 50 sec, 67 °C for 50 sec, and 72 °C for 20 sec, and a final extension at 72 °C for 30 sec. Each sample was then cleaned with 1.4 × Serapure beads and concentrations were quantified using fluorescence in a EnSpire multimode plate reader. In total, 10 ng of each indexed and cleaned sample was pooled together. The final pooled library was cleaned with 1.5 × Serapure bead-to-sample ratio and the library was submitted to the Australian Genome Research Facility, Melbourne for sequencing on an Illumina MiSeq using a 500 cycle MiSeq v2 Nano Kit.

Data analysis

Sequences obtained by Sanger sequencing were aligned by individual locus in Geneious v.8.1.4 (Biomatters Ltd.) and a consensus sequence was generated and used as the reference for the reads obtained by TAS. The demultiplexed TAS Illumina MiSeq files were imported into Geneious v.8.1.4. Reads were trimmed to remove adapters and low-

quality sequence. The map-to-reference option was selected to map reads for each sample to the different reference loci using High Sensitivity/Medium settings and a minimum mapping quality of 20. A consensus sequence for each locus was generated for each individual with Generate Consensus Sequence (Threshold = 65%, with Ns called if coverage was less than 10). The forward and reverse reads of the low-copy nuclear genes (LCNG) overlapped so it was possible to phase these loci into separate alleles, but this was not possible for the nuclear ribosomal DNA loci (ETS and ITS) as the reads were not overlapping due to unexpected length variation in both of these loci. Alignments of individual consensus sequences for each locus were generated using MUSCLE (Edgar 2004) in Geneious v.8.1.4 and adjusted manually. For each LCNG, samples with multiple alleles were assessed for topological concordance between the different copies using neighbour-joining trees (using the Geneious tree-builder, HKY model) and Neighbour-Net networks (SplitsTree4, default settings, Huson and Bryant 2006), to ensure that a conflicting signal was not introduced from distantly related allelic variants (see Suppl. material 2: SHMT network and tree and Suppl. material 3: RBPCO network and tree). Allelic variants within samples were largely concordant with one-another permitting consensus sequences for those samples to be used for subsequent phylogenetic analyses.

Alignments of all nuclear loci (ncDNA; with consensus sequences for LCNG alignments) were analysed individually to explore gene tree topologies in IQ-TREE v.1.6.12 on the web server (http://iqtree.cibiv.univie.ac.at/, Trifinopoulos et al. 2016) with support estimated with 1,000 ultra-fast bootstrap replicates (UFBS) (Minh et al. 2013). After comparing topologies, four ncDNA loci (ETS, ITS, RBPCO, SHMT) were concatenated into a single matrix as no major incongruencies were observed. The combined ncDNA dataset was partitioned into six partitions corresponding to each locus with the ITS region further divided in ITS1, 5.8S and ITS2 for subsequent analyses. IQ-TREE was used to perform maximum likelihood (ML) analyses on the concatenated ncDNA alignment. The analysis was run with the alignment partitioned and allowing ModelFinder (Kalyaanamoorthy et al. 2017) to identify the optimal substitution models for each partition (Table 2). Node support was estimated using 1,000 UFBS. Bayesian Inference (BI) was performed, with the alignment partitioned by locus. The best model of substitution for each partition was estimated with IQ-TREE model selection using the options: selection criteria of Bayesian (BIC), candidate models JC, F81, K80, HKY, SYM, GTR, heterogeneity types I, G, I+G, and the genomic source of nuclear (Table 2). MrBayes v.3.2.7a (Ronquist et al. 2012) was run using the CIPRES Science Gateway (Miller et al. 2010). Two parallel runs each with eight Monte Carlo Markov Chains were run for five million generations, sampling a tree every 1,000 generations and a burn-in of 25%.

A consensus network of the combined ncDNA dataset was constructed in SplitsTree4 (Huson and Bryant 2006) using the last 101 sampled BI trees (edge weights = mean, threshold = 0.05). This method allows for the visualisation of conflict in a set of trees and provides an alternative method of interpretation to a single fixed topology of a consensus tree.

All chloroplast (cpDNA) loci were concatenated into a single matrix for phylogenetic analyses. IQ-TREE was used to perform ML analyses on the cpDNA matrix, with

Table 2. ncDNA data partitions and best fit substitution models. Models estimated by IQ-TREE model selection and applied for BI.

Partition	Model
ETS	HKY+F+G4
ITS1	GTR+F+G4
5.8S	SYM+I+G4
ITS2	HKY+F+G4
SHMT	HKY+F+G4
RBPCO	K2P+I

the alignment partitioned by locus, using ModelFinder to identify the optimal substitution model for each locus, and support was estimated using 1,000 UFBS replicates. The resulting topology was very poorly supported (though similar groups to the ncDNA phylogeny were discovered within the genus *Archidendron*). To further investigate cpDNA relationships within *Archidendron*, the outgroups were removed, and the IQ-TREE analysis was performed on the reduced dataset. The UFBS replicates were then used to create a consensus network in SplitsTree4 (edge-weights = mean, threshold = 0.20).

Pollen morphology of *Archidendropsis* subg. *Basaltica*

Pollen size and surface texture are key morphological features differentiating the subgenera of *Archidendropsis* but one of the three species of subg. *Basaltica* (*A. xanthoxylon* (C.T. White & W.D. Francis) I.C. Nielsen) was not examined by Nielsen et al. (1983b). To fill this gap and ensure consistency of results with published data, pollen from *A. xanthoxylon* (BRI AQ0199126, BRI AQ0874091, BRI AQ0199129 and BRI AQ0648303) and *A. basaltica* (F. Muell.) I.C. Nielsen (BRI AQ1003764, BRI AQ0199029, BRI AQ0625292 and BRI AQ0648454) of subg. *Basaltica* was examined. Pollen grains were obtained from flowers of herbarium specimens under a Zeiss dissecting microscope at the Queensland Herbarium (BRI) using clean forceps and a fine brush. Samples were mounted on aluminium stubs using double-sided carbon tabs and coated with gold using an Agar Scientific Automatic Sputter Coater. Pollen grains were observed and photographed using a Phenom G2 5keV (kiloelectronvolt) desktop scanning electron microscope (PhenomWorld). Pollen diameter for 10 grains of *A. basaltica* and eight grains of *A. xanthoxylon* was measured using ToupView (TOUPTEK PHOTONICS) software; overall fewer grains were available on specimens of *A. xanthoxylon* for microscopy.

Results

Targeted amplicon sequencing loci

Of the eight nuclear loci only four were included in the final phylogenetic analyses: SHMT, RBPCO, ITS and ETS. ETS and ITS amplified well, were variable, and are

commonly used phylogenetic markers in Caesalpinioideae phylogenetic studies. Of the LCNGs, SHMT was the most informative, followed by RBPCO; allelic variation was found in some individuals for all LCNGs. Exploring allelic variation in the SHMT (36 samples with alleles) and RBPCO (24 samples with alleles) showed that for samples with more than one allele, the copies were closely related to each other (Suppl. material 2: SHMT network and tree and Suppl. material 3: RBPCO network and tree). Two LCNGs were excluded because few individuals of the target genera were successfully sequenced; only 12 sequences of *Archidendron* and two sequences of *Archidendropsis* were obtained for AlGP, and only 16 sequences of *Archidendron* and one *Archidendropsis* were obtained for Eif3E. The remaining two LCNG loci (CYB6 and UDPG) are not included in the analyses due to their short lengths, 240 bp and 202 bp respectively, and lack of variation.

Of the four chloroplast loci, *trn*K-*mat*K was the most informative, followed by *psb*D-*trn*T and then *trn*V-*ndh*C. However, only one of the three blocks of *trn*V-*ndh*C was successfully sequenced. The internal primers designed allowed 100% coverage for the *trn*K-*mat*K, 81% coverage for the *psb*D-*trn*T, and less than 30% coverage for the *trn*V-*ndh*C. It was not possible to obtain sequences for all samples for all blocks in which the three cpDNA regions were divided; as a result the cpDNA dataset was patchy. The *trn*L-*rpl*32 intergenic spacer did not amplify well, with 10 samples partially sequenced, and it was not included in final analyses.

Phylogenetic analyses

The topologies of the combined ncDNA Bayesian and IQ-TREE analyses were congruent (nodes supported with UFBS ≥ 95; PP ≥ 0.90) and the Bayesian tree is presented (Fig. 2A,B). The Archidendron clade was recovered as monophyletic (PP 1.0) with six well supported clades (A–F) resolved within it. However, the relationships between clades A–F were not well resolved or supported with a polytomy in the backbone of the phylogeny. Clade A (PP 0.99) includes all three species of *Archidendropsis* subg. *Basaltica*, clade B (PP 1.0) includes the three samples of *Pararchidendron pruinosum* (Benth.) I.C. Nielsen, and clade C (PP 1.0) includes the two sampled representatives of *Archidendropsis* subg. *Archidendropsis*. Four monophyletic genera are grouped together in clade D (PP 1.0), with *Acacia* sister to *Paraserianthes* in clade D1 (PP 1.0) and *Falcataria* sister to *Serianthes* (PP 1.0) in clade D2 (Fig. 2A). Clade E (PP 1.0) comprises all but two sampled representatives of *Archidendron* ser. *Clypeariae*, and all other samples of *Archidendron* are placed in clade F (PP 1.0). Clades C, D and *Wallaceodendron* are related (PP 0.98) and together are sister to Clade E (PP 0.96; Fig. 2A).

Within *Archidendron*, only one of Nielsen's eight series is resolved as monophyletic (ser. *Ptenopae*) within subclade F1 (Fig. 2A). Clade E, the Clypeariae clade had two main lineages and several smaller supported subclades within them. Clade F, the Archidendron s.s. clade is segregated into three well supported subclades: the lucyi subclade (F1, PP 1.0) that includes three fully supported lineages; the grandiflorum subclade (F2, PP 1.0) that is poorly resolved; and the vaillantii subclade (F3, PP 1.0) that comprises two well supported lineages (PP 0.99; Fig. 2A–C).

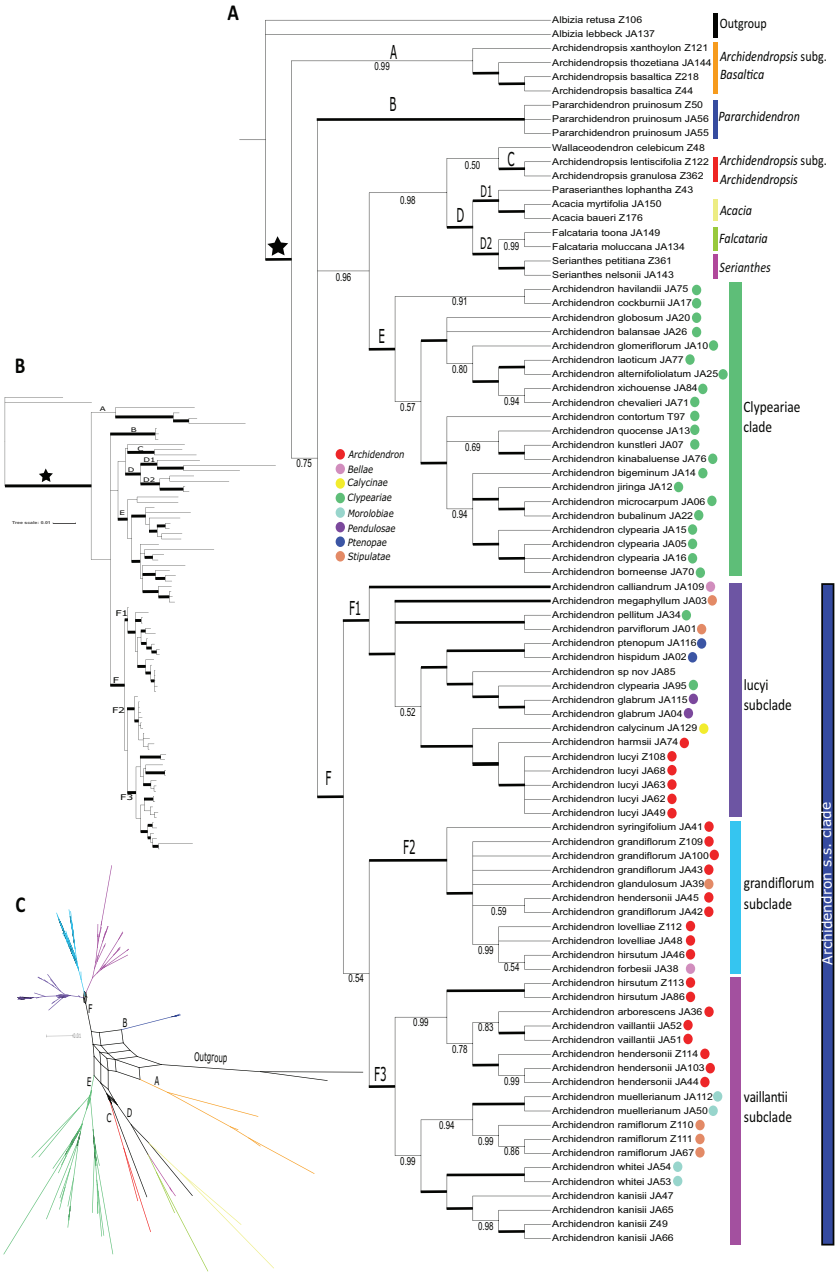

Figure 2. Combined ncDNA phylogeny of the Archidendron clade. The Bayesian Inference (BI) cladogram, phylogram, and consensus network for the combined ncDNA dataset are presented **A** Cladogram: the star indicates the Archidendron clade sensu Koenen et al. (2020). Nodes with PP = 1.0 are shown in bold while other nodes with PP ≥ 0.50 are noted under the node. Clades are labelled with letters above the node. Coloured bars to the right of clades are names discussed in the text. Nielsen's series of *Archidendron* are shown as coloured circles next to the sample name; key to colour and series in legend **B** Phylogram: clades are labelled as per **A** and nodes with a PP = 1.0 are shown in bold **C** Consensus network: branches are colour coded and labelled as per the clades of **A**.

Of the 12 species of *Archidendron* that included more than one accession, seven are monophyletic (*A. glabrum* (K. Schum.) K. Schum. & Lauterb., *A. kanisii* R.S. Cowan, *A. lucyi* F. Muell., *A. muellerianum*, *A. ramiflorum* (F. Muell.) Kosterm., *A. vaillantii* (F. Muell.) F. Muell. and *A. whitei*), one is unresolved (*A. lovelliae* (F.M. Bailey) I.C. Nielsen), and four are not monophyletic (*A. clypearia* (Jack) I.C. Nielsen, *A. grandiflorum* (Sol. ex. Benth.) I.C. Nielsen, *A. hendersonii* (F. Muell.) I.C. Nielsen and *A. hirsutum* I.C. Nielsen). Three of the four samples of *A. clypearia* form a clade (within clade E, Fig. 2; PP 1.0) with *A. borneense* (Benth.) I.C. Nielsen nested among them. One sample of *A. hendersonii* (JA45) is related to *A. grandiflorum* within clade F2; all other samples of *A. hendersonii* (Z114, JA103, JA44) form a clade within F3 (PP 1.0; Fig. 2A). Another species falling in both subclades F2 and F3 is *A. hirsutum*, with one sample (JA46) related to *A. forbesii* Baker f. and *A. lovelliae* in subclade F2 (PP 0.99), and the other two (Z113 and JA86) forming a sister pair in subclade F3 (PP 1.0; Fig. 2A).

The consensus network of the final 101-sampled BI trees shows the degree of topological uncertainty between the genera in the Archidendron clade (Fig. 2C). While each respective genus is well-supported as monophyletic (except *Archidendropsis* and *Archidendron* as described above) the relationships between the genera are highly uncertain, reflecting the lack of support in the consensus phylogenies. However, the network reinforces the distinction between the two clades of *Archidendropsis*, and the distinction of the Clyperiae clade from the rest of *Archidendron*.

The phylogeny of the three cpDNA loci combined lacks support for nearly all nodes (Suppl. material 4: cpDNA tree). Of the supported nodes there are two that are incongruent with the ncDNA tree (Fig. 2): *Paraserianthes* is sister to *Falcataria* (UFBS 100), and *A. harmsii* Malm is supported in the grandiflorum subclade (UFBS 95) sister to *A. grandiflorum* JA100 (UFBS 97; Suppl. material 4: cpDNA tree). The consensus network of the UFBS replicates (with splits present in at least 20% of trees) reflects the patterns in the ncDNA phylogeny, with four distinct groupings within *Archidendron* (Fig. 3). Within these groupings, several individuals are placed in different clades to the ncDNA tree: *A. hendersonii* JA45 is placed in the vaillantii subclade rather than the grandiflorum subclade, and *A. harmsii* JA74 is in the grandiflorum subclade rather than the lucyi subclade (Fig. 3).

Pollen morphology of *Archidendropsis* subg. *Basaltica*

The pollen measurement results are consistent with Nielsen et al. (1983a, 1983b). The pollen of the two species examined (*A. basaltica* and *A. xanthoxylon*) are aggregated into symmetrical 16-celled polyads with a diameter of 55–62 μm for *A. basaltica* and 62–68 μm for *A. xanthoxylon* (Fig. 4). Fossules were present on the surface of all grains of both species, but they were fainter on the peripheral cells compared to the central ones and overall fainter on *A. basaltica* compared to *A. xanthoxylon* (Fig. 4).

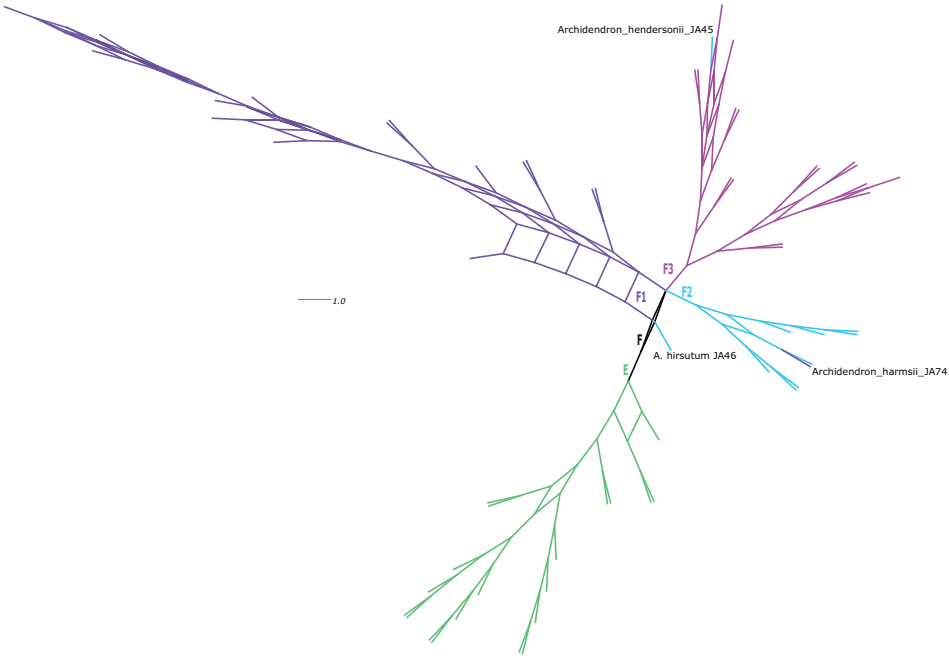

Figure 3. Combined cpDNA consensus network of clades within the genus *Archidendron*. The branches are labelled, and colour coded according to clades in Fig. 2A. Samples that have changed position relative to the ncDNA tree (as discussed in the text) are labelled with their name on the network.

Discussion

Phylogeny of the Archidendron clade

Our study presents the most taxon-rich sampling of the Archidendron clade of any phylogenetic analyses to date. We confirm that the Archidendron clade sensu Koenen et al. (2020) of Indomalayan-Australasian genera (*Acacia*, *Archidendron*, *Archidendropsis*, *Falcataria*, *Serianthes*, *Pararchidendron*, *Paraserianthes* and *Wallaceodendron*) is robustly supported, yet the relationships between the constituent clades are poorly resolved and lack support. This result is not unexpected given we used only four ncDNA loci and that phylogenomic studies based on hundreds of loci also yield short branches with low support across the backbone of the Archidendron clade (Koenen et al. 2020; Demeulenaere et al. 2022; Ringelberg et al. 2022). It has been suggested that this lack of resolution may be the result of extremely rapid speciation and that the backbone of this clade could be best regarded as a polytomy within the Ingoid legumes (Koenen et al. 2020). The differences in published topologies of the Archidendron clade are illustrated in Demeulenaere et al. (2022) but it is clear that further work based on increased sampling of phylogenomic data is required to uncover the evolutionary history of the clade.

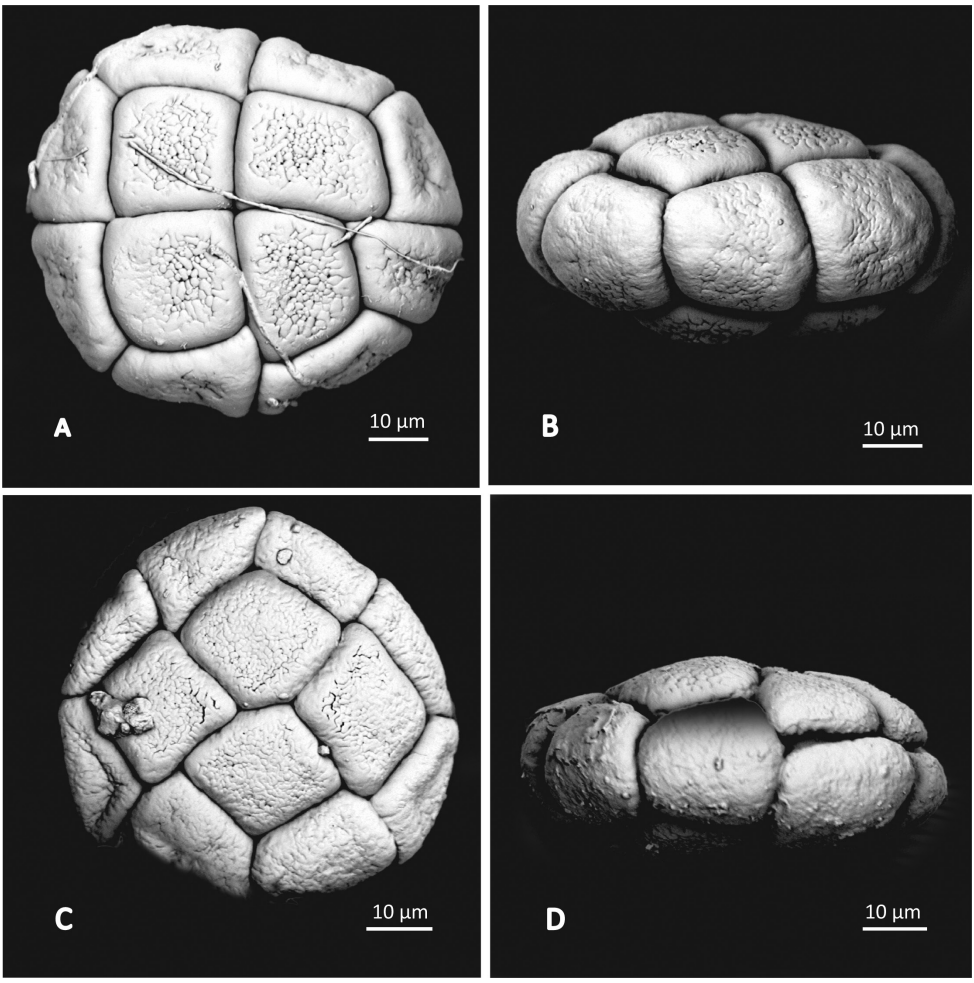

Figure 4. Scanning electron micrographs of *Archidendropsis* subg. *Basaltica* pollen. *Archidendropsis xanthoxylon* (**A** BRI AQ0199126 and **B** BRI AQ0874091) and *Archidendropsis basaltica* (**C** BRI AQ0199029 and **D** BRI AQ01003764).

Despite the poorly resolved backbone of the Archidendron clade, many clades within it are robustly supported and corroborate published phylogenies, as well as shedding new light on the genera *Archidendron* and *Archidendropsis* (Fig. 2). Four genera of the Archidendron clade are confirmed to be monophyletic – *Acacia* (Miller and Bayer 2001; Luckow et al. 2003; Miller et al. 2003; Brown et al. 2008), *Falcataria* (Brown et al. 2011), *Pararchidendron* and *Serianthes* (Demeulenaere et al. 2022) – and the previously suggested non-monophyly of *Archidendron* and *Archidendropsis* (Brown et al. 2008, 2011; Iganci et al. 2016; Demeulenaere et al. 2022; Ringelberg et al. 2022) is confirmed and clarified by increased sampling within these genera.

Phylogenetic relationships within *Archidendron*

The genus *Archidendron* is not monophyletic, and the eight series, while useful for identification purposes, do not coincide with evolutionary lineages (Fig. 2). The only series confirmed to be monophyletic was series *Ptenopae* from the island of New Guinea, the smallest series comprising just two species with two-winged leaf rachises and pinnae: *A. ptenopum* Verdc. and *A. hispidum* (Mohlenbr.) Verdc. (Nielsen et al. 1984b). The monophyly of series *Calycinae* and *Pendulosae* was not tested, as only one species of each was sampled, however, all other series (*Archidendron*, *Bellae*, *Clypeariae*, *Morolobiae*, and *Stipulatae*) are not monophyletic. *Archidendron* is instead resolved into two well supported lineages, one of which is primarily distributed in western Malesia and mainland Asia (the Clypeariae clade; clade E, Figs 1–3) and the other (the Archidendron s.s. clade; clade F, Figs 1–3) mostly restricted to eastern Malesia and Australia. These two lineages have been identified in previous phylogenetic studies but the sampling for each was extremely limited, with at most seven species of one lineage included (Brown et al. 2008, 2011; Iganci et al. 2016; Demeulenaere et al. 2022; Ringelberg et al. 2022). The further segregation of the Archidendron s.s. clade into three well supported lineages, the lucyi (F1), the grandiflorum (F2), and the vaillantii subclades (F3; Figs 2–3), is novel.

These three subclades of the Archidendron s.s. clade reflect geographic distributions to some extent, but no macromorphological characters have been identified to clearly delineate them. The grandiflorum and vaillantii subclades are predominantly Australian with some southern New Guinean species included, while the lucyi subclade is geographically more broadly distributed in the Lesser Sunda Islands, the Moluccas, through New Guinea to the Solomon Islands with only one species, *A. lucyi*, extending into northern Australia. Morphologically, the lucyi subclade includes all the sampled species lacking stipules that are not from ser. *Clypeariae* (i.e. *A. calliandrum* de Wit, *A. harmsii*, and *A. glabrum*), although stipules are reported for other species in this clade, three with stipular glands (*A. lucyi*, *A. megaphyllum* Merr. & L.M. Perry, *Archidendron* sp. nov. JA85), two with stipules only (*A. ptenopum* and *A. hispidum*) and *A. parviflorum* Pulle having both stipular glands and stipules (AAU Balgooy 6769; Nielsen et al. 1984b). All sampled species in the grandiflorum and vaillantii subclades have stipules, except *A. arborescens* (Kosterm.) I.C. Nielsen and *A. forbesii*, which have stipular glands (BM000946689; BRI AQ0380081; BRI AQ052589; Nielsen et al. 1984b) The placement of an undescribed species (*Archidendron* sp. nov. JA85) from the Aru Islands (Moluccas) in the lucyi subclade fits the geographic range. Ivan Nielsen noted this as a putative new species in October 1998 (AAU Balgooy 6769) but it does not align with any of the 20 imperfectly known species he outlined (Nielsen et al. 1984b), highlighting that further taxonomic work is required.

Three species in the Archidendron s.s. clade were not resolved as monophyletic (Fig. 2A), although it is unlikely these are issues with species delimitation. The paraphyly of *A. grandiflorum* (Fig. 2), a morphologically consistent species across a large geographic range (Brown pers. obs.), could be the result of potentially rapid and recent divergence

or may be due to insufficient phylogenetically informative characters in this study. The latter could also apply to the polyphyletic species (*A. hendersonii* and *A hirsutum*), as *A. hendersonii* JA45, which is placed separately from the other conspecific samples is missing data for two of the four ncDNA loci (Table 1). However, this was not the case for *A. hirsutum* JA46. Re-examination of the vouchers of all accessions of *A. hendersonii* and *A. hirsutum* confirmed their identifications, suggesting that incomplete lineage sorting or paralogy problems associated with one or more nuclear loci could explain these non-monophyletic species; further data are required to investigate this.

The Clypeariae clade (clade E, Figs 2–3) includes all sampled species of ser. *Clypeariae* (19/51), except one accession of *A. clypearia* (JA95) from Papua New Guinea and *A. pellitum* (Gagnep.) I.C. Nielsen from Vietnam. Series *Clypeariae* was previously recognised in *Pithecellobium* as section *Clypearia* until Nielsen et al. (1984b) expanded *Archidendron* based on evidence from shared wood anatomy, inflorescence and pod morphology (Nielsen et al. 1984b). Characters of the pods are also useful to differentiate series *Clypeariae* from the rest of *Archidendron*. Nielsen et al. (1984b) described six pod types and most species of ser. *Clypeariae* have pod type 2 (long funicle, opens ventral suture first) or 6 (straight pods with overgrown seeds), while the other series primarily have pod type 1 (opens dorsal suture first, short funicles). Seeds of ser. *Clypeariae* are usually flattened and are not embedded in the pericarp, which is possibly linked to characteristics of the pod, such as dryness (de Wit 1942; Nielsen 1981, 1992; Nielsen et al. 1984b). Additionally, the combination of lack of stipules and solitary, stipitate ovaries delineates ser. *Clypeariae* (Nielsen et al. 1984b). Individually though, these characters are not diagnostic, as some species with sessile ovaries are placed in ser. *Clypeariae* (e.g. *A. occultatum* (Gagnep.) I.C. Nielsen and *A. turgidum* (Merr.) I.C. Nielsen), other species lacking stipules are placed in series *Archidendron* (e.g. *A. harmsii* and *A. tjendana* (Kosterm.) I.C. Nielsen), and two Philippine species of ser. *Clypeariae* (*A. apoense* (Elmer) I.C. Nielsen and *A. merrillii* (J.F. Macbr.) I.C. Nielsen) have more than one ovary but both are stipitate (Nielsen et al. 1984b). Given these morphological differences of ser. *Clypeariae* from the rest of *Archidendron*, together with the non-monophyly of the genus, there are grounds for segregating *Clypeariae* as a distinct genus; however, we are not proposing such a taxonomic change here for several reasons. First, there are many shared morphological characters between species of *Archidendron* s.l.; second, the shallow backbone of the ncDNA tree remains poorly supported with topological uncertainty between lineages; third, the placement of two species of ser. *Clypeariae* within the Archidendron s.s. clade (clade F; *A. clypearia* var. *velutinum* (Merr. & L.M. Perry) I.C. Nielsen and A. *pellitum*) raises further doubts; and fourth, phylogenetic sampling of species remains incomplete. All these issues suggest that denser taxon sampling and larger phylogenomic datasets are required before re-classifying *Archidendron* as two genera.

Archidendron clypearia is the most widespread species of *Archidendron*, found from India through to Papua New Guinea. The morphological variation within *A. clypearia* has been used to recognise four infraspecific taxa (Legume Phylogeny Working Group 2021): subsp. *clypearia*, subsp. *subcoriaceum* (Thwaites) M.G. Gangop & Chakrab.,

var. *sessiliflorum* (Merr.) I.C. Nielsen, and var. *velutinum*. The one accession of *A. clypearia* placed outside the Clypeariae clade (JA95) (Fig. 2A) has been identified as var. *velutinum* (Brown, pers. obs. of CANB525617; previously only identified to species level by the collector), the only infraspecific taxon found in eastern Malesia (Sulawesi, Moluccas and PNG). The three other samples of *A. clypearia* included in the phylogeny have not been assigned to infraspecific taxa but they are not likely var. *velutinum*, as they are from Malaysia and Vietnam and lack the woolly to velutinous hairs on the lower surface of the leaflets (Brown per. obs.). Taxonomic revision and denser phylogenetic sampling of *A. clypearia* from across its morphological and geographic range is required to verify this placement, delineate the taxa and investigate if var. *velutinum* should be raised to species level (Merrill and Perry 1942) or if there are intermediate forms as suggested by Kostermans (1966). The only other species of series *Clypeariae* that extends into eastern Malesia, *A. palauense* (Kaneh.) I.C. Nielsen, from the Moluccas through to the Solomon Islands (Nielsen et al. 1984b), was not sampled here. There are no obvious morphological characters that support placement of *A. pellitum* outside the Clypeariae clade, as it has the full combination of diagnostic characters of ser. *Clypeariae*: compressed pods with a long (3–5 mm) funicle, stipitate single ovary and no visible stipules (US 2515891; P01818442; Nielsen 1981). In addition, no evidence of paralogy in the nuclear loci of *A. pellitum* and *A. clypearia* var. *velutinum* (JA95) was noted in this study; all sequences suggest they fall in the A. lucyi subclade.

The last revision of the genus *Archidendron* (Nielsen et al. 1984b) significantly advanced our understanding of the genus but more detailed taxonomic study is still required, focusing especially on the large number of species known from incomplete material and widespread morphologically variable species, such as *A. clypearia*. To resolve the backbone of the Archidendron clade and inform decisions about generic delimitation to deal with the non-monophyly of *Archidendron*, we recommend further sampling of ser. *Clypearia*, particularly from the Wallacean region of Malesia (i.e. Moluccas, Sulawesi, Philippines), together with further genomic sampling.

Phylogenetic relationships within *Archidendropsis*

While *Archidendropsis* is not monophyletic, its two subgenera (*Archidendropsis* and *Basaltica*) are (Fig. 2). The species within each subgenus have long been recognised as closely related (Bentham 1875; Nielsen 1981) but the two subgenera themselves have not always been associated with each other. For example, Bentham (1875) placed the species of each subgenus in different sections of *Albizia* based on inflorescence shape. Species of subgenus *Archidendropsis* that have flowers arranged in cylindrical spikes were placed by Bentham (1875) in *Albizia* section *Lophantha* Benth. (an illegitimate name later corrected to *Albizia* section *Pachysperma* (Benth.) Fosberg by Fosberg (1965)). Within this section they were separated from the other taxa, which are now recognised as *Paraserianthes*, into series *Platyspermae* Benth. because they have flattened, broadly orbiculate seeds (Bentham 1875). The two species of subgenus *Basaltica* known at that time (*A. basaltica* and *A. thozetiana* (F. Muell.) I.C. Nielsen) were placed by Bentham in his

large section *Eualbizzia* distinguished by flowers in globular heads and flattened orbicular seeds (Bentham 1875). Within that section, these taxa were placed into series *Obtusifolia*, which corresponds to the Australian species with 1–2 jugate leaves, ovate, oblong or obtuse leaflets, short petioles, pedunculate heads in the axils, and small sessile flowers.

It was only recently that the species of the two subgenera were united within *Archidendropsis* by Nielsen (1983) based on characters of the fruit and seed: pods dehiscent along both sutures, and seeds that are winged, thin-walled and lack a pleurogram. However, Nielsen himself questioned whether the subgenera should be congeneric, noting that if they were not, "*the evolution of the winged thin walled seeds without pleurogram should have happened twice*" (Nielsen et al. 1983a: p. 337). The results presented here (Fig. 2) alongside two recent phylogenomic analyses (Demeulenaere et al. 2022; Ringelberg et al. 2022) show that the two subgenera of *Archidendropsis* do not form a monophyletic group, suggesting these seed characteristics are indeed the result of convergent evolution.

The presence of a pleurogram is common in mimosoid genera (Gunn 1984), and is considered to have evolved multiple times (Maumont 1993). Within the Archidendron clade, *Archidendron* and *Archidendropsis* are the only two genera whose seeds lack a pleurogram (Nielsen 1992). The absence of a pleurogram has been associated with short-lived 'recalcitrant' seeds (i.e. seeds which lack dormancy and can be viviparous; Nielsen 1992) and has been thought to be an adaptive response to humid environments (Corner 1951 in Nielsen 1992; Maumont 1993). Like the absence of a pleurogram, winged seeds are also rare in mimosoids occurring in only eight genera, including *Archidendropsis* (Gunn 1984). The possession of a winged seed has been suggested to be an adaptation for wind-dispersal but there have been no published observations of this in *Archidendropsis* (Gunn 1984; Nielsen 1992). The short viability of *Archidendropsis* seeds has been linked to the restricted geographic ranges of individual species (Nielsen 1983). However, humidity may be a more important determinant of these distributions, as the ranges of the two Australian species occurring in drier, non-rainforest habitats are more than 10 times larger than the rainforest species (e.g. *A. basaltica* ≥ 750,000 km^2 compared to *A. xanthoxylon* c. 8,750 km^2 (AVH 2021)). The habitats of *A. basaltica* and *A. thozetiana* are also more open than for *A. xanthoxylon*, but these two species generally have narrower wings on their seeds than the rainforest species *A. xanthoxylon* (Cowan 1998), suggesting that the wing is unlikely to have an impact on wind dispersal. Morphological features that have been used to unite the two subgenera in *Archidendropsis* are thus homoplasious and not useful for generic delimitation.

The non-monophyly and clear morphological distinctions between them means that the two subgenera can no longer be treated as congeneric and need to be placed in separate genera. As the type of *Archidendropsis* (*A. fulgens* (Labill.) I.C. Nielsen) is from subg. *Archidendropsis*, it is subg. *Basaltica* that requires a new name. No name exists at the generic level for these taxa, as they have previously been placed in *Acacia*, *Albizia* and *Archidendropsis* (Mueller 1859; Bentham 1875; Fosberg 1965; Nielsen 1983), names which are all typified by other taxa.

In addition to the aforementioned morphological differences between the two subgenera, species of subg. *Basaltica* are endemic to Australia, whereas those of subg. *Archidendropsis* are found in New Caledonia, New Britain, the Solomon Islands and

on the island of New Guinea (Fig. 1B). Furthermore, there are several pollen characters separating the two subgenera (Nielsen et al. 1983a). Pollen of subg. *Basaltica* has isometric channels in the tectum and is aggregated into smaller polyads (55–68 μm), cf (80–120 μm) for subg. *Archidendropsis* where the tectum has non-isometric channels (Fig. 4; Nielsen et al. 1983a). The pollen surface of subg. *Basaltica* has fossules on the central cells, with either faint fossules or smooth peripheral cells, while in subg. *Archidendropsis* the surface of all pollen cells has small rounded areoles or deep fossules (Fig. 4; Nielsen et al. 1983a). Species of subg. *Basaltica* have sessile flowers arranged in globular pedunculate heads, rather than in spikes or racemes. Although one species of subg. *Archidendropsis*, *A. fournieri* (Vieill.) I.C. Nielsen, also has flowers arranged in globular pedunculate heads, it does not share the other diagnostic characters of subg. *Basaltica*, it is endemic to New Caledonia, its seeds are not winged, and the diameter of the pollen polyads is larger, fitting within the size range for subg. *Archidendropsis* (Nielsen 1983). Another character noted by Nielsen et al. (1983a) to differentiate the two subgenera, was the shape of the stipules, with those of subg. *Basaltica* being small and often developed into stipular spines (to 1.2 mm long; Brown pers. obs.; Fig. 5F) that are early caducous. However, the stipules of *A. xanthoxylon* were not recorded by Nielsen et al. (1983a) and are not like other Australian species being 1.2–3 mm long, ovate to triangular, dark gland-like and persistent (Brown, pers. obs., BRI AQ022813, BRI AQ0234095, BRI AQ0771148, BRI AQ199127, BRI AQ0199128; Fig. 5G). These stipules do differ, however, from those of the species of subg. *Archidendropsis* which, if present, are usually small (c. 1 mm), ovate or filiform and often caducous (Nielsen 1983).

Flowers arranged in globular heads, seeds lacking a pleurogram with a narrow peripheral membranous wing and flat, narrowly oblong, brown pods opening along both sutures distinguish this new genus from other Australian mimosoid legumes, and the keys in Flora of Australia (Cowan 1998) and available on KeyBase (Bean 2021; KeyBase 2021) still remain suitable.

Taxonomic treatment

Heliodendron **Gill.K. Br. & Bayly, gen. nov.**
urn:lsid:ipni.org:names:77303797-1
Fig. 5

Diagnosis. A genus of mimosoid legumes similar to *Archidendropsis* but differing in the following combination of features: inflorescences of glomerules, calyx and corolla with hairs (restricted to the lobes in *H. xanthoxylon*); stipules either small (to 1.2 mm) rigid and caducous or glandular (1.2–3 mm long) and persistent; pollen arranged in polyads diameter of 55–68 μm; pollen tectum with isometric channels. In contrast, *Archidendropsis* has inflorescences of spikes, spiciform racemes, racemes or in one species glomerules, but when in glomerules the calyx and corolla are glabrous; stipules (if present) either small (c. 1mm) ovate or filiform and often caducous, or large auriculate, orbicular, or cordate and persistent; pollen polyad diameter of 80–120 μm, pollen tectum with non-isometric channels.

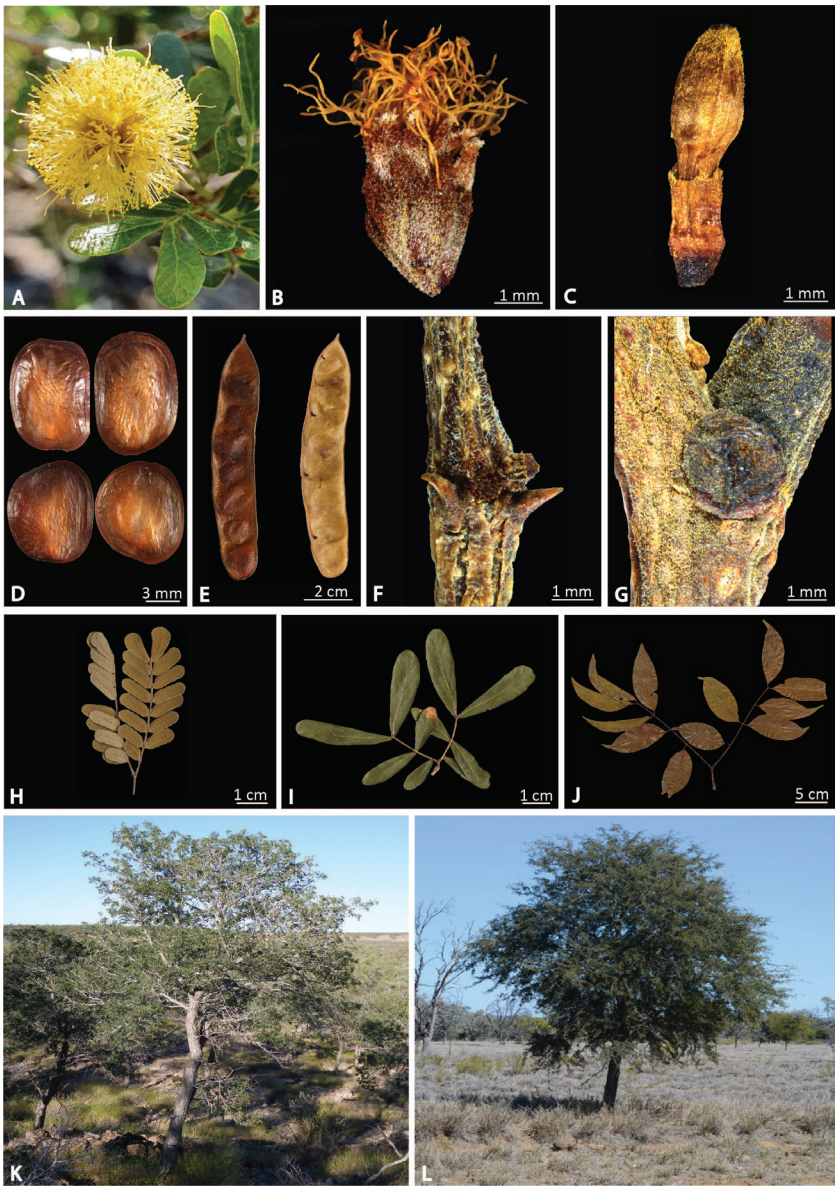

Figure 5. Morphology of *Heliodendron*. Plate showing diagnostic features of the new genus *Heliodendron* **A** inflorescence of *H. thozetianum*, Hazelwood Gorge, west of Mackay, Queensland (photo, Stuart Worboys, Australian Tropical Herbarium) **B** single flower of *H. basalticum* (BRI AQ0648454) showing hairs on calyx and corolla **C** mature bud of *H. xanthoxylon (*BRI AQ0874091) showing hairs on the lobes of the calyx and corolla **D** seeds of *H. basalticum* (BRI AQ0746724) **E** overall pod shape of *H. xanthoxylon* (BRI AQ0234095) **F** small rigid stipules of *H. basalticum* (BRI AQ0673898) **G** glandular stipule of *H. xanthoxylon* (BRI AQ0771148). Whole leaf showing overall leaflet size and shape of **H** *H. basalticum* (BRI AQ0648454) **I** *H. thozetianum* (BRI AQ0611464), and **J** *H. xanthoxylon* (BRI AQ0874091). Habit of *H. basalticum* from **K** Bladensberg National Park, Queensland (photo, Dale Richter, Queensland Herbarium) **L** 65 km west south-west of Blackall, Queensland (photo, Murray Fagg, Australian Plant Image Index, Australian National Botanic Gardens).

Description. Trees or shrubs, with terete branchlets. Stipules either resembling small thorns to 1.2 mm long that are early caducous, or persistent circular-ovate glands 1–3 mm in diameter. Leaves bipinnate, pinnae 1–2 pairs with 1.5–11 leaflet pairs per pinna; glands at the junction of pinnae circular or triangular to rhombic, +/- circular glands at the junction of leaflet petiolules. Leaflets opposite, subsessile (0.2–0.7 mm) or long (3.5–7 mm) petiolulate; elliptic to elliptic-lanceolate or oblong, 2–38 mm × 1.5–15 mm, glabrous to puberulous. Inflorescence of globular heads 0.5–1.7 mm in diameter, either simple or arranged into a panicle up to 35 cm long. Flowers: homomorphic, yellow to cream, sessile. Calyx 1.5–3 mm long, tubular to subcampanulate; corolla 2.5–7 mm long, tubular to narrowly campanulate. Ovary 0.8–2 mm long, solitary and shortly stipitate; stamens numerous 5–9 mm long, united basally into a tube that equals or slightly exceeds the corolla tube. Pollen 16-celled polyads with a diameter of 55–68 μm, tectum with isometric channels. Pod brown, valves chartaceous, 6–22 cm × 0.5–2.5 mm, oblong, flat and dehiscing along both sutures. Seeds lacking a pleurogram, flat, circular to ovate or obliquely ovate, 5–13 mm, with a narrow 0.2–1 mm peripheral, membranous wing. Fig. 5.

Type. *Heliodendron basalticum* (F. Muell.) Gill.K. Br. & Bayly ≡ *Acacia basaltica* F. Muell., *Journal of the Proceedings of the Linnean Society*, *Botany* 3: 146 (1859)

Etymology. From the Greek *helios* (sun) and *dendron* (tree) alluding to the endemic distribution of the genus in the Australian state of Queensland, widely known as the "sunshine state", the globular, sun-like inflorescences of yellow flowers, and the tree habit (Fig. 5A, K, L) and also in reference to the genera *Archidendropsis* (in which the species were previous placed) and *Archidendron* (which they resemble).

Homotypic synonym. *Archidendropsis* subg. *Basaltica* I.C. Nielsen, *Bulletin du Muséum National d'Histoire Naturelle*. *Section B*, *Adansonia*: *Botanique Phytochimie* 5(3): 325 (1983).

Notes. We have chosen to create a new name for this genus rather than making a new combination based on the name *Archidendropsis* subg. *Basaltica*. This is because using the name "Basaltica" at generic rank would require a change of epithet for the most widespread species in the genus under Art. 23.4 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). To minimise taxonomic change, and to avoid potential confusion, we would rather that the species retains its well-known epithet, which has been in continuous use since 1859.

The genus includes the following three species, all endemic to Queensland, Australia (Fig. 1B).

Heliodendron basalticum **(F. Muell.) Gill.K. Br. & Bayly, comb. nov.**

urn:lsid:ipni.org:names:77303798-1

Basionym. *Acacia basaltica* F. Muell., *Journal of the Proceedings of the Linnean Society*, *Botany* 3: 146 (1859). ≡ *Albizia basaltica* (F. Muell.) Benth., *Flora Australiensis* 2: 422 (1864); *Archidendropsis basaltica* (F. Muell.) I.C. Nielsen, *Bulletin du Muséum National d'Histoire Naturelle*. *Section B*, *Adansonia*: *Botanique Phytochimie* 5(3): 326 (1983).

Type. Peak Downs, *F. Mueller 42* (holotype: MEL 594732A image!; isotype K000822321 image!).

***Heliodendron thozetianum* (F. Muell.) Gill.K. Br. & Bayly, comb. nov.**
urn:lsid:ipni.org:names:77303799-1

Basionym. *Acacia thozetiana* F. Muell., *Fragmenta Phytographiae Australiae* 4(24): 9 (1863). ≡ *Albizia thozetiana* (F. Muell.) F. Muell. ex Benth., *Flora Australiensis* 2: 422 (1864); *Archidendropsis thozetiana* (F. Muell.) I.C. Nielsen, *Bulletin du Muséum National d'Histoire Naturelle*. *Section B*, *Adansonia*: *Botanique Phytochimie* 5(3): 326 (1983).

Type. Fort Cooper, *[A. Thozet?] no. 29*. (Lectotype, designated by R.S. Cowan, *Nuytsia* 11: 13 (1996)): MEL 595338A image!; residual syntypes: MEL 595339A, MEL 595340A, MEL 595342A, MEL 595377A].

***Heliodendron xanthoxylon* (C.T. White & W.D. Francis) Gill.K. Br. & Bayly, comb. nov.**
urn:lsid:ipni.org:names:77303800-1

Basionym. *Albizia xanthoxylon* C.T. White & W.D. Francis, *Proceedings of the Royal Society of Queensland* 41: 141, t. X (1929). *Archidendropsis xanthoxylon* (C.T. White & W.D. Francis) I.C. Nielsen, *Bulletin du Muséum National d'Histoire Naturelle*. *Section B, Adansonia*: *Botanique Phytochimie* 5(3): 326 (1983).

Type. Atherton District, North Queensland, *Overseer brothers s.n.* (Provisional Forestry Board), end of October, 1927 (Lectotype, designated by I.C. Nielsen as "Type", *Bulletin du Muséum National d'Histoire Naturelle*. *Section B*, *Adansonia*: *Botanique Phytochimie* 5(3): 341 (1983): BRI AQ022813! [2 sheets]; isolectotypes: DNA D0053218 image!, K000822329 image!, MEL 1562403A image!).

Notes. The protologue of *Albizia xanthoxylon* (White and Francis 1929) gave a location, collector name and month of the collection but did not indicate the herbarium in which the type was held, thus meaning that all specimens of this gathering could be considered syntypes. However, it appears that Nielsen inadvertently typified this taxon, according to Art. 7.11 of the ICN (Turland et al. 2018), when providing the description for the new combination of *Archidendropsis xanthoxylon* with the text "*Type*: *Overseer Brothers*, *Australia*, *N. Queensland*, *Atherton District*, *Oct 1927*, *fl. fr.* (*holo-*,*BRI*; *iso-K*)" (Nielsen et al. 1983a: p. 341). We believe this satisfies the requirements of Art. 7.11 to effectively lectotypify the name, which means that the BRI specimen is the lectotype and the K specimen is the isolectotype. Interestingly, the material illustrated in the protologue is clearly the isolectotype at K, as it is the only type specimen of *Heliodendron xanthoxylon* with pods, and the structure of the inflorescence and leaves is almost identical (K000822329; White and Francis 1929).

In Flora of Australia, Cowan (1998) cited BRI as holding an isotype as well as the holotype of this taxon; however, the two sheets have the same collection details,

are labelled as sheet 1 of 2 and sheet 2 of 2, and share a single accession number (BRI AQ022813). Therefore, it is herein determined that these are the one collection, and both represent the holotype (now lectotype; BRI AQ022813).

Conclusion

We present the most densely sampled phylogeny of the genera *Archidendron* and *Archidendropsis* to date and confirm that both genera are not monophyletic. The well supported clades within the Archidendron clade based on four nuclear markers agree with more data-rich phylogenomic data sets now being generated. A new genus, *Heliodendron*, endemic to Queensland (Australia), is described for the Australian members of the former *Archidendropsis* subg. *Basaltica*. Further sampling of species from subg. *Archidendropsis* would be beneficial, particularly to ascertain the relationships of the globular flowered *A. fournieri* and the non-New Caledonian representatives of *Archidendropsis* s.s. While *Archidendron* is also not monophyletic, no nomenclatural changes are made, because low phylogenetic support and high topological uncertainty between genera of the Archidendron clade mean that the relationships between the two clades of *Archidendron* remain uncertain. In addition, discrete macromorphological characters need to be identified to distinguish the two lineages of *Archidendron* as the basis for generic re-delimitation. A taxonomic revision of the widespread polymorphic *A. clypearia* would aid this, as our results indicate var. *velutinum* from eastern Malesia may represent a distinct species. Phylogenomic data and additional sampling of this species would be beneficial before taxonomic changes are made.

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Supplementary material 1

Primer sequences and PCR variations

Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay

Data type: Pdf file.

Explanation note: The reference for the primer and their PCR conditions are provided, along with the variations for PCR reagents and cycling conditions for the initial PCR in the two-step PCR process. * only used for sanger sequencing so no variations to note. Standard PCR reagents prior to variation consisted of 2X QIAGEN PCR buffer (QIAGEN), 5 mM of each dNTP (Bioline), 1 µl of each primer (10 µM), 1.25 µl of dimethyl sulfoxide (DMSO, 99.5%; Sigma-Aldrich), 1 U of Taq DNA polymerase, 100 ng of template and made up to 25 µl with ultra pure water per reaction. Reagent variations, A: not varied; B: 200 ng DNA, 1.2 µl BSA instead of DMSO; C: 200 ng DNA; D: 200ng DNA, 6 µM each primer, 1.5 µl MgCl2, 0.9 µl DMSO and 0.1 µl Taq; E: 6 µM each primer. Cycle variations: Z: 94 °C for 15 mins; 30 cycles of 94 °C for 20 sec, 61 °C for 20 sec, 72 °C for 2 mins; 72 °C for 5 mins; Y: 94 °C for 15 mins; 35 cycles of 94 °C for 20 sec, 61 °C for 20 sec, 72 °C for 2 mins; 72 °C for 5 mins; X: 94 °C for 15 mins; 35 cycles of 94 °C for 20 sec, 55 °C for 30 sec, 72 °C for 2 mins; 72 °C for 7 mins; W: 94 °C for 15 mins; 40 cycles of 94 °C for 20 sec, 50 °C for 1 min, 72 °C for 3 mins; 72 °C for 7 mins; V: 80 °C for 5 mins; 40 cycles of 95 °C for 1 min, 50 °C for 1 min with 0.3 °C/sec ramp, 65 °C for 4 mins; 65 °C for 5 mins; U: 94 °C for 5 mins; 30 cycles of 94 °C for 30 sec, 53 °C for 30 sec, 72 °C for 1 min; 72 °C for 7 mins; T: 80 °C for 5 mins; 30 cycles of 95 °C for 1 min, 50 °C for wwith 0.3 °C/sec ramp, 65 °C for 4 mins; 65 °C for 5 mins.

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Link: https://doi.org/10.3897/phytokeys.205.79381.suppl1

Supplementary material 2

SHMT network and tree

Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay

Data type: Pdf file.

Explanation note: Neighbour-joining tree and NeighbourNet network are presented with individual samples with more than one allele coloured to highlight their positions. The samples are coloured the same in both the tree and network. The clades that are congruent with Fig. 2 (B, C, D, D1, D2, F1, F2) are labelled. The sequences from species of *Albizia* (Z106, JA137) were removed as they occur on a very long branch relative to the rest of the samples in the network.

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Link: https://doi.org/10.3897/phytokeys.205.79381.suppl2

Supplementary material 3

RBPCO network and tree

Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay

Data type: Pdf file.

Explanation note: Neighbour-joining tree and NeighbourNet network are presented with individual samples with more than one allele coloured to highlight their positions. The samples are coloured are the same in both the tree and network. Clade B, which is congruent with Fig. 2 is labelled.

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Link: https://doi.org/10.3897/phytokeys.205.79381.suppl3

Supplementary material 4

cpDNA tree

Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay

Data type: Pdf file.

Explanation note: IQ-Tree of combined cpDNA loci, with all UFBS values shown. The two clades that are congruent with of Fig. 2 are labelled (A and F). Arrows indicate the placement of the two supported incongruences mentioned in the results text.

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Phylogenomic assessment prompts recognition of the Serianthes clade and confirms the monophyly of *Serianthes* and its relationship with *Falcataria* and *Wallaceodendron* in the wider ingoid clade (Leguminosae, Caesalpinioideae)

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Abstract

The Indo-Pacific legume genus *Serianthes* was recently placed in the Archidendron clade (sensu Koenen et al. 2020), a subclade of the mimosoid clade in subfamily Caesalpinioideae, which also includes *Acacia*, *Archidendron*, *Archidendropsis*, *Falcataria*, *Pararchidendron*, *Paraserianthes* and *Wallaceodendron*. *Serianthes* comprises ca. 18 species, five subspecies and two varieties that are characterised by bipinnately compound leaves with alternate sessile leaflets, branched axillary corymbiform panicles and woody indehiscent pods. Generic relationships, as well as species relationships within genera in the Archidendron clade, remain uncertain. While the sister relationship between *Serianthes* and the genus *Falcataria* is strongly supported by molecular data, the distinction between *Serianthes* and the monotypic genus *Wallaceodendron* has been questioned, based on their similar flower and fruit morphologies. We combined three gene-enriched hybrid capture DNA sequence datasets (generated from the 964 mimobaits v1 probe set, the expanded

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997 mimobaits v2 probe set and the GoFlag angiosperm 408 probe set) and used their overlapping markers (77 loci of the target exonic and flanking regions) to test the monophyly of *Serianthes* and to investigate generic relationships within the Archidendron clade using 55 ingoid plus two outgroup taxa. We show that *Serianthes* is monophyletic, confirm the *Serianthes* + *Falcataria* sister relationship to *Wallaceodendron* and recognise this combined clade as the Serianthes clade within the Archidendron clade. We also evaluated the use of overlapping loci across datasets in combination with concordance analyses to test generic relationships and further investigate previously unresolved relationships across the wider ingoid clade. Concordance analysis revealed limited gene tree conflicts near the tips of the Archidendron clade, but increased discordance at the base of the clade, which could be attributed to rapid lineage divergence (radiation) and/or incomplete lineage sorting.

Keywords
Archidendron clade, Fabaceae, mimosoid clade, monophyly, phylogenomics, targeted enrichment sequencing

Introduction

In the recent re-classification of legume subfamilies (LPWG 2017), the former subfamily Mimosoideae that is nested within the re-circumscribed Caesalpinioideae, was informally recognised as the mimosoid clade. Within the mimosoid clade, phylogenetic analyses (e.g. Luckow et al. 2003; Bruneau et al. 2013; LPWG 2017; Koenen et al. 2020) consistently show that none of the tribes in the traditional tribal classification of Bentham (1844) are monophyletic. Recent phylogenomic analyses provided greater resolution across the mimosoid phylogeny (Koenen et al. 2020) and Caesalpinioideae as a whole (Ringelberg et al. 2022), establishing the basis for the recognition of a number of informally-named clades, including the large pantropical ingoid clade (Koenen et al. 2020) that contains all genera of tribe Ingeae plus *Acacia* Mill. and all its segregates, except *Vachellia* Wight & Arn. Morphologically, this clade is characterised by flowers with > (10–)30 stamens that are often fused into a tube (Fig. 1; Brown et al. 2008; Koenen et al. 2020).

Koenen et al. (2020) found that the Indomalayan/Australasian Archidendron clade falls within the ingoid clade (Fig. 1). The Indo-Pacific genus *Serianthes* Benth., which is the focus of this study, is included in the Archidendron clade, together with seven other genera (Koenen et al. 2020; Table 1, Fig. 2): *Acacia* s.s., *Archidendron* F. Muell., *Archidendropsis* I.C. Nielsen, *Falcataria* (I.C. Nielsen) Barneby & J.W. Grimes, *Pararchidendron* I.C. Nielsen, *Paraserianthes* I.C. Nielsen and *Wallaceodendron* Koord. The Archidendron clade is restricted to the Indomalayan and Australasian realms, with highest species diversity and endemism in Malesia, Papua New Guinea, New Caledonia and Australia (Table 1).

Nielsen (1992) and Nielsen et al. (1983, 1984a, 1984b) solidified the classification of the genera in the Archidendron clade and this generic system is still largely followed today. However, apart from *Acacia* s.s. (Brown et al. 2008), the monophyly of most of the ingoid genera in the Archidendron clade has not been tested with modern

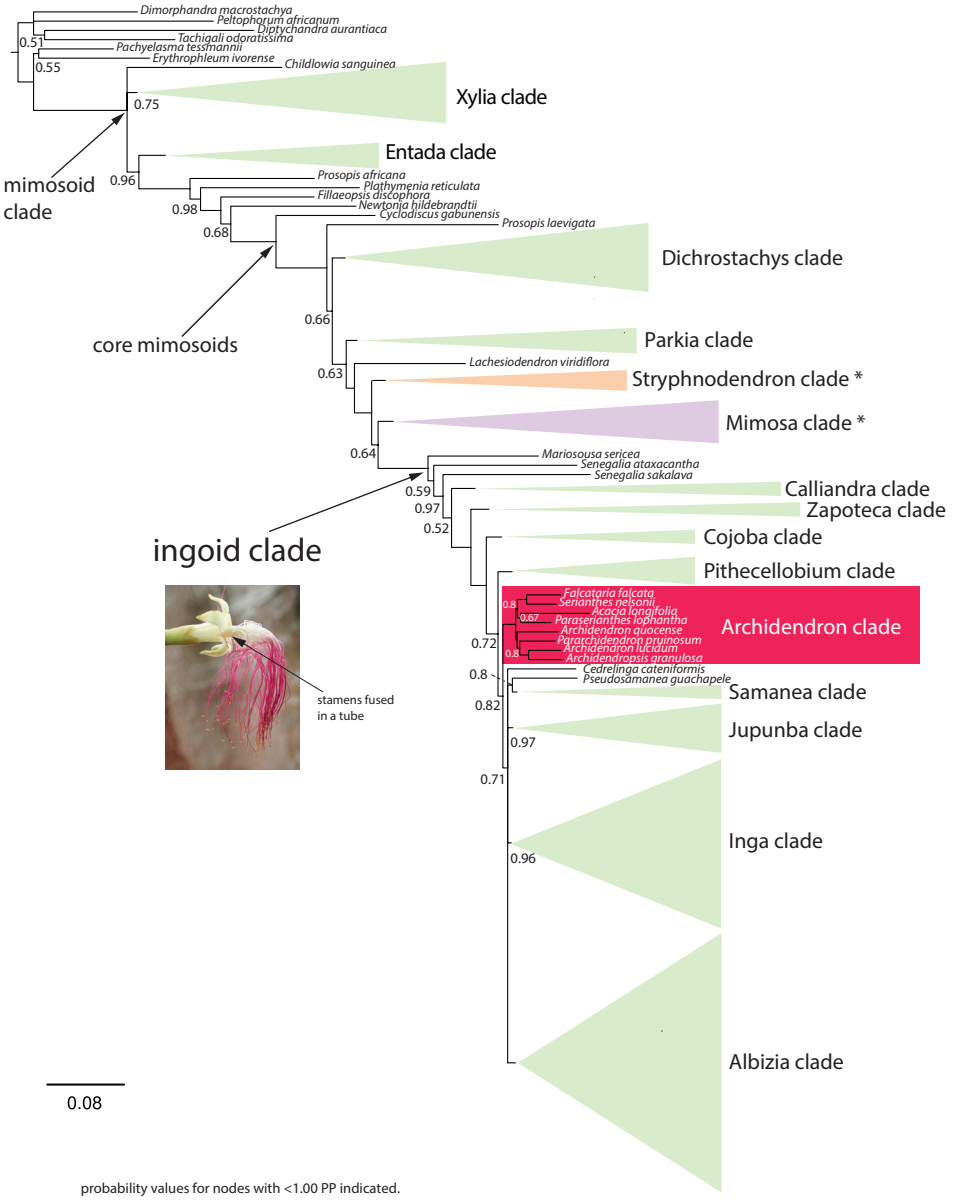

Figure 1. Phylogeny of the mimosoid clade modified from Koenen et al. (2020), based on the mimosoid 964 nuclear dataset with the Archidendron clade highlighted in red. Clade names follow Koenen et al. (2020) with branches collapsed and represented by green triangles. The Stryphnodendron and Mimosa clades, taxa from which were used to root trees in this study, are highlighted in orange and purple, respectively and indicated with an asterisk.

phylogenetic and phylogenomic analyses until recently (Brown et al. 2022; Ringelberg et al. 2022). Recent efforts to resolve phylogenetic relationships within the species-rich Archidendron clade have been hampered by a paucity of molecular data or incomplete taxon sampling in previous studies (Brown et al. 2008; Brown et al. 2011; Koenen et al. 2020). These uncertainties are compounded by nomenclatural instability (Barneby and Grimes 1996; Brown et al. 2008), lack of fertile herbarium specimens and morphological homoplasy (Fosberg 1960; Nielsen et al. 1984a; Koenen et al. 2020), as well as extensive geographic ranges for some species spanning the Indo-Pacific and Australia (Strijk et al. 2020). In the age of museomics and collection-based phylogenomics, the ability to sequence DNA from historical museum specimens (Zedane et al. 2016; Moreno-Aguilar et al. 2020; Renner et al. 2021) provides new opportunities to analyse phylogenetic relationships within the species-rich Archidendron clade by expanding taxon sampling geographically and including expert-identified specimens. Targeted enrichment sequencing (e.g. Hyb-Seq) can generate phylogenomic data by extracting DNA from small amounts of leaf tissue from archived herbarium specimens to build phylogenies with greatly enhanced gene and taxon representation (Bossert and Danforth 2018; Johnson et al. 2019; Escudero et al. 2020; Bateman et al. 2021; Eriksson et al. 2021).

Serianthes is a genus of tropical trees and shrubs distributed in the Indo-Pacific (Southeast Asia, the Pacific Islands and Australia). The genus was described by Bentham (1844) and has been revised by Fosberg (1960) and Kanis (1979, only the Malesian species). The most recent revision of *Serianthes* (Nielsen et al. 1984b) recognised 18 species, five subspecies and four varieties. The infrageneric classification

Table 1. Genera of the Archidendron clade: diversity, distribution and sampling included in the current study.

Genus	# of spp.	Distribution	# of spp. incl.	Literature Cited
***Acacia* Mill. s.s.**	986–1045	Mostly from Australia incl. 19 phyllodinous spp. from Hawai'i to Madagascar	3	Brown et al. (2008); Koenen et al. (2020)
***Archidendron* F. Muell.**	96	Endemic to SE Asia, the Pacific Islands and Australia	3	Fosberg (1960); Brown et al. (2008, 2010); Koenen et al. (2020)
***Archidendropsis* I.C. Nielsen**	11	Endemic to northern Australia (Queensland), New Caledonia, the Bismarck Archipelago and New Guinea	2	Nielsen et al. (1983, 1984a, 1984b); Brown et al. (2011); Koenen et al. (2020)
***Falcataria* (I.C. Nielsen) Barneby & J.W. Grimes**	3	Endemic to SE Asia, Papua New Guinea, the Solomon Islands and Australia	1	Brown et al. (2011); Koenen et al. (2020)
***Pararchidendron* I.C. Nielsen**	1, two subspecies and one variety	Java, Saleier Island, Bali, Lombok, Sumba, Sumbawa, Flores, Timor, Papua New Guinea and Australia (Queensland & New South Wales)	1	Nielsen et al. (1983, 1984a, 1984b); Brown et al. (2011); Koenen et al. (2020)
***Paraserianthes* I.C. Nielsen**	1	Java, Sumatra, the Lesser Sunda Islands and Australia	1	Nielsen et al. (1983, 1984a, 1984b); Brown et al. (2011); Koenen et al. (2020)
***Serianthes* Benth.**	18	Indo-Pacific Region	8	Nielsen et al. (1983, 1984a, 1984b); Koenen et al. (2020)
***Wallaceodendron* Koord.**	1	North Sulawesi and the Philippines	1	Nielsen et al. (1983, 1984, 1984a, 1984b); Brown et al. (2011)

of Nielsen et al. (1984a) recognised two subgenera, based on the basic unit of the inflorescence, subgenus *Minahassae* Fosberg with racemosely arranged pedunculate spikes and subgenus *Serianthes* with racemosely arranged pedunculate racemes, umbels or glomerules, while pod dehiscence and pod valve morphology were used to define sections within subgenus *Serianthes*. Although the monophyly of *Serianthes* has not been questioned, certain *Albizia* and *Acacia* taxa have been transferred to *Serianthes* in taxonomic revisions (Fosberg 1960).

Most *Serianthes* species are island endemics confined to small archipelagos in the Indo-Pacific Ocean. These endemic species face varying degrees of extinction threat caused by habitat loss and spread of invasive species. The IUCN Red List of Threatened Species lists 12 species of *Serianthes*, with three designated as critically endangered (IUCN 2021). In addition, *Serianthes nelsonii* Merr., endemic to the Mariana Islands, Guam and Rota, is listed as critically endangered by the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1987); only a single mature tree remains in Guam (Indigenous name [IN] for *S. nelsonii* on Guam: Håyun Lågu) and fewer than 50 individuals on Rota (IN: Tronkon Guåfi). As traditional uses and endemic languages are intrinsically connected to these endemic species, the islands' biocultural diversity is also vulnerable to extinction. Indigenous island communities traditionally use *Serianthes* trees for building canoes, boats and meeting houses, as ethnomedicines, in agriculture and in handicrafts (Demeulenaere et al. 2021).

Nielsen et al. (1983, 1984a, 1984b) discussed the generic limits of *Serianthes* and the other Malesian, Australian and Pacific Ingeae, based on comparative morphology. Nielsen et al. (1983) considered *Serianthes* to be closely related to *Falcataria* (as *Paraserianthes falcataria*) and *Wallaceodendron*, based on their wood anatomy and postulated that they were more closely related to the group of *Paraserianthes* s.s., *Archidendropsis* and *Pararchidendron* than to *Archidendron*. The eophylls of *Falcataria* and *Serianthes* are bipinnate, while all other genera in the Archidendron clade have once-pinnately compound eophylls (Nielsen et al. 1983). In 1996, Barneby and Grimes established *Falcataria* as a new genus, based on Nielsen's *Paraserianthes* section *Falcataria*, which included three species. This treatment was validated by the phylogenetic study of Brown et al. (2011), which concluded that *Paraserianthes* was paraphyletic and provided strong evidence for a well-supported *Falcataria* clade (incl. *Falcataria falcata* (L.) Greuter & R. Rankin, *Falcataria pullenii* (Verdc.) Gill. K. Br. and *Falcataria toona* (F.M. Bailey) Gill. K. Br., D.J. Murphy & Ladiges), distinct from *Paraserianthes lophantha* (Willd.) I.C. Nielsen of Nielsen's *Paraserianthes* section *Paraserianthes.*

A recent phylogenomic study of the mimosoid clade included seven of the eight genera of the Archidendron clade (Koenen et al. 2020) and was the first study to include one of the 18 species of *Serianthes*, but it did not sample the monotypic *Wallaceodendron.* Here, we used data from targeted sequence capture to evaluate the monophyly of *Serianthes* by combining a large dataset for mimosoid legumes (Koenen et al. 2020) with a separate phylogenomic dataset for *Serianthes* and genera of the Archidendron clade.

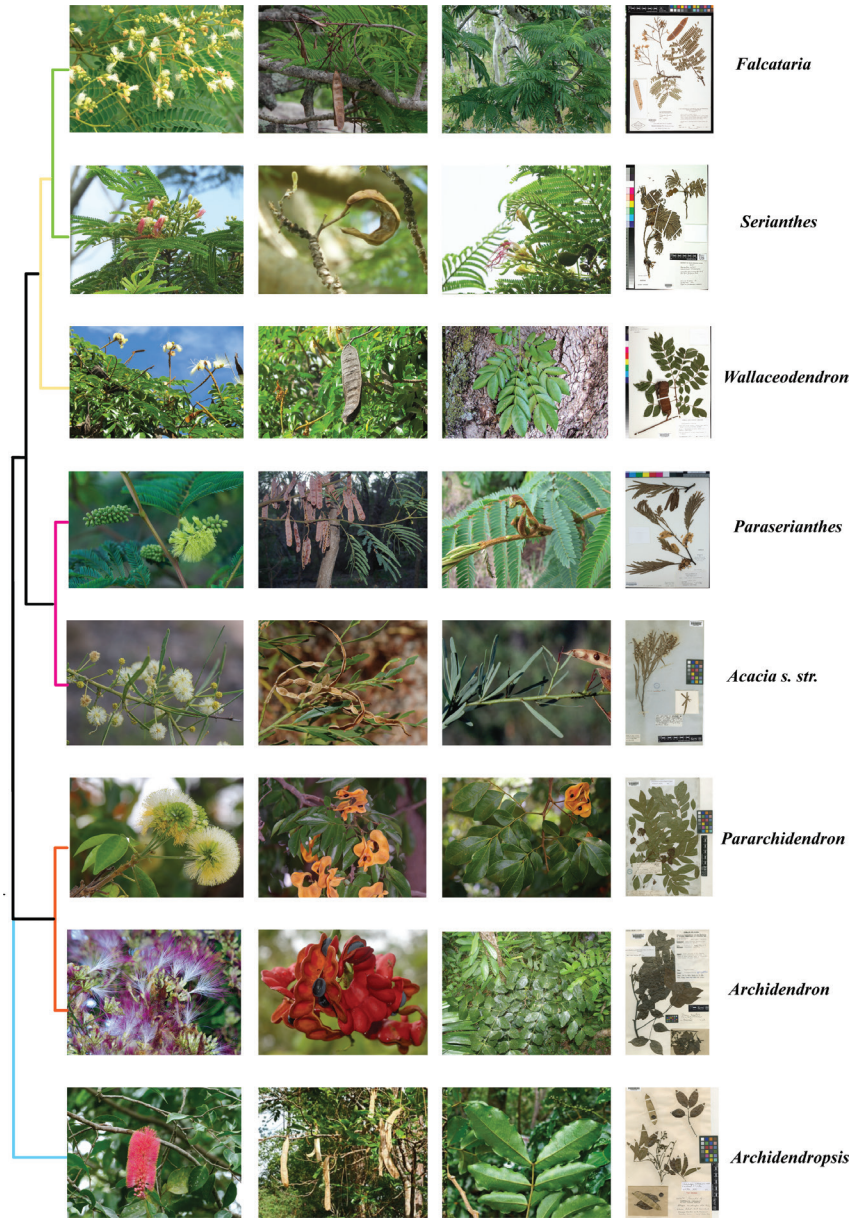

Figure 2. Morphology and relationships of the genera of the Archidendron clade, based on relationships recovered in our ASTRAL analysis. The colour scheme follows that in Fig. 7. Images are used with permission from Flickr: *Acacia rostellifera* (PC: Russell Cumming, HS: K000779891), *Archidendron grandiflorum* (PC: fl, le: Russell Cumming, HS: K000724398), *Archidendron lucyi* (PC: fr: Russell Cumming), *Archidendropsis paivana* subsp. *balansae* I.C. Nielsen (PC: fl: Benoît Henry), *Archidendropsis streptocarpa* (Fournier) I.C. Nielsen (PC: fr, le: Benoît Henry, HS: K000822329), *Falcataria falcata* (Photo credits [PC]: flower [fl]: JB Friday), *Falcataria toona* (PC: fruit [fr], leaf [le]: Russell Cumming, herbarium sheet [HS]: NY0149795, *Serianthes nelsonii* (PC: Else Demeulenaere, HS: US00689615), *Pararchidendron pruinosum* (PC: Russell Cumming, HS: K000759556), *Paraserianthes lophantha* (PC: fl: Eric Hunt; fr: Russell Cumming, le: Forest Starr and Kim Starr, HS: OBI126697), *Wallaceodendron celebicum* (PC: Plantaholic Sheila, HS: LSU00096994).

Methods

Sampling

We used sequences generated from three target capture probe sets: 1) The Mimobaits probe set v1 including 964 nuclear genes of Koenen et al. (2020; https://github.com/erikkoenen/mimobaits/), 2) the Mimobaits probe set v2 (expanded from v1 including 997 nuclear genes, Ringelberg et al. 2022) and 3) the GoFlag angiosperm 408 probe set which includes 408 nuclear exons and their flanking regions (Breinholt et al. 2021a). Merging these datasets resulted in alignments with 57 taxa of the ingoid clade and outgroups, of which 19 belong to the Archidendron clade (Tables 1, 2). Eight of the 18 species of *Serianthes* were included, covering the distribution range of the genus and members of both subgenera and the two sections in subgenus *Serianthes*. Outgroup selection followed previous phylogenies of mimosoid legumes (Koenen et al. 2020) to select *Stryphnodendron pulcherrimum* Hochr. and *Mimosa grandidieri* Baill. as the outgroup.

DNA extraction, library preparation and enrichment

DNA extractions of the *Serianthes* samples for sequencing the GoFlag angiosperm 408 probe set followed the protocol of Breinholt et al. (2021a). Following bead clean-up, DNA was normalised and Illumina-compatible libraries were prepared following standard procedures (Breinholt et al. 2021a). Library construction, target enrichment and sequencing of *Serianthes* samples were done by RAPiD Genomics (Gainesville, Florida, U.S.A.) using protocols of Breinholt et al. (2021a). Target enrichment used the angiosperm version of the GoFlag 408 probe set (Breinholt et al. 2021a) that covers 408 conserved nuclear exons across 229 of the single- or low-copy genes identified by the 1KP transcriptome sequencing project (Leebens-Mack et al. 2019). All enriched samples were sequenced using an Illumina HiSeq 3000 (Illumina, San Diego, California, USA) with paired-end 100 base-pair reads.

Data filtering and assembly

For the GoFlag 408 samples, we used a modified version of the iterative baited assembly pipeline of Breinholt et al. (2021a, b) to recover the targeted nuclear exon loci and the more variable flanking intron regions from enriched Illumina data. Our modified pipeline differed from the original pipeline in that: 1) reference sequences used in the *de novo* assembly of the loci were from 690 angiosperm samples extracted from the 1KP alignments of single copy nuclear loci (Leebens-Mack et al. 2019) corresponding to the 408 target regions; 2) we used 10 angiosperm genomes, rather than flagellate land plant genomes, to assess orthology; 3) to filter non-angiosperm contaminants, we performed a tBLASTx (Camacho et al. 2009) search against the respective angiosperm and flagellate land plant reference sequences for each locus. If a sequence's best hit was not from an angiosperm, that sequence was removed as a potential contaminant. The pipeline outputs sequences for each locus. To minimise the possibility of including

paralogs, we removed loci from a sample's alignment when multiple sequences were recovered for a single locus alignment. For the eight *Serianthes* samples, we removed an average of 6.6% of loci due to presence of multiple sequences.

To recover sequences with as many shared loci as possible from the 964 and 997 gene *Mimobaits* datasets of Koenen et al. (2020) and Ringelberg et al. (2022), we downloaded raw reads for these samples from the NCBI Sequence Read Archive (SRA) database. We ran the same pipeline to recover sequences from as many of the GoFlag angiosperm 408 loci as possible. This resulted in 77 shared loci for 57 taxa, each containing the targeted exon and flanking regions. We excluded samples for which fewer than 10 GoFlag loci were recovered. Specimens with more than 72% gaps or ambiguities in the concatenated alignment were removed from gene alignments. The 72% threshold coincides with the gap/ambiguity value for *Falcataria*, a key taxon in our analysis that was inferred to be sister to *Serianthes* by Koenen et al. (2020). Other studies have applied similar (75%; Koenen et al. 2020) or more stringent (50%; Spillane et al. 2021) thresholds to account for compositional bias. Based on the 72% threshold, we retained 19 taxa of the Archidendron clade. By excluding taxa with fewer than 10 loci or more than 72% gaps or ambiguities, 43 of the 115 taxa in the original *Mimobaits* 964 nuclear dataset (Koenen et al. 2020; Table 2) and six taxa from the expanded mimosoid 997 gene dataset (Ringelberg et al. 2022; Table 2) were retained. We aligned sequences from these 49 species with seven *Serianthes* samples and one outgroup generated using the GoFlag angiosperm 408 dataset (Table 2) using MAFFT version 7.425 (Katoh and Standley 2013). The presence of indels in the flanking intron regions of the GoFlag target exons and the substantial variation in the amount of flanking sequence recovered from each sample resulted in regions of the alignment with nucleotide data from only one or a few samples. To reduce this missing data, we used a Perl script to eliminate any columns in the alignment of each locus that included fewer than ten nucleotides.

Concatenated, gene tree and concordance analyses

A partitioned ML analysis of the concatenated multi-locus alignment was run in IQ-TREE (Nguyen et al.2015; Minh et al. 2020b). ModelFinder (Kalyaanamoorthy et al. 2017) was used to identify the best-fit substitution model for each locus. Ultrafast bootstrap approximations (UFBoot) were calculated to evaluate branch support in a single IQ-TREE run. ASTRAL-III (Zhang et al. 2018) was used to infer a species tree while accounting for possible incomplete lineage sorting amongst gene trees (Koenen et al. 2020). Each of the 77 gene trees was constructed using Maximum Likelihood analyses comparable to the partitioned analysis of the concatenated alignment. These gene trees served as input for the ASTRAL analysis to infer a species tree with local posterior probabilities (PP) as node support values. Polytomy tests (Sayyari and Mirarab 2018) to assess if polytomy null models could be rejected at a particular node ($p < 0.05$) were conducted in ASTRAL-III. Gene tree (dis)concordance analyses were performed in IQ-TREE to assess levels of gene tree conflict across the species tree (Chan et al. 2020; Minh et al. 2020a).

Table 2. Sample information for the taxa included in the ingoid clade phylogeny. This table includes sampling code/accession and voucher information for 57 taxa with the herbarium acronym shown in parentheses, dataset name and publication. Taxa belonging to the Archidendron clade are indicated with an asterisk.

Species	Accession	Voucher	Database	Publication
***Abarema cochliacarpos* (Gomes) Barneby & J.W. Grimes**	ERS4812838	L.P. de Queiroz 15538 (HUEFS)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
Acacia rostellifera* Benth.	ERS11697109	Murphy 466 (MELU)	expanded mimosoid 977 nuclear dataset	Ringelberg et al. (2022)
***Acacia victoriae* Benth. ***	ERS11697114	Ariati 260 (MELU)	expanded mimosoid 977 nuclear dataset	Ringelberg et al. (2022)
***Albizia adianthifolia* (Schumach.) W. Wight**	ERS4812846	J.J. Wieringa 6278 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia altissima* Hook.f.**	ERS4812847	C. Jongkind 10709 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia atakataka* Capuron**	ERS4812849	E. Koenen 229 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia aurisparsa* (Drake) R. Vig.**	ERS4812850	E. Koenen 230 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia ferruginea* (Guill. & Perr.) Benth.**	ERS4812857	C. Jongkind 10762 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia grandibracteata* Taub.**	ERS4812858	E. Koenen 159 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia inundata* (Mart.) Barneby & J.W. Grimes**	ERS4812859	J.R.I. Wood 26530 (K)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia mahalao* Capuron**	ERS4812860	E. Koenen 216 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia masikororum* R. Vig.**	ERS4812861	E. Koenen 237 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia obbiadensis* (Chiov.) Brenan**	ERS4812862	Thulin 4163 (UPS)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia obliquifoliolata* De Wild.**	ERS4812863	J.J. Wieringa 6519 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia retusa* Benth.**	ERS4812865	Hyland 2732 (L)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia sahafariensis* Capuron**	ERS4812866	E. Koenen 405 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia saponaria* (Lour.) Blume**	ERS4812867	Jobson 1041 (BH)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia umbellata* (Vahl) E.J.M. Koenen**	ERS4812882	Jobson 1037 (BH)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia versicolor* Welw. ex Oliv,**	ERS4812868	O. Maurin 560 (JRAU)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia viridis* E. Fourn.**	ERS4812869	Du Puy M251 (K)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Albizia zygia* (DC.) J.F. Macbr.**	ERS4812870	J.J. Wieringa 5915 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Archidendron grandiflorum* (Soland. ex Benth.) I.C. Nielsen ***	ERS11697138	Clarkson 6233 (L)	expanded mimosoid 977 nuclear dataset	Ringelberg et al. (2022)
***Archidendron lucidum* (Benth.) I.C. Nielsen ***	ERS4812873	Wang and Lin 2534 (L)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Archidendron quocense* (Pierre) I.C. Nielsen ***	ERS4812874	Newman 2094 (E)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Archidendropsis granulosa* (Labill.) I.C. Nielsen ***	ERS4812875	McKee 38353 (L)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Archidendropsis xanthoxylon* ***	ERS11697143	Hyland 9229 (L)	expanded mimosoid 977 nuclear dataset	Ringelberg et al. (2022)
***Balizia pedicellaris* (DC.) Barneby & J.W. Grimes**	ERS4812877	L.P. de Queiroz 15529 (HUEFS)	mimosoid 964 nuclear dataset	Koenen et al. (2020)

Species	Accession	Voucher	Database	Publication
***Balizia* sp.nov.**	ERS4812878	M.P. Morim 577 (RB)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Blanchetiodendron blanchetii* (Benth.) Barneby & J.W. Grimes**	ERS4812879	L.P. de Queiroz 15616 (HUEFS)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Chloroleucon tenuiflorum* (Benth.) Barneby & J.W. Grimes**	ERS4812885	L.P. de Queiroz 15514 (HUEFS)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Cojoba arborea* (L.) Britton & Rose**	ERS4812886	M.F. Simon 1545 (CEN)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Falcataria falcata* (L.) Greuter & R. Rankin**	ERS4812898	Ambri & Arifin W826A (K)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Havardia pallens* (Benth.) Britton & Rose**	ERS4812900	C.E. Hughes 2138 (FHO)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Hesperalbizia occidentalis* (Brandegee) Barneby & J.W. Grimes**	ERS4812901	C.E. Hughes 1296 (FHO)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes [2]**	ERS4812903	J.R. Iganci 862 (RB)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Jupunba trapezifolia* (Willd.) Britton & Killip**	ERS4812839	M.F. Simon 1600 (CEN)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Leucochloron bolivianum* C.E. Hughes & Atahuachi**	ERS4812907	C.E. Hughes 2608 (FHO)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Leucochloron limae* Barneby & J.W. Grimes**	ERS4812908	MWC8250 (K)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Mariosousa sericea* (M. Martens & Galeotti) Seigler & Ebinger**	ERS4812911	MWC18949 (K)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Mimosa grandidieri* Baill.**	ERS4812912	E. Koenen 207 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Pararchidendron pruinosum* (Benth.) I.C. Nielsen ***	ERS4812919	Jobson 1039 (BH)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Paraserianthes lophantha* (Willd.) I.C. Nielsen ***	ERS4812920	M. van Slageren & R. Newton MSRN648 (K)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Pithecellobium dulce* (Roxb.) Benth.**	ERS4812927	B. Marazzi 309 (ASU)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Samanea saman* (Jacq.) Merr.**	SRR18455122	Demeulenaere E, GUAM	GoFlag 408 dataset	This contribution
***Senegalia ataxacantha* (DC.) Kyal. & Boatwr.**	ERS4812938	C. Jongkind 10603 (WAG)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Serianthes calycina* Benth. ***	ERS11697309	Barrabé 1158 (NOU)	expanded mimosoid 977 nuclear dataset	Ringelberg et al. (2022)
***Serianthes germanii* Guillaumin ***	SRR17180693	MacKee HS 5036 (L), L.2034754	GoFlag 408 dataset	This contribution
***Serianthes hooglandii* Fosberg ***	SRR17180692	Schodde R 2750 (L), L.2034739	GoFlag 408 dataset	This contribution
***Serianthes kanehirae* var. *kanehirae* (Ukall, Kumer - Palau) ***	SRR1718091	Demeulenaere E, PAL006	GoFlag 408 dataset	This contribution
***Serianthes melanesica* Fosberg ***	SRR1718090	Drake DR; 256 (US); US2191202	GoFlag 408 dataset	This contribution
***Serianthes minahassae* (Koord.) Merrill & Perry ***	SRR1718089	Pullen R, 6484 (L); L.1995177	GoFlag 408 dataset	This contribution
***Serianthes nelsonii* (Håyun Lågu - Guam) ***	SRR1718088	Demeulenaere E, GUA002	GoFlag 408 dataset	This contribution
***Serianthes vitiensis* A. Gray ***	SRR1718087	Gardner RO, 6872 (US); US942100	GoFlag 408 dataset	This contribution
***Sphinga acatlensis* (Benth.) Barneby & J.W. Grimes**	ERS4812941	C.E. Hughes 2112 (FHO)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Stryphnodendron pulcherrimum* (Willd.) Hochr.**	ERS4812942	L.P. de Queiroz 15482 (HUEFS)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Viguieranthus glaber* Villiers**	ERS4812947	E. Koenen 325 (Z)	mimosoid 964 nuclear dataset	Koenen et al. (2020)
***Wallaceodendron celebicum* Koord. ***	ERS11697328	Tim Flynn 7173 (NYBG)	expanded mimosoid 977 nuclear dataset	Ringelberg et al. (2022)

PP values of 1 provided unambiguous support for each branch (Fig. 3, Table 3). Gene concordance factors (gCF, the percentage of gene trees containing a specific branch in the species tree) and site concordance factors (sCF, the percentage of alignment sites supporting that branch) were calculated (Minh et al. 2020a, Table 4; Stubbs et al. 2020). sCF values have a lower bound of 33% because they are based on a quartet-based approach to calculate the value at each node (Burbrink et al. 2020). Robustly or fully supported branches with high bootstrap values in the species tree can still show conflicting signals in the gene trees due to incomplete lineage sorting (ILS), hybridisation, inconsistent paralog retention in polyploids, introgression, model misspecification and stochastic error inherent in sequencing techniques. New methods may help to elucidate these processes using target capture data from nuclear loci in the future (e.g. Morales-Briones et al. 2021; Tiley et al. 2021).

The two gene discordance factors, gDF_1 and gDF_2, quantify the support for the two nearest-neighbour interchange partitions. The third gene discordance factor, gDF_P ("paraphyletic discordance factor"), calculates the support for all possible topologies (Minh et al 2020a; Thomas et al. 2021). There are three possible quartets around each branch it supports (based on sites), the first one is the sCF, the second one sDF_1 calculates the support amongst sites for alternative quartets and sDF_2 calculates the support for a second alternative arrangement (Minh et al. 2020a; Thomas et al. 2021). The sum of sCF, sDF_1 and sDF_2 values is 100%. Correlations between concordance factors and support values were visualised in R (R Core Team 2021). The pipeline to run the analyses in IQ-TREE, ASTRAL-III and the visualisation of relationships between concordance factors in R followed Lanfear (2018) and Matschiner (2020).

Results

Assembly

The matrix comprised 77 exons and flanking regions for 57 taxa (Table 2) and was 115,160 bp in length. Of the 45,600 variable sites, 15,210 were parsimony-informative and 30,390 were singleton sites.

Phylogenetic inference and quantification of gene tree and site conflicts

The ASTRAL species tree and the concatenated ML tree from IQ-TREE have largely similar Archidendron clade topologies (Fig. 4), with higher support values (BS and PP) in the ASTRAL tree compared to the concatenated ML analysis (Figs 3, 4). Although there are topological differences between the ASTRAL species tree and the concatenated ML analysis from IQ-TREE outside of the Archidendron clade, the ASTRAL tree is better resolved.

Local posterior probability values and polytomy *p*-values of the ASTRAL species tree analysis are strongly negatively correlated (r = -0.917; Figs 5, 6; Lanfear 2018).

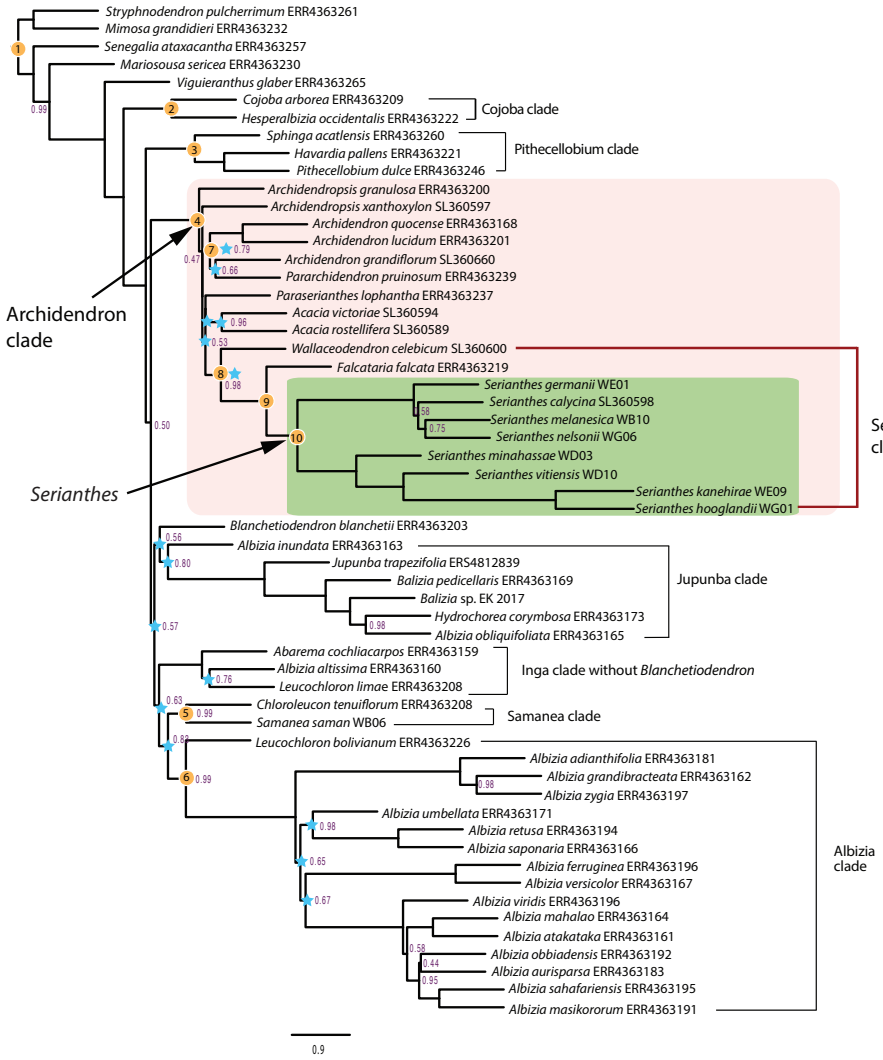

Figure 3. Phylogeny of the ingoid and Archidendron clades. ASTRAL species tree, based on 77 gene trees. Nodes of particular interest are labelled with numbered orange circles and are discussed in the text and Table 3. Unambiguously supported relationships shown with PP = 1 unless indicated at the nodes. Blue stars show nodes where a polytomy cannot be rejected by the data using the polytomy test ($p \leq 0.05$). Clade names follow (Koenen et al. 2020), except for the Serianthes clade, which is newly recognised here.

Fig. 6 shows that almost all the nodes for which the polytomy null model was rejected ($p < 0.05$) have high local posterior probability values.

The tree topology is described, based on the ASTRAL analysis focusing on 10 nodes for which the polytomy null model could be rejected (numbered in Fig. 3; Table 3). Bootstrap values and polytomy test *p*-values of the concatenated analysis are listed in

Table 3. Comparison of support values for individual nodes from concatenated analysis vs. gene tree analysis. BS and *p*-value (polytomy test) generated by concatenated analysis. BS, PP and *p*-value (polytomy test) generated by gene tree analysis.

ID	Name	Concatenated analysis		Gene Tree Analysis		
		BS	*p*-value	PP	BS	*p*-value
1	ingoid clade	100	0.000	1.000	100	0.000
2	Cojoba clade	100	0.009	1.000	100	0.000
3	Pithecellobium clade	NA	NA	1.000	100	0.000
4	Archidendron clade	100	0.270	1.000	100	0.000
5	Samanea clade	NA	NA	0.99	99	0.001
6	Albizia clade	100	0.000	0.99	100	0.011
7	*Archidendron* + *Pararchidendron*	100	0.000	0.79	100	0.285
8	Serianthes clade (*Wallaceodendron* + *Serianthes* + *Falcataria*)	100	0.000	0.980	100	0.056
9	*Falcataria* + *Serianthes*	100	0.000	1.000	100	0.000
10	*Serianthes*	100	0.000	1.000	100	0.000

Table 3. The gCF and sCF values showed a strong positive correlation (r = 0.888; Fig. 5) and high PP values mostly coincide with medium to high gCF and sCF values (Fig. 7A).

Clade names used in this manuscript follow the mimosoid clade classification of Koenen et al. (2020). The ingoid clade (sensu Koenen et al. 2020) (node 1) is well supported by high PP and BS values and the null hypothesis of the node being replaced by a polytomy is rejected (p = 0.001). Low sDF_1, sDF_2, gDF_1, gDF_2, gDF_P and medium sCF provide confidence that this split is well supported (Table 4, Fig. 7B). The backbone of the ingoid clade is only partly resolved. The Cojoba clade (node 2), Pithecellobium clade (node 3), Archidendron clade (node 4), Samanea clade (node 5) and Albizia clade (node 6) were all recovered with high PP and BS values and their polytomy null models were rejected (p = 0.001) (Fig. 3; Table 3). We recovered *Albizia* and *Leucochloron* as polyphyletic. The relationship between the Jupunba clade and the Inga clade remained unresolved along the backbone of the ingoid clade (Fig. 3). Note that, in our analyses, the ingoid clade does not include representatives from the Calliandra and Zapoteca clades. The gCF and sCF values are medium to high for all selected clades with the exception of the Archidendron clade (node 4), the Samanea clade (node 5), the Albizia clade (node 6) and the Wallaceodendron + Serianthes + Falcataria clade (node 8; Fig. 3; Table 3). gDFs and sDFs estimates are low, while values of gDF_P are rather high for most of the numbered clades, except the ingoid clade (node 1), the Cojoba clade (node 2), the Falcataria + Serianthes clade (node 9) and the Serianthes clade (node 10) (Fig. 3, Table 3), which also had longer branch lengths (Table 4). The concatenated analysis retained unresolved relationships across the ingoid backbone, except for the Pithecellobium clade (Fig. 3).

Our analyses strongly support the monophyly of the Archidendron clade (PP = 1, BS = 100), with a polytomy rejected at this node in the gene tree analysis (p = 0.001) (node 4 on Fig. 3, Table 3). The concordance analysis for this node provided a gCF value of 21.33% and sCF value of 69.59%. Discordance analysis returns low sDF_1 and sDF_2 values of 15.69% and 14.72%, respectively and low gDF_1 and gDF_2 values of 0% and

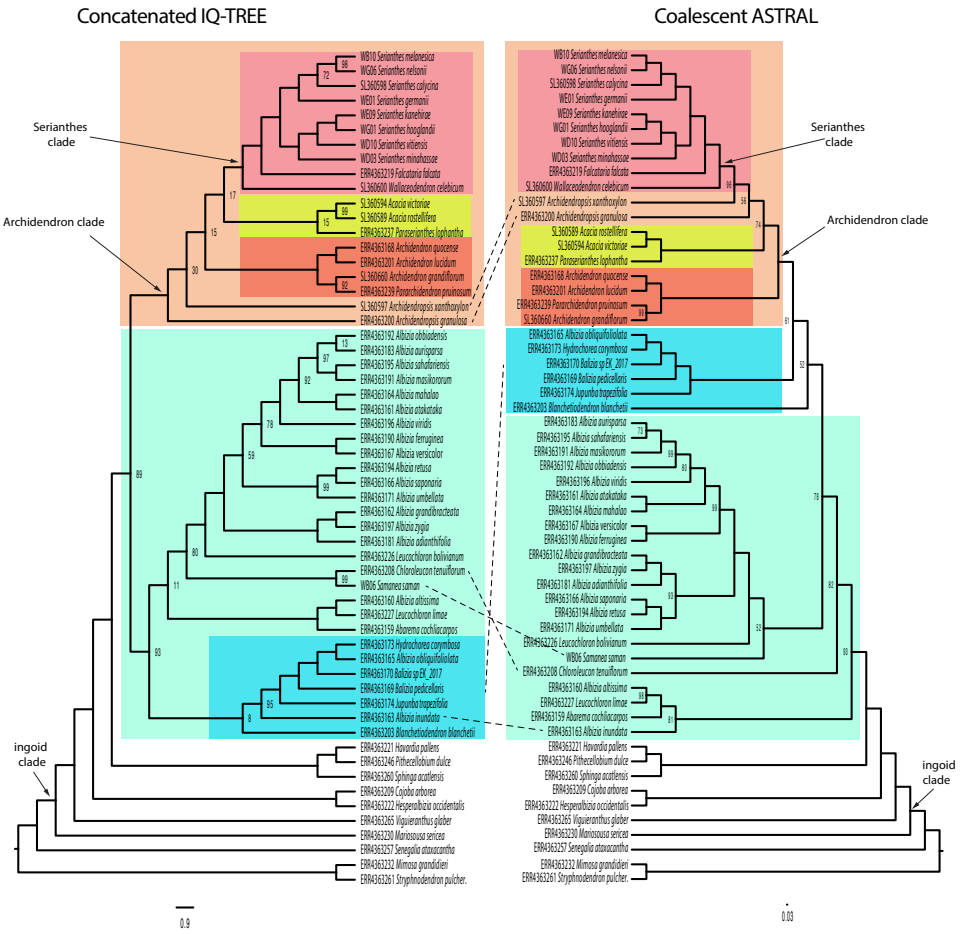

Figure 4. Backbone phylogeny of the ingoid clade. Comparison between the concatenated ML tree (left) and ASTRAL partition tree analysis (right). Bootstrap values < 100% are indicated below the nodes. Major clades in the IQ-tree and phylogenetic grades in the ASTRAL tree are shown in colour blocks with the incongruences between them indicated by dashed lines.

high gDF_P of 78.67%. Taking the low support from the gene concordance factors and gene discordance factors into account, it is important to note that the polytomy in the concatenated analysis phylogeny was not rejected ($p = 0.270$) in the ASTRAL analysis.

Furthermore, our analyses support the sister relationship of *Serianthes* and *Falcataria* with unambiguous BS and PP support, with a high gCF value of 44.83% and a sCF value of 69.28% (node 9) (Fig. 3; Tables 3, 4). The polytomy test for this node is rejected at $p < 0.001$ (Table 3). The gDF_P value is 44.83%, while low gDF_1 (5.17%), gDF_2 (5.17%), sDF_1 (12.31%) and sDF_2 (18.41%) values are recovered. *Wallaceodendron* is resolved as sister to the Serianthes + Falcataria clade (node 8)

Table 4. Comparison of concordance, discordance factors and branch lengths calculated in IQ-TREE for individual nodes in the Mimosoid phylogeny.

ID	Name	Concordance Analysis							
		gCF	sCF	gDF_1	gDF_2	gDF_P	sDF_1	sDF_2	BranchL
1	ingoid clade	53.61	51.32	18.84	17.39	10.14	22.51	26.18	0.474
2	Cojoba clade	52.46	65.79	3.28	3.28	40.98	14.86	19.35	0.743
3	Pithecellobium clade	40.00	64.25	0.00	0.00	60.00	16.620	19.13	0.760
4	Archidendron clade	21.33	69.59	0.00	0.00	78.670	15.69	14.72	0.748
5	Samanea clade	29.410	45.54	5.88	4.41	60.29	26.72	27.74	0.283
6	Albizia clade	25.37	51.25	5.97	2.99	65.67	22.56	26.20	0.278
7	*Archidendron* + *Pararchidendron*	9.86	46.67	0.00	2.82	87.32	25.78	27.56	0.118
8	Serianthes clade (*Wallaceodendron* + *Serianthes* + *Falcataria*)	16.92	58.08	0.00	3.80	80.00	19.73	22.19	0.241
9	*Falcataria* + *Serianthes*	44.83	69.28	5.17	5.17	44.83	12.31	18.41	0.707
10	*Serianthes*	46.97	65.60	12.12	13.64	27.27	17.13	17.27	0.480

(Fig. 3; Tables 3, 4). For this relationship, we also find unambiguous BS and PP for both gene tree and concatenated analyses and a gCF value of 16.92% and sCF value of 58.08%. The polytomy test is not rejected at $p < 0.056$ and gDF_P (80.00%) is high, but the gDF (0% and 3.8%) and sDF (19.73%, 22.19%) are very low. Based on our results, we informally name the Serianthes clade (node 8, Fig. 3) to include the genera *Falcataria*, *Serianthes* and *Wallaceodendron*.

The ASTRAL species tree topology, using a representative sample of eight species of *Serianthes*, confirmed its monophyly (node 10) with unambiguous BS and PP support in the gene tree analysis (Fig. 3; Table 3). The polytomy test for this node was rejected ($p < 0.001$) and a high gCF value of 46.97% and an sCF value of 65.60% coincided with a low gDF_P value of 27.27%. The discordance analysis further showed low gDF1 (12.12%), gDF_2 (13.64%), sDF_1 (17.13%) and sDF_2 (17.27%) values. We identify two well-supported subclades within *Serianthes*. The first one comprises taxa from Malesia, Papuasia and southern Micronesia (*S. minahassae* (Koord.) Merrill & Perry, *S. vitiensis* A. Gray, *S. kanehirae* Fosberg, S. *hooglandii* Fosberg), while the other clade unites all taxa from Polynesia and northern Micronesia (*S. germanii* Guillaumin, *S. calycina* Benth., *S. melanesica* Fosberg, *S. nelsonii* Merr.).

Our analyses also confirm the close relationship between *Archidendron* and *Pararchidendron* (node 7; Fig. 3; Table 3). This topology did not reject the polytomy at $p = 0.285$, but has a BS = 100% and PP = 0.79 for the gene trees and a BS = 100 for the concatenated analyses and a gCF value of 9.86% and a sCF value of 46.67%. The gDFP (87.32%) value is very high and the gDF_1, gDF_2 (0.00% and 2.82%) and sDF_1, sDF_2 (25.78%, 27.56%) values were low.

Low gDF_P values were found for the tips of the generic clades, while high gDF_P values were found along the backbone of the ingoid and Archidendron clades. Polytomies were rejected for the tips of the clades, for instance, in the Albizia and Serianthes clades, which are accompanied by high gCF and sCF, low gDFs and sDFs and low gDF_P values.

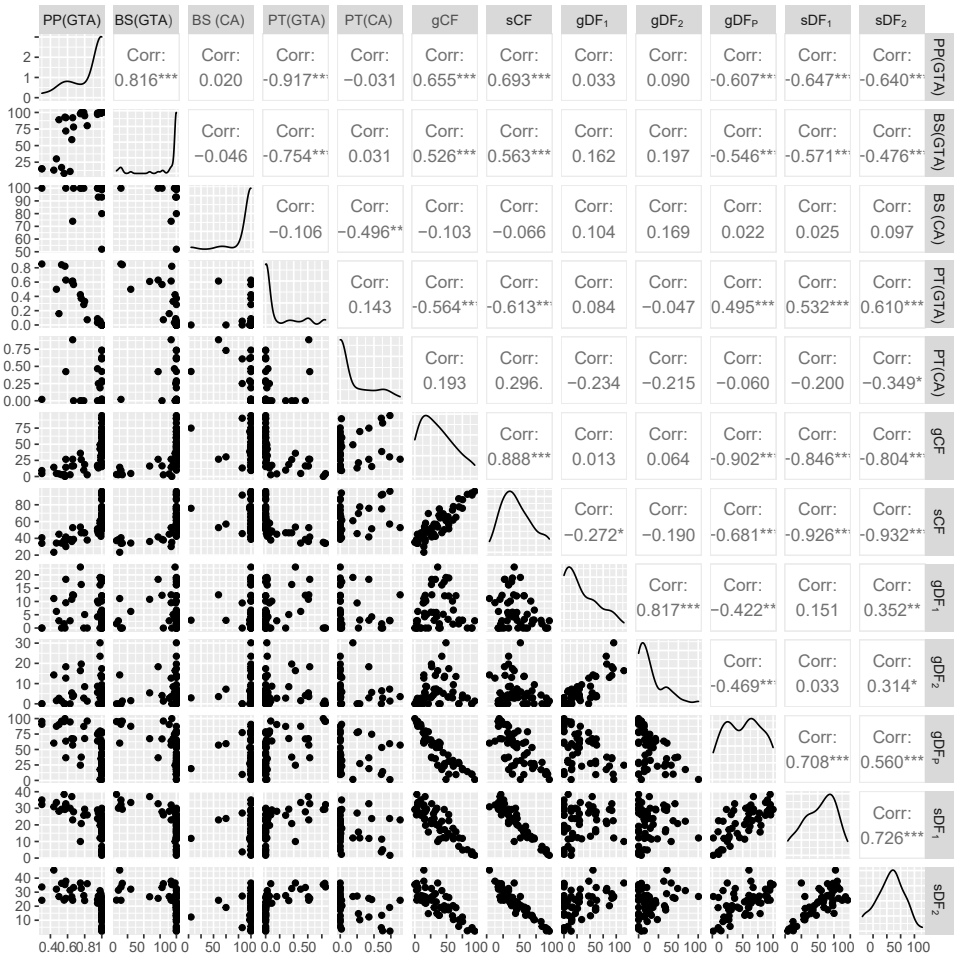

Figure 5. Scatter plots from gene discordance analysis. The graphs show the relationships between PP (gene tree analysis [GTA]), BS (GTA), BS (concatenated analysis [CA]), polytomy test [PT] (GTA), PT (PA), gene concordance factor (gCF), site concordance factor (sCF), gene discordance factors (gDF1, gDF2), gene discordance factor (P stands for paraphyly) (gDFP) and site discordance factors (sDF1, sDF2). The strength and direction of correlations (r) between variables are described as follows: r = -1, perfect negative relationship; -1 < r ≤ -0.70, strong negative relationship; -0.70 < r ≤ -0.50, moderate negative relationship; -0.50 < r ≤ -0.30, weak negative relationship; -0.30 < r < 0.30, no relationship; 0.30≥ r < 0.50, weak positive relationship; 0.50 ≥ r < 0.70, moderate positive relationship; 0.70 ≥ r < 1, strong positive relationship; r = 1, perfect positive relationship.

Discussion

Our study provides the first molecular evidence that *Serianthes*, as delineated by Nielsen et al. (1984a), is monophyletic (node 10) (Fig. 3; Tables 3, 4). Diagnostic features of *Serianthes* include bipinnately compound leaves with alternate sessile

leaflet insertion, branched axillary corymbiform panicles and woody indehiscent pods (Fosberg 1960; Nielsen et al. 1984b), as opposed to bipinnately compound leaves with opposite leaflets and dehiscent pods in *Wallaceodendron* and *Falcataria.* The spiciform racemes of *Wallaceodendron* are solitary, while they are compound in *Falcataria*. Nielsen et al. (1984a) also commented on differences in pollen morphology between *Serianthes* and other genera in the Archidendron clade (Table 5), whereby the tectum of *Wallaceodendron* and *Serianthes* (except for subgenus *Serianthes* sect. *Minahassae*) is perforated by non-isometric channels, as compared to isodiametric channels in the other genera of the Archidendron clade (Nielsen et al. 1984a). Further research is needed to evaluate the taxonomic significance of pollen exine stratification across the Archidendron clade as a whole.

The close relationship amongst *Serianthes*, *Falcataria*, and *Wallaceodendron* as suggested by Nielsen et al. (1983), based on morphology, is corroborated by our phylogenomic analysis and this group is here referred to as the Serianthes clade (Fig. 3). The centre of diversity of the Serianthes clade is the Malesian and Papuasian region. Of this clade, *Serianthes* is the only genus with Pacific Island representatives, while *Falcataria* is the only genus occurring in Australia. *Serianthes* is the most widespread, most likely because of its indehiscent pods, which are dispersed via ocean currents (Demeulenaere and Ickert-Bond 2022).

The monophyly of *Serianthes* and the relationships within the Serianthes clade (nodes 8, 9 and 10; Fig. 3; Tables 3, 4) received full support, suggesting that the alignments were informative and provided a clear signal for these relationships. Nielsen et al. (1983, 1984a) postulated that *Paraserianthes falcataria* (now *Falcataria falcata*) is closely related to *Serianthes*, observing that the bracts of the two are large and concave and have barely distinguishable wood anatomy (Nielsen et al. 1983). *Serianthes* and

Table 5. Morphology of *Serianthes*, *Falcataria* and *Wallaceodendron,* based on Fosberg (1960), Nielsen (1992), Nielsen et al. (1983, 1984a, b) and Verdcourt (1979).

	Wallaceodendron	***Falcataria***	***Serianthes***
Inflorescence	Solitary axillary unbranched spiciform raceme	Unbranched elongated raceme	Umbel, raceme or panicle composed of pedunculate spikes, pedunculate racemes or 1–4 flowered glomerules
Pod	Dehiscent, unwinged	Dehiscent, narrow wing	Indehiscent, unwinged
Epicarp	Chartaceous to woody	Chartaceous to woody, dehiscent, narrow wing	Thin, coriaceous, chartaceous to woody
Endocarp	Membranaceous to chartaceous Endocarp forms a papery envelope around each seed, which is the basic dispersal unit	Chartaceous	Parchment-like, woody
Germination	Not known	Epigeal	Epigeal
First two foliar leaves of the seedling	Not known	Opposite and bipinnate	Opposite and bipinnate
Leaf phyllotaxy	Spiral	Alternate	Alternate
Leaflet insertion	Opposite	Opposite	Alternate
Pollen exine	Tectum perforated by non-isometric channels	Tectum perforated by isometric parallel channels	Tectum perforated by non-isometric channels (except in subgenus *Serianthes* sect. *Minahassae*)

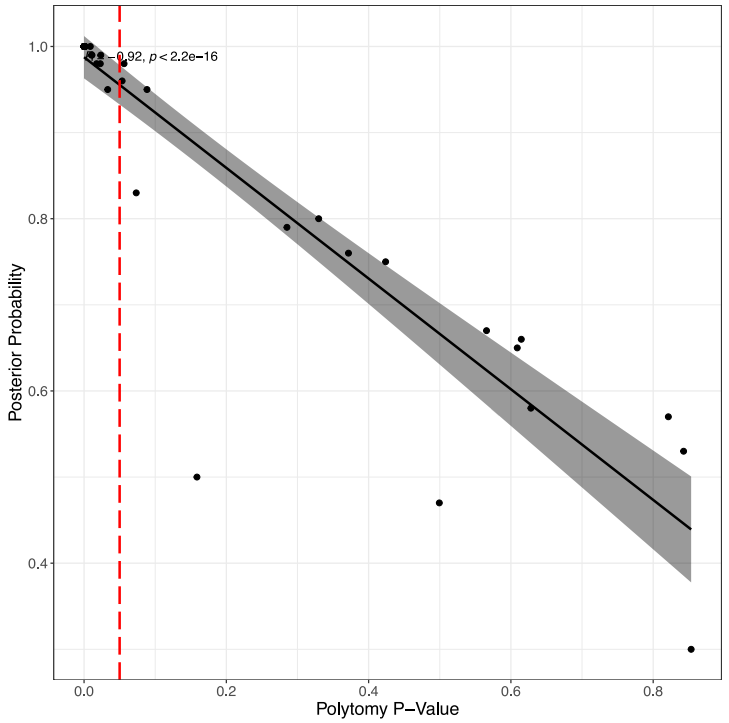

Figure 6. Pearson correlation showing the relationship between polytomy *p*-value and PP (gene tree analysis). We visualise the branches for which the polytomy null model could be rejected, based on the ASTRAL polytomy test at $p < 0.05$, indicated by the red dashed line.

Falcataria also share opposite and bipinnate seedling leaves, while mature leaves of *Serianthes*, in contrast to *Falcataria*, have alternate leaflet insertion (Table 5). This phylogenomic study provides the first evidence of two deeply-divergent and robustly-supported subclades within *Serianthes*, one comprising *S. germanii*, *S. calycina*, *S. melanesica* and *S. nelsonii* and the second *S. minahassae*, *S. hooglandii*, *S. vitiensis* and *S. kanehirae*. The placements of other *Serianthes* species within these subclades and how they correspond to the classification of subgenera and sections from Nielsen et al. (1984a) will require more complete taxon sampling.

Serianthes and *Falcataria* are sister genera in our phylogenomic study (Fig. 3), corroborating the results of Ringelberg et al. (2022), but not Brown et al. (2022). Both genera have alternate leaves, while *Wallaceodendron* has leaves that are spirally arranged (Sosef et al. 1998). *Wallaceodendron* was recovered as sister to *Serianthes* + *Falcataria* in our study (Fig. 3). Fosberg (1960) treated these three genera as distinct, noting that, while the flowers and the fruits of *Wallaceodendron* and *Serianthes* are very similar, *Serianthes* has flowers arranged in panicles, rather than racemes in *Wallaceodendron*, the pods of *Serianthes* are indehiscent, compared to the dehiscent pods of *Wallaceodendron* (tardily dehiscent) and *Falcataria*, and *Wallaceodendron* and *Falcataria* have strictly

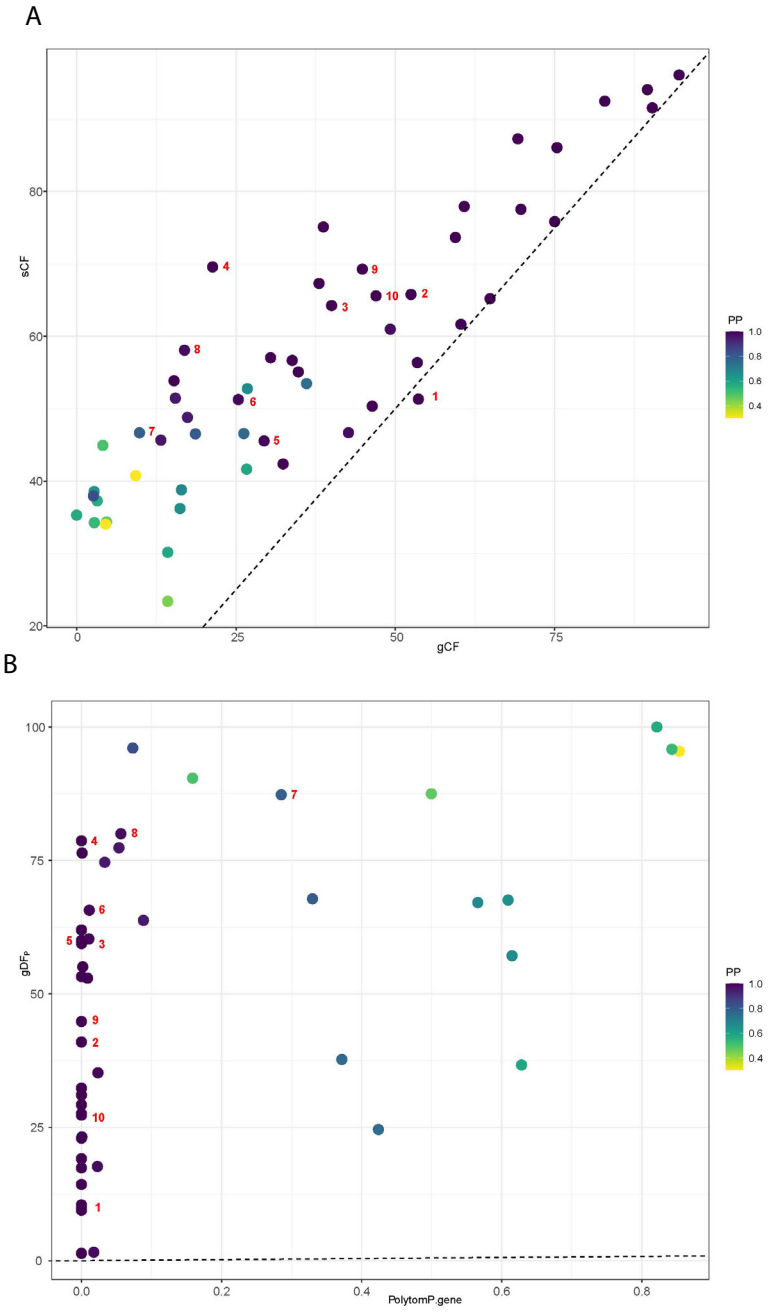

Figure 7. A scatter plot showing PP values and the relationship to gene concordance factors (gCF) and site concordance factors (sCF) (gene tree analysis). The red numbers coincide with the branch numbers of Table 4 and Fig. 3 **B** scatter plot showing p-value (polytomy test) and the relationship to gene discordance factors (paraphyly) (gDFP). Points show each bipartition in the full dataset phylogeny, with red numbers coinciding with the branch numbers in Fig. 3 and Table 4.

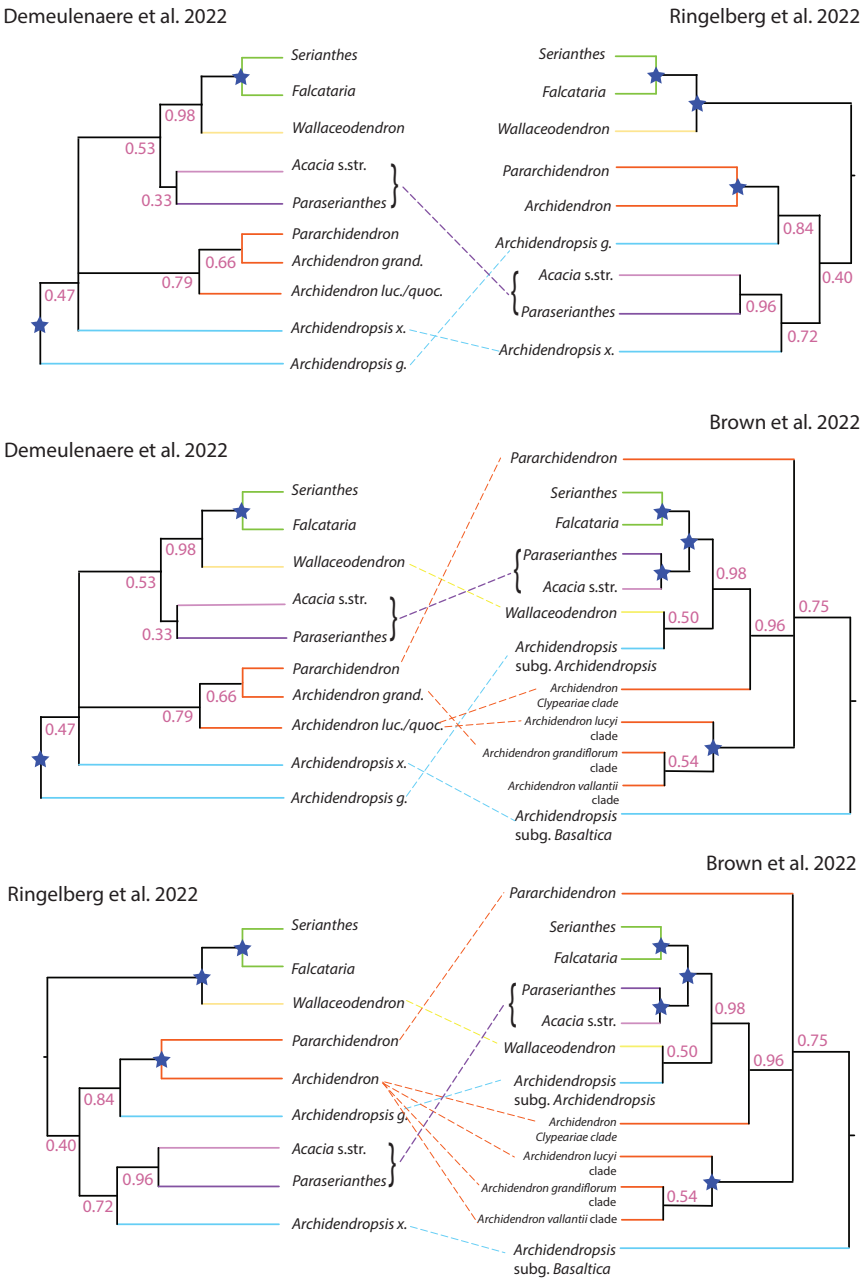

Figure 8. Comparison of relationships of the Archidendron clade recovered by different authors. Colour schemes follow those in Fig. 2. The branches that are fully supported (either by PP = 1.00 or BS = 100%) are indicated by blue stars and discordant placements of genera are indicated by dashed lines. The following abbreviations are used: *Archidendron grandi.* = *Archidendron grandiflorum*, *Archidendron luc.* = *Archidendron lucidum*, *Archidendron quoc.* = *Archidendron quocense*, *Archidendropsis g.* = *Archidendropsis granulosa* and *Archidendropsis x.* = *Archidendropsis xanthoxylon*.

opposite leaflets as opposed to alternate leaflets in *Serianthes* (Fosberg 1960; Kanis 1979; Nielsen et al. 1983). This combination of inflorescence, leaf, and fruit dehiscence differences supports recognition of three distinct genera.

Our phylogeny suggests that *Pararchidendron* is nested within *Archidendron*, rendering *Archidendron* paraphyletic (Fig. 8) as also found by Brown et al. (2022). Many nodes along the backbone of the Archidendron clade remain poorly resolved (Fig. 8). The sister relationship of *Paraserianthes* and *Acacia* s.s. agrees with Brown et al. (2022) and Ringelberg et al. (2022). A recent phylogeny of legumes as a whole found full support for the sister relationship between the monophyletic *Acacia* s.s. and a clade containing *Falcataria*, *Pararchidendron* and *Archidendron* (Zhao et al. (2021), but this study did not include *Paraserianthes*. The position of *Archidendropsis* within the Archidendron clade remains uncertain, but the genus is not supported as monophyletic in our analyses (Fig. 8) – see Brown et al. (2022). Increased taxon sampling with phylogenomic data is needed to resolve the relationships of *Archidendron*, *Archidendropsis* and *Pararchidendron*.

Conflicting topologies amongst sites and genes occurred where nodes showed low sCF and gCF values (nodes 4, 5 and 8 in Fig. 3; Table 4), which are indicative of discordant signals between gene trees. This was also shown by the short internode distances (expressed in coalescent units) at these branches in our phylogeny (Fig. 3). High gDF_p values coincided with short branches and likely indicate rapid lineage divergence (evolutionary radiation) and/or ILS (nodes 3, 5, 6, 7 and 8; Fig. 3; Table 4). This is consistent with the large putative hard polytomy in the ingoid clade discovered by Koenen et al. (2020), which likely represents a rapid radiation of a set of six or seven lineages. The Archidendron clade (node 4 in Fig. 3; Tables 3, 4) is one of the lineages derived from that putative hard polytomy along part of the backbone of the ingoid clade. The gene tree analysis provided high node support (PP = 1, BS = 100) and a high sCF value of 69.59% supporting the obtained tree topology at this node. The observed low discordance factor values (between 0 and 14.72%; Minh et al. 2020a; Thomas et al. 2021), however, indicated notable conflicts between gene concordance and discordance factors. The concordance analysis provided high gDF_p values of 78.67%, indicating that the gene trees lacked a clear signal (Minh et al. 2020a; Thomas et al. 2021). The fact that high PP and BS values coincided with low gCF values illustrates that classical node support measures, such as PP and BS, do not capture all aspects of variation in large phylogenomic datasets (Brower 2006, 2018; Thomas et al. 2021).

Conclusions

Sequence capture (Grover et al. 2012) provides a cost-effective way to generate hundreds of informative markers for plant phylogenomics that can be used across taxonomic scales (Zimmer and Wen 2015), including recent radiations of species and in intraspecific phylogeography (Nicholls et al. 2015). There is growing interest in combining data from different probe sets and, particularly, the merger of data from universal probe sets with data from clade-specific probes (e.g. Hendriks et al. 2021). Our study shows

that the merger of data from different probe sets can yield enough overlapping loci to resolve intergeneric relationships. Our ingoid dataset increased resolution in the ingoid and Archidendron clades and generated a well-supported phylogeny, representing the evolution of unlinked markers across the genome. In many cases, the concordance analysis provided a new perspective on bootstrap values, local posterior probability support levels and polytomy tests, which may be inflated in large, concatenated alignments (Minh et al. 2020a; Thomas et al. 2021). Our analyses provide robust evidence for: (1) the monophyly of *Serianthes* and two main lineages within the genus; (2) the Serianthes clade, which sets the stage for future biogeographic analysis of this clade and highlights the close sister relationship between *Wallaceodendron* and *Serianthes* + *Falcataria*; (3) rapid radiations across the backbones of the ingoid and Archidendron clades, which may be difficult to resolve without extensive genomic data; the concordance analysis clarified the interpretation of phylogenetic relationships; in particular, we found limited gene conflicts near the tips of the Archidendron clade, but an increase in discordance at the base of the clade; and (4) the utility of the polytomy test to further evaluate if gene tree discordance affects node support values. Continued sampling and sequencing of *Serianthes* species and other genera in the Archidendron clade are necessary to fully evaluate the generic delimitation and relationships within the Archidendron clade.

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On the taxonomic affinity of *Albizia carbonaria* Britton (Leguminosae, Caesalpinioideae-mimosoid clade)

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Abstract

Recent phylogenomic analyses placed *Albizia carbonaria* Britton as the sister-group of the two currently known species of *Pseudosamanea* Harms, clearly outside *Albizia* section *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes where it has until now been included. Its morphological similarities to *Pseudosamanea* are discussed, including characteristics of the polyad, and it is concluded that the species is compatible with the generic description of that genus except for its much more finely divided leaves with smaller leaflets, and its smaller flowers and fruits. Since these are merely quantitative differences, the species can readily be accommodated in *Pseudosamanea*. The new combination *Pseudosamanea carbonaria* (Britton) E.J.M. Koenen is made, and a diagnosis distinguishing it from the other two species of *Pseudosamanea* is presented.

Keywords

Albizia sect. *Arthrosamanea*, polyads, *Pseudosamanea*, taxonomy

Introduction

Recent phylogenomic analysis (Ringelberg et al. 2022) placed *Albizia carbonaria* Britton as the sister-group to *Pseudosamenea* Harms, separate from other Neotropical species of *Albizia* Durazz. that Barneby and Grimes (1996) placed in their section *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes. Given the finely divided microphyllidious

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foliage and slender inflorescences of *A. carbonaria*, with much smaller flowers than those of the macrophyllidious species of *Pseudosamanea*, this may at first sight seem an unexpected phylogenetic relationship. However, on closer inspection, the similarities between *A. carbonaria* and *Pseudosamanea* are immediately apparent (Fig. 1) from the umbellate capitula with distinctly pedicellate peripheral flowers and a single enlarged sessile central flower (Fig. 1H), the ferrugineous indumentum on the twigs, leaf axes, peduncles, flowers and pods, the distinctive exfoliating bark (Fig. 1B, G), and the plano-compressed fruits and papery texture of the pod valves (Fig. 1D, I). In particular, the strongly dimorphic nature of the capitula, with only the much larger central flower being sessile, is unlike any of the species in *Albizia* sect. *Arthrosamanea*, but is effectively a miniature version of the capitula of *Pseudosamanea guachapele* (Kunth) Harms (Fig. 1C, F, H).

Albizia carbonaria clearly differs from *Ps. guachapele* and *Pseudosamanea cubana* (Britton & Rose) Barneby & J.W. Grimes in having more numerous and smaller leaflets (i.e. microphyllidious instead of macrophyllidious, Barneby and Grimes 1996), that are otherwise similar by being discolorous and in possessing a single midrib with pinnate secondary venation which also differs from the typically palmate or palmately-pinnate venation of leaflets of *Albizia* sect. *Arthrosamanea*. The stipitate, indehiscent or tardily dehiscent fruits of *A. carbonaria* are more similar to those of *Ps. cubana*, while those of *Ps. guachapele* dehisce actively along the ventral suture while the pods are still on the tree. Pods in all three species have the same characteristic ferrugineous indumentum. Thus, the flowers, leaflets and pods of *A. carbonaria* are merely quantitatively different from those of *Pseudosamanea*, being (much) smaller relative to *Ps. guachapele* and *Ps cubana*.

Evidence from polyad grain numbers

Based on its 32-celled polyads (Niezgoda and Nevling 1979a: figs 1 and 2; confirmed by my own observation, *G.P. Lewis 3862*), *A. carbonaria* was previously excluded from *Albizia* by Niezgoda and Nevling (1979a) who suggested it was preferable to restrict (Neotropical) *Albizia* to those species with 16-celled polyads. They placed *A. carbonaria* in *Pithecellobium* Mart., generating the only homotypic synonym of the species that I am aware of, which is somewhat remarkable for a species of the ingoid clade that was first described nearly a century ago, but all other authors (Nielsen 1985; Barneby and Grimes 1996; Rico-Arce et al. 2008) included it without question in *Albizia*. It is notable that *Pithecellobium*, under its current circumscription, is reported as having consistently 16-celled polyads, while *Albizia* sect. *Arthrosamanea* has either 16- or (28-)32-celled polyads (Guinet and Grimes 1997). Unfortunately, Guinet and Grimes (1997) described the characteristics of the pollen by genus, and failed to list which *Albizia* species have 32-celled polyads. However, Niezgoda and Nevling (1979a) compared the 32-celled polyads of *Pithecellobium daulense* Spruce ex Benth., which is (somewhat ironically) now a synonym of *Albizia pistaciifolia* (Willd.) Barneby & J.W. Grimes, with 16-celled polyads of *Albizia retusa* Benth. However, no voucher is cited for the *P. daulense* polyad in that publication, but in Niezgoda et al. (1983) the same species is included, with

voucher *Maguire 56150* which has since been re-identified as *Enterolobium gummiferum* J.F. Macbr. in NY (specimen consulted online, http://sweetgum.nybg.org/science/vh/, Barcode: 00924167). Further reason to doubt that *A. pistaciifolia* has 32-celled polyads is that in mimosoid species with polyads the fruit is usually pollinated by a single polyad (Niezgoda and Nevling 1979a; see also Banks et al. 2010), suggesting that species with 16-celled polyads should have a maximum of 16 seeds per fruit, and *A. pistaciifolia* is described as having 11–15 seeded fruits (Barneby and Grimes 1996). If *A. pistaciifolia* indeed has 16-celled polyads, it is possible that when *A. carbonaria* is excluded, *Albizia* sect. *Arthrosamanea* will be fundamentally characterized by 16-celled polyads. This seems likely for two reasons: (1) all taxa whose pollen has been studied in the genera *Hydrochorea* Barneby & J.W. Grimes (sensu Soares et al. 2022), *Jupunba* Britton & Rose and *Punjuba* Britton & Rose (i.e. the "Abarema alliance" of Barneby and Grimes 1996), that together form the sister-group of *Albizia* sect. *Arthrosamanea* in the Jupunba clade (sensu Koenen et al. 2020; Ringelberg et al. 2022), consistently have 16-celled polyads (Guinet and Grimes 1997); (2) all species included by Barneby and Grimes (1996) in *Albizia* sect. *Arthrosamanea* have fruits that are usually c. 11–15 seeded (although occasionally up to 18-seeded in *Albizia inundata* (Mart.) Barneby & J.W. Grimes, which accordingly appears to have 16(-20?)-celled polyads, see Vossler 2019: fig. 2c & e), except for *A. carbonaria* that has 20–26-seeded fruits (Barneby and Grimes 1996).

Pseudosamanea guachapele has 32-celled polyads (Niezgoda and Nevling 1979b; Guinet and Grimes 1997); therefore those of *A. carbonaria* are compatible with *Pseudosamanea*. The polyads of *Ps. cubana* are reported to be 24-celled (Guinet and Grimes 1997), but the fruit is described as 24–30 seeded (Barneby and Grimes 1996), casting doubt on the reported number of grains per polyad, or suggesting that the species is perhaps variable in grain number per polyad. Given the variation in the number of cells per polyad within several genera as well as within species or even individuals (e.g. *Leucochloron* Barneby & J.W. Grimes; Guinet and Grimes 1997), this character has been viewed as unimportant for generic delimitation in recent decades, despite mention by Guinet and Grimes (1997) that several groups are invariant in this regard. Phylogenetic studies are now revealing that polyad grain number may be more useful than previously thought. For example, the Calliandra clade (sensu Koenen et al. 2020) comprising *Acaciella* Britton & Rose, *Calliandra* Benth. and *Afrocalliandra* E.R. Souza & L.P. Queiroz has consistently 7 or 8-celled polyads, which is unusual in the ingoid clade where species usually have ≥ 16 cells per polyad. Similarly, I suggest that the entire Jupunba clade sensu Koenen et al. (2020) may be fundamentally 16-celled, and many of the genera that Guinet and Grimes (1997) described as having > 16 cells per polyad or of variable polyad number are placed in the Inga clade of Koenen et al. (2020; see also Ringelberg et al. 2022). All this suggests that the utility of polyad grain number should be re-evaluated in the light of recent phylogenomic evidence. In conclusion, the decision of Niezgoda and Nevling (1979a) to exclude *A. carbonaria* from *Albizia* based on the grain number per polyad was correct and in line with the other morphological differences discussed here; however, they did not place it in the correct genus. Instead, the 32-celled polyads provide further evidence in support of placing the species in *Pseudosamanea*.

Inclusion of *A. carbonaria* in *Pseudosamanea*

An important character used by Barneby and Grimes (1996) to define *Pseudosamanea* is inflorescences axillary to coeval leaves (although in *Ps. guachapele* flowers often develop before the leaves). The inflorescences of *A. carbonaria* appear somewhat similar to those typically found in *Albizia* sect. *Arthrosamanea* and many other mimosoid genera where the capitula form a compound inflorescence resembling a pseudo-raceme or a complex panicle of pseudo-racemes with suppression or early shedding of leaves. However, it is questionable whether the description of the inflorescences of *Pseudosamanea* by Barneby and Grimes (1996) is completely accurate, as specimens at K (*S.C. Sant'Ana 1023* and *C.E. Hughes 753*) have short compound pseudo-racemose inflorescences, comprising multiple umbellate capitula arising from a leaf axil (rather than only singly as described for *Ps. guachapele* by Barneby and Grimes 1996), with the subtending leaves being caducous. Another key feature of the inflorescences of *Pseudosamanea* is that the meristem at the apex of reproductive branches continues to grow (i.e. is indeterminate), producing new leaves below which the fruits develop. Unlike in other species of Neotropical *Albizia*, this is clearly also the case in *A. carbonaria*, see e.g. *E. Suclli & J. Farfán 1258* – NY, Barcode 1300235; *J. Leon 4372* – F, https://collections-botany.fieldmuseum.org/, Catalog number 1578909), providing evidence that the inflorescences of *A. carbonaria* are not qualitatively different from *Pseudosamanea*, while being unlike the efoliate pseudoracemes typically found in *Albizia* sect. *Arthrosamanea* where the meristem is not continuous.

Barneby and Grimes (1996: 226) noted that "among related albizias with multifoliolate leaves, *A. carbonaria* is notable for the dorsally pallid leaflets, the dense golden indumentum of the inflorescence, the distinctly pediceled flowers, and the papery tomentulose pod." All these characters distinguishing it from other *Albizia* sect. *Arthrosamanea*, are in agreement with the generic description of *Pseudosamanea* (sensu Barneby and Grimes 1996). *Albizia carbonaria* differs from *Pseudosamanea* as delimited by Barneby and Grimes (1996) in the dimensions and number of leaflets per leaf, flower dimensions and inflorescence structure, but these are minor quantitative differences that do not constitute sufficient reason for not including the species in *Pseudosamanea*, an option which would require segregation of a new monotypic genus. I therefore propose to include the species in *Pseudosamanea* and hence the new combination is made:

***Pseudosamanea carbonaria* (Britton) E.J.M. Koenen, comb.nov.**
urn:lsid:ipni.org:names:77303801-1
Fig. 1A–D

Albizia carbonaria Britton, Sci. Surv. Porto Rico & Virgin Islands 6: 348. 1926. Basionym

Albizia malacocarpa Standl. ex Britton & Rose, N. Amer. Fl. 23: 44. 1928. - Types: *Calderón 2024* (lectotype: NY, [NY00001767], chosen here; isolectotypes: US, [US00000471], GH [GH00069258]); *Williams 952* (paratype: NY, [NY01300065]).

Albizia sumatrana Steenis, in Encycl. Ned.-Ind. ed. 2, Suppl. Vol. vi. 864. 1931. - Type: *Keuchenius s.n.* (holotype: BO, isotypes: A, [A00058480]; A, [A00058481]; BO).
Pithecellobium carbonarium (Britton) Niezgoda & Nevling, Phytologia 44: 310. 1979.
Albizia filicina Standl. & L.O. Williams ex L. Holdridge & Poveda, Arboles de Costa Rica 1: 134. 1975. nomen nudum.

Type. *C.L. Bates s.n.* (holotype: NY, [NY00001778]; isotype: K!, [K000528017]).

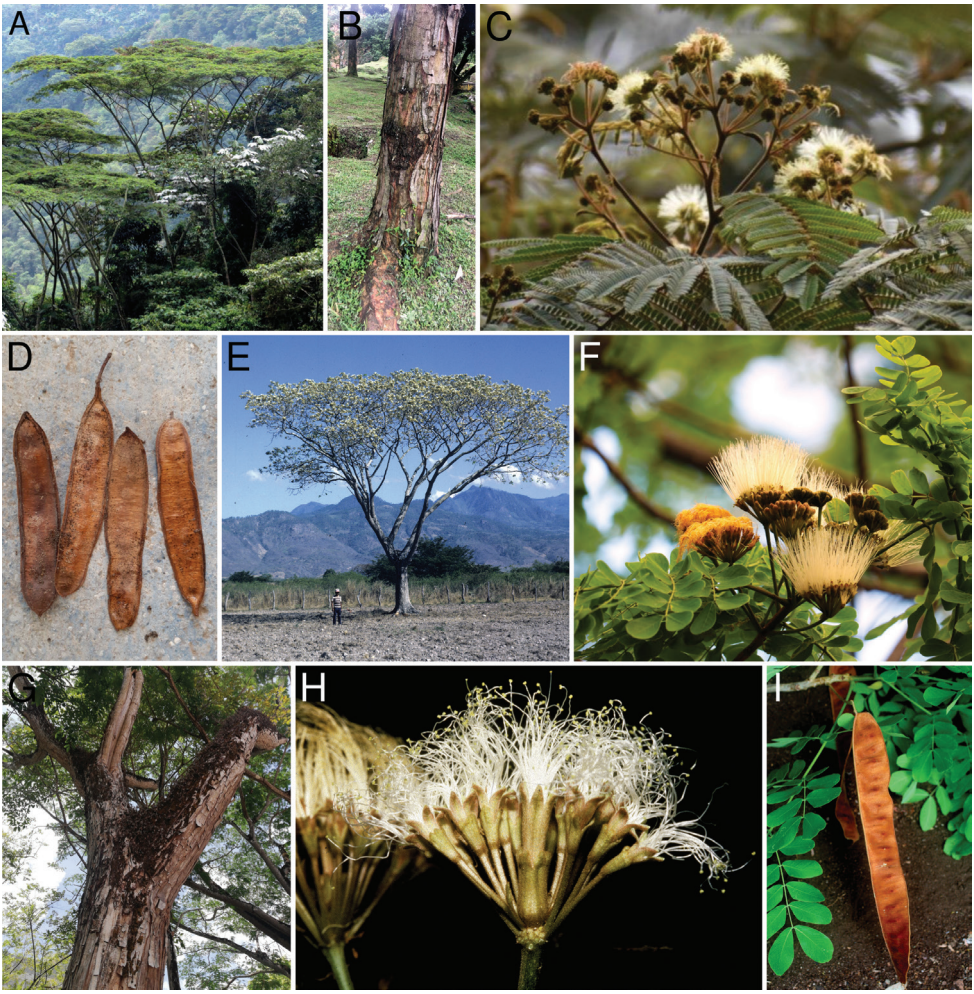

Figure 1. A–D *Pseudosamanea carbonaria* (Britton) E.J.M. Koenen **A** habit **B** trunk with exfoliating bark **C** inflorescences **D** pods **E–I** *Pseudosamanea guachapele* **E** habit **F** inflorescences **G** trunk with exfoliating bark **H** close-up of strongly heteromorphic inflorescence typical of the genus **I** pod **A** Bioexploradores Farallones **B** Karen Osorio **C** Juan Manuel de Roux **D** Juan Carlos Delgado Madrid **E, H** Colin Hughes **F** Cynthia Tercero **G** Bribrábrico **I** Daniel H Janzen **A, B, C, D, F, G, I** from https://www.gbif.org, distributed under a Creative Commons BY-NC-SA 3.0 License.

Pseudosamanea carbonaria can easily be distinguished from the other two currently known species of *Pseudosamanea* by having 8–13 pairs of pinnae and (18–)20–30 leaflet pairs, compared to 3–6 pairs of pinnae and 5–8 leaflet pairs, as well as leaflet size (the larger ones 4.5–8 mm long vs. 23–50 mm) and flower size (corolla of peripheral flowers (4–)4.4–6.4 mm long vs 9.5–11 mm in *Ps. guachapele* and 11–13 mm in *Ps. cubana*; the stamen filaments 13–16.5 mm vs. 41–45 mm in *Ps. guachapele* and 25–27 mm in *Ps. cubana*) and fruit size 7–12 × 1.5–2.35 cm long (excluding the stipe) vs. c. 12–22 × 2–4.5 cm in the other two species. [All measurements taken from Barneby and Grimes (1996)].

Representative material studied. *Ps. carbonaria*: Colombia: *G.P. Lewis 3862* (K, 2 sheets, fls & frts), R.T. Pennington *694* (K, fls), *H.P. Fuchs & L. Zanella 22388* (K, fls); Peru: *A. Daza & T.D. Pennington 16353* (K, fls & frts), *E. Suclli & J. Farfán 1258* (K, 2 sheets, fls & frts).

Ps. guachapele: Mexico: *C.E. Hughes* 665 (K, frts), *E.A. Pérez-García* 1035 (K, fls); Honduras: *C.E. Hughes & B.T. Styles 117* (K, frts), *C.E. Hughes 753* (K, fls). Guatemala: *D.J. Macqueen 68* (K, fls & frts), *C.E. Hughes 1103* (K, fls).

To identify the species of the genus *Pseudosamanea*, the following identification key, based on that of Barneby and Grimes (1996), but with an additional identification step to include *Ps. carbonaria*, can be used:

Key to the species of *Pseudosamanea*

1 Leaves with 8–13 pairs of pinnae and (18–)20–30 pairs of leaflets per pinna ..... ***Ps. carbonaria***

– Leaves with 3–4 pairs of pinnae and 5–8 pairs of leaflets per pinna..... **2**

2 Pedicel of outer peripheral flowers 11–22 mm; pods sessile 10–20-seeded; SE Mexico to Venezuela and NE Peru..... ***Ps. guachapele***

– Pedicel of outer peripheral flowers 4–6.5 mm; pods stipitate 24–30-seeded; Cuba..... ***Ps. cubana***

With the addition of *Pseudosamanea carbonaria*, the genus now comprises three species with native distribution from S Mexico to N Peru and in Cuba (*Ps. cubana*, endemic), occurring in seasonally dry deciduous forest and gallery forest up to 1000 m (*Ps. guachapele*), moist upland forest up to 1800 m (*Ps. carbonaria*), and palm savannas and along watercourses below 50 m (*Ps. cubana*). Two species, *Ps. carbonaria* and *Ps. guachapele*, are cultivated including outside their native range on the Atlantic coast of Brazil, Cameroon (*Ps. guachapele*) and Indonesia (*Ps. carbonaria*). While *Ps. guachapele* is naturally widespread across the range of the genus (except for Cuba), the native range of *Ps. carbonaria* is not known with certainty, but is presumed to be from Colombia to Panama and Venezuela, and it is introduced as a shade tree in coffee plantations in Central America, the Caribbean, Peru and SE Brazil (Barneby and Grimes 1996).

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Re-establishment of the genus *Pseudalbizzia* (Leguminosae, Caesalpinioideae, mimosoid clade): the New World species formerly placed in *Albizia*

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Abstract

Following recent mimosoid phylogenetic and phylogenomic studies demonstrating the non-monophyly of the genus *Albizia*, we present a new molecular phylogeny focused on the neotropical species in the genus, with much denser taxon sampling than previous studies. Our aims were to test the monophyly of the neotropical section *Arthrosamanea*, resolve species relationships, and gain insights into the evolution

* These authors made equal contributions to this paper.

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of fruit morphology. We perform a Bayesian phylogenetic analysis of sequences of nuclear internal and external transcribed spacer regions and trace the evolution of fruit dehiscence and lomentiform pods. Our results find further support for the non-monophyly of the genus *Albizia*, and confirm the previously proposed segregation of *Hesperalbizia*, *Hydrochorea*, *Balizia* and *Pseudosamanea*. All species that were sampled from section *Arthrosamanea* form a clade that is sister to a clade composed of *Jupunba*, *Punjuba*, *Balizia* and *Hydrochorea*. We find that lomentiform fruits are independently derived from indehiscent septate fruits in both *Hydrochorea* and section *Arthrosamanea*. Our results show that morphological adaptations to hydrochory, associated with shifts into seasonally flooded habitats, have occurred several times independently in different geographic areas and different lineages within the ingoid clade. This suggests that environmental conditions have likely played a key role in the evolution of fruit types in *Albizia* and related genera. We resurrect the name *Pseudalbizzia* to accommodate the species of section *Arthrosamanea*, except for two species that were not sampled here but have been shown in other studies to be more closely related to other ingoid genera and we restrict the name *Albizia* s.s. to the species from Africa, Madagascar, Asia, Australia, and the Pacific. Twenty-one new nomenclatural combinations in *Pseudalbizzia* are proposed, including 16 species and 5 infraspecific varietal names. In addition to the type species *Pseudalbizzia berteroana*, the genus has 17 species distributed across tropical regions of the Americas, including the Caribbean. Finally, a new infrageneric classification into five sections is proposed and a distribution map of the species of *Pseudalbizzia* is presented.

Keywords
Arthrosamanea, hydrochory, monophyly, Neotropics, phylogeny, taxonomy

Introduction

The genus *Albizia* Durazz. has a complicated taxonomic history but has generally been treated as a pantropical genus with 120–140 species, of which 36 are endemic to Africa, with c. 30 species in Madagascar, of which c. 24 are endemic, c. 35 species in Asia, one in Australia, and 22 in tropical America (Lewis and Rico Arce 2005; Rico Arce et al. 2008). All species are woody, forming trees of variable stature and inhabit a wide range of lowland tropical biomes (Figs 1 and 2), including rain forests, seasonally dry tropical forests, and savannas, with one species, *Albizia julibrissin* Durazz., the type species of the genus, in subtropical and warm temperate forests in Asia. However, *Albizia* remains poorly defined; its delimitation remains one of the most challenging taxonomic problems in the legume family, and it is currently considered the main "dustbin" genus in tribe Ingeae (Koenen et al. 2020). In the past, the most problematic genus of tribe Ingeae was *Pithecellobium* Mart., but its taxonomy has been gradually clarified (Barneby and Grimes 1996). Resolution of the taxonomic status of *Albizia* has lagged behind that of *Pithecellobium* and only really started at the end of the twentieth century. For example, several new neotropical genera have been segregated from *Albizia*: *Balizia* Barneby & J.W. Grimes; *Hesperalbizia* Barneby & J.W. Grimes, and *Hydrochorea* Barneby & J.W. Grimes. Barneby and Grimes (1996) also re-established the genus *Pseudosamanea* Harms, which previously had been treated as a synonym within *Albizia* (Table 1). However, at the time they were established, the monophyly of these new and re-established genera had not been tested using phylogenetic analyses of molecular data.

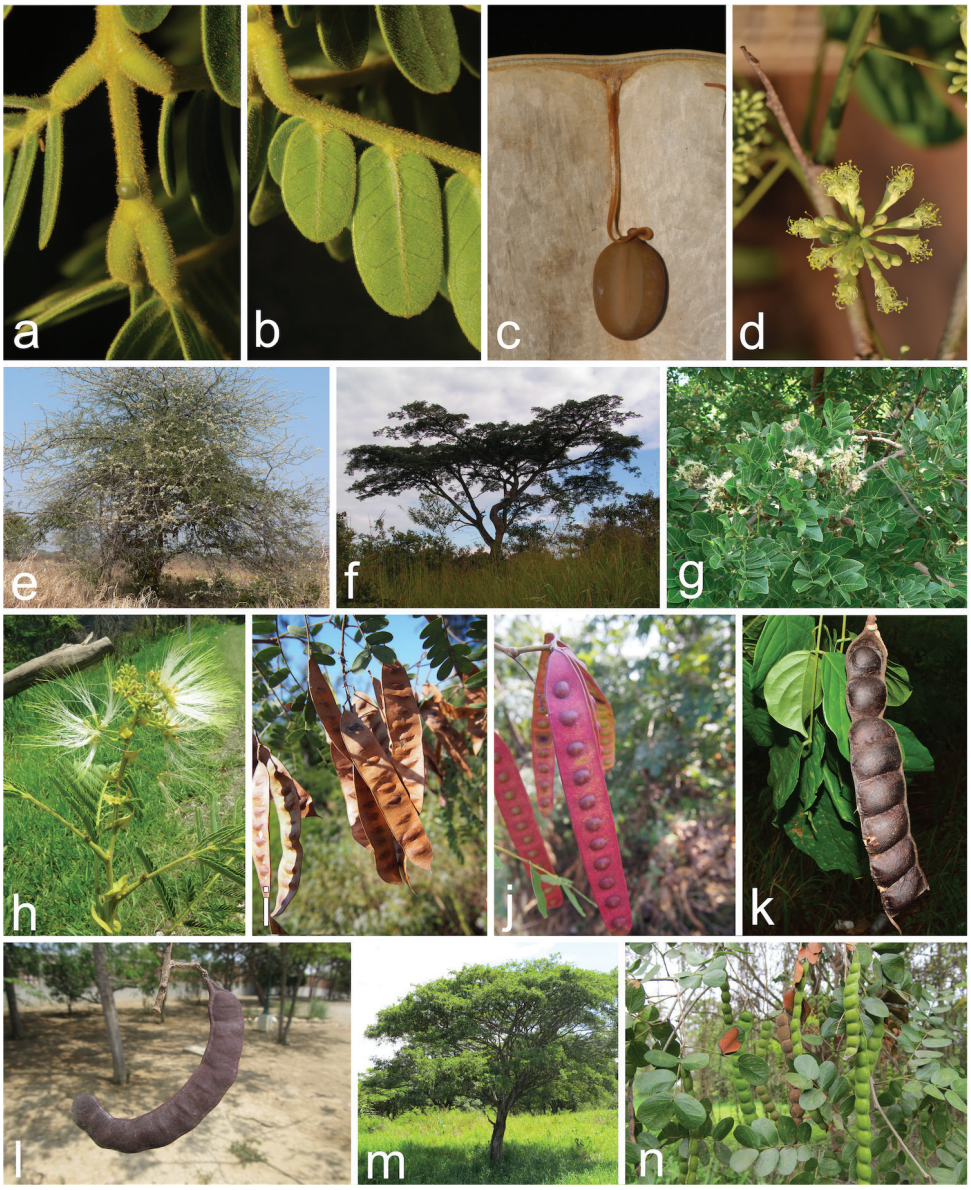

Figure 1. Morphology of *Albizia* s.l. showing selected members of the genera *Albizia* and *Pseudalbizzia* **a–c** *Albizia ferruginea* (Guill. & Perr.) Benth. in Congo **a** detail of leaf rachis and gland between terminal pinnae **b** detail of leaflets of a terminal pinna **c** seed and funiculus attached to the valve **d** *Albizia glaberrima* (Schumach. & Thonn.) Benth. in Malawi, detail of inflorescence **e** *Albizia anthelmintica* Brongn. in Malawi, habit **f** *Albizia adianthifolia* (Schumach.) W. Wight in Congo, habit **g** *Albizia glaberrima* in Malawi, branches and inflorescences **h** *Albizia chinensis* (Osbeck) Merr. in Thailand, inflorescences **i** *Albizia odoratissima* (L. f.) Benth. in Thailand, fruits **j** *Albizia procera* (Roxb.) Benth. in Thailand, fruits **k** *Albizia splendens* Miq. in Thailand, woody fruit **l** *Pseudalbizzia multiflora* var. *multiflora* in Ecuador, woody fruit **m, n** *Pseudalbizzia pistaciifolia* (Willd.) E.J.M Koenen & Duno in Ecuador **m** habit **n** woody fruit. Photos: **a, b** David J. Harris / With permission from RBG Edinburgh **c** Claude Boucher Chisale **d–f** Günter Baumann **g** Jos Stevens **h** Natcha Sutjaritjai **i–k** Prateep Panyadee **l–n** Xavier Cornejo.

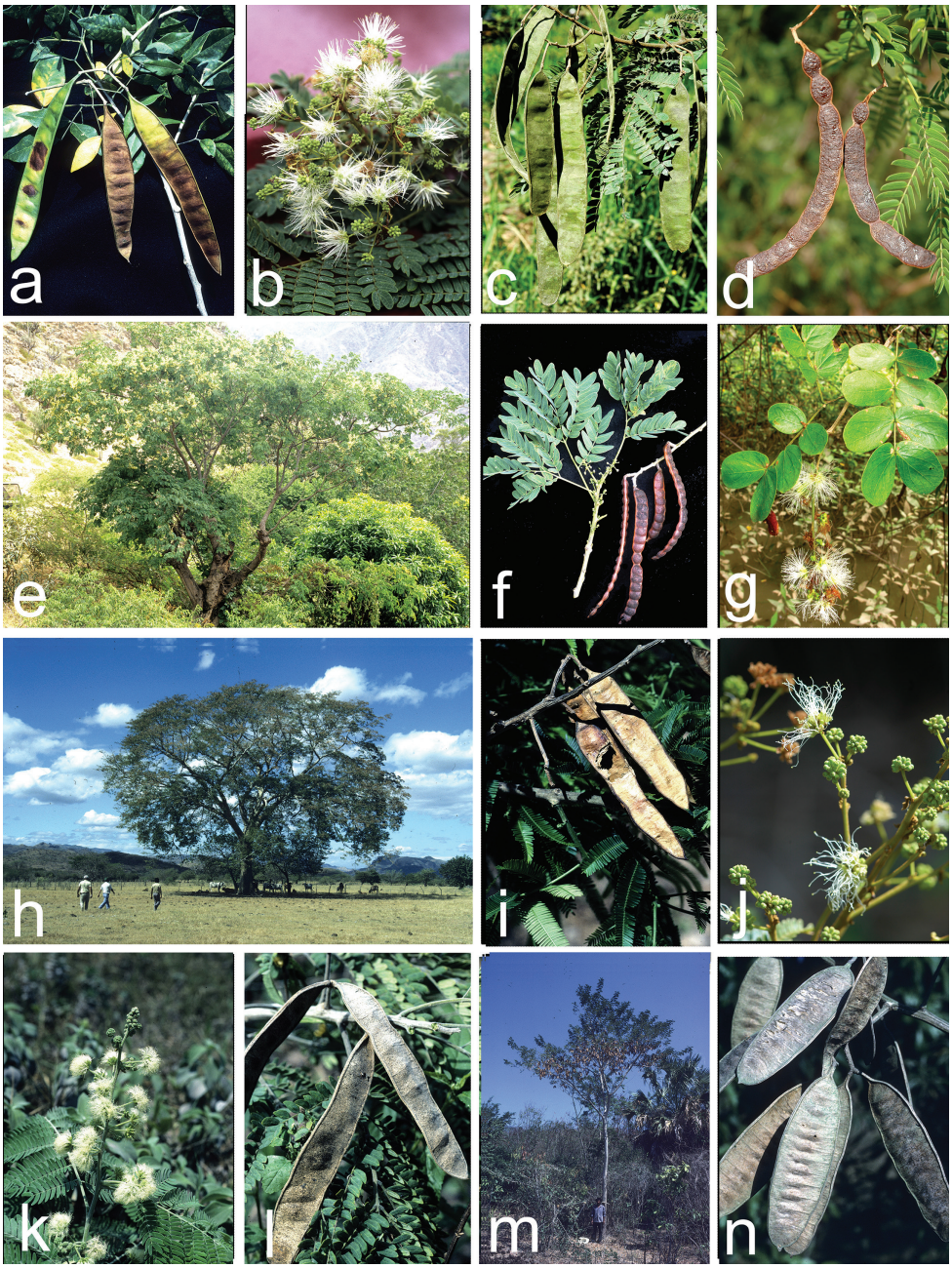

Figure 2. Habit, flower and fruit variation in the genus *Pseudalbizzia* **a** *P. adinocephala* pods (*Hughes 1913*) **b** *P. coripatensis* inflorescence (*Hughes 2433*) **c** *P. coripatensis* pods (*Hughes 2433*) **d** *P. inundata* pods (*JRI Wood 26530*) **e** *P. multiflora* habit (*Hughes 2214*) **f** *P. multiflora* leaves and pods (*Hughes 2214*) **g** *P. pistaciifolia* leaves and inflorescence (*Cornejo 8426, GUAY*) **h** *P. niopoides* habit (*Hughes 419*) **i** *P. niopoides* pods (*Rivera 2245*) **j** *P. polycephala* inflorescence (*de Queiroz 15515*) **k** *P. tomentosa* inflorescence (*Hughes 1143*) **l** *P. sinaloensis* pods (*Hughes 1576*) **m** *P. tomentosa* habit (*Hughes 1335*) **n** *P. tomentosa* pods (*Hughes 1307*). All photos by Colin Hughes except **g**, Xavier Cornejo.

Table 1. Main taxonomic changes related to *Albizia*, Ingeae tribe [1981–2008]. Modified from Rico Arce et al. (2008).

Nielsen (1981)	Barneby and Grimes (1996)	Lewis and Rico Arce (2005)	Rico Arce et al. (2008)	Iganci et al. 2015
Albizia	***Albizia***	***Albizia***	***Albizia***	***Albizia***
	Balizia			***Balizia***
Cathormion	***Cathormion***	***Cathormion***	*	*
	Hydrochorea		*	***Hydrochorea***
	Hesperalbizia	***Hesperalbizia***		
	Pseudosamanea	***Pseudosamanea***		

* Not explicitly mentioned in the study.

Barneby and Grimes (1996) placed the remaining New World species of *Albizia* in their section *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes. They characterized this section as forming a group that is homogeneous in most respects, but diverse in the late developmental stages of the fruit, which vary in: 1) fruit opening type: dehiscent, indehiscent, or breaking, 2) lateral shape: flat to conspicuously raised above the seed chambers, 3) texture and consistency of the valves: papery, chartaceous or woody, 4) longitudinal shape: straight to weakly falcate (Barneby and Grimes 1996) (Figs 1, 2 and 4). Within section *Arthrosamanea*, four series were proposed by Barneby and Grimes (1996): series *Paniculatae* with papery, plano-compressed, inertly dehiscent pods with continuous valves (13 species); series *Arthrosamanea* comprising 3 species with lomentiform, plano-compressed pods, where the ripe valves crack transversely between seeds but the wiry sutures persist at maturity; series *Multiflorae* (2 species) characterized by lomentiform fruits only reluctantly separating into articles, the thick-textured valves and sutural keels breaking transversely under pressure; and the monospecific series *Inundatae* which bears crypto-lomentiform pods, dehiscent through the sutures and with the valves differentiating into a continuous exocarp and a segmented endocarp separating into 1-seeded segments (Barneby and Grimes 1996).

Series *Paniculatae* is widespread across Mexico, Central and South America, occurring mainly in seasonally dry forests, grasslands, and less often in humid forests (in South America). All species of series *Paniculatae* have papyraceous, dehiscent fruits with one exception, *A. berteroana* (DC.) Fawc. & Rendle (the earlier combination *A. berteroana* (DC.) M. Gómez was invalidly published due to incorrect citation of the basionym, see Barneby and Grimes 1996), whose fruits are indehiscent and fall to the ground entire. In contrast, the other three series are distributed from Panama to South America and are most diverse in the Amazon basin (Barneby and Grimes 1996), and usually have more or less woody fruits, which are articulated and indehiscent, some dividing into monospermous segments through the grooves of the valves, considered to be an adaptation for hydrochory, i.e., seed dispersal in riparian and seasonally inundated forests (*e.g.*, *A. inundata* (Mart.) Barneby & J.W. Grimes, A. *pistaciifolia* (Willd.) Barneby & J.W. Grimes, and *A. subdimidiata* (Splitg.) Barneby & J.W. Grimes).

The segregate genera established by Barneby and Grimes (1996) have not been universally accepted. For example, in the most recent taxonomic treatment of *Albizia* for Mexico and Central America (Rico Arce et al. 2008), the genera *Balizia*, *Hesperalbizia*,

and *Pseudosamanea* were not recognized (Table 1). However, subsequent phylogenetic analyses have confirmed that these genera were rightfully segregated as distinct evolutionary lineages, *Hesperalbizia* being more closely related to *Lysiloma* Benth. (Duno de Stefano et al. 2021), and the closely related *Balizia* and *Hydrochorea* (the former reduced to synonymy of the latter, Soares et al. 2022) being placed as the sister-group of *Jupunba* Britton & Rose (Iganci et al. 2015; Soares et al. 2021, 2022). Phylogenomic analysis of the mimosoid clade, based on DNA sequences of 964 targeted nuclear genes confirmed these findings and, furthermore, showed that the species from the Americas (i.e., sect. *Arthrosamanea*) form a separate lineage from the African, Madagascan and Asian species (Koenen et al. 2020). Koenen et al. (2020) also showed that *Pseudosamanea*, although difficult to place in any clade, is not closely related to either *Albizia* s.s. or section *Arthrosamanea* and is perhaps most closely related to *Samanea* Merr. and *Chloroleucon* Britton & Rose ex Record.

While the data of Koenen et al. (2020) provided a robust phylogenomic backbone for the mimosoid and ingoid clades, and clearly demonstrated the non-monophyly of *Albizia* by sampling 25 species of that genus, only three of the 19 species from Central and South American sect. *Arthrosamanea* were included in that study, leaving doubts about the monophyly of that section and whether it should be segregated under the circumscription of Barneby and Grimes (1996), or whether there are further potential segregates, given the possibility that some of these species are more closely related to other neotropical genera. That possibility was suggested by the occurrence of lomentiform fruits in some species of section *Arthrosamanea* as reflected in the classification into separate series by Barneby and Grimes (1996). Similar lomentiform fruits also occur in *Hydrochorea* (Barneby and Grimes 1996; Soares et al. 2022) and *Albizia* s.s. (*Albizia dolichadena* (Kosterm.) I.C. Nielsen, *Albizia moniliformis* (DC.) F. Muell., *Albizia rosulata* (Kosterm.) I.C. Nielsen and *Albizia umbellata* (Vahl) E.J.M. Koenen), as well as a few other ingoid lineages (Barneby and Grimes 1996: 204; Koenen 2022a). For this reason, several species of neotropical *Albizia* have homotypic synonyms in *Arthrosamanea* Britton & Rose, *Samanea* or *Cathormion* Hassk., genera which previously had been recognized and defined based mainly on characters of fruit texture and dehiscence (Barneby and Grimes 1996). Barneby and Grimes (1996: 204) considered these fruit types to have arisen multiple times in parallel in different genera, and this was confirmed by subsequent phylogenetic (Iganci et al. 2015; Soares et al. 2021) and phylogenomic studies (Koenen et al. 2020), although the neotropical lomentiform *Albizia* species were not included in these studies, or remained unresolved.

Here we investigate whether *Albizia* sect. *Arthrosamanea* is monophyletic and thereby provide a more rigorous basis for recognizing its evolutionary distinctiveness from *Albizia* s.s. as a segregate genus. We infer a new phylogeny with emphasis on the neotropical species and make use of further insights offered by the phylogenomic analysis of Ringelberg et al. (2022). In addition, we use a tree topology inferred from data from the latter study to evaluate whether lomentiform fruits in *Albizia* sect. *Arthrosamanea* are independently derived from other lineages in which this fruit type occurs.

Based on our phylogenetic results and the recent findings of Koenen et al. (2020) and Ringelberg et al. (2022), we update the taxonomy of neotropical *Albizia* by resurrecting the genus *Pseudalbizzia* Britton & Rose.

Materials and methods

We used the nuclear ribosomal External and Internal Transcribed Spacer (ETS and ITS) regions that previously been used to study sister-group relationships within tribe Ingeae (Brown et al. 2008; Iganci et al. 2015; Souza et al. 2016). Our combined dataset included 123 accessions, of which 50 are from Genbank and 73 are newly sequenced here, including 25 species of *Albizia* s.l. sequenced for the first time. The outgroup, *Vachellia farnesiana* (L.) Wight & Arn., was designated to root the tree (Table 2). The plastid *trnK* region was initially explored but preliminary analyses suggested it is not sufficiently phylogenetically informative and these data were excluded from this study.

Fresh leaf material collected in the field plus herbarium material from the Jardín Botánico Regional Roger Orellana (CICY) were used for DNA extraction. Herbarium specimens used in these analyses came from AAU, CICY, FCME, MA, MEXU, and MO (acronyms as in Thiers 2016). Additional sequences were downloaded from GenBank (Table 2).

DNA from leaf fragments was obtained using the DNeasy Plant Mini Kit (QIAGEN Inc., Valencia, California) following the manufacturer's specifications. To assess concentration and relative quality of DNA, 3 µl of final volume plus 2 µl loading buffer were run for 30 minutes at 6 V cm^{-1} on a 1% agarose gel prepared with 0.5× TBE. The resulting gel was developed by immersion for 20–30 minutes in a 0.1 µg ml^{-1} ethidium bromide solution and later observed in a DigiDoc-It Imaging System (version 6.7.1; UVP, Inc., Cambridge, UK) transilluminator. DNA purity and concentration were quantified with a NanoDrop 2000c. Afterwards, DNA samples were standardized to 10 ng $µl^{-1}$.

PCR amplifications were performed in an Applied Biosytems Veriti 96 Well Thermal Cycler. Volumes of reagents and conditions for the amplifications were as follows: **ITS**: 30 µL of mix containing 3 µl 10× Buffer, 2.5 µl $MgCl_2$, 0.6 µl (~10 ng) primer, 4 µl Q solution, 1 µl 1.25 mM L^{-1} dNTP, 0.2 µl (1 U) TAQ polymerase, 2 µl (~10 ng) DNA, then completed to volume (approx. 16.1 µl) with ultra-pure water. PCRs were conducted under the following protocol: 94 °C × 3 min + 30 cycles (94 °C × 1 min + 60.5 °C × 1 min + 72 °C × 2 min) + 72 °C × 7 min. Primers were S3 (AACCTGCGGAAGGATCATTG) (Käss and Wink 1997), and 26S (TAGAATTCCCCGGTTCGCTCGCCGTTAC) (Sun et al. 1994). **ETS**: 30 µl of mix containing 3 µl 10× Buffer, 2.5 µl $MgCl_2$, 0.6 µl (~10 ng) primer, 4 µl Q solution, 1 µl 1.25 mM l^{-1} dNTP, 0.2 µl (1 U) TAQ polymerase, 2 µl (~10 ng) DNA, then completed to volume (approx. 16.1 µl) with ultra-pure water. PCR amplifications were conducted under the following protocol: 94 °C × 3 min + 30 cycles (94 °C × 1 min + 60.5 °C × 1 min + 72 °C × 2 min) + 72 °C × 7 min. Primers used were 18S-IGS (5'-GAGACAAGCATATGACTACTGGCAGGATCAACCAG-3') and 26S-IGS (5'-GGATTGTTCACCCACCAATAGGGAACGTGAGCTG-3') (Baldwin and Markos 1998).

Table 2. Voucher information of taxa included in the phylogenetic analysis with their corresponding GenBank accession numbers.

Accessions ITS	Accessions ETS
Albizia adianthifolia (Schumach.) W. Wight, MW699934, BGRO 001	*Albizia adianthifolia*, MW699372, BGRO 001
Albizia amara (Roxb.) Boivin, MW699936, BGRO 003	*Albizia amara*, MW699374, BGRO 003
Albizia anthelmintica Brongn., MW699937, BGRO 004	*Albizia anthelmintica*, MW699375, BGRO 004
Albizia arenicola R. Vig., MW699938, R. Randrianaivo 642, MO	*Albizia antunesiana* Harms, MW699376, S.H.C.P. 966, MO
Albizia brevifolia Schinz, MW699940, BGRO 005	*Albizia arenicola*, MW699377, R. Randrianaivo 642, MO
Albizia glaberrima Hutch. & Dalziel, MW699943, R.E. Gereau 6203, MA	*Albizia brevifolia*, MW699378, BGRO 005
Albizia gummifera (J.F. Gmel.) C.A. Sm., MW699944, J.E. Lawesson 5094, AAU	*Albizia chinensis* (Osbeck) Merr., MW69379, A. Ntemi & A. Athumani 478, MO
Albizia harveyi E. Fourn., MW699945, BGRO 006	*Albizia crassiramea* Lace, MW699380, K. Larsen et al. 46378, AAU
Albizia julibrissin Durazz., MW699946, BGRO 007	*Albizia ferruginea* (Guill. & Perr.) Benth., MW699382, *C.H. Jongkind 2098*, MA
Albizia kalkora (Roxb.) Prain, MW699947, E. Bouflord 26356, MO	*Albizia glaberrima*, MW699383, R.E. Gereau 6203, MA
Albizia lebbeck (L.) Benth., MW699948, C. Chan 7539, CICY	*Albizia gummifera*, MW699384, J.E. Lawesson 5094, AAU
Albizia petersiana (Bolle) Oliv., MW699950, BGRO 008	*Albizia harveyi*, MW699385, BGRO 006
Albizia procera (Roxb.) Benth., MW699953, BGRO 009	*Albizia julibrissin*, MW699387, BGRO 007
Albizia retusa Benth., MW699954, K. Yasuda 1804, MO	*Albizia kalkora*, MW699388, E. Bouflord 26356, MO
Albizia tanganyicensis Baker f., MW699956, BGRO 010	*Albizia lebbeck* (L.) Benth., MW699389, C. Chan 7539, CICY
Albizia umbellata (Vahl) E. J. M. Koenen, EF638182.1	*Albizia lebbekioides* (DC.) Benth., MW699390, H. Balslev 9333, AAU
Balizia leucocalyx (Britton & Rose) Barneby & J.W. Grimes, MW699959, S. Aguilar & F. Aguilar 1833, M	*Albizia lucidior* (Steud.) I.C. Nielsen ex H. Hara, MW699391, J.F. Maxwell 95–259, MO
Lysiloma acapulcense (Kunth) Benth., MW699960, H. Gómez D. 2003, MO	*Albizia petersiana* (Bolle) Oliv., MW699394, BGRO 008
Lysiloma latisiliquum (L.) Benth., MW699961, P. Simá 2287, CICY	*Albizia procera*, MW699396, BGRO 009
Pseudalbizzia adinocephala (Donn. Sm.) E.J.M. Koenen & Duno, MW699935, BGRO 002	*Albizia retusa*, MW699397, K. Yasuda 1804, MO
MW699958, J.L. Linares 5406, FCME	*Albizia sahafariensis* Capuron, MW699398, R. Randrianaivo et al. 1387, MO
Pseudalbizzia berteroana (Balb. Ex DC.) Britton & Rose, MW699939, *A.* Jimenez 2113, MO	*Albizia tanganyicensis*, MW699400, BGRO 010
Pseudalbizzia edwallii (Hoehne) E.J.M. Koenen & Duno, MW699942, J.M. Silva & L.M. Abe 4237, MEXU	*Albizia umbellata*, EF638157.1
Pseudalbizzia multiflora (Kunth) E.J.M. Koenen & Duno, MW699949, X. Cornejo 1922, GUAY	*Balizia leucocalyx*, MW699403, S. Aguilar & F. Aguilar 1833, M
Pseudalbizzia pistaciifolia (Willd.) E.J.M. Koenen & Duno, MW699951, *X.* Cornejo 5323, GUAY	*Balizia pedicellaris* (DC.) Barneby & J.W. Grimes, MW699404, P.R. House 1880, MA
Pseudalbizzia polycephala (Benth.) E.J.M. Koenen & Duno, MW699952, L.P. Queiroz 9578, MEXU	*Havardia mexicana*, MW699405, S. Foldi s.n., CICY
Pseudalbizzia sinaloensis (Britton & Rose) E.J.M. Koenen & Duno, MW699955, C.E. Hughes et al. 1576, FCME	*Hesperalbizia occidentalis*, MW699406, J.G. Hernandez Oria 21, FCME
Pseudalbizzia tomentosa (Micheli) E.J.M. Koenen & Duno, MW699957, *A.* Dorantes et al. 165, CICY	*Lysiloma acapulcense*, MW699407, H. Gómez D. 2003, MO
Pseudosamanea cubana (Britton & P. Wilson) Barneby & J.W. Grimes, MW699941, GHBG 001	*Lysiloma latisiliquum*, MW699408, P. Simá 2287, CICY
Pseudosamanea guachapele (Kunth) Harms, MW699962, BGRO 011	*Paraserianthes lophantha*, MW699409, H. Balslev et al. 62450, AAU
Zapoteca formosa (Kunth) H.M. Hern., MW699963, R. Duno s.n. CICY. Additional accessions (ITS): *Acacia acradenia* F.Muell., AF487765.1	*Pithecellobium diversifolium*, MW699410, J.F.B. Pastore & R.M. Harley 2599 MO
Acacia longifolia (Andrews) Willd., HM007655.1	*Pithecellobium excelsum*, MW699411, G. P. Lewis et al 2339, MO
Acaciella angustissima (Mill.) Britton & Rose, EF638169.*1*	*Pseudalbizzia adinocephala*, MW699373, BGRO 002
Balizia pedicellaris (DC.) Barneby & J.W. Grimes, JX870657.1	MW699402, J.L. Linares 5406, FCME
Calliandra dysantha Benth., JX870684.1	*Pseudalbizzia edwallii*, MW699381, *J.M. Silva & L.M. Abe 4237*, MEXU

Accessions ITS	Accessions ETS
Calliandra foliosa Benth., EF638181.1	*Pseudalbizzia inundata* (Mart.) E.J.M. Koenen & Duno, MW699386, H. Balslev et al. 97355, AAU
Cojoba arborea (L.) Britton & Rose, JX870758.1	*Pseudalbizzia multiflora* (Kunth) E.J.M. Koenen & Duno, MW699392, X. Cornejo & T. Andres 8705, GUAY
Cojoba undulatomarginata L. Rico, EF638187.1	*Pseudalbizzia niopoides* (Spruce ex Benth.) E.J.M. Koenen & Duno, MW699393, J.R. Grande 374, VEN
Ebenopsis ebano (Berland.) Barneby & J.W. Grimes, JX870759.1	*Pseudalbizzia polycephala* MW699395, L.P. Queiroz 9578, MEXU
Enterolobium contortisiliquum (Vell.) Morong, EF638190.1	*Pseudalbizzia sinaloensis*, MW699399, C.E. Hughes et al. 1576, FCME
Enterolobium cyclocarpum (Jacq.) Griseb., EF638191.1	*Pseudalbizzia tomentosa*, MW699401, A. Dorantes et al. 165, CICY
Enterolobium timbouva Mart., JX870760.1	*Pseudosamanea cubana* (Britton & P. Wilson) Barneby & J.W. Grimes, MW699412, BJ FTGH 2000
Faidherbia albida (Delile) A. Chev., EU812008.1	*Pseudosamanea guachapele*, MW699413, BGRO 011
Havardia mexicana (Rose) Britton & Rose, JX870762.1	*Samanea tubulosa* (Benth.) Barneby & J.W. Grimes, MW699414, *G.A. Parada & V.D. Rojas* 2480, MO. Additional accessions: *Acacia acradenia*, EF638116.1
Havardia pallens (Benth.) Britton & Rose, KF921656.1	*Acacia longifolia*, EF638115.1
Hesperalbizia occidentalis (Brandegee) Barneby & J.W. Grimes, EF638195.*1*	*Acaciella angustissima* EF638082.1
Hycrochorea corymbosa (Rich.) Barneby & J.W. Grimes, JX870763.1	*Pseudalbizzia adinocephala* EF638144.1
Jupunba trapezifolia (Vahl.) Moldenke, EF638166.1	*Albizia kalkora* EF638158.1
Mariosousa coulteri (Benth.) Seigler & Ebinger, EF638198.1	*Albizia lebbeck* EF638155.1
Mariosousa dolichostachya (S.F. Blake) Seigler & Ebinger, EF638199.1	*Albizia saponaria* (Lour.) Blume, EF638085.1
Paraserianthes lophantha (Willd.) I.C. Nielsen, EF638204.1	*Archidendropsis basaltica* (F. Muell.) I.C. Nielsen, EF638141.1
Pithecellobium diversifolium Benth., JX870768.1	*Archidendropsis thozetiana* (F. Muell.) I.C. Nielsen, EF638140.1
Pithecellobium dulce (Roxb.) Benth., EF638207.1	*Calliandra dysantha* EF638121.1
Pithecellobium excelsum (Kunth) Mart., EF638208.1	*Calliandra foliosa* EF638122.1
Samanea saman (Jacq.) Merr., JX870770.1	*Cojoba arborea* EF638095.1
Samanea tubulosa (Benth.) Barneby & J.W. Grimes, EF638212.1	*Cojoba undulatomarginata* EF638096.1
Pseudosamanea guachapele (Kunth) Harms, JX870769.1	*Ebenopsis confinis* (Standl.) Britton & Rose, EF638100.1
Senegalia berlandieri (Benth.) Britton & Rose, KY688777.*1*	*Ebenopsis ebano* EF638101.1
Sphinga acatlensis (Benth.) Barneby & J.W. Grimes, EF638214.1	*Enterolobium contortisiliquum* EF638151.1
Vachellia campechiana (Mill.) Seigler & Ebinger, EF638215.1	*Enterolobium cyclocarpum* EF638149.1
Vachellia farnesiana (L.) Wight & Arn., EF638219.1	*Faidherbia albida* EF638163.1
Viguieranthus ambongensis (R. Vig.) Villiers, JX870773.1	*Havardia pallens* EF638146.1
Viguieranthus densinervus Villiers, JX870774.1	*Hesperalbizia occidentalis* EF638139.1
Viguieranthus megalophyllus (R. Vig.) Villiers, JX870776.1	*Hycrochorea corymbosa* EF638138.1
Viguieranthus subauriculatus Villiers, JX870778.1	*Jupunba trapezifolia* (Vahl.) Moldenke, EF638110.1
Zapoteca tetragona (Willd.) H.M. Hern., JX870784.1	*Mariosousa coulteri* (Benth.) Seigler & Ebinger, EF638124.1
	Mariosousa dolichostachya EF638084.1
	Pararchidendron pruinosum (Benth.) I.C. Nielsen, EF638129.1
	Paraserianthes toona (Bailey) I.C. Nielsen, EF638106.1
	Pithecellobium dulce EF638142.1
	Pseudosamanea guachapele EF638160.1
	Samanea saman EF638136.1
	Samanea tubulosa EF638135.1
	Senegalia berlandieri EF638162.1
	Sphinga acatlensis EF638145.1
	Vachellia farnesiana EF638128.1
	Viguieranthus ambongensis KR997873.1
	Viguieranthus densinervus JX870891.1
	Viguieranthus megalophyllus KR997871.1
	Viguieranthus subauriculatus KR997076.1
	Zapoteca formosa EF638134.1
	Zapoteca tetragona EF638133.1.

The quality of the PCR products was evaluated by agarose electrophoresis (3 µl of final volume plus 2 µl of bromophenol blue, gel prepared with 0.5× TBE and 1% agarose, run at 120 volts and 25 amperes 30 min). PCR products were sequenced at Macrogen (http://www.macrogen.com/eng/) using the same amplification primers. The sequencing products were assembled and edited using the Sequencher v. 5.2.3. An initial automated alignment was conducted with MAFFT (Katoh et al. 2002) using the E-INS-i algorithm option, a 100PAM/k = 2 scoring matrix, a gap opening penalty of 1.3, and an offset value of 0.123. The alignments were visually inspected and manually edited for further improvement. The Akaike Information Criterion (AIC), implemented in jModeltest (Posada 2008) was used to select the best model of nucleotide substitution for each alignment. The selected models were TVM+I+G for ETS and GTR+I+G for ITS. Phylogenetic analyses were performed with MrBayes v.3.2.5 (Ronquist et al. 2012) separately for each dataset, and subsequently concatenated with each partition treated as independent and associated with its own evolutionary model. Analyses were performed using default parameters for 5 million generations. Two independent threads were run. Convergence was assessed with both MrBayes and Tracer (Rambaut et al. 2018). Posterior Probabilities (PP) ≤ 0.95 were considered weakly supported whereas PP of 0.95–1.0 were deemed strongly supported (Alfaro et al. 2003).

To examine the evolution of fruit types within New World *Albizia* we utilize a phylogeny derived from a new analysis based on data of Ringelberg et al. (2022) for the Jupunba clade, as described in Soares et al. (2022), because it is based on a large set of 560 nuclear exons and flanking non-coding regions, and therefore shows enhanced resolution within this clade compared to the ITS + ETS phylogeny.

Results

Alignments of our combined datasets recovered by MAFFT required few manual adjustments. The ETS sequences had 381 bp and, once aligned, 52% of the data were informative. In the case of ITS, the sequences were slightly longer, 551 bp but only 34% were informative.

None of the molecular-based analyses (ETS, ITS, and ETS+ITS) using Bayesian inference recovered the genus *Albizia* as monophyletic. The combined ETS + ITS phylogeny (Fig. 3) is used as the basis for discussing the results in detail. The outgroup *Vachellia farnesiana*, plus *Acaciella angustissima* (Mill.) Britton & Rose, *Senegalia berlandieri* (Benth.) Britton & Rose and two species of *Mariosousa* Seigler & Ebinger form a paraphyletic grade subtending a fully supported clade (PP = 1) that includes all members of the tribe Ingeae as well as *Acacia* s.s.

The most relevant clade from the perspective of this study is highly supported (PP = 0.96) and includes all members of the genus *Albizia* and a few other genera of tribe Ingeae (clade A). The genus *Albizia*, as currently circumscribed, is non-monophyletic with species placed in two separate, strongly supported clades (Fig. 3). As in Koenen et al. (2020), species of *Albizia* sect. *Arthrosamanea* are placed in clade B (PP = 0.96),

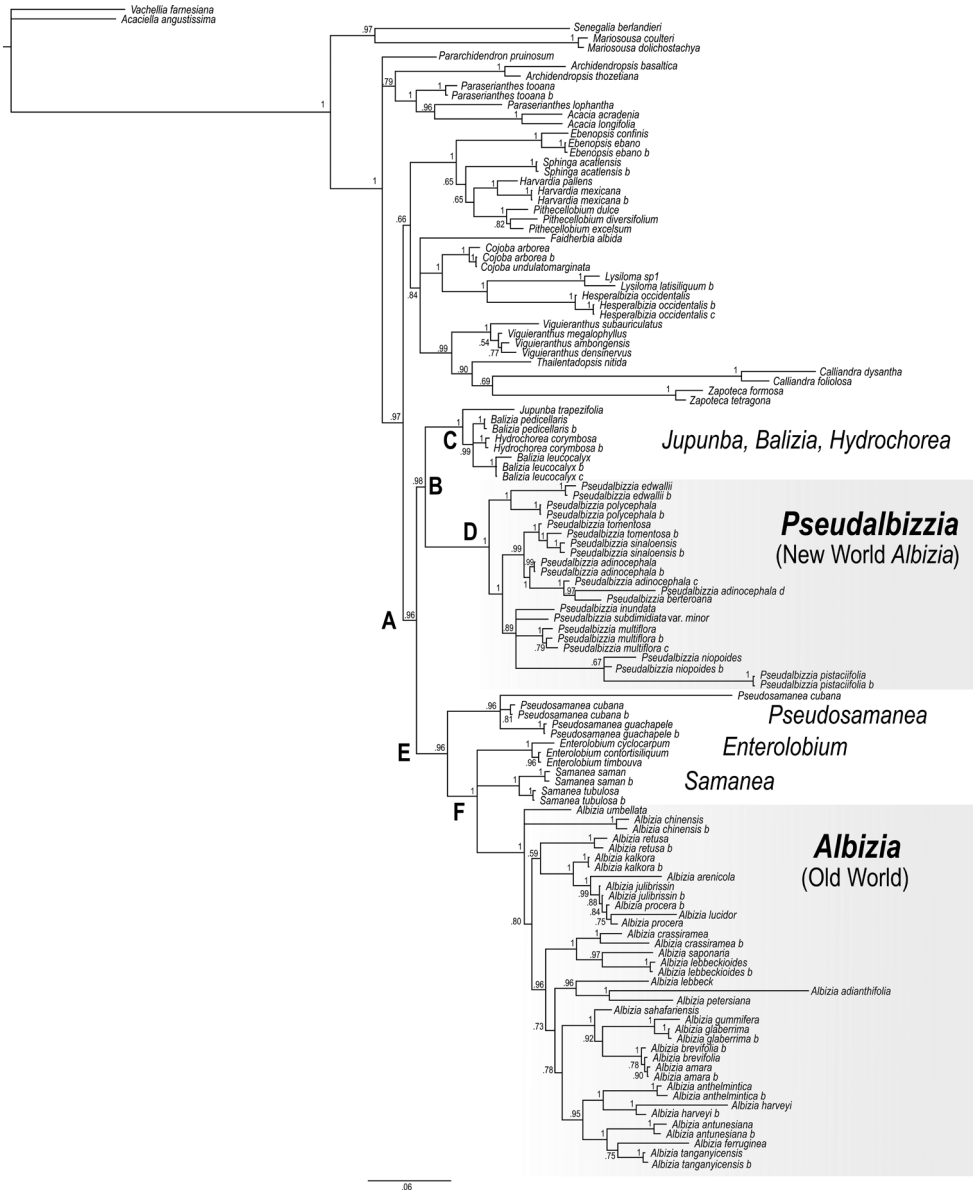

Figure 3. Phylogeny of the ingoid clade (sensu Koenen et al. 2020), i.e., the traditionally recognized tribes Ingeae + Acaciaeae (excl. *Vachellia*). Phylogram derived from Bayesian analysis in MrBayes of the combined ETS and ITS data for *Albizia* and related genera. Main clades are labeled **A–F** (see text). Posterior support values are indicated above branches.

which equates to the Jupunba clade of Koenen et al. (2020). All species that were sampled from this section are included in this clade (Fig. 3 clade D), which received full support (PP = 1), and as in Koenen et al. (2020) this section is sister to clade C (PP = 1) comprising the genera *Jupunba*, *Balizia* and *Hydrochorea*.

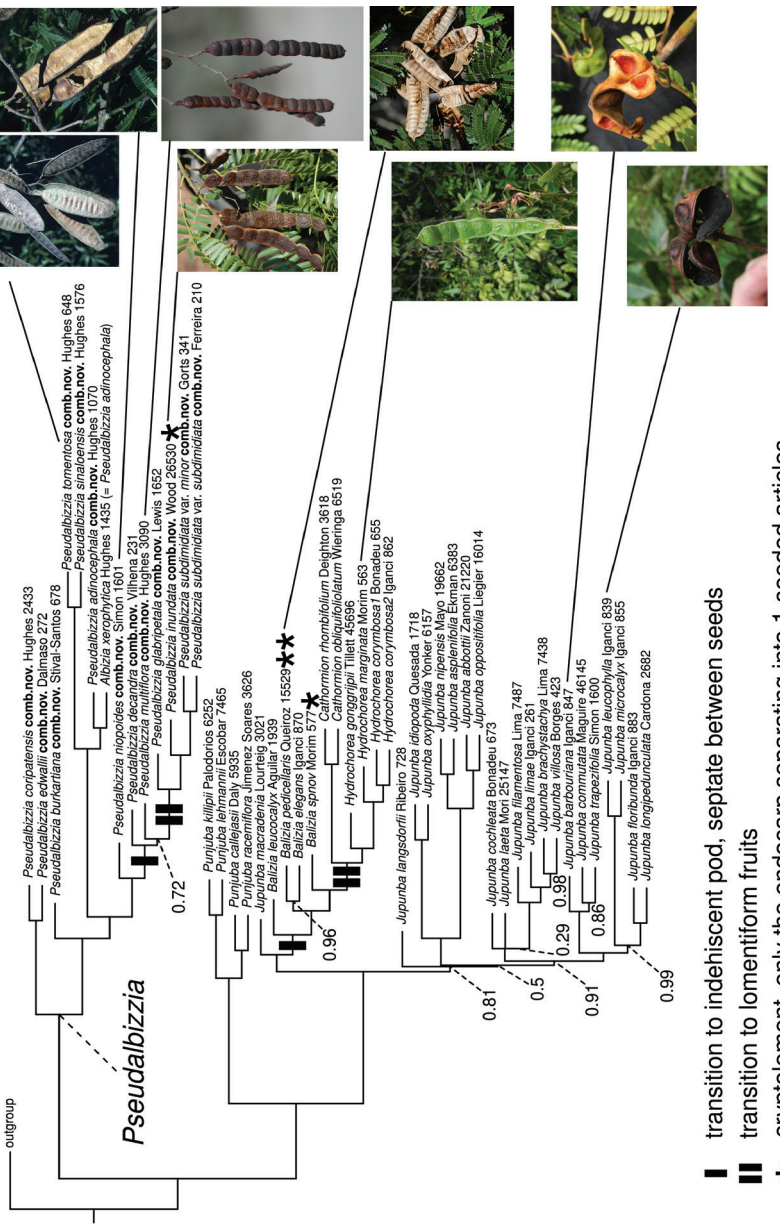

Figure 4. Phylogeny of the Jupunba clade redrawn from an ASTRAL species tree analysis by Soares et al. (2022) that utilizes data from Ringelberg et al. (2022) showing the evolutionary transitions from ancestrally papery, plano-compressed fruits to septate indehiscent fruits and subsequently to lomentiform hydrochorous fruits associated with species growing in seasonally inundated habitats in *Pseudalbizzia* and similar parallel transitions in *Balizia* and *Hydrochorea*. Photos of *Pseudalbizzia inundata*, *P. multiflora*, *P. niopoides P. tomentosa* and *Balizia pedicellaris*, by Colin Hughes, of *Hydrochorea marginata*, *Jupunba barbouriana* and *J. leucophylla*, by Erik Koenen.

Within sect. *Arthrosamanea*, three clades are well supported, one comprising *Albizia polycephala* (Benth.) Killip ex Record and *Albizia edwallii* (Hoehne) Barneby & J.W. Grimes of ser. *Paniculatae*, a second clade comprising species of ser. *Paniculatae* endemic to Mexico, Central America, and the Caribbean, and a third clade that includes *Albizia niopoides* (Benth.) Burkart (also ser. *Paniculatae*) and the species from the other three series. The phylogeny of Ringelberg et al. (2022) presented here in Fig. 4 based on a new analysis of the Jupunba clade accessions from Soares et al. (2022), has greater resolution within sect. *Arthrosamanea* and shows that ser. *Paniculatae* forms a well-resolved paraphyletic grade in which the other three series are nested. The other two non-monospecific series also appear to be non-monophyletic, with the monospecific ser. *Inundatae* nested inside ser. *Arthrosamanea* and these together in turn nested in ser. *Multiflorae*, although support for the paraphyly of ser. *Multiflorae* is only 0.72 pp.

The Old World species of *Albizia* form a monophyletic group (PP = 1) placed in clade E (PP = 0.96) (Fig. 3), with the genera *Enterolobium* Mart., *Samanea*, and *Pseudosamanea*. Within clade E *Pseudosamanea* (PP = 0.96) is sister to clade F which includes *Enterolobium*, *Samanea* and Old World *Albizia*. All these clades have high support (PP = 1). These analyses also support the transfer of *Cathormion umbellatum* Kosterm., which is placed in the Old World *Albizia* clade (Fig. 3), to *Albizia*, as proposed by Koenen et al. (2020).

Our analyses also confirm that the monotypic genus *Hesperalbizia*: *H. occidentalis* (Brandegee) Barneby & J.W. Grimes is sister to *Lysiloma*, in the Cojoba clade (sensu Koenen et al. 2020), unrelated to either New World *Albizia* (clade D) or Old World *Albizia* (clade F), as previously shown by Duno de Stefano et al. (2021). Furthermore, *Pseudosamanea guachapele* (Kunth) Harms (previously *Albizia guachapele* (Kunth) Dugand in Rico Arce et al. (2008)) is also unrelated to New World *Albizia* but is instead a member of clade E, sister to clade F which includes *Enterolobium*, *Samanea* and Old World *Albizia*.

In both *Albizia* sect. *Arthrosamanea* and the closely related *Balizia* and *Hydrochorea*, these phylogenies suggest that lomentiform fruits were independently derived from indehiscent fruits that are septate between the seeds, as species with the latter fruit type form paraphyletic grades to the lomentiform species in both cases (Fig. 4). In turn, these indehiscent septate fruits are nested within paraphyletic assemblages of species with fruits that dehisce along one or both sutures in both groups. Interestingly, in both cases, a single species with crypto-lomentiform fruits is found, but it is not clear whether these were derived from the same ancestral fruit type or not. In *Hydrochorea* this crypto-lomentiform species appears as an intermediate between indehiscent and lomentiform species, while in *Albizia* sect. *Arthrosamanea* the crypto-lomentiform-fruited *A. inundata* appears to be derived from a lomentiform-fruited ancestor. Another difference between these two groups is that the follicular dehiscence of *Balizia pedicellaris* (DC.) Barneby & J.W. Grimes fruits appears to be secondarily derived from indehiscent fruits, but we note that similar dehiscence is also found in a few species of *Jupunba*.

Discussion

This study addresses the non-monophyly of the genus *Albizia* and our results provide important insights into the evolutionary history of the neotropical species placed in sect. *Arthrosamanea*, with implications for their taxonomic classification. We show that sect. *Arthrosamanea*, with expanded taxon sampling relative to Koenen et al. (2020), and as also shown by the study of Ringelberg et al. (2022), is monophyletic with only two exceptions: *Albizia leonardii* Barneby & J.W. Grimes which is placed among taxa of the 'senegalioid grade' (Ringelberg et al. 2022; Terra et al. 2022) and *Albizia carbonaria* Britton that is more closely related to *Pseudosamanea* (Koenen 2022b; Ringelberg et al. 2022).

The geographically-based splitting of a large genus in tribe Ingeae, such as *Albizia*, which occupies a pantropical distribution, is not unprecedented, nor unexpected, especially given the lack of pantropical monographic synthesis or geographically widely sampled phylogenies for the mimosoid clade. For example, the genus *Pithecellobium*, once the largest genus of tribe Ingeae, has been progressively divided during the last 50 years into multiple genera (see Brown et al. 2008 for a general history of the tribe). Another example is the genus *Calliandra* Benth. for which the New World species of *Calliandra*. ser. *Laetevirentes* were segregated into *Zapoteca* H.M. Hern. (Hernández 1986), and almost all Old World species allocated progressively to other segregated genera: *Viguieranthus* Villiers (Villiers 2002), *Thailentadopsis* Kosterm. (Lewis and Schrire 2003), *Sanjappa* E.R. Souza & M.V. Krishnaraj (Souza et al. 2016) and *Afrocalliandra* E.R. Souza & L.P. Queiroz (Souza et al. 2013). All these taxonomic rearrangements were supported by morpho-anatomical and molecular phylogenetic analyses. Molecular data have also demonstrated that *Abarema* is polyphyletic (Iganci et al. 2015), prompting reinstatement of the genera *Jupunba* and *Punjuba* Britton & Rose (Soares et al. 2021). Finally, neither *Zygia* P. Browne nor *Marmaroxylon* Killip are monophyletic, although a new generic classification for those genera has yet to be proposed (Ferm et al. 2019). The non-monophyly of *Albizia* documented here and elsewhere (Koenen et al. 2020; Ringelberg et al. 2022) is thus not a surprise and reflects the state of flux surrounding generic delimitation in mimosoids, especially within the ingoid clade.

Some of the taxonomic proposals of Barneby and Grimes (1996) relative to the American segregates of *Albizia* s.l. are confirmed by our results. The genera *Balizia* and *Hydrochorea* form part of the Jupunba clade (sensu Koenen et al. 2020) (Figs 3 and 4) (Iganci et al. 2015), although neither *Hydrochorea* nor *Balizia* are monophyletic in our phylogeny (Figs 3 and 4, see Soares et al. 2022). Two neotropical species, included in *Albizia* by Rico Arce et al. (2008) are also placed outside New World *Albizia* (Fig. 3): *Hesperalbizia occidentalis* is closely related to *Lysiloma*, in agreement with previous results (Iganci et al. 2015; Duno de Stefano et al. 2021); similarly, *Pseudosamanea guachapele*, is also placed outside *Albizia* in our phylogeny, emerging, as expected, together with the other species *Pseudosamanea cubana* (Britton & Rose) Barneby & J.W. Grimes, although relationships within this clade are unresolved (Fig. 3).

Here we show that the dehiscent, papery, plano-compressed fruit type is ancestral within *Albizia* sect. *Arthrosamanea* (Fig. 4) and is associated with species growing predominantly in seasonally dry tropical forest and woodland, with successive shifts to septate indehiscent fruits and then lomentiform fruits with hydrochorous seed dispersal associated with species growing in seasonally inundated varzea forest, riverine habitats and low-lying margins of palm and white-sand savannas (Fig. 4). Interestingly, in the sister group of *Albizia* sect. *Arthrosamanea*, the mainly neotropical clade composed of *Jupunba*, *Punjuba*, *Balizia*, and *Hydrochorea*, a similar parallel evolutionary transition in fruit types is apparent. In *Jupunba* and *Punjuba*, fruits are always dehiscent, while a transition to septate indehiscent fruits occurred in *Balizia*, an exception being *Balizia pedicellaris* which has follicular dehiscence and a newly described species with crypto-lomentiform fruits (Fig. 4, and Soares et al. 2022). Nested within the paraphyletic *Balizia* is a clade comprising the genus *Hydrochorea* plus two African species of *Cathormion*, all species of which have indehiscent lomentiform fruits adapted for hydrochory and are found in riparian or other periodically flooded habitats in the Amazon basin, West Africa and the Congo basin (Fig. 4, and Soares et al. 2022).

Barneby and Grimes (1996) pointed out that a radiation of species with similarly heterogeneous fruit types to that seen in section *Arthrosamanea* occurs in Madagascan *Albizia* s.s. and that the association between lomentiform fruits, hydrochorous seed dispersal, and seasonally flooded habitats is also apparent in Old World *Albizia* s.s. For example, *Albizia dolichadena*, *A. moniliformis*, *A. rosulata*, and *A. umbellata* from Australasia also have lomentiform fruits and are distributed near streams or in riparian and swamp forests (Rico Arce et al. 2008). Furthermore, as indicated above and pointed out by Barneby and Grimes (1996), similar transitions to lomentiform fruits have occurred in parallel in several other lineages across the ingoid clade, including *Cathormion altissimum* (Hook.f.) Hutch. & Dandy (sometimes referred to as *Albizia altissima* Hook.f.; Koenen 2022a) and *Senegalia rostrata* (Humb. & Bonpl. ex Willd.) Seigler & Ebinger (syn. *Dugandia rostrata* (Humb. & Bonpl. ex Willd.) Britton & Killip, syn. *Manganaroa articulata* Speg.; Barneby and Grimes 1996: 204) in all cases apparently also closely associated with riparian and/or periodically inundated habitats. These repeated parallel derivations of similar, but not strictly homologous fruit types attest to the high evolvability of the mimosoid fruit more generally. In the light of phylogenetic evidence, it is now clear that these evolutionarily highly labile morphological adaptations of the fruit related to seed dispersal syndrome do not provide reliable characters for generic delimitation, supporting inclusion of the species that were placed in ser. *Arthrosamanea*, ser. *Inundatae* and ser. *Multiflorae* within *Albizia* sect. *Arthrosamanea* by Barneby and Grimes (1996), i.e., the clade of New World *Albizia* that is recovered in our analysis.

Taxonomic treatment

There are two validly published generic names – *Pseudalbizzia* of Britton and Rose (1928) and *Arthrosamanea* of Britton and Killip (1936) – that could be applied to the New World clade of *Albizia*. In accordance with Principle III of the International

Code of Nomenclature (Turland et al. 2018), we reinstate *Pseudalbizzia*, the earlier name associated with this clade, and provide the corresponding new combinations for its constituent species.

Pseudalbizzia Britton & Rose, N. Am. Fl. 23: 48. 1928.

Type. *Pseudalbizzia berteroana* Britton & Rose.

Arthrosamanea Britton & Rose, in Britton & Killip, Ann. New York Acad. Sci. 35: 128, 1936. *Albizia* section *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 206. 1996. Type: *Arthrosamanea pistaciifolia* Britton & Rose.

Description. Unarmed ***trees*** with sympodial growth, up to 30 m, rarely small treelets of c. 3 m, microphyllidious to macrophyllidious; trunk 35–120(–150) cm dbh; young stems and all leaves and inflorescence-axes more or less densely tomentellous to pilosulous; stipules puberulent to glabrous, deltate, narrowly triangular, triangular-ovate, narrowly ovate, or narrowly lanceolate, veinless or faintly 3-veined, falling early to tardily, perhaps sometimes obsolete and/or lacking on mature leaves. ***Leaves*** bipinnate, not sensitive, (1–)2–15(–19) pairs of pinnae; leaflets (2–)16–52(–63) pairs per pinna; a nectary immediately below first pair of pinnae, near or well below mid-petiole, sometimes lacking or reduced to a minute pore, round, elliptic or vertically elongate, either shallow-cupular or almost plane, thick-rimmed, sometimes immersed in petiolar groove or even obsolete, much smaller nectaries at some distal pinnae, at the tip of most pinnae, and between 1–2 furthest pairs of leaflets; leaflets gently decrescent toward each end of the rachis or toward the base of the rachis or sub-equilong, the first pair of leaflets often reduced to paraphyllidia, sometimes minute, sometimes absent or perhaps falling early, the blades of the remaining leaflets elliptic, elliptic-ovate, oblong-elliptic, narrowly oblong-elliptic, lance-oblong to linear-lanceolate, base obliquely truncate to shallowly semi-cordate, apex deltately subacute, deltately acute to subacute, obtuse or apiculate, the larger ones (1.5–)2–4(–6) times as long as wide, margin strongly to slightly revolute; venation generally palmate, of 2–4(–5) veins from the pulvinule, the nearly straight main vein a little forwardly displaced and giving rise on each side to 2–13 major secondary veins, the inner of 2(–3) posterior primary veins incurved-ascending to anastomose slightly beyond mid-blade, the outer posterior vein and sometimes a faint anterior one very short and weak, all venation immersed on upper face. ***Inflorescence*** primary axis up to 30 cm long; peduncles (1–)2–8(–10) per node of the capitulate or corymbose-umbellate inflorescence, capitula 8–26(–40)-flowered; bracts heteromorphic or homomorphic, ovate, oblong-obovate or spatulate, linear-spatulate, falling early or persistent, sessile or shortly pedicellate, the flowers moderately to strongly dimorphic, the terminal ones generally longer. ***Flowers*** 5-merous, rarely 6-merous, glabrous to densely pubescent externally. Peripheral flowers: calyx campanulate, turbinate, turbinate-campanulate or narrowly campanulate, sessile or short pedicellate, lobes very short, depressed-deltate, ovate or triangular, glabrous or puberulent; corolla narrowly trumpet-shaped, erect or recurved, lobes ovate to lance-ovate; androecium with

9–30(–32) stamens, up to 20 mm long, united at the base forming a clear stemonozone, the staminal tube as long or longer than the stemonozone; ovary sessile or shortly stipitate, slenderly ellipsoid, conical at apex, glabrous or pubescent; style a little longer than the stamens, slightly dilated at the stigma. Terminal flowers: sessile or almost so, calyx shallowly campanulate to broadly campanulate, corolla tubular; androecium with 16–38(–42) stamens, 8.5–11.5(–13) mm long, united at the base forming a clear stemonozone, staminal tube equalling or longer than the stemonozone. ***Fruits*** solitary, or rarely 2–4 per capitulum, sessile, subsessile or cuneately contracted at base into a short pseudo-stipe, the body linear, linear-elliptic, narrowly elliptic-oblong, straight or nearly straight, sometimes decurved, plano-compressed, apex rounded but minutely apiculate to obtuse, (8–)13(–15)-seeded; valves papery, coriaceous, or grossly ligneous, olivaceous, castaneous, fuscous-greenish, or brown becoming tan-brown, closely transverse venulose, minutely puberulous, tomentulose, glabrescent to glabrous, framed by straight sutures or dilated, sometimes 3-angulate but not winged, transversely or horizontally, dehiscence tardy to very tardy, inert, through both sutures or dehiscence 0, in the latter, the pod crypto-lomentiform, incipiently lomentiform or lomentiform, then the whole fruit long persistent on the tree, commonly falling entire and breaking on the ground into 8–12 individually indehiscent segments, funicle apically sigmoid or ribbon-like (not sigmoid), lentiform; ***seeds*** obliquely ascending or straight, disciform, oblong-ellipsoid, elliptic, strongly compressed, the translucent, brownish or greyish testa produced as a peripheral wing, adherent to the embryo, which does not fill the testa-cavity, the pleurogram small, inversely U-shaped or U-shaped.

Notes. The genus forms a group that is homogeneous in most respects, but diverse in the late developmental stages of the fruit, including: 1) fruit opening type: dehiscent, indehiscent, or irregularly breaking, 2) lateral shape: flat to conspicuously raised over the seed chambers, 3) texture and consistency of the valves: papery, chartaceous to woody (Barneby and Grimes 1996). Figs 1, 2 and 4.

Pseudalbizzia (clade D) is the sister group of the *Jupunba-Punjuba-Balizia-Hydrochorea* clade (Fig. 3). *Jupunba* and *Punjuba* are markedly different morphologically, having spirally twisted dehiscent fruits with a red or ochre endocarp, reminiscent of the fruits of several other genera in tribe Ingeae (e.g., some *Pithecellobium* species, and some species of *Archidendron* F. Muell. and *Cojoba* Britton & Rose). The red or red-brown testa of the seeds of *Jupunba* and *Punjuba* are very distinctive, and are never black, and the embryo is nearly always aniline-blue due to the presence of delphinidin (an anthocyanidin). *Punjuba* is furthermore distinguished by its spicate inflorescences, which are not seen in *Pseudalbizzia*. *Balizia* has ligneous, indehiscent or tardily dehiscent pods, their seeds being released sometimes only after decay of the valves on the floor of terra firme forest, whereas in *Hydrochorea* the fruits are lomentiform, adapted to dispersal by water. The fruits of *Hydrochorea* recall some species of *Pseudalbizzia* adapted to similar riparian habitats. However, the species of *Pseudalbizzia* are markedly different in form of inflorescence, leaflet-venation, and shape of the ovary.

Two species previously placed in *Albizia* from the New World which were not included in our phylogenetic analysis, *Albizia carbonaria* and *A. leonardii*, have since been shown to be placed outside the New World *Albizia* clade (Ringelberg

et al. 2022; Koenen 2022b; Terra et al. 2022). Two other species, also not sampled here, nor by Ringelberg et al. (2022), are here tentatively included in *Pseudalbizzia*: *Albizia barinensis* L. Cárdenas and *Albizia buntingii* Barneby & J.W. Grimes (see below for discussion about the placement of these species). The genus *Pseudalbizzia* was published in the Flora of North America (Britton and Rose 1928) and included just a single species, *P. berteroana*. The original description of *Pseudalbizzia* closely matches *Albizia* and no characters distinguishing the two genera were discussed by Britton and Rose (1928). The generic name *Arthrosamanea* was also published by Britton & Rose, again with a single species, *A. pistaciifolia* (Willd.) Britton & Rose, in an account of the Mimosaceae and Caesalpiniaceae of Colombia (Britton and Killip 1936), but again no differences between the genus and *Albizia* or *Pseudalbizzia* were mentioned.

Pseudalbizzia as circumscribed here comprises 17 species and 5 varieties ranging in distribution from northwestern Mexico to northern Argentina and including the Greater Antilles (Figs 5 and 6). Full synonymy, detailed species descriptions, geographical distributions, representative samples of all species and keys for their identification can be found (under the name *Albizia*) in Barneby and Grimes (1996), Linares (2005) and Rico Arce et al. (2008). Finally, we propose a new sectional classification of

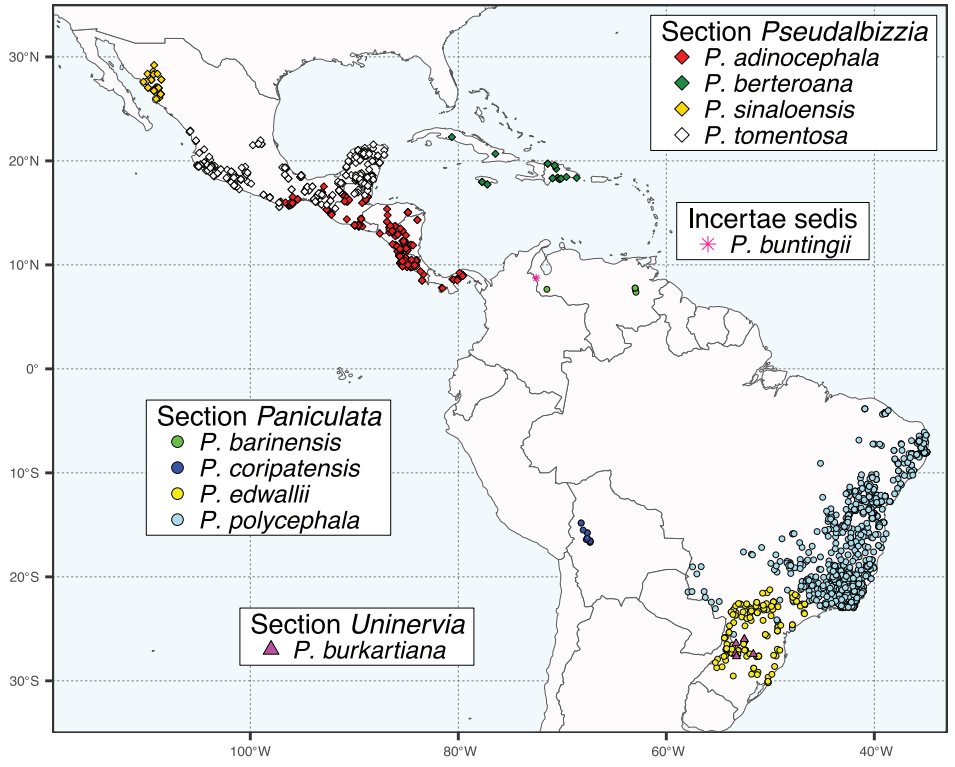

Figure 5. Distribution map of *Pseudalbizzia* sections *Paniculata*, *Pseudalbizzia*, *Uninervia* and *Pseudalbizzia buntingii* (incertae sedis), as per the legend.

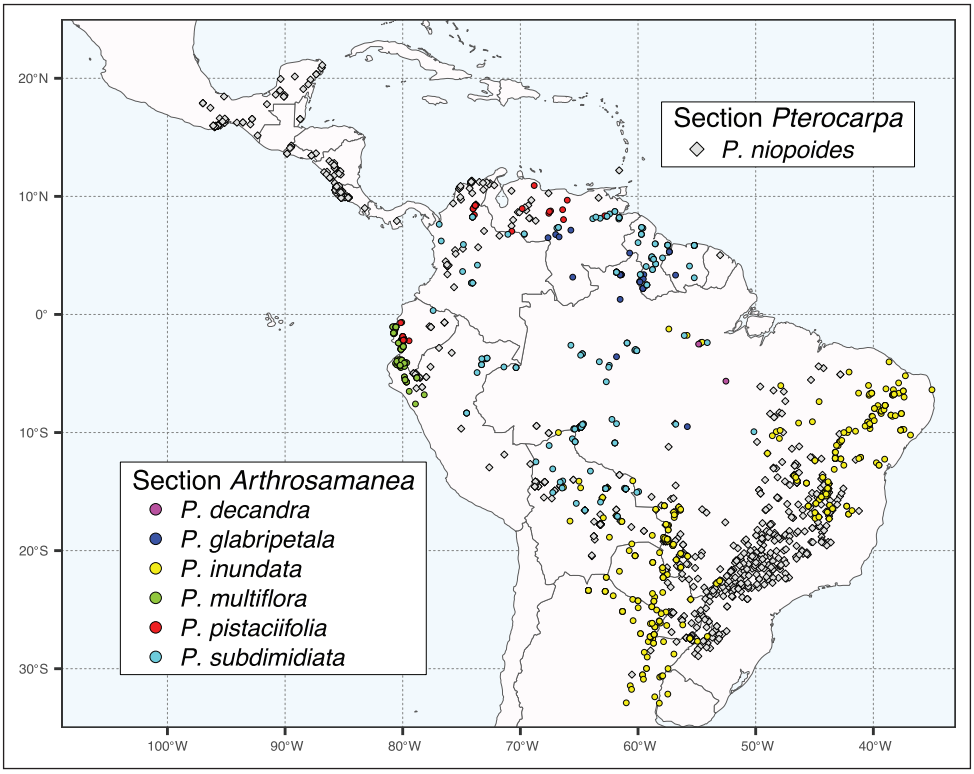

Figure 6. Distribution map of *Pseudalbizzia* sections *Arthrosamanea* and *Pterocarpa*, as per the legend.

Pseudalbizzia to account for the non-monophyly of the series of Barneby and Grimes (1996), based on the phylogenies (Figs 3 and 4) which sampled nearly all species. A key to the sections is provided.

Key to the sections of the genus *Pseudalbizzia*

1 Leaflets with a single vein from the pulvinule..... **sect. *Uninervia***
– Leaflets with 3–5 veins from the pulvinule..... **2**
2 Fruits with a narrowly winged margin, seeds oblique, foliage microphyllidious..... **sect. *Pterocarpa***
– Fruit margins not winged, or if winged, then foliage macrophyllidious and seeds straight..... **3**
3 Fruits indehiscent and septate or lomentiform ..... **sect. *Arthrosamanea***
– Fruits dehiscent, plano-compressed, valves papery, not septate..... **4**
4 Micro- to mesophyllidious foliage, distributed in South America..... ..... **sect. *Paniculata***
– Macro- or microphyllidious foliage, distributed in Mexico, Central America and the Caribbean ..... **sect. *Pseudalbizzia***

***Pseudalbizzia* sect. *Paniculatae* (Benth.) E.J.M. Koenen & Duno, stat. nov. and sect. nov.**
urn:lsid:ipni.org:names:77303802-1

Pithecellobium sect. *Samanea* ser. *Paniculatae* Benth. pro parte, London J. Bot. 3: 219. 1844.
Albizia sect. *Arthrosamanea* ser. *Paniculatae* (Benth.) Barneby & J.W. Grimes pro parte, Mem. New York Bot. Gard. 74(1): 208. 1996. Type species (designated by Barneby and Grimes, Mem. New York Bot. Gard. 74(1): 208. 1996.): *Pithecellobium polycephalum* Benth. = *Pseudalbizzia polycephala* (Benth.) E.J.M. Koenen & Duno.
Pithecellobium sect. *Samanea* ser. *Parviflorae* [sic] Benth. pro parte, Trans. Linn. Soc. London 30: 591 (exclus. sp. 77). 1875 & in Martius, Fl. Bras. 15(2): 445. 1876. Type species (designated by Barneby and Grimes, Mem. New York Bot. Gard. 74(1): 208. 1996.): *Pithecellobium polycephalum* Benth. = *Pseudalbizzia polycephala* (Benth.) E.J.M. Koenen & Duno.

Type. *Pithecellobium polycephalum* Benth. = *Pseudalbizzia polycephala* (Benth.) E.J.M. Koenen & Duno.

Notes. Micro- to mesophyllidious trees with paniculate compound inflorescences of efoliate pseudoracemes and dehiscent plano-compressed papery fruits. Four species of humid, semi-deciduous and seasonally dry tropical and extratropical forests and woodland in South America (Fig. 5).

***Pseudalbizzia barinensis* (L. Cárdenas) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303803-1

Basionym. *Albizia barinensis* L. Cárdenas, Ernstia 21: 5, f. sn. 1983.

Type. Venezuela. Barinas, muy cerca de Punta de Piedra, 3 Apr 1976, *L. Cardenas de Guevara 2273* (holotype: MY; isotypes: BM!, F! [F0093839F], K! [K000527984], NY! [NY00001781], RB! [RB00539860], US! [US00385615], VEN).

Notes. This species has not been included in any phylogenetic analysis, but its foliage, efoliate pseudoracemes and plano-compressed papery fruits leave little doubt that it should be placed in *Pseudalbizzia*. It is here included in section *Paniculata* based on these characters and its South American distribution.

***Pseudalbizzia coripatensis* (Rusby) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303804-1

Basionym. *Pithecellobium coripatense* Rusby, Bull. New York Bot. Gard. 4: 349. 1907.

Type. Bolivia. La Paz, Sur Yungas, at Coripata, 6 May 1894, *M. Bang 2176* (holotype: NY! [NY00334642]; isotypes: BM! [BM000952433], G-2! [G00364414, G00364429], GH-2! [GH00064010, GH00064011], M! [M0218258], K! [K000527985], MINN, MO! [MO-954213], US).

***Pseudalbizzia edwallii* (Hoehne) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303805-1

Basionym. *Pithecellobium edwallii* Hoehne, Bol. Inst. Brasil. Sci. 2: 243. 1926.

Type. Brazil, São Paulo, *G. Edwall 5608* (lectotype: SP, designated by Barneby and Grimes, Mem. New York Bot. Gard. 74(1): 209. 1996).

***Pseudalbizzia polycephala* (Benth.) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303806-1

Basionym. *Pithecellobium polycephalum* Benth., London J. Bot. 3: 219. 1844.

Type. Brazil. Rio de Janeiro, *J.B.E. Pohl 1420* (lectotype: K! (*herb. Bentham*) [K000528000], designated by Barneby and Grimes, Mem. New York Bot. Gard. 74(1): 208. 1996).

***Pseudalbizzia* sect. *Uninervia* E.J.M. Koenen & Duno, sect. nov.**
urn:lsid:ipni.org:names:77303807-1

Type. *Albizia burkartiana* Barneby & J.W. Grimes = *Pseudalbizzia burkartiana* (Barneby & J.W. Grimes) E.J.M. Koenen & Duno.

Notes. Microphyllidious trees with the inflorescences of section *Paniculata*, but with a single vein from the pulvinule at the base of the leaflets. A single, narrowly endemic species in Paraná pine woodland and the Southern Mata Atlantica of Brazil (Fig. 5).

***Pseudalbizzia burkartiana* (Barneby & J.W. Grimes) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303808-1

Basionym. *Albizia burkartiana* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 211–212. 1996.

Type. Brazil. Santa Catarina, Capinzal, on upper Rio Uruguai, 700 m, 21 Dec 1973, *P.R. Reitz & R. M. Klein 14359* (holotype: NY! [NY00001783]; isotype: US! [US00811452]).

Notes. In the protologue the fruits were not described as these were not known at that time. This rare, locally endemic species has since been collected in fruit (*Stival-Santos 678*, BR), and we here provide a description of these. Fruits sessile but with a narrow pseudo-stipitate base, dehiscent along both slightly thickened sutures, the valves plano-compressed, papery in texture, light brown with finely prominent transverse veins, 6.5–12 × 1.2–1.6 cm, 7–12-seeded when well-fertilized.

***Pseudalbizzia* sect. *Pseudalbizzia*.**
Type as for the genus.

Notes. Trees with micro- or macrophyllidious foliage, inflorescences composed of efoliate pseudoracemes arising singly from a leaf axil or sometimes the capitula solitary or paired in the leaf axils, or the pseudoracemes combined into a terminal panicle, fruits plano-compressed with papery valves, dehiscent along both sutures or more rarely indehiscent (in *P. berteroana*), sometimes with a winged margin, seeds straight. Four species predominantly of seasonally dry tropical forests in Mexico, Central America and the Caribbean (Fig. 5).

***Pseudalbizzia adinocephala* (Donn. Sm.) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303809-1

Albizia xerophytica J. Linares, syn. nov., Revista Mex. Biodiversidad 76: 7. 2005. Type: Honduras. El Paraíso, Municipio Morocelí, orillas de Quebrada Grande c. 3.9 km al NE de Morocelí por el camino hacia El Plan. 2002. *J.L. Linares et al. 5674* (holotype: MEXU! [MEXU01160777]; isotype: EAP).

Basionym. *Pithecellobium adinocephalum* Donn. Sm., Bot. Gaz. Crawfordsville. 57: 419. 1914.

Type. Costa Rica. San José, Ad fundum La Verbena prope Alajuelita, 100 m, Aug 1894, *A. Tonduz 8932* (US-3); Dec 1894 (lectotype: *A. Tonduz* 9077 [US-212774]!; isolectotypes: BR-3! [BR0000005189519, BR0000005189182, BR0000005189847], G! [G00364416], designated by Barneby and Grimes, Mem. New York Bot. Gard. 74(1): 218. 1996).

Notes. *Albizia xerophytica* was described from material from dry forest habitats in southern Honduras based on minor differences in leaf and fruit morphology, but we do not consider these to be significantly different from the range of variation that is observed in *P. adinocephala* and prefer the broader concept of the species as described in Barneby and Grimes (1996: 218–220). The difference in habitat (i.e., lower rainfall regions) also appears to be minor, as some specimens from wetter sites have been identified as *A. xerophytica* (see map in Rico Arce et al. 2008) while specimens of *P. adinocephala* have been collected across the full range of drier and wetter sites. Finally, the distribution of *A. xerophytica* is entirely enclosed by the much wider range of *P. adinocephala*.

***Pseudalbizzia berteroana* (Balb. ex DC.) Britton & Rose, N. Amer. Fl. 23: 48. 1928.**

Basionym. *Acacia berteroana* Balb. ex DC., Prodr. 2: 470. 1825.

Type. Republica Dominicana, Sto. Domingo, *C.L.G. Bertero, herb. Balbis s.n.*, 1821 (holotype: G; isotype: M! [M0218254]).

***Pseudalbizzia sinaloensis* (Britton & Rose) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303810-1

Basionym. *Albizia sinaloënsis* in Britton & Rose, N. Amer. Fl. 23(1): 45. 1928.

Type. Mexico. Sinaloa, vicinity of Fuerte, 26 March 1910, *J.N. Rose, P.C. Standley & Russell 13559* (holotype: NY! [NY00001775]; isotype: US! [US00000483]).

***Pseudalbizzia tomentosa* (M. Micheli) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303811-1

Basionym. *Pithecellobium tomentosum* M. Micheli, Mém. Soc. Phys. Genève 34: 285, t. 28. 1903.

Type. Mexico. Michoacán, rives de l'Espiritu Santo, 600 m, 19 April 1898 [*E. Langlassé*] *107* (G): Zilmatango, 30 m, aout 1898, n *280* (G). (lectotype: *E. Langlassé 107* G-385667!; isolectotypes: K! [K000082098], NY (fragm.)! [NY00001777], designated by Standley, Contr. U.S. Natl. Herb. 23: 396. 1922).

***Pseudalbizzia tomentosa* var. *nayaritensis* (Britton & Rose) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303812-1

Basionym. *Albizzia nayaritensis* Britton & Rose, N. Amer. Fl. 23: 47. 1928.

Type. Mexico. Nayarit; San Blas, La Palma, 20 m, 1923, *J. González Ortega 90N* (holotype: US! [US00918691]; isotypes: K! [K000082100], NY-2! [NY00001768, NY00001769]).

***Pseudalbizzia tomentosa* var. *purpusii* (Britton & Rose) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303813-1

Basionym. *Albizzia purpusii* Britton & Rose, N. Amer. Fl. 23: 45. 1928.

Type. Mexico. Veracruz, Rancho Remudadero, 19°15'N, 96°34'W, April 1922, *C.A. Purpus 8723* (holotype: NY! [NY00001773]; isotypes: GH! [GH00069252], MO! [MO-120564], UC! [UC214372], US! [US00000479]).

Pseudalbizzia tomentosa* var. *tomentosa

***Pseudalbizzia* sect. *Pterocarpa* E.J.M. Koenen & Duno, sect. nov.**
urn:lsid:ipni.org:names:77303814-1

Type. *Pithecellobium niopoides* Spruce ex Benth. = *Pseudalbizzia niopoides* (Spruce ex Benth.) E.J.M. Koenen & Duno.

Notes. Microphyllidious trees with the inflorescence usually composed of axillary efoliate pseudoracemes, sometimes a partly or wholly terminal panicle (but not surpassing the foliage), the fruit with a narrowly winged margin and seeds oblique. A single widespread species found in deciduous seasonally dry forests, gallery forest, and evergreen forests in Mexico, Central and South America (Fig. 6).

***Pseudalbizzia niopoides* (Spruce ex Benth.) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303815-1

Basionym. *Pithecellobium niopoides* Spruce ex Benth., Trans. Linn. Soc. London 30: 591. 1875.

Type. Brazil, Pará, Santarem, Nov 1851, *R. Spruce 1088*, *Herb. Bentham* (holotype: K! [K000528013]).

***Pseudalbizzia niopoides* var. *colombiana* (Britton) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303816-1

Albizia niopoides var. *colombiana* (Britton) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 222. 1996.

Basionym. *Albizzia colombiana* Britton, in Britton & Killip, Ann. New York Acad. Sci. 35: 131. 1936.

Type. Colombia. Magdalena, near Bonda, Santa Marta, 3 August 1899, *H.H. Smith 38* (holotype: NY! [NY00001784]; isotypes: BR! [BR0000005111176], E! [E00313853], K! [K000527990], NY!, U-2! [U0003354, U1253389]).

Pseudalbizzia niopoides* var. *niopoides

***Pseudalbizzia* sect. *Arthrosamanea* (Britton & Rose) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303817-1

Arthrosamanea Britton & Rose, Ann. New York Acad. Sci. 35: 128, pro gen. 1936, *sensu stricto*. *Albizia* sect. *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes

pro parte, Mem. New York Bot. Gard. 74(1): 206. 1996. Type species: *Arthrosamanea pistaciifolia* (Willd.) Britton & Rose = *Mimosa pistaciifolia* Willd. = *Pseudalbizzia pistaciifolia* (Willd.) E.J.M. Koenen & Duno.

Albizia sect. *Arthrosamanea* ser. *Multiflorae* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 234. 1996.

Albizia sect. *Arthrosamanea* ser. *Inundatae* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 238. 1996.

Notes. Micro- or macrophyllidious trees, usually the efoliate pseudoracemes arising singly and only rarely arranged in panicles, fruits indehiscent and septate, or lomentiform, one species crypto-lomentiform. Six species of usually humid, often seasonally inundated forest or riparian habitats in South America (Fig. 6).

***Pseudalbizzia decandra* (Ducke) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303818-1

Basionym. *Pithecellobium decandrum* Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 121. 1930.

Type. Brazil. Pará, habitat in silvis non inundatis civitatis Pará circa Óbidos, *A. Ducke* (Herb. Amaz. Mus. Pará 15.724, et H.J.B.R. 10.174) et loco Serra do Dedal ad lacum Faro, *A. Ducke* (H.J.B.R. 20.198), ubi florebat Januario 1927, *A. Ducke* (lectotype: *A. Ducke 10174* RB!; isolectotypes: G! [G00364418], K-2!: [K000527990, K000527998], U-2! [U0003349, U0003350], designated by Barneby and Grimes, Mem. New York Bot. Gard. 74(1): 234. 1996.).

***Pseudalbizzia glabripetala* (H.S. Irwin) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303819-1

Basionym. *Pithecellobium glabripetalum* H.S. Irwin, in Mem. New York Bot. Gard. 15(1): 109. 1966.

Type. Guyana. Orealla, Corantyne River, Oct 1879, *G.S. Jenman 364* (holotype: NY! [NY00334664]; isotypes: BM!, P!).

***Pseudalbizzia inundata* (Mart.) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303820-1

Basionym. *Acacia inundata* Mart., Spix & Mart. in Reise Bras. 1: 555. 1823.

Type. Brazil. Minas Gerais, Rio Sao Francisco, 1818, *C.F.P. von Martius 1659* (holotype: M! [M0218478]; isotypes: K! [K000797598], NY!).

***Pseudalbizzia multiflora* (Kunth) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303821-1

Basionym. *Acacia multiflora* Kunth, Nov. Gen. Sp. (quarto ed.) 6: 277–278. 1823.

Type. Peru. Cajamarca, Prov. Jaén, San Felipe, 980 m, *Aime Bonpland & F.W.H.A. von Humboldt 3562* (holotype: P! [P00679365]).

Pseudalbizzia multiflora* var. *multiflora

***Pseudalbizzia multiflora* var. *sagasteguii* (Barneby & J.W. Grimes) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303822-1

Basionym. *Albizia multiflora* var. *sagasteguii* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 237–238. 1996.

Type. Peru. Cajamarca, Prov. Contumazá, in a quebrada near San Benito, *A. Sagástegui 15410* (holotype: F! [F0042945F]; isotypes: MO! [MO-149743], NY!, US! [US00624358]).

***Pseudalbizzia pistaciifolia* (Willd.) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303823-1

Basionym. *Mimosa pistaciaefolia* [sic] Willd., Sp. Pl. 4: 1028. 1806.

Type. Venezuela. Caracas. *F. Bredemeyer s.n.*, *herb. Willdenow* (holotype: B).

***Pseudalbizzia subdimidiata* (Splitg.) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303824-1

Albizia subdimidiata (Splitg.) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 234. 1996.

Basionym. *Acacia subdimidiata* Splitg. Tijdschr. Natuurl. Gesch. Physiol. 9: 112 (1842).

Type. Suriname. “ad ripas fluminis Surinami superioris”, 27 April 1838. *Splitgerber 917* (holotype: L [L0018505]).

***Pseudalbizzia subdimidiata* var. *minor* (Barneby & J.W. Grimes) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303825-1

Basionym. *Albizia subdimidiata* var. *minor* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 234. 1996.

Type. Guyana. Basin of Essequibo river, Kuyaliwak Falls, 1 Jan 1937, *A.C. Smith 2156* (holotype: NY! [NY00001790]; isotypes: A! [A00069262], G! [G00364427], K! [K000528004], P, U! [U0003358]).

Pseudalbizzia subdimidiata* var. *subdimidiata

Incertae sedis

***Pseudalbizzia buntingii* (Barneby & J.W. Grimes) E.J.M. Koenen & Duno, comb. nov.**
urn:lsid:ipni.org:names:77303826-1

Basionym. *Albizia buntingii* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 223. 1996.

Type. Venezuela. Zulia, alrededores de Casigua El Cubo, 100 m, al este del empalme de la via hacia Casigua con la carretera Machiques-La Fría, 25 Feb 1985, *G.S. Bunting 13370* (holotype: NY! [NY00001782]).

Notes. Fruits of this species are unknown and the species is only known from the type locality (Fig. 5), but it is similar in leaf and inflorescence morphology to several South American species of *Pseudalbizzia*, as described in the protologue. Especially the efoliate pseudoracemes point to this species most likely being correctly accommodated in *Pseudalbizzia.* Collection of fruits and/or inclusion of the species in phylogenetic studies is needed to confirm its generic and sectional placements.

Non-native species

Some cultivated and sometimes naturalized Old World *Albizia* species are found in the New World, including: *A. procera* (Roxb.) Benth., *A. julibrissin*, *A. lebbeck* (L.) Benth., and *A. chinensis* (Osbeck) Merr. For these species, Barneby and Grimes (1996) proposed *Albizia* section *Albizia*, now considered as *Albizia* s.s.

Author contributions

GAP, RR, GCFC, IVM, and RDD designed the study. GAP, LLCI, ELC, RDD contributed labwork. RDD, GCFC, IRM contributed data by supervising students in the lab. EJMK, RDD, XC, SM and CEH contributed taxonomic knowledge, JR contributed species distribution data and the maps. GAP, RDD, ITC, JRP, and RR undertook the phylogenetic analyses. EJMK, RDD, RR, GCFC, CEH and JR contributed to writing the manuscript.

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A new generic circumscription of *Hydrochorea* (Leguminosae, Caesalpinioideae, mimosoid clade) with an amphi-Atlantic distribution

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Abstract

Hydrochorea and *Balizia* were established to accommodate four and three species, respectively, that were previously included in different ingoid genera, based primarily on differences in fruit morphology. Both genera have Amazonia as their centre of diversity, extending to Central America and the Brazilian Atlantic Rainforest. Previous phylogenetic evidence showed *Balizia* to be paraphyletic with respect to *Hydrochorea*, and species of *Hydrochorea* and *Balizia* were placed in a large unresolved polytomy with species of *Jupunba*. Here we present a new phylogenomic analysis based on 560 exons, from which 686 orthologous alignments were derived for gene tree inference. This analysis confirms a paraphyletic *Balizia* in relation to *Hydrochorea*, together with two African species formerly placed in *Albizia* nested within the clade. *Jupunba macradenia* was resolved as sister to the clade combining those taxa. However, quartet support is low for several of the branches at the base of the clade combining the genera *Jupunba*, *Balizia* and *Hydrochorea*, suggesting that rapid initial divergence in this group led to extensive incomplete lineage sorting and consequently poor phylogenetic resolution. Because of these phylogenomic complexities, we decided to use morphology as the main guide to consider *Hydrochorea* as a distinct genus from *Jupunba*, and *Balizia* as

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a new synonym for *Hydrochorea*. The taxonomic treatment includes the study of collections from various herbaria and fieldwork expeditions. We present a re-circumscribed *Hydrochorea* accommodating a total of 10 species, including six new combinations, five new synonyms, one new taxonomic status, two corrections of nomenclature category for lectotypes, and a second step lectotype and three new lectotypes. A new species from the Brazilian Amazon is described and illustrated. An identification key for all species of *Hydrochorea* is presented, together with comments and illustrations.

Keywords
Albizia, *Balizia*, *Cathormion*, Fabaceae, nomenclature, taxonomy

Introduction

Rupert C. Barneby and James W. Grimes established a new generic system for most of the ingoid mimosoids of the Americas in a landmark monographic series (Barneby and Grimes 1996, 1997; Barneby 1998). In it they created seven new genera, including *Hydrochorea* Barneby & J.W. Grimes and *Balizia* Barneby & J.W. Grimes, which were established to accommodate four and three species, respectively, that were previously included (as many ingoid species have been) in several different genera such as *Albizia* Durazz., *Arthrosamanea* Britton & Rose, *Cathormion* Hassk. and *Pithecellobium* Mart., among others (Lewis and Rico Arce 2005; Brown 2008). While Barneby and Grimes (1996: p. 35) stated that *Hydrochorea* and *Balizia* "have arisen from common ancestry", these were nonetheless treated as separate genera based on differences in fruit morphology that were ascribed to adaptation to different habitats and seed dispersal strategies: *Hydrochorea* was defined based on lomentiform fruits adapted to water-borne dispersal in seasonally inundated habitats, while *Balizia* was described as a genus of "terra firme" forest (even though at least two of its three species were mentioned to also often occur on riverbanks), and recognized mainly based on having indehiscent or follicular fruits, with a septate endocarp but not lomentiform. Barneby and Grimes (1996) recognized *Balizia*, *Hydrochorea*, and *Abarema* Pittier s.l. as closely related genera, distinguished by fruit morphology (Iganci and Morim 2009, 2012). However, *Abarema* was shown to be polyphyletic (Iganci et al. 2016) and the type species of the genus, *Abarema cochliacarpos* (Gomes) Barneby & J.W. Grimes is placed in the Inga clade, together with the recently described *A. diamantina* E. Guerra, M.P. Morim & Iganci (Guerra et al. 2016, 2019). The other species of *Abarema* s.l. were segregated in the two genera *Jupunba* Britton & Rose and *Punjuba* Britton & Rose (Soares et al. 2021). These findings question all the former classifications of those taxa, which were mostly based on fruit morphology, and call for further studies aiming to better understand fruit and seed morphology in the context of the evolution of dispersal strategies and ecological adaptations.

Recent phylogenetic evidence (Iganci et al. 2016; Koenen et al. 2020b; Soares et al. 2021; Ringelberg et al. 2022; and a new analysis presented here) has shown *Balizia* to be paraphyletic with respect to *Hydrochorea*. Furthermore, two African species that were formerly placed in several genera including *Albizia* Durazz. and *Cathormion* Hassk.

were also shown to be most closely related to *Hydrochorea* (Koenen et al. 2020b), and their general morphological features and ecology are virtually indistinguishable from Neotropical species of *Hydrochorea*.

Besides the advances in phylogenetic and phylogenomic methods, recent fieldwork collecting programmes have greatly contributed to herbarium collections of Amazonian taxa (Milliken et al. 2010; Cardoso et al. 2017; Ulloa et al. 2017; BFG 2021), and furthermore, the Reflora Program has led to the online availability of nearly all Brazilian plant collections (Pearce et al. 2020; BFG 2021), providing excellent opportunities for synoptic taxonomic revisions.

Here we present a taxonomic update including a new generic circumscription of *Hydrochorea* based on phylogenomic and morphological evidence, along with a nomenclatural review presented as a synopsis of the genus, which includes new combinations, new synonyms, and the description of a newly discovered species from the Upper Rio Negro. We include an identification key, illustrations, and distribution maps for the 10 species now accommodated in *Hydrochorea*.

Materials and methods

Taxonomy

Standard herbarium taxonomy practices were used for analysis of all species studied in the present work. The collections (including digital images) of the following herbaria were analysed: A, BM, BR, CTBS, E, F, G, GH, HUEFS, IAN, INPA, K, MG, MO, NY, P, PEL, R, RB, SP, US and Z (Thiers 2022). Fieldwork was carried out especially in the Upper Rio Negro region of Amazonian Brazil, where we collected four species of *Balizia* and *Hydrochorea*, including a species new to science. All the new collections were incorporated into the RB herbarium, in the Rio de Janeiro Botanical Garden, and duplicates were sent to partner institutions. Fresh leaf samples were stored in silica gel for total DNA extraction. We also visited the collections in NY to study the specimens that Barneby and Grimes (1996) worked with for their taxonomic account. Combined with studying the large number of new collections that have been made in the past 25 years since publication of the Barneby and Grimes (1996) taxonomic account, we were able to review their taxonomic decisions based on the relatively limited herbarium material available to them at the time.

Online databases were used to view digital images of specimens including types, especially the Reflora Virtual Herbarium (REFLORA -Herbário Virtual 2022), National Institute of Science and Technology (INCT-Splink 2022), and JSTOR (2022). Geographic distributions of each species were inferred based on specimen labels and literature (Barneby and Grimes 1996; Soares 2015). The morphological characters were described following Beentje (2016) and Iganci and Morim (2009, 2012), for habit, leaves, inflorescences, flowers, pods, and seeds. Original descriptions of all taxa were analysed, and nomenclature was revised according to the International Code of Nomenclature of algae, fungi and plants (the Shenzen code; Turland et al. 2018). Except for the new

species described here, and the two African species now placed in *Hydrochorea*, all other species have been described earlier in detail by specialists (Barneby and Grimes 1996). Thus, for those species, here we only present new combinations, taxonomic notes and a reference to the literature where the complete description is available. Synonyms are accepted following Barneby and Grimes (1996) and are only listed here when either lectotypification or nomenclatural correction is needed.

Exon selection, matrix assembly and phylogenomic analysis

To better evaluate the evidence for monophyly of the studied genera, or lack thereof, we have performed new analyses based on a selection of exons with flanking non-coding regions derived from the sequencing data of Koenen et al. (2020b) and Ringelberg et al. (2022), including network analyses and quantification of supporting bipartitions across gene trees for alternative topologies. The sequencing methods are described in those publications and here we only briefly describe our methods when they differ from Koenen et al. (2020b) and Ringelberg et al. (2022). In the original *Mimobaits* probe design (Koenen et al. 2020b), exons were predicted, and flanking untranslated regions (UTRs) were also (partially) included. From this reference exon set, we selected all of those that are longer than 500bp, which for initial or terminal exons includes the UTR. Read data of Koenen et al. (2020b) and Ringelberg et al. (2022) for the accessions of the Jupunba clade plus six outgroup accessions were mapped against these exons and non-matching reads discarded. Read quality filtering and *de novo* assembly methods followed Koenen et al. (2020b), and after clustering the assembled contigs to the reference sequences of the exons, initial alignments and gene trees were inferred using MAFFT (Katoh et al. 2005) and RAxML (Stamatakis 2014), respectively. Then, mono- and paraphyletic groups per species were collapsed to select a single allele in case multiple alleles were reconstructed (Yang and Smith 2014), followed by cutting long internal branches to splice potential paralogs into separate alignments using the cut_long_branches.py script of Yang and Smith (2014). The resulting clusters were then realigned with MAFFT and used to infer multilabeled gene trees using RAxML. Finally, gene trees with a single tip per species were extracted from these gene trees using the maximum inclusion (MI) method of Yang and Smith (2014) and used in species tree analysis in ASTRAL-III (Zhang et al. 2018) with default settings and nodes with less than 10% bootstrap support collapsed as suggested by the authors of the software. A filtered supernetwork was constructed in SplitsTree4 (Huson 1998) from the same set of gene trees but with nodes with less than 50% bootstrap support collapsed and with the mintrees parameter set to 100 (25% of the total number of gene trees). Quantification of supporting bipartitions across gene trees for alternative topologies followed the same methodology as Koenen et al. (2020a).

Results

Our herbarium taxonomic work has resulted in the synopsis presented below. This includes a total of six new combinations, including a new status for a species that had

been treated at varietal rank by Barneby and Grimes (1996), as well as the description of a new species. *Balizia* and its sections are placed in the synonymy of *Hydrochorea* and two new heterotypic synonyms, one at species and one at varietal rank, are proposed, as well as two lectotype corrections. A second step lectotype and three new lectotypes are designated.

Phylogenomic analysis

A total of 560 exons were selected for gene tree inference, from which 398 MI gene trees were extracted after clustering and filtering (Suppl. materials 1, 2). The species tree based on these gene trees (Fig. 1A, Suppl. material 3) does not provide qualitatively different results from those of Ringelberg et al. (2022), showing a paraphyletic *Balizia* relative to *Hydrochorea* together with the two African *Cathormion*/*Albizia* species. All currently recognised species of *Balizia* and *Hydrochorea*, including the type species of both genera, were sampled, with the exception of *H. marginata*, although this species was included in the studies of Iganci et al. (2016) and Soares et al. (2021). Also, *Jupunba macradenia* (Pittier) M.V.B. Soares, M.P. Morim & Iganci was found as sister of the clade combining these genera. However, quartet support is low for several of the branches at the base of the clade combining the genera *Jupunba*, *Balizia* and *Hydrochorea*, suggesting that rapid initial divergence in this group led to extensive incomplete lineage sorting and consequently poor phylogenetic resolution. This is further reinforced by the filtered supernetwork (Fig. 1B), which also clearly shows the paraphyly of *Balizia*, and shows that *Hydrochorea* and *Balizia* together form a group that is separate from *Jupunba*, but with a complex network structure indicative of incomplete lineage sorting. When the monophyly of these genera and their sister-group relationships are evaluated based on the number of compatible bipartitions across gene trees, it is clear that *Albizia* sect. *Arthrosamanea* (Britton & Rose) Barneby & J.W. Grimes, *Punjuba* and *Hydrochorea* (including the two African *Cathormion*/*Albizia* species) are each monophyletic, while *Balizia* and *Jupunba* are only supported to be monophyletic by a small number of gene trees (Fig. 1C). Support for the sister-group relationship of *Jupunba macradenia* with *Balizia* + *Hydrochorea* is supported by c. 10% of the gene trees. This is higher than what is found for some other species of *Jupunba* that are sister to *Balizia* + *Hydrochorea* in some gene trees, but nonetheless the separation between these genera is not very clear likely due to significant incomplete lineage sorting.

Discussion

In this study, we have made an in-depth investigation of the generic delimitation issues surrounding the genera *Balizia*, *Cathormion* and *Hydrochorea*, to reconcile morphological characters of the group with phylogenetic relationships and to propose a revised classification. While the uncovered phylogenomic complexity adds further difficulty to the goal of achieving a stable classification for these taxa, we conclude that the taxa with either indehiscent, follicular or lomentiform fruits, that are septate between the seeds at least in

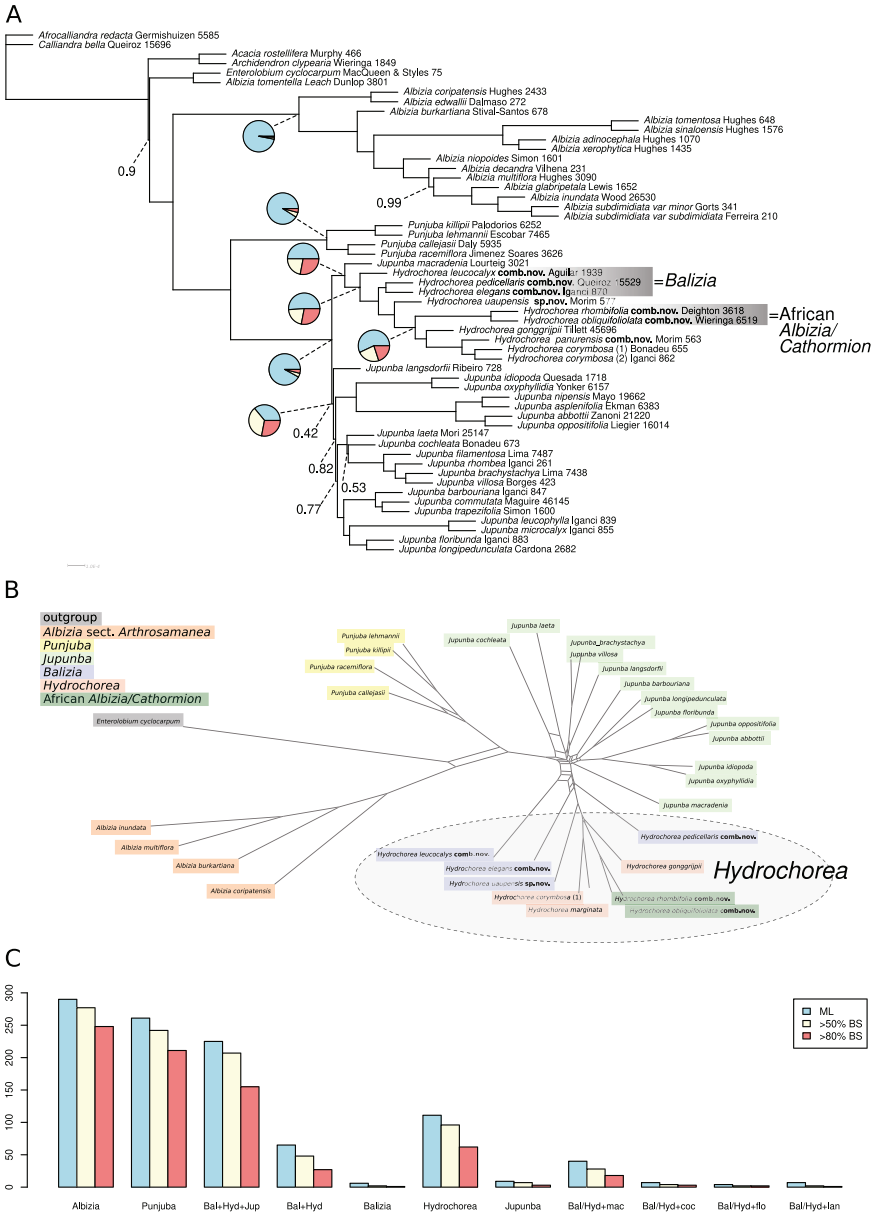

Figure 1. Phylogenomics of the Jupunba clade **A** ASTRAL-III species tree based on 398 gene trees, posterior probability values are shown only for those nodes for which support is lower than 1.0, and pie charts on several crucial nodes indicate alternative quartet support **B** filtered super-network of the same gene tree set with the genus *Hydrochorea* as circumscribed in this study indicated by a grey ellipse **C** bar graphs indicating numbers of compatible bipartitions across the same gene tree set in the maximum-likelihood estimate (ML) and when only taking into account bipartitions that receive at least 50 or 80% bootstrap support. The abbreviations that are used are Bal = *Balizia*, Hyd = *Hydrochorea*, and Jup = *Jupunba*. Note that the taxonomy of *Albizia* sect. *Arthrosamanea* is updated in this volume by Aviles Peraza et al. (2022), where new binomials in the genus *Pseudalbizzia* are presented for the majority of the species of this section.

the endocarp, are preferably all classified within a recircumscribed *Hydrochorea*, separate from the genus *Jupunba* which is characterized by dehiscent fruits that are never septate between the seeds. Extensive incomplete lineage sorting surrounding the early evolution of these genera means that they are phylogenomically not well separated (Fig. 1), but in order to ensure both diagnosability and stability of names, we believe keeping these as separate genera is justified (i.e., transferring some species to *Hydrochorea* to account for the non-monophyly of *Balizia* is preferable to moving all taxa to a morphologically heterogeneous *Jupunba*).

One of the most interesting aspects of *Hydrochorea* is the evolution of its fruit morphology and dehiscence in adaptation to water-borne seed dispersal, which presumably led to its distribution in riparian, swamp and periodically inundated forests on both sides of the Atlantic, as trans-oceanic dispersal is presumed to be relatively likely in hydrochorous plants. Much attention was traditionally given to pod morphology in mimosoids, in attempts to classify the ingoid genera, as one of the most easily observable characters to visually distinguish the taxa (Barneby and Grimes 1996; Lewis and Rico-Arce 2005). Lomentiform pods are typical of most species of *Hydrochorea*, but are also found in *Albizia* s.s. (*Albizia dolichadena* I.C. Nielsen, *Albizia moniliformis* (DC.) F. Muell., *Albizia rosulata* (Kosterm.) I.C. Nielsen and *Albizia umbellata* (Vahl) E.J.M. Koenen) and *Albizia* sect. *Arthrosamanea* (Barneby and Grimes 1996; Aviles Peraza et al. 2022). The craspedia, as found in *Mimosa* L., *Adenopodia* C. Presl and *Entada* Adans., are somewhat similar, but in those genera there is a replum (a persistent framework formed by the upper and lower suture of the craspedium) that stays attached to the infructescence after the 1-seeded articles have been shed. The fruit of *Cathormion altissimum* (Hook. f.) Hutch. & Dandy (which is transferred to a new genus by Koenen 2022) is also similar, but the fruit of that species differs in containing aerenchymous tissue on the seminiferous nuclei to promote floating. These various lomentiform ingoid fruits also differ in whether they break up while still attached to the tree as is the case in most species of *Hydrochorea* and some species of *Albizia* sect. *Arthrosamanea*, or whether the fruit falls from the tree entire and only tardily breaks up into 1-multiple seeded articles afterwards, as appears to be the case in most of the other genera. Phylogenetic evidence clearly indicates that these fruits have all evolved independently from one another (Ringelberg et al. 2022), presumably in response to adaptation to riparian and periodically inundated habitats. The homoplasious nature of these similar fruits has led to many species having been moved around between different genera, based on their fruit morphology (Nielsen 1981). We note that the legume fruit appears to be amenable to the evolution of lomentiform fragmentation, given the similar craspedia that were independently derived at least twice and, moreover, lomentiform fruits are also present in several lineages of subfamily Papilionoideae.

Recent advances in molecular systematics of ingoid legumes also demonstrated the pod morphology to be less informative than previously thought (Souza et al. 2013; Iganci et al. 2016; Koenen et al. 2020b; Soares et al. 2021; Souza et al. 2022). Barneby and Grimes (1996) stated that *Balizia* and *Hydrochorea* closely resemble *Albizia* but are distinguished by indeterminate inflorescence-axes and vegetative branches arising from

sylleptic and proleptic buds, pinnate leaflet venation, and truncate ovaries. The authors also highlighted the strong similarities in flower morphology shared between *Abarema* s.l., *Balizia* and *Hydrochorea*.

Iganci et al. (2016) found the species of *Hydrochorea* and *Balizia* in a large unresolved polytomy together with *Jupunba* species. The Bayesian results of Soares et al. (2021) are in line with the generic delimitation proposed here, with 1.0 posterior probability supporting *Jupunba*, *Hydrochorea* and *Balizia* as monophyletic considering matK sequences only, and a monophyletic *Jupunba* and paraphyletic *Hydrochorea* in relation to *Balizia* when considering ETS sequences only. However, there was no bootstrap support for a monophyletic *Jupunba* and neither for the clade uniting *Hydrochorea* and *Balizia*. The results of Ringelberg et al. (2022) show that *J. macradenia* is more closely related to *Hydrochorea* and *Balizia* than to other species of *Jupunba*, in contrast to the phylogenetic position of the same accession in Soares et al. (2021), but in accordance with the phylogenomic results presented here. Notably, Soares et al. (2021) included three accessions of *J. macradenia*, which were firmly nested in a monophyletic *Jupunba*, suggesting that further phylogenomic analyses with more accessions included will need to be carried out to further test the monophyly of *Jupunba*.

Phylogenetic evidence (Iganci et al. 2016; Koenen et al. 2020b; Soares et al. 2021; Ringelberg et al. 2022; and a new analysis presented here) that shows *Balizia* to be paraphyletic with respect to *Hydrochorea*, as well as the field discovery of a new species that is morphologically intermediate between the two genera, with crypto-lomentiform pods that resemble more the follicle of *Balizia pedicellaris* (DC.) Barneby & J.W. Grimes than the lomentiform pods of *Hydrochorea*, but a species of seasonally inundated forest with hydrochorous seed dispersal, prompted us to decide that the two genera are best combined. Furthermore, two African species that were formerly placed in several genera, including *Albizia* and *Cathormion*, were shown to be closely related to *Hydrochorea* based on phylogenomic evidence (Koenen et al. 2020b). These species are therefore best accommodated within *Hydrochorea*, as their general morphological features and ecology are virtually indistinguishable from Neotropical species of *Hydrochorea*.

Koenen et al. (2020b) and Ringelberg et al. (2022) also show that *Albizia* sect. *Arthrosamanea* is placed in the Jupunba clade, being more closely related to *Jupunba*, *Punjuba*, *Balizia* and *Hydrochorea* than to *Albizia* s.s. These results are reinforced by Aviles Peraza et al. (2022) who proposed nomenclatural updates to solve this situation based on more extensive sampling of *Albizia* sect. *Arthrosamanea*. In our study (Fig. 1), we have still referred to these species as *Albizia* sect. *Arthrosamanea* but we refer the reader to Aviles Peraza et al. (2022) for presentation of a new taxonomy of the group.

Based on parsimony analysis of morphological characters only, Barneby and Grimes (1996) recognized pollen polyads comprising 16 grains as a synapomorphy for the Abarema alliance, while other alliances that they recognized (e.g., the Samanea, Chloroleucon and Inga alliances) presented a polymorphic polyad number. Indeed, Guinet and Grimes (1997) studied all Neotropical species of *Hydrochorea* and *Balizia* for their polyads and we observed that the nested African species *Cathormion obliquifoliolatum* (De Wild.) G.C.C. Gilbert & Boutique (*Deighton 3618*, K) and *Cathormion rhombifolium*

(Benth.) Keay (Germain 87, K) also have 16-celled polyads. Polyad morphology was also highlighted as diagnostic for the recognition of *Afrocalliandra* E.R. Souza & L.P. Queiroz, a genus segregated from *Calliandra* Benth. (Souza et al. 2013), and more attention should be given to this character in future studies. Furthermore, the taxa in the Jupunba clade share the simultaneous presence of vegetative and reproductive branches (sylleptic), a character considered by Grimes (1999) as uncommon amongst the ingoid legumes. Thus, possessing polyads with 16 grains and sylleptic branches could circumscribe either the clade comprised of *Hydrochorea*, *Jupunba* and *Punjuba*, or a more conservative *Jupunba* s.l. Forthcoming studies, including more samples of unstable taxa in current molecular analyses, new field collections and advances in phylogenomic analysis, will hopefully resolve this question.

We did not include *Hydrochorea acreana* (J.F. Macbr.) Barneby & J.W. Grimes in our synopsis and the name is here considered as *incertae sedis*. Pods from this species were not known to Barneby and Grimes (1996), and herbarium specimens are difficult to identify when flowers and especially fruits are unavailable. The type specimen (*Krukoff 5631*, NY334624) includes flowers arranged in a large terminal panicle composed of umbelliform pseudoracemes of capitula, differing from the axillary to terminal inflorescences in *Hydrochorea* and *Jupunba* that are not paniculate, and always have sylleptic branches present. Citing fruiting Central American collections, *Hydrochorea acreana* was combined into *Abarema* s.l. by Rico-Arce (1999) as *Abarema acreana* (J.F. Macbr.) L. Rico. However, the Central American collections cited by Rico-Arce (1999) were identified by Barneby and Grimes as either *Abarema macradenia* (Pittier) Barneby & J.W. Grimes or *Abarema adenophora* (Ducke) Barneby & J.W. Grimes, with which we agree. Interestingly, a specimen from Acre which was collected in 1995 (*Oliveira 691*; NY00662831) and was presumably not seen by Barneby and Grimes (1996), but was identified as *A. acreana* by L. Rico-Arce, does include unripe pods and this material is likely conspecific with the type material of *H. acreana*. However, as discussed before, fruit morphology often has been shown to be rather misleading in mimosoid taxonomy due to homoplasy, and we point out the differences in inflorescence structure from *Jupunba* as discussed above. Soares et al. (2021) resolved *H. acreana* as sister to *Albizia subdimidiata* (Splitg.) Barneby & J.W. Grimes, and not closely related to *Hydrochorea* nor *Jupunba*, but these analyses were based on ETS sequences only and morphologically the material does not bear much resemblance to species of *Albizia* sect. *Arthrosamanea*, in which *Albizia subdimidiata* is placed. Given the taxon's unusual combination of morphological characters, it may well represent an isolated lineage that merits recognition as a distinct genus; this decision is pending further study.

Taxonomic treatment

Hydrochorea **Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 23. 1996.**
Figs 2, 3

Balizia Barneby & J.W. Grimes, syn. nov., Mem. New York Bot. Gard. 34(1). 23. 1996. Type: *Balizia pedicellaris* (DC.) Barneby & J.W. Grimes.

Balizia sect. *Leucosamanea* Barneby & J.W. Grimes, syn. nov., Mem. New York Bot. Gard. 34(1). 36. 1996. Type: *Balizia leucocalyx* (Britton & Rose) Barneby & J.W. Grimes.

Balizia Barneby & J.W. Grimes sect. *Balizia* syn. nov., Mem. New York Bot. Gard. 34 (1). 37. 1996. Type: *Balizia pedicellaris* (DC.) Barneby & J.W. Grimes.

Type. *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes.

Description. Shrubs and **trees**, unarmed; branches grey to brown pilosulous to glabrescent, cylindrical; stipules persistent or caducous. **Leaves** bipinnate, with 1–15 pairs of pinnae; petiole canaliculate or cylindrical, grey to brown pilosulous or glabrous; nectaries sessile to stipitate, orbicular, patelliform, or cupuliform, the first either near mid-petiole or between the first pinnae pair, and often along the leaf rachis, between the leaflet pairs; leaflets 2–33 pairs per pinna, petiolate to subsessile, rhombic-ovate, rhombic-lanceolate, rhombic-oblong, rhombic-obovate, ovate, elliptic, oblong, lanceolate or oblanceolate, grey to brown pilosulous, ciliate or glabrous, concolorous or more often discolorous, venation pinnate. **Inflorescence** consisting of umbelliform capitula or corymbiform racemes, arising singly or fasciculate from the axils of coeval or hysteranthous leaves, bracts generally caducous; bracteoles persistent or caducous. **Flowers** heteromorphic, pedicellate in peripheral flowers, mostly pentamerous, and sessile in the larger terminal flower, 5–8-merous; calyx green, gamosepalous, campanulate, or tubular, pubescent, ciliate or glabrous; corolla pinkish to reddish, yellowish or whitish, gamopetalous, infundibuliform, campanulate, or tubular, glabrous, puberulent, ciliate or pilose at the apex; androecium with (10–)12–60(–75) stamens; filaments white, greenish or roseate, fused into a tube, included in peripheral flowers or exserted beyond the corolla in the terminal flower; stemonozone present, anthers dorsifixed; ovary superior, sessile, truncate at the apex, usually pubescent or sometimes glabrous. **Fruits** sessile or shortly stipitate, straight or slightly recurved, either lomentiform, the seeds released in one-seeded articles, or woody and indehiscent, the exocarp with transverse fibres and the endocarp hard and septate, or follicular, with similar exocarp but the septate endocarp papyraceous and shed along with the seeds, or crypto-lomentiform with follicular dehiscence, the exocarp smooth and the endocarp remaining attached to the seeds forming 1-seeded articles. **Seeds** with a hard testa, with pleurogram complete or narrowly U-shaped.

Distribution and habitat. North America (Mexico), Central America (Belize, Costa Rica, Guatemala, Honduras and Nicaragua), South America (Brazil, Bolivia, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname and Venezuela) and Africa (Congo Basin and West Africa) (Fig. 2A). *Hydrochorea* species occur in riparian habitats, inundated and non-inundated wet tropical forests of the Orinoco and Amazon basins, pre-Andean Amazonia along the Nor-Yungas and Pando in Bolivia, Vaupés in Colombia and Huánuco in Peru, Central Brazilian Savanna, the Atlantic Rainforest of Brazil and extending to northern South America in Venezuela and the Guianas and the Gulf-Caribbean lowlands until Mexico, and one species in coastal tidal swamp forests in Upper Guinea (West Africa) and one species in riparian and seasonally inundated forests in the Congo Basin.

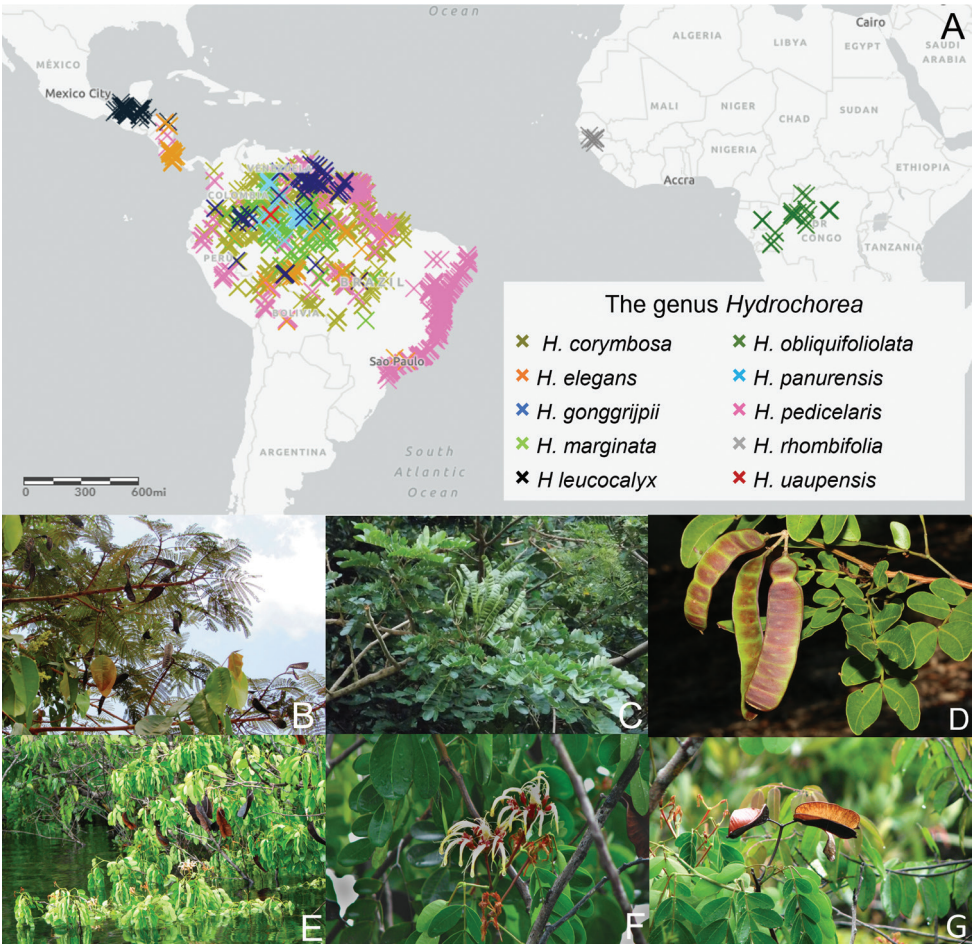

Figure 2. The genus *Hydrochorea* Barneby & J.W. Grimes **A** The amphi-atlantic geographic distribution of *Hydrochorea* **B** *Hydrochorea pedicellaris* (DC.) M.V.B. Soares, Iganci & M.P. Morim foliage and fruits **C** *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes foliage and fruits **D** *Hydrochorea panurensis* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci foliage and fruits **E** *Hydrochorea uaupensis* M.P. Morim, Iganci & E.J.M. Koenen in habitat, with foliage and fruits **F** Flowers of *H. uaupensis* after rain **G** mature fruits of *H. uaupensis.* **B, C** from M.V.B Soares **D** from D. Cardoso **E–G** from J.R.V. Iganci.

Note. Since the names *Hydrochorea* and *Balizia* were published in the same publication (Barneby and Grimes 1996), neither has priority, although *Hydrochorea* was treated as genus 1 and *Balizia* as genus 2, *Hydrochorea* thus appearing first in the publication. The name *Hydrochorea* is here chosen to represent the recircumscribed genus, especially since the name is appropriate for most of its species, and most *Balizia* species are also thought to frequently use water-borne seed dispersal, and all but one species (*B. elegans*) are reported to often occur along river-banks. The name *Balizia*, being an anagram of *Albizia*, is less appropriate

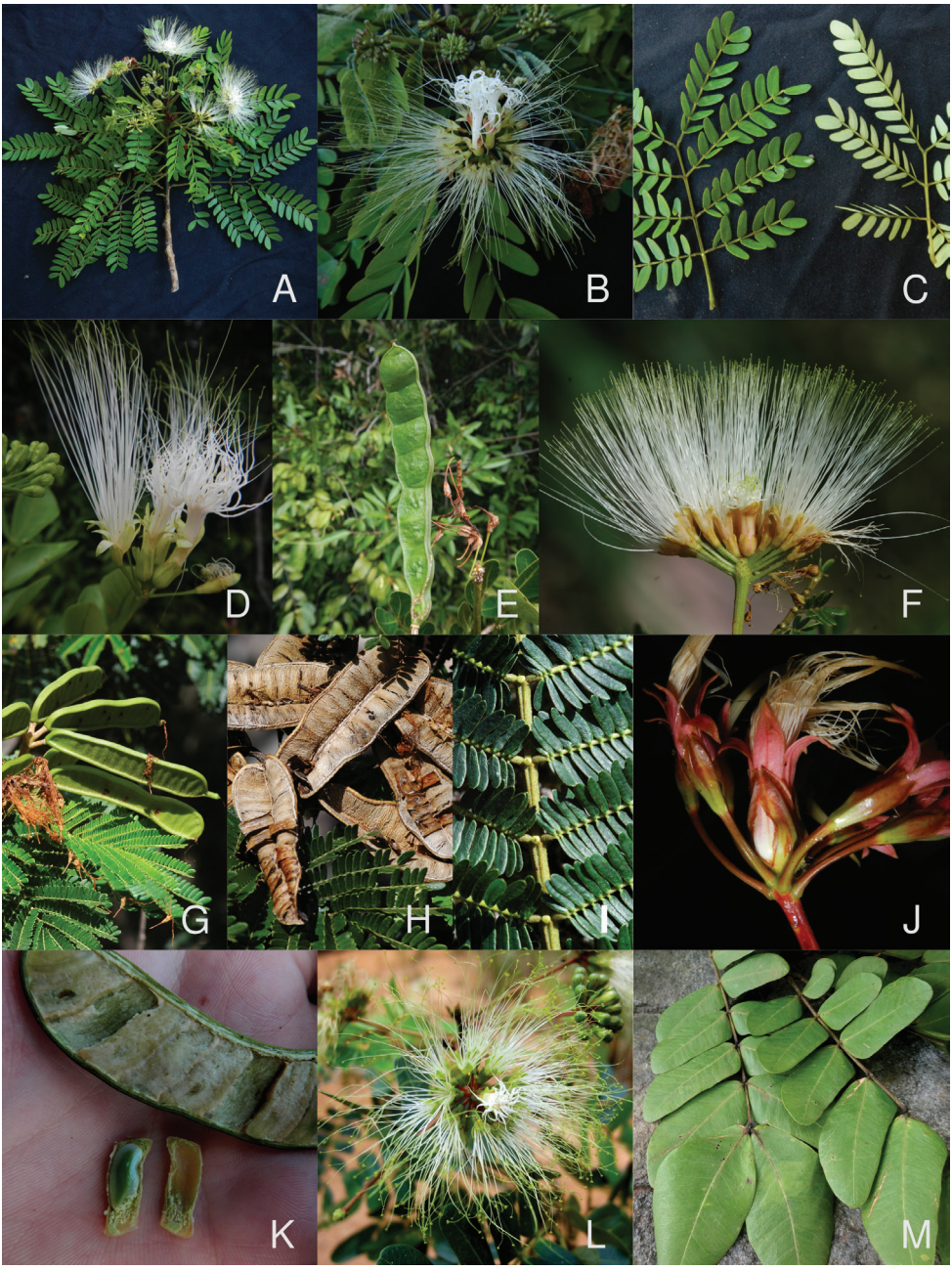

Figure 3. The genus *Hydrochorea* Barneby & J.W. Grimes (continued). Species from the Americas **A** flowering branch of *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes **B** close-up of inflorescence of *H. corymbosa* **C** discolorous leaves of *H. corymbosa* **D** close-up of inflorescence of *Hydrochorea panurensis* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci **E** unripe lomentiform pod of *H. panurensis* **F** close-up of inflorescence of *Hydrochorea pedicellaris* (DC.) M.V.B. Soares, Iganci & M.P. Morim, with a few peripheral flowers removed to expose sessile terminal flowers **G** unripe pods of *H. pedicellaris* **H** dehisced follicular pods of *H. pedicellaris* showing papery septate endocarp **I** detail of primary rachis

of *H. pedicellaris* showing interpinnal extra-floral nectaries **J** inflorescence of *Hydrochorea uaupensis* M.P. Morim, Iganci & E.J.M. Koenen showing large sessile central flower and pedicellate peripheral flowers **K** unripe crypto-lomentiform pod and seed enveloped by septate endocarp of *H. uaupensis*; African species **L** inflorescence of *Hydrochorea obliquifoliolata* (De Wild.) E.J.M. Koenen **M** pinnae of *Hydrochorea rhombifolia* (Benth.) E.J.M. Koenen showing rhombic leaflets. **A–E, J, K** Erik Koenen **F-I** Colin Hughes **L** Jan Wieringa **M** William Hawthorne. Vouchers **A–C** *J.R.V. Iganci 862* **D, E** *M.P. Morim 563* **F–I** *L.P. Queiroz 15529* **J, K** *M.P. Morim 577* **L** *J.J. Wieringa 6519* **M** unvouchered.

given that several of its species have previously been placed in *Albizia* and therefore the name may suggest close kinship, while actually being most closely related to the genus *Jupunba*.

Identification key to the species of *Hydrochorea*

1a Species from Congo Basin and West Africa **2**

2a Adaxial leaflet surface shiny, abaxial leaflet surface glabrous, apart from the ciliate midrib or with few scattered short hairs especially on and near the midrib; calyx and corolla green to greenish white, corolla lobes glabrous or with a few short white hairs around the apex, Congo Basin (Democratic Republic of Congo, Central African Republic and Gabon) ..... **6. *H. obliquifoliolata***

2b Adaxial leaflet surface dull, abaxial leaflet surface pilose with varying density of hairs (rarely nearly glabrous); calyx and corolla white, upper half of corolla lobes rusty pilose to villous, West Africa (Senegal, Guinea-Bissau, Guinea, and Sierra Leone) ..... **9. *H. rhombifolia***

1b Species from North, Central and South America **3**

3a Pinnae 1–jugate on every leaf (seldom 2-jugate and then the true petiole very short) **4**

4a Calyx covering the corolla in bud; flowers glabrous, terminal flower with tubular calyx ..... **7. *H. panurensis***

4b Calyx not covering the corolla in bud; flowers puberulous, terminal flower with campanulate calyx ..... **5. *H. marginata***

3b Pinnae 2– or more jugate (seldom 1–jugate on some leaves of the same individual) **5**

5a Leaflets up to 10 pairs per pinna **6**

6a Pinnae 1–2 jugate, leaflets ovate to rhombic-ovate, corolla of peripheral flowers up to 1.5 mm long; follicular crypto-lomentiform fruit ..... **10. *H. uaupensis***

6b Pinnae (2–)3–6-jugate; leaflets rhombic-oblong, rhombic-ovate or rhombic-lanceolate; corolla of peripheral flowers with more 1.5 mm long; fruit indehiscent or lomentiform **7**

7a Leaflets rhombic-oblong; corolla of peripheral flowers more than 7 mm long ..... **4. *H. leucocalyx***

7b Leaflets rhombic-ovate to rhombic-lanceolate; corolla of peripheral flowers up to 6 mm long ..... **1. *H.corymbosa***

5b	Leaflets in more than 10 pairs per pinna 8
8a	Corolla of peripheral flowers 8–10 mm long, fruit indehiscent, not lomentiform ..... **2. *H. elegans***
8b	Corolla of peripheral flowers up to 7.5 mm long, fruit lomentiform or follicular **9**
9a	Pinnae 3–5-jugate; fruit lomentiform ..... **3. *H. gonggrijpii***
9b	Pinnae 6–17-jugate; fruit follicular, with septate endocarp and transverse fibers in the exocarp ..... **8. *H. pedicellaris***

1. *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes, New York Bot. Gard. 74(1): 27. 1996.
Fig. 2A, C, 3A-C, 4

Pithecellobium subcorymbosum Hoehne [as *Pithecolobium*], Comiss. Linhas Telegr. Estratég., Mato Grosso-Amazonas, Bot. 8: 18, Ic. 133. 1919. Type: Brazil, Mato Grosso, São Luiz de Cáceres, nas margens do rio Paraguai, perto da Campina, *Hoehne 4582* (lectotype, designated here from amongst the syntypes: R! [R000003169]; isolectotype: SP).

Basionym. *Mimosa corymbosa* Rich., Actes Soc. d'Hist. Nat. Paris 1: 113. 1792.

Type material. French Guiana, frequens in sylvis ripariis fluvii Kourou, *Louis Claude Richard s.n.* (lectotype, designated by Barneby and Grimes 1996, p. 27, as holotype, here corrected: P [P02142909] digital image!).

Distribution and habitat. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Venezuela. *Hydrochorea corymbosa* occurs in periodically or permanently inundated riparian forest, gallery forest, and open vegetation, up to 480 m elevation (Barneby and Grimes 1996).

Notes. *Hydrochorea corymbosa* is morphologically similar to *H. gonggrijpii* by its leaves with (2–)3–6 pairs of pinnae (3–5 pairs of pinnae in *H. gonggrijpii*), but differs by presenting (4–)5–11(–14) leaflet pairs per pinnae (vs. (12–)14–35 in *H. gonggrijpii*). *Hydrochorea corymbosa* has a wide distribution in the Brazilian Amazon, and displays wide morphological plasticity. Barneby and Grimes (1996) recognised the specimen *Louis Claude Richard s.n.* (P02142909) as holotype, although the species protologue did not present a type specimen. The specimen does represent original material that the author associated with the taxon, being a specimen collected by the author and annotated as *Mimosa corymbosa*. Thus, *Louis Claude Richard s.n.* (P02142909) is here corrected to lectotype (Art. 9.3, 9.4, 9.8 and 9.10; Turland et al. 2018).

Selected specimens examined. Brazil, Amazonas: São Gabriel da Cachoeira, entre Assunção do Içana e Camarão, mato de Igapó, margem do rio, 10 July 2012, *J.R.V. Iganci 862* (RB). Bolivia, Pando: Federico Roman, bordo del Río Abuna, 18 November 2006, *S. Altamirano & H. Ramos 4293* (K). Colombia, Vaupés: Mitú

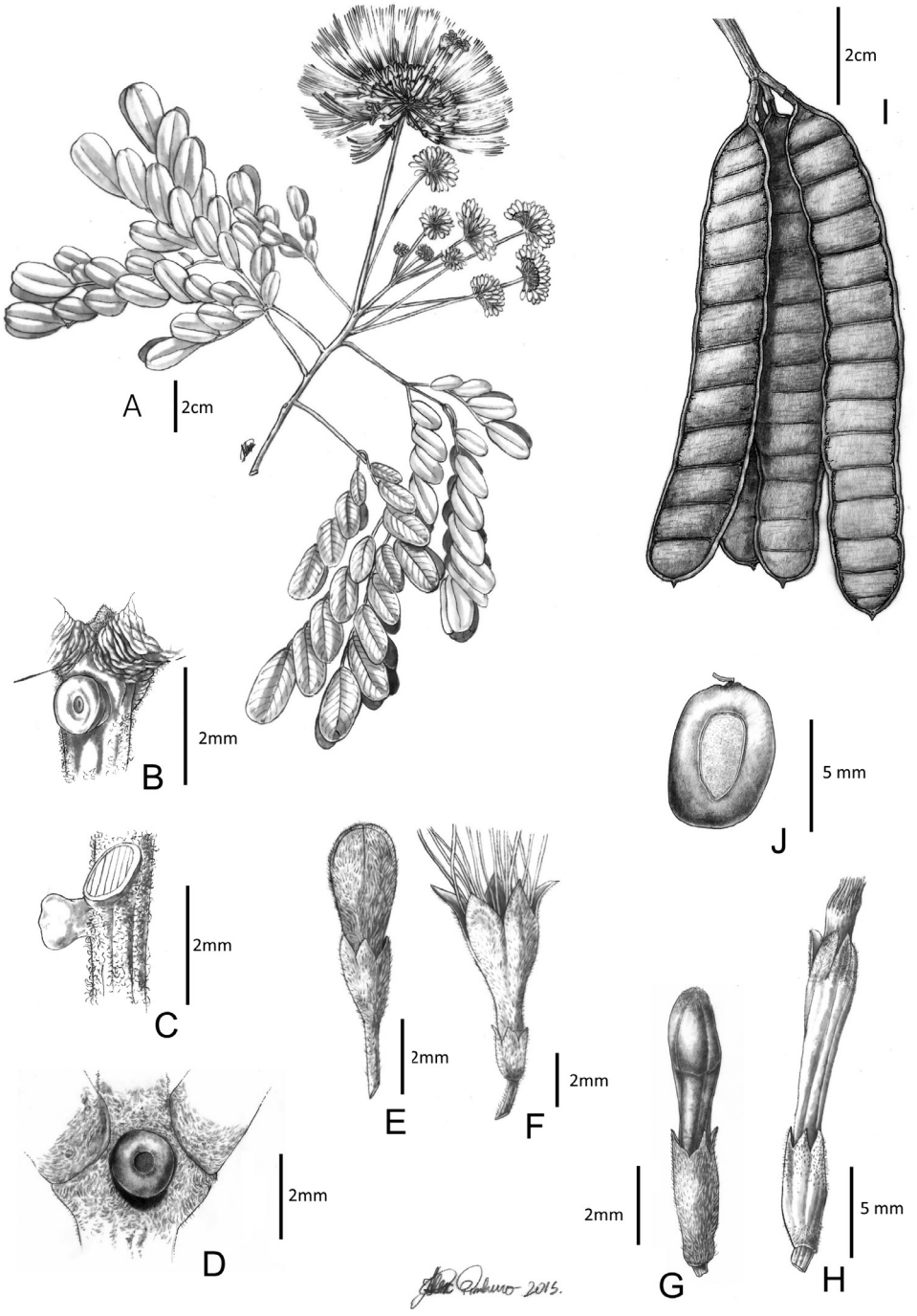

Figure 4. *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes **A** branch with inflorescences **B–D** extra-floral nectaries **E** peripheral flower bud **F** peripheral flower **G** terminal flower bud **H** terminal flower **I** fruit **J** seed. **A, E–H** from *M.V.B. Soares 75* **B–D** from *M.V.B. Soares 180* **I–J** from *M.V.B. Soares 174*. Illustration by Alex Pinheiro.

and Vicinity, lower rio Kubiyú, 26 September 1976, *Zarucchi 2147* (INPA). Ecuador, Francisco de Orellana: Estación Científica Yasuní, Río Tiputini, este de la Carretera Repsol-YPF, km 7 desvío hacia el pozo Tivacuno, Laguna Herradura, 20 April 1999, *G. Villa 177* (K). Guyana: Potaro-Siparuni, riparian zone lower Kuribrong, April 2010, *Zartman et al. 8002* (INPA). Peru, Loreto: Jenaro Herrena, Cano Supay, flooded forest along cano, 23 May 2002, *T.D. Pennington et al. 17430* (K). Venezuela, Amazonas: Departamento Rio Negro, middle part of the Río Baria, 21 July 1984, *G. Davidse 27570* (K).

2. *Hydrochorea elegans* (Ducke) M.V.B. Soares, Iganci & M.P. Morim, comb. nov.
urn:lsid:ipni.org:names:77303827-1
Fig. 2A

Balizia elegans (Ducke) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 40 1996. *Albizia elegans* (Ducke) L. Rico, Novon, 9(4): 556. 1999.
Albizia duckeana L. Rico, syn. nov., Kew Bull. 55(2): 404. 2000. Type: based on *Pithecellobium elegans* Ducke.

Basionym. *Pithecellobium elegans* Ducke [as *Pithecolobium*], Arch. Jard. Bot. Rio de Janeiro 3: 64. 1922.

Type material. Brazil, in silvis non inundatis, prope Alcobaca (Tocantins), *A. Ducke 16271* (lectotype, designated by Barneby and Grimes 1996, p. 40: MG [MG00016271], digital image!; isolectotypes: G [G00359898] digital image!, MG, P [P03093819] digital image!, R [R000002384] digital image!, RB [RB10177]!, US [US1040853] digital image!, US [US00000336] digital image!, US [US00610722] digital image!).

Distribution and habitat. Bolivia, Brazil, Costa Rica, Ecuador, Honduras, Nicaragua, Peru. *Hydrochorea elegans* occurs in primary rain forest, up to 350 m elevation (Barneby and Grimes 1996).

Notes. *Hydrochorea elegans* has a morphological affinity with *H. pedicellaris*, as already pointed out by Ducke (1922) and by Barneby and Grimes (1996). However, the corolla of peripheral flowers is larger (8–10 mm long) in *H. elegans* than in *H. pedicellaris* (up to 7.5 mm long). Ducke (1922) and Barneby and Grimes (1996) also commented on the similarity between the fruit of both species, but the fruits of *H. elegans* are indehiscent (vs. follicular dehiscence in *H. pedicellaris*). *Hydrochorea elegans* has a disjunct distribution between hylaean Brazil and Costa Rica and Nicaragua.

Selected specimens examined. Brazil, Rondônia: Porto Velho, área do Reservatório da Usina Hidrelétrica de Samuel, 15 June 1986, *C.A.C. Ferreira 7458* (K). Costa Rica, Limón: Talamanca, Fila Carbon, Finca de Pedro Bolivar, 25 May 1999, *O. Valerde 1175* (K).

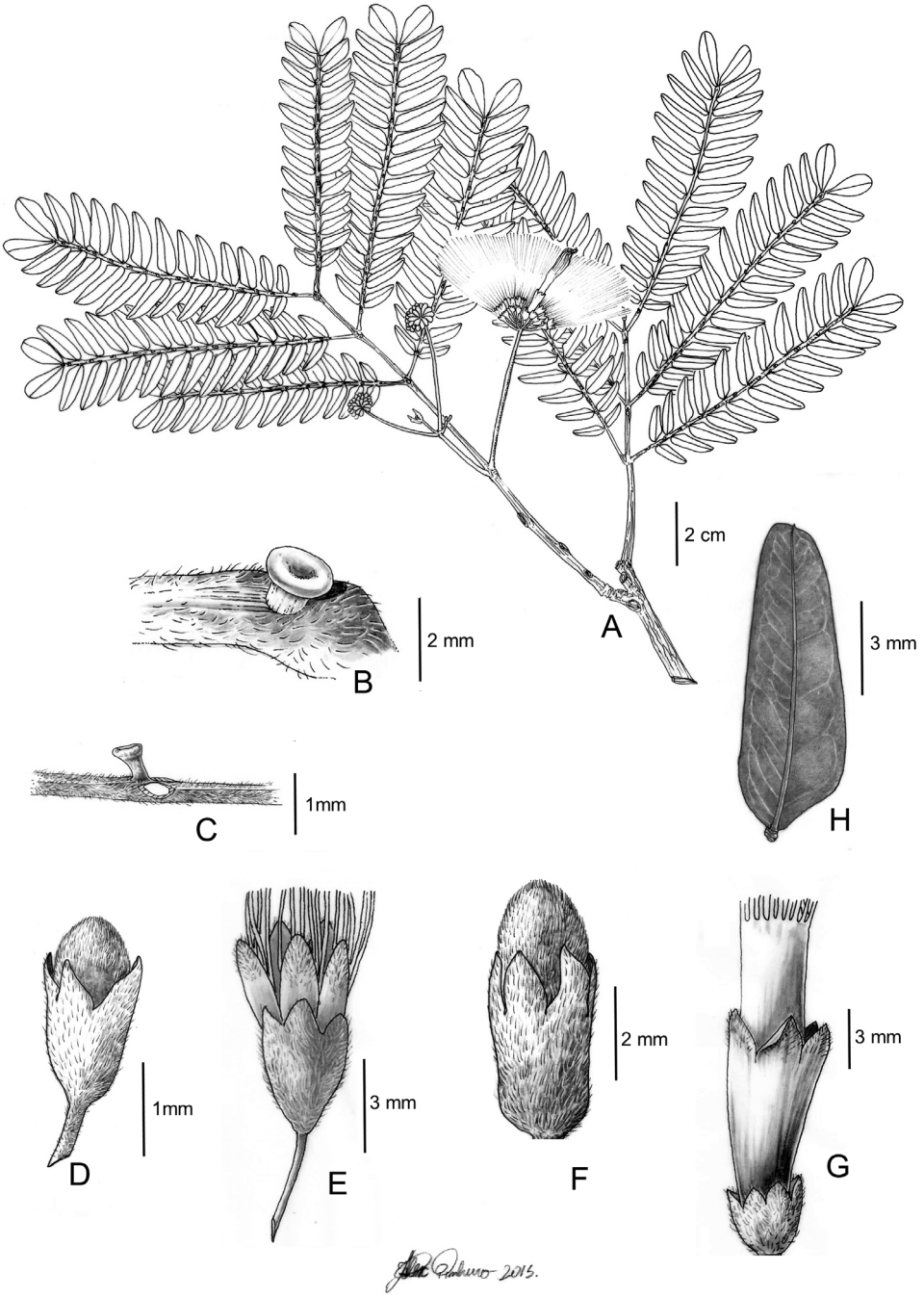

Figure 5. *Hydrochorea gonggrijpii* (Kleinhoonte) Barneby & J.W. Grimes **A** branch with inflorescences **B, C** extra-floral nectaries **D** peripheral flower bud **E** peripheral flower **F** terminal flower bud **G** terminal flower **H** leaflet. **A–H** from *Fróes 28045*. Illustration by Alex Pinheiro.

3. *Hydrochorea gonggrijpii* (Kleinhoonte) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74 (1): 25. 1996.
Figs 2A, 5

Basionym. *Pithecellobium* [as *Pithecolobium*] *gonggrijpii* Kleinhoonte Recueil Trav. Bot. Néerl. 22: 414. 1926.

Type material. Suriname, im Reservat der Zanderij I, die nummerierten Baume n. 102 (Herb. [Acad.Rhenotraiect.J n. 1529, im Dez. 1915, und n. 4350bl. im Juli 1919) und n. 141 (Herb. n. 4357, bl. Im Juli 1919.)" 141, 10/VII/1919", *Forest Bureau 4357* (lectotype, designated here from amongst the syntypes: IAN [IAN49436]!; isolectotypes: A [A00064017] digital image!, BR [BR0000005170067] digital image!, K [K000527996]!, K [K000527995]!, MO [MO954361] digital image!, NY [NY00334660] digital image!, NY [NY00334661] digital image!, NY [NY00334662] digital image!, P [P01818508] digital image!, U [U U0003385] digital image!, U [U0003384] digital image!, US [US00629380] digital image!).

Distribution and habitat. Brazil, Colombia, Guyana, French Guiana, Suriname, Venezuela. *Hydrochorea gonggrijpii* occurs along riverbanks, gallery forest margins, and low-lying swamp forests, at 40–1400 m elevation (Barneby and Grimes 1996).

Notes. In the nomenclatural treatment of *H. gonggrijpii* Barneby and Grimes (1996: p. 25) maintained the specimens "Surinam: im Reservat der Zanderij I, die nummerierten Baume n. 102 (Herb. [Acad. Rhenotraiect. J n. 1529, im Dec. 1915, und n. 4350 bl. im Juli 1919) und n. 141 (Herb. n. 4357, bl. im Juli 1919.)" as syntypes. In the present work, the specimen *Forest Bureau 4357* (IAN49436) is designated as lectotype (Art. 9.3, Turland et al. 2018).

Selected specimens examined. Brazil, Amazonas: Presidente Figueiredo, Cachoeira do boto, 21 September 2007, *Carvalho-Sobrinho et al 1632* (RB). Colombia, Vaupés: Mitú and vicinity, lower Río Kubiyú, along river, 26 September 1976, *J.L. Zarucchi s.n.* (K). Suriname. Plantas de Tafelberg (Table Mountain), 10 August 1944, *Maguire 24273* (RB). Venezuela, Bolivar: Distrito Piar, gallery forest bordering savana, vicinity of Guadequen (Buadequen), Río Acanán (affluent of Río Carrao), Cerros Los Hermanos, 20 May 1986, Lat 5°26'N, Long 62°17'W, alt 470 meters, *J.A. Steyermark et al. 131865* (NY).

4. *Hydrochorea leucocalyx* (Britton & Rose) Iganci, M.V.B. Soares & M.P. Morim, comb. nov.
urn:lsid:ipni.org:names:77303828-1
Fig. 2A

Balizia leucocalyx (Britton & Rose) Barneby & J.W. Grimes, in Mem. New York Bot. Gard. 74(1): 85. 1996.

Basionym. *Samanea leucocalyx* Britton & Rose, N. Amer. Fl. 23: 34. 1928.

Type material. Mexico. Tabasco, El Limon, *J. N. Rovirosa 976* (lectotype, designated by Barneby and Grimes 1996, p. 36, as holotype, here corrected: US [US13198371] digital image!, clastotypus (fragm. + photo): NY [NY00003824] digital image!).

Distribution and habitat. Belize, Guatemala, Honduras, Mexico. *Hydrochorea leucocalyx* occurs in wet tropical forests, often along riverbanks, seldom in anthropogenic pastures, up to 400 m elevation (Barneby and Grimes 1996).

Notes. Amongst the species of *Hydrochorea*, *H. leucocalyx* is one of the few that does not occur in Amazonia. It has affinities with the new species described in this treatment (see *H. uaupensis*) and is mainly distinguished by the lomentiform indehiscent fruit (vs. the cryptoloment in *H. uaupensis*). Barneby and Grimes (1996) recognised the specimen *J. N. Rovirosa 976* as holotype, but in the species protologue (Britton and Rose 1928), the authors did not indicate the herbarium where the type specimen was deposited. Thus, following Art. 9.10 of the International Code of Botanical Nomenclature (Turland et al. 2018), the specimen *J. N. Rovirosa 976* (US13198371) is here corrected to lectotype.

Selected specimens examined. Honduras: 7 September 1932, *W.S. Schipp 1024* (K). Mexico, Chiapas: km 12 carretera Pénjamo-Chancalá, 8 June 1960, *J.P. Chavelas et al. s.n.* (K).

5. *Hydrochorea marginata* (Spruce ex Benth.) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74(1): 29. 1996.

Figs 2A, D, 6

Basionym. *Pithecellobium* [as *Pithecolobium*] *marginatum* Spruce ex Benth., Trans. Linn. Soc. London 30: 586. 1875.

Type material. Brazil, Barra, by a stream [Prov. Rio Negro], *Spruce 1658* (lectotype, designated by Barneby and Grimes 1996, p. 31: K [K000528011]!; isolectotypes: E [E00313848] digital image!, F [V0058733F] digital image!], G [G275450] digital image!, P [P03094432] digital image!, P [P03094430] digital image!).

Distribution and habitat. Brazil and Venezuela. *Hydrochorea marginata* occurs in Amazonia, in flooded areas and along riverbanks and lake shores.

Notes. Barneby and Grimes (1996) considered *H. marginata* to comprise three varieties, *H. marginata* var. *panurensis* (Benth.) Barneby & J.W. Grimes, *H. marginata* var. *scheryi* Barneby & J.W. Grimes, and *Hydrochorea marginata* var. *marginata*. *Hydrochorea marginata* var. *panurensis* is recognized at the species level in this treatment, and *H. marginata* var. *scheryi* is placed as a synonym of *H. panurensis* because we identified no morphological diagnostic characters that support them as independent taxa. Both these taxonomic decisions are discussed under *H. panurenis*.

Selected specimens examined. Brazil: Amazonas, Rio Negro between Moreira and Rio Arirahá, 13 October 1971, *G.T. Prance 15206* (NY).

6. *Hydrochorea obliquifoliolata* (De Wild.) E.J.M. Koenen, comb.nov.
urn:lsid:ipni.org:names:77303829-1
Figs 2A, 3L

Pithecellobium obliquifoliolatum (De Wild.) J. Léonard, in Compt. Rend. Sem. Agric. Yangambi Comm. No. 67, 868 (1947).
Pithecellobium obliquifoliolatum (De Wild.) Aubrév., Fl. Forest. Soudano-Guin. 290 (1950), in obs., Aubrev. in Not. Syst., ed. Humbert, xiv. 57 (1950) nom. illeg.;
Arthrosamanea obliquifoliolata (De Wild.) G.C.C. Gilbert & Boutique, Fl. Congo Belge & Ruanda-Urundi iii. 194 (1952).
Cathormion obliquifoliolatum (De Wild.) G.C.C. Gilbert & Boutique, Bull. Soc. Roy. Bot. Belgique 90: 309 (1958).

Basionym. *Albizia obliquifoliolata* De Wild., Bull. Jard. Bot. État Bruxelles 7: 253 (1920).

Type material. Democratic Republic of the Congo, Congo Belge, Eala, *Laurent 1823* (lectotype, designated here: BR [BR0000008916334]!; isolectotype: BR [BR0000008916662]!).

Description. Trees up to 30 m in height and up to 1m DBH, the bark with both small scattered and long transverse linear lenticels, the indumentum consisting of a dense rusty to golden-brown pubescence covering the young twigs, petiole and primary rachis, with more sparse pubescence on peduncles and pinna-rachises except for dense rows of hairs at the margins of the otherwise glabrous canaliculate adaxial side of the pinna rachises, often also the canaliculate primary rachis of the leaf sparsely pubescent to glabrous adaxially. **Stipules** linear deltoid to falcate, 2–3 mm long, adaxially glabrous except at apex, densely pubescent, caducous. **Leaves** with (1–)2(–3) pairs of pinnae, petiole pulvinate and slightly flattened at base, (1.5–)2–3.5(–4.5) cm long, with a sessile concave circular to triangular nectary at the apex, c. 0.8–1.5 mm in diameter, rachis usually canaliculate adaxially, (0–)1.5–3(–6) cm long, if the leaf 3-jugate then usually with an inter-pinnal nectary, similar to the petiolar one, in between the middle pair of pinnae, apical nectary usually lacking, pinnae distinctly pulvinate, and usually with minute paraphyllidia at the apex of the pulvini, pinna-rachises canaliculate adaxially, the groove glabrous, c. (3–)4–11(–15) cm long, with short stipitate circular to elliptical cupular or trumpet-shaped nectaries c. (0.2–)0.5–1 mm in diameter. Leaflets in (3–)5–7(–8) pairs per pinna, subsessile on a c. 0.5 mm long pulvinule, widely spaced so that the margins do not overlap, bicolorous, dark green and shiny above, pale dull green beneath, rhomboid and often distinctly curved towards pinna apices, base asymmetrically obtuse or slightly oblique and the apex rounded or shallowly emarginate, sometimes mucronate, (1.4–)2.2–3.5(–4.7) × (0.6–)1.1–1.8(–2.2) cm, except the apical pair that is asymmetrically elliptic with oblique base and emarginate apex, (1.8–)2.7–4.8(–5.5) × (1.0–)1.5–2.5 cm, venation pinnate with (6–)12–16(–18) secondary veins brochidodromous, prominent on both surfaces or prominulous to slightly sunken on upper surface, and reticulate tertiary venation, often prominent on upper surface, obscure beneath, margins and midrib ciliate on both surfaces, lamina glabrous but for a few short scattered appressed hairs. **Inflorescences** (10–)15–20 flowered umbelliform capitula, on long slender peduncles arising 1–2 from axillary buds of coeval or caducous leaves, held

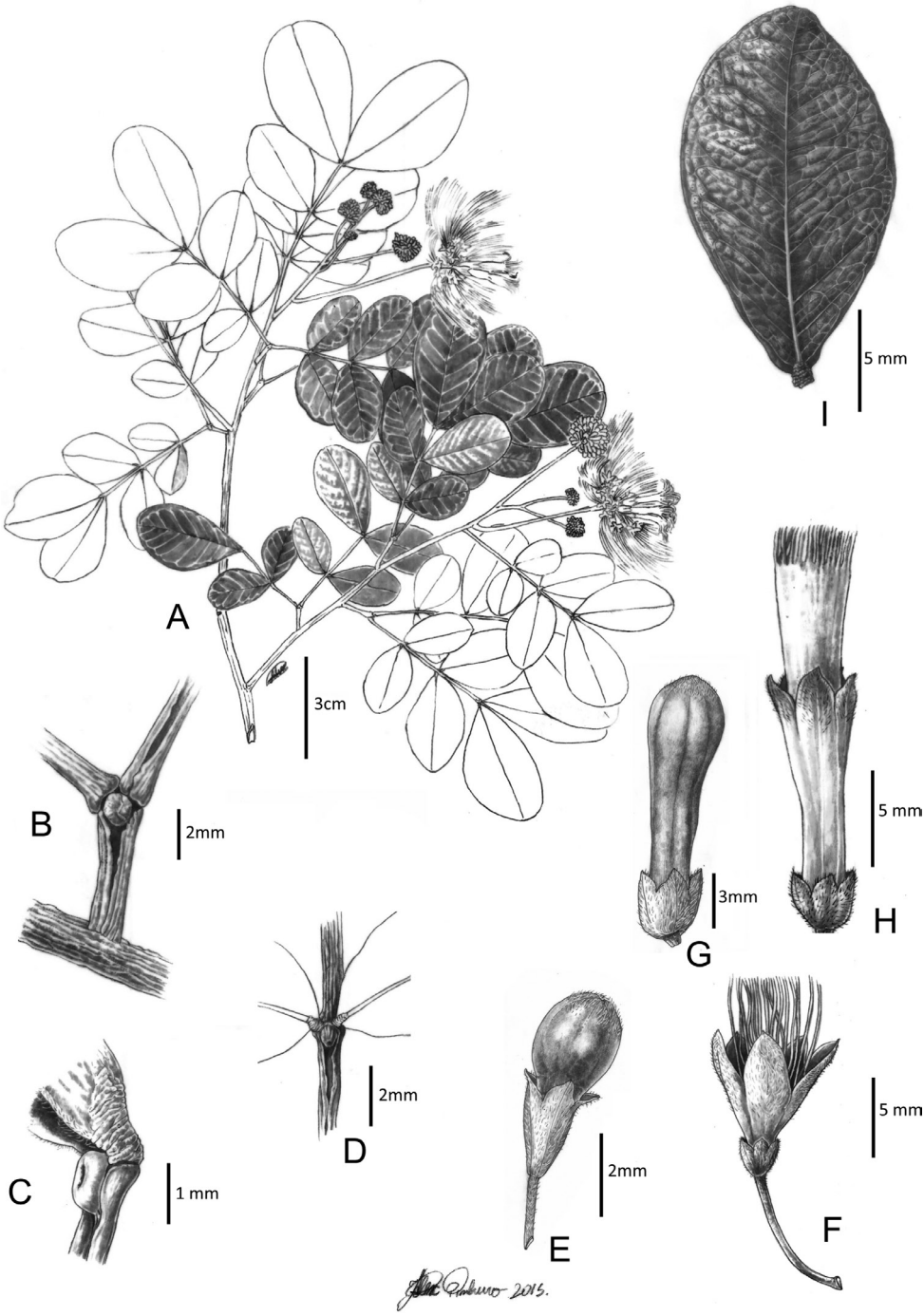

Figure 6. *Hydrochorea marginata* (Spruce ex Benth.) Barneby & J.W. Grimes **A** branch with inflorescences **B–D** extra-floral nectaries **E** peripheral flower bud **F** peripheral flower **G** terminal flower bud **H** terminal flower **I** leaflet. **A–D, F, H, I** from *A. Carlos et al. 066* **E, G** from *C. Ferreira et al. 7260*. Illustration by Alex Pinheiro.

above the foliage, the axillary meristems usually not continuous beyond the peduncles and aborted prior to fruit set, dimorphic with a single enlarged terminal flower and often one dispositioned peripheral flower c. 0.5 cm below the others, on peduncles 4–8(–12) cm long. Bracts linear to spatulate, sometimes bilobed at apex, c. 2–3.5 × 0.5 mm, pubescent with longer hairs at apex. Peripheral flowers on pedicels 2–6 mm long, calyx pentamerous, green to greenish white, c. 3–4 mm long, the deltoid lobes c. 0.5 × 0.5 mm, glabrous, corolla pentamerous, green to greenish white, c. 5–6 mm long, the lobes c. 2–3 × 2 mm, glabrous or with short white hairs around the apices of the lobes, androecium consisting of c. 20–30 stamens, c. 2.1–2.5 cm long, the filaments white to pale green at apex, fused into a tube c. 3 mm long, with dorsifixed pale yellowish green anthers, pollen in 16-celled plano-compressed disc-shaped polyads, pistil c. 2.5–2.8 cm long, ovary c. 3 mm long, pubescent in upper half, the pale green to white style emerging from it at an angle of c. 45°, with a green funnel-shaped stigma, extending beyond the stamens. Terminal flower sessile to subsessile, similar to peripheral flowers but broadly campanulate and larger, calyx c. 3.5–5 mm and corolla c. 7.5–9 mm long, the filaments thicker and staminal tube c. 8–10 mm long, exserted well beyond the corolla tube. **Pods** falcate and weakly articulated, base often tapering into a c. 5 mm long stipe, (3–)6–12 seeded with a thin papery fruit wall and slightly thickened rim, dark brown to black outside when ripe, light brown inside, (3.7–)5.5–9.6 × 1.2–1.4 cm, breaking up into 1-seeded articles 0.4–0.7(–1.0) cm long, the basal and apical articles up to 1 cm long, seed c. 6.5 × 4.5 × 0.5 mm, the testa hard, light brown with a darker brown closed elliptic pleurogram, c. 4 × 2 mm.

Distribution and habitat. Gabon, Central African Republic, Congo-Brazzaville, Democratic Republic of the Congo. *Hydrochorea obliquifoliolata* occurs in the Congo Basin, and is a species of swamp forests, seasonally inundated forests and riverbanks.

Notes. The similarities to *Cathormion rhombifolium*, the other African species that is here transferred to *Hydrochorea*, are discussed below.

Selected specimens examined. Gabon: Ogooué-Lolo, road Okondja to Bambidie and Lastoursville, 21 km SW of Okondja, 7 February 2008, *J.J. Wieringa 6519* (BR, K). Democratic Republic of Congo: Yafunda, rive guache, près d'Isangi, 8 September 1938, *J. Louis 11175* (BR). Boendu, August 1938, *Du Bois 904* (BR), *G. Couteaux 55* (BR). Bolomba, 7 November 1957, *C. Évrard 2746* (BR). Bongoy, 4 January 1958, *C. Évrard 3191* (BR). Botsima, route station-village, 28 January 1991, *J.B.M.M. Dhetchuvi 321* (BR). Yangambi, île Tutuku en face du plateau de l'Isalowe, 3 January 1940, *R.G.A. Germain 87* (BR). Bokondji, 28 September 1959, *De Wanckel 162* (BR).

7. *Hydrochorea panurensis* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci, comb. nov.

urn:lsid:ipni.org:names:77303830-1

Figs 2A, 7

Hydrochorea marginata var. *panurensis* (Benth.) Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74: 32. 1996. Type: based on *Pithecellobium panurense* Spruce ex Benth., syn. nov.

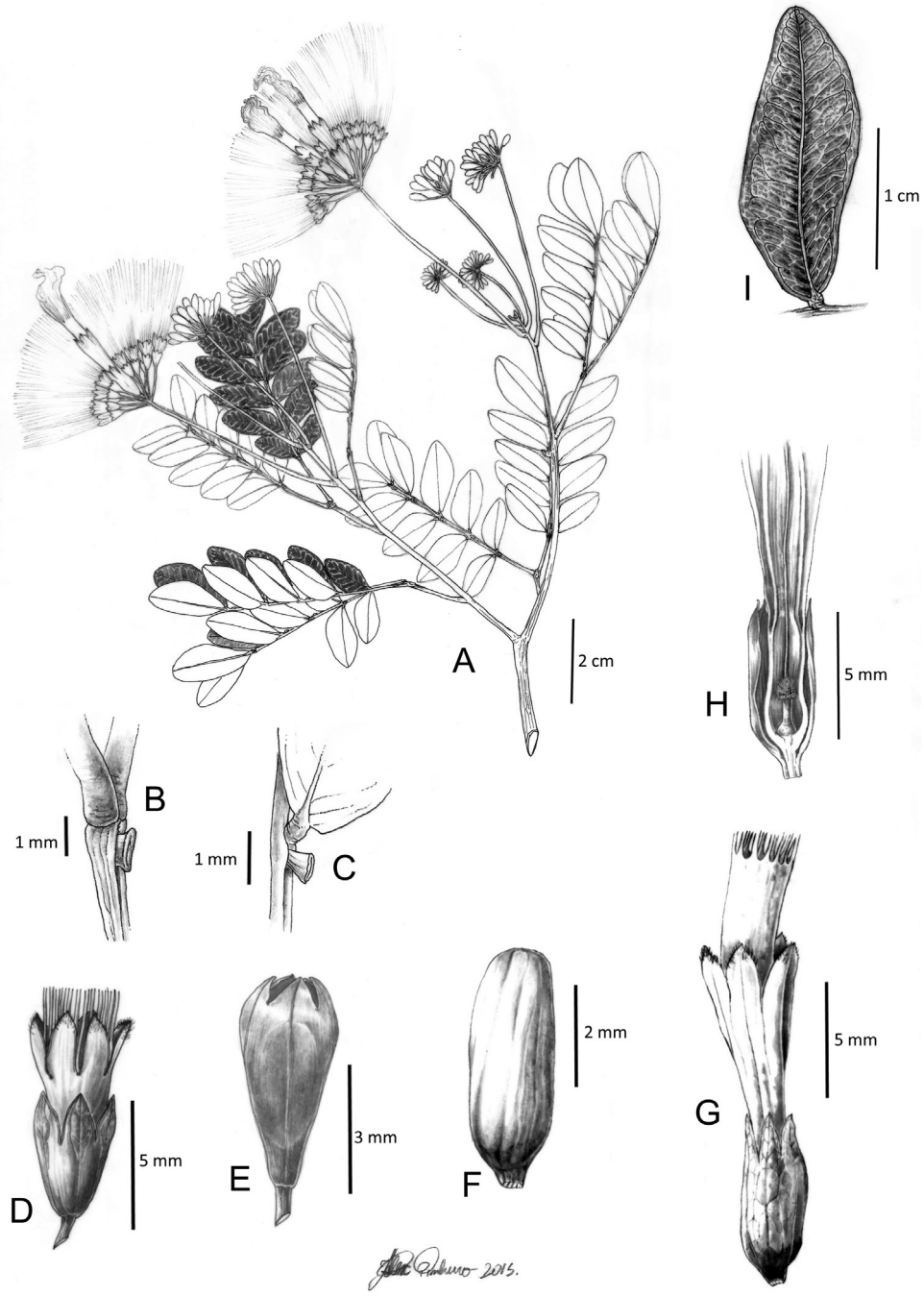

Figure 7. *Hydrochorea panurensis* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci **A** branch with inflorescences **B, C** extra-floral nectaries **D** peripheral flower **E** peripheral flower bud **F** terminal flower bud **G** terminal flower **H** terminal flower longitudinal section **I** leaflet. **A–I** from *Wurdack & Adderley 43618*. Illustration by Alex Pinheiro.

Hydrochorea marginata var. *scheryi* Barneby & J.W. Grimes, Mem. New York Bot. Gard. 74: 32. 1996. Type: Venezuela, at Sanariapo, Territorio Federal Amazonas, *Llewellyn Williams 15953* (lectotype first step, designated by Barneby and Grimes 1996, p. 32, as holotype, here corrected: F; lectotype second step, here designated: F [V0058706F], digital image!; isotypes: F [V0058707F] digital image!), G [G00365761] digital image!, GH [GH00060404] digital image! K [K0005279] digital image!, MO [MO954357] digital image!, MO [MO954358] digital image!), NY [NY00334620] digital image! US [US00000401] digital image!, US [US00385625] digital image!, VEN [VEN2237] digital image!, syn. nov.

Basionym. *Pithecellobium* [as *Pithecolobium*] *panurense* Spruce ex Benth., Trans. Linn. Soc. London 30: 586. 1875.

Type material. Brazil, in silvis 'Gapó' ad flumen Uaupés prope Panuré, prov. do Alto Amazonas, *Spruce 2425* (lectotype first step, designated by Barneby and Grimes 1996, p. 32, as holotype, here corrected: K; lectotype second step, here designated: K [K000528008]!; isolectotypes: E [E00313845] digital image!, F, [V0058739F] digital image!, G [G00365356] digital image!, G [G00365687] digital image!, GH [GH00063965] digital image!, K [K000528007]!, NY [NY334690], P [P03094382] digital image!, P [P03094383] digital image!, RB [RB00708599]!).

Distribution and habitat. Brazil, Venezuela. *Hydrochorea panurensis* occurs in seasonally flooded Amazonian sites along rocky stream banks and ecotone with gallery forests.

Notes. Ducke (1949) considered *Pithecellobium panurense* as a form of *P. marginatum*, considering the vegetative characters to be more important taxonomically than the differences between the flowers of those taxa. Barneby and Grimes (1996) moved *P. panurense* to *Hydrochorea* as *H. marginata* var. *panurensis*. However, *Hydrochorea panurense* has diagnostic floral characters which distinguish it from *H. marginata*. The floral buds of *H. panurense* have the corolla covered by the calyx; the flowers are glabrous and the terminal flower has a tubular calyx (vs. calyx not covering the corolla in the floral buds, pubescent flowers, and calyx of the terminal flower campanulate in *H. marginata*). Barneby and Grimes (1996) also described *H. marginata* var. *scheryi*, distinguishing it from *H. marginata* var. *panurensis* only by the pedicel of the peripheral flowers, this 4–5 mm long. (vs. 6.5–13 mm long in *H. marginata* var. *panurensis*). Barneby and Grimes (1996) emphasized, however, that this is the only character to distinguish between the two taxa. In the present study we consider *H. marginata* var. *scheryi* to be a synonym of *H. panurensis*.

A second step lectotypification is designated here for both *H. panurensis* and *H. marginata* var. *scheryi*, since the material that Barneby and Grimes (1996) recognised as holotypes consists of two sheets in both cases and they did not select lectotypes from amongst these sheets (Art. 9.10,9.17; Turland et al. 2018).

Selected specimens examined. Brazil, Amazonas: Barcelos, Serra do Araçá, Rio Araçá à 13 h de Barcelos, 28 July 1985, *Silva 389* (INPA); São Gabriel da Cachoeira. Margem do Rio Içana em direção a comunidade Camarão, 0°48'35.8"N, 67°32'10"W, 19 July 2012, *Morim*, *M.P.*, *Iganci*, *J.R.V*, *Bonadeu F & Koenen*, *E. 563* (RB, Z). Venezuela, Amazonas: Rio Casiquiare, 11 November 1959, *Wurdack & Adderley 43407* (IAN).

8. *Hydrochorea pedicellaris* (DC.) M.V.B. Soares, Iganci & M.P. Morim, comb. nov.
urn:lsid:ipni.org:names:77303831-1
Figs 2A, B, 3F-I

Balizia pedicellaris (DC.) Barneby & J.W. Grimes, in Mem. New York Bot. Gard. 74(1): 85. 1996.
Albizia pedicellaris (DC.) L. Rico, in Novon 9(4): 555. 1999.

Basionym. *Inga pedicellaris* DC., Prodr. 2: 441. 1825.

Type material. French Guiana, "...in Cayenna" (lectotype, designated by Barneby and Grimes 1996, p. 36, as holotype, here corrected: G-DC = F Neg. 6972, digital image!).

Distribution and habitat. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Venezuela. *Hydrochorea pedicellaris* occurs in non-inundated primary rainforest in Amazonia, in the lowlands of the Atlantic Rainforest, and in gallery forests, up to 200 m elevation, and occasionally at 700–800 m elevation in Bolivia, Ecuador and eastern Brazil (Barneby and Grimes 1996).

Notes. *Hydrochorea pedicellaris* is the only species of the genus that occurs in a range of environments including areas of the Brazilian Atlantic Forest. It has an affinity with *H. elegans* (see comment under that species), but when it is in fruit it is easily recognized by its follicular dehiscence, and an exocarp with deep, transversal fissures. Barneby and Grimes (1996) recognised a specimen in the G-DC herbarium as holotype, but in the species protologue (De Candolle 1825), the author did not indicate a type specimen. Thus, the specimen at G-DC should be considered a lectotype, here corrected (Art. 9.10; Turland et al. 2018).

Selected specimens examined. Bolivia, La Paz: Province of Larecaja, Tuiri, 12 September 1989, *B. Krukoff 10886* (K). Brazil, Amazonas: São Gabriel da Cachoeira, Rio Içana, na comunidade Camarão, terra firme, 0°37'23"N, 67°26'57"W, 20 July 2012, *Iganci*, *J.R.V*, *Morim*, *M.P.*, *Bonadeu F.*, *Koenen*, *E.* 870 (RB); Espírito Santo: Linhares Fragmento em frente a casa do Reis, Sítio Santo Domingo, Restinga arbórea de cordões arenosos, 19°21'6"S, 39°43'31"W, 13 March 2007, *R.D. Ribeiro et al. 812* (RB). Guyana: Territorio Federal Delta Amacuro, 29 May 1964, *L.M. Berti 225* (K). Peru: Palcazú, Pasco Oxapampa, localidad Mayro, 20 May 2010, *R. Vásquez et al. 36546* (K). Suriname: Zenderij, November 1944, *M. Koeleroe 237* (RB). Venezuela: Altiplanicie de Nuria, 15 July 1960, *J.A. Steyermark 86335* (K).

9. *Hydrochorea rhombifolia* (Benth.) E.J.M. Koenen, comb. nov.
urn:lsid:ipni.org:names:77303832-1
Figs 1A, 3M

Feuilleea rhombifolia (Benth.) Kuntze, Revis. Gen. Pl. 1: 189 (1891).

Cathormion rhombifolium (Benth.) Keay, Kew Bull. 8(4): 489 (1953).

Basionym. *Albizia rhombifolia* Benth., London J. Bot. 3: 87 (1844).

Type material. Guinée, Conakry, *Heudelot 735* (lectotype designated here from amongst the syntypes: K [K000043955]!; isolectotypes: K [K000043954]!, K [K000043949]!, P [P00418271] digital image!, P [P00418272] digital image!, P [P00418270] digital image!).

Description. Trees or **shrubs** up to 12 m tall, the young stems, all leaf-axes and peduncles puberulent-tomentulose with rusty brown hairs. **Stipules** deltoid, c. 1 mm long, puberulent-tomentulose, caducous. **Leaves** with 2–3 pairs of pinnae, petiole pulvinate, ventrally flattened above pulvinule and with central groove in upper half, 2–3.5(–8.5) cm long, rachis ventrally grooved, 1.5–4(–12.5) cm long, pinna rachises pulvinate, ventrally grooved, (3.2–)4–6(–12) cm long. Nectaries present at the petiole apex just below the first pair of pinnae as well as just below each further pair of pinnae, sessile or shortly stipitate on stipe to 0.5 mm, cupular or sometimes concave, circular and 0.8–2.2 mm in diameter, and between the upper 2–3 pairs of leaflets, trumpet-shaped and then on a short stipe 0.5 mm or cupular and (sub)sessile, the lower ones circular and the upper ones elliptical, 0.8–1.5 × 0.8–1.1 mm. Minute paraphyllidia sometimes present at the apex of the pinna-pulvinus. Leaflets in 4–6 pairs per pinna, closely spaced, bicoloured leaflets often with partly overlapping margins, bright green above and pale green beneath, dull on both surfaces, rhomboid with a pulvinate sessile oblique base and rounded to slightly emarginate apex, increasing in size towards pinna apex, (1.1–)1.7–3.5(–5.1) × (0.5–)1.2–1.8(–2.3) cm, except for the apical pair which has a less oblique to nearly acute base, (2.1–)2.5–4.5(–5.7) × (1.1–)1.5–2.5(–3.2) cm; venation pinnate with 8–12(–18) secondary veins brochidodromous, tertiary venation reticulate, prominulous on both surfaces, midribs ciliate on both sides, the lower leaflet surface pilose with a variable density of brownish to white hairs, rarely almost glabrous, sometimes villose particularly near the midrib giving a rusty orange-brown appearance. **Inflorescences** umbelliform capitula, axillary to co-eval leaves on peduncles (4.5–)5–9.5 cm long, dimorphic with 6–16 peripheral flowers and 1–2 terminal flower(s) with elongated exserted staminal tubes. Bracts spatulate, c. 1.8 mm long, puberulent with minute rusty hairs, caducous. Peripheral flowers on pedicels of 1–4 mm, calyx pentamerous, white, 3–3.5 mm long, fused, the deltoid lobes 1–1.3 mm long, glabrous or with few minute hairs, corolla pentamerous, white, 6–8 mm long, fused in the lower half, glabrous, pilose to villose in the upper half, androecium 1.6–2.3 cm long, consisting of 20–28 stamens with white filaments fused at the base into a short tube of c. 2 mm, anthers dorsifixed, pollen in 16-celled plano-compressed disc-shaped polyads, gynoecium with a c. 2 mm long ovary, pubescent on the upper half, the 1.6–2.5 cm long white style emerging from it at an angle of c. 45°, with a funnel-shaped stigma, extending beyond the stamens. Terminal flower(s) similar but larger and more robust in appearance, calyx c. 4.5 mm long with c. 1.5 mm long lobes, corolla c. 9 mm long, androecium with 30–36 stamens that are thicker and fused into a tube 7–10 mm long, exserted well beyond the corolla tube, and with a sunken nectariferous disk be-

low the base of the ovary, gynoecium otherwise similar to that of the peripheral flowers. **Pods** straight to falcate, 6–12-seeded with a thin papery fruit wall and thickened rim, dark brown outside when ripe, whitish grey inside, (4.5–)7–12.5 × 1.4–1.9 cm, breaking up into 1-seeded articles 0.6–1.1 cm long, seed c. 7 × 4.5 × 2 mm, the testa hard, light brown with a wide lighter brown closed pleurogram.

Distribution and habitat. Known from the tidal riverine systems near the coast from Senegal to Sierra Leone. *Hydrochorea rhombifolia* occurs often abundantly, in permanent or tidal swamp forest, including on the edge of mangrove swamps, and in gallery forests.

Notes. Bentham (1844) described *Albizia rhombifolia*, before designation of holotypes was required by the International Code of Botanical Nomenclature. Keay (1953) made the new combination *Cathormion rhombifolium* and cited the holotype as being at Kew. However, there are three specimens of *Heudelot 735* at K, the type that was cited by Bentham, leaving it ambiguous as to which one of these represents the holotype. Therefore, the specimen from Herbarium Benthamianum (the oldest deposited specimen dating to 1854) is here designated as a lectotype: it has leaves and flowers, and is more richly annotated than the other two specimens.

Hydrochorea obliquifoliolata and *H. rhombifolia* are morphologically very similar and have sometimes been confused in herbaria, despite their clearly different geographical distributions. The species are readily separated by the darker appearance of the leaflets of *H. obliquifoliolata*, which have a distinct shine on the upper surface and the lower surface usually (sub-)glabrous (vs. a usually rusty pilose lower leaflet surface in *H. rhombifolia*). The leaflets of *H. rhombifolia* are also more closely spaced than those of *H. obliquifoliolata*, the latter not having overlapping margins. Furthermore, the flower colour of the two species is clearly different (as per the key), a characteristic which remains apparent when comparing dried flowering specimens in the herbarium, and the corolla lobes of *H. obliquifoliolata* are glabrous or with a few short apical hairs (vs. pilose to villous on the upper half in *H. rhombifolia*).

Selected specimens examined. Sierra Leone: Mange, 7 February 1939, *F.C. Deighton 3618* (K), Rokupr, 25 May 1953, *F.C. Deighton 5925* (K), Kasanko (Mafore), 3 December 1950, *T.S. Jones 52* (K), near Tassin and Kukum, 17 January 1892, *G.F. Scott Elliot 4418* (K); Guinée-Bissau: Gabu, Ponte do rio Colufe, 10 June 1949, *Espirito Santo 2500* (K).

10. *Hydrochorea uaupensis* M.P. Morim, Iganci & E.J.M. Koenen, sp. nov.

urn:lsid:ipni.org:names:77303833-1

Figs 2A, E-G, 3J, K, 8

Diagnosis. *Hydrochorea uaupensis* is morphologically similar in appearance to *H. leucocalyx* (Britton & Rose) Iganci, M.V.B. Soares & M.P. Morim by its leaflets and inflorescence, however it differs by having a red or green calyx, pink corolla, 1–2 pairs of pinnae, and crypto-lomentiform fruits (vs. white calyx and corolla, 3–5(–6) pairs of pinnae and indehiscent fruits in *H. leucocalyx*).

Type material. Brazil, Amazonas, São Gabriel da Cachoeira. Igarapé Tibuari, afluente do Vaupés 0°05'5"N, 67°23'16"W, 23 July 2012, fl. and fr., *M.P. Morim*, *J.R.V. Iganci*, *F. Bonadeu*, *E. Koenen 577* (holotype: RB [RB00728413]!; isotypes: HUEFS!, INPA!, K!, MBM!, MG!, MO!, NY!, PEL!, S!, US!, Z!).

Description. Trees 2–6 m tall, trunk not observed, partially underwater during seasonal inundation. Branches, leaf axes and peduncles sparsely pubescent to glabrescent. **Stipules** linear, to 1.2 cm long, densely pubescent on outer surface. **Leaves** with 1–2 pairs of pinnae; petiole including pulvinus 1.5–4.5 cm, cylindrical; rachis 0 or 3–4(–9) cm, glabrous, canaliculate; extrafloral nectaries borne between first or both pairs of pinnae, sessile, patelliform and smaller nectaries usually present between the leaflet pairs; pinnae 3–5 jugate; leaflets subsessile on pulvinules, chartaceous, c. 2–4(–6) × 1.5–2(–3) cm, rhomboid or ovate, apex emarginate or obtuse, sometimes with a minute mucro, base asymmetrically oblique to acute; adaxial and abaxial surfaces glabrous, discolorous, adaxial surface sometimes lustrous; venation pinnate with c. 11–17 secondary veins, tertiary venation reticulate and prominent on both surfaces when leaflets dry. **Inflorescences** dimorphic, umbelliform with 7–10 peripheral flowers and an enlarged sessile terminal flower, peduncle 4–6(–8) cm. Bracts and bracteoles not seen. Flowers with a reddish or green calyx, pink corolla and white filaments, the flower buds oblong, ca. 8 mm long, with the corolla concealed by the calyx prior to anthesis, peripheral flowers on pedicels 0.7–1.5 cm, calyx campanulate, c. 9 mm long, 5-angulate due to prominently raised veins, sparsely puberulent or ciliate at the apex of the lobes, corolla tubular, with a prominulous midvein on the lobes, c. 1.5 cm long, sparsely puberulent on the upper half of the lobes, stamens c. 50–60, the filaments white, c. 3 cm long, exserted from the corolla ca. 2 cm; ovary glabrous, 3–4 mm, sub-truncate to truncate at the apex, style 3.5–4 cm, stigma funnel-shaped; terminal flower similar to peripheral flowers but more robust and c. 5 mm wide at base, calyx c. 1.2 cm long, corolla 1.6 cm long, stamens ca. 75, ca. 3.5 cm long. **Pods** typically 1–3 per infructescence, crypto-lomentiform, up to 15-seeded, oblong, slightly curved, lignescent, c. 9.5 × 2.5 cm excluding a ca. 5 mm long mucro, dehiscence follicular, the smooth exocarp and transversely fibrous mesocarp continuous, the endocarp septate, enveloping the seeds which are released in monospermous articles. **Seeds** not seen in mature state, oblong, c. 1.6 × 0.4–0.7 cm, pleurogram extending from apex to base, c. 1.3 × 0.3–0.4 cm, closed.

Distribution and habitat. Brazil. Known only from the Upper Rio Negro region in the Brazilian Amazon (Amazonas state), in seasonally inundated "campinarana" vegetation.

Phenology. Flowering and fruiting in July.

Etymology. The specific epithet refers to the type locality, near the River Uaupés, in the state of Amazonas, Brazil. The indigenous people living in this area (e.g., the Tucanos) were known as Uaupés, and later the river took the same name.

Notes. *Hydrochorea uaupensis* is only known from Amazonas state, Brazil, where it was collected at "Igarapé Tibuari", in the municipality of São Gabriel da Cachoeira, during fieldwork in July 2012. The species grows in open vegetation on white sand, known in Brazil as campinarana in the Amazon Domain. During times of flood, only the treetops are exposed above the water line. A second herbarium collection from close to the type locality (Rio Tourí, afl. do Rio Negro, igapó; *R.L. Fróes 28691*, IAN [IAN78279]),

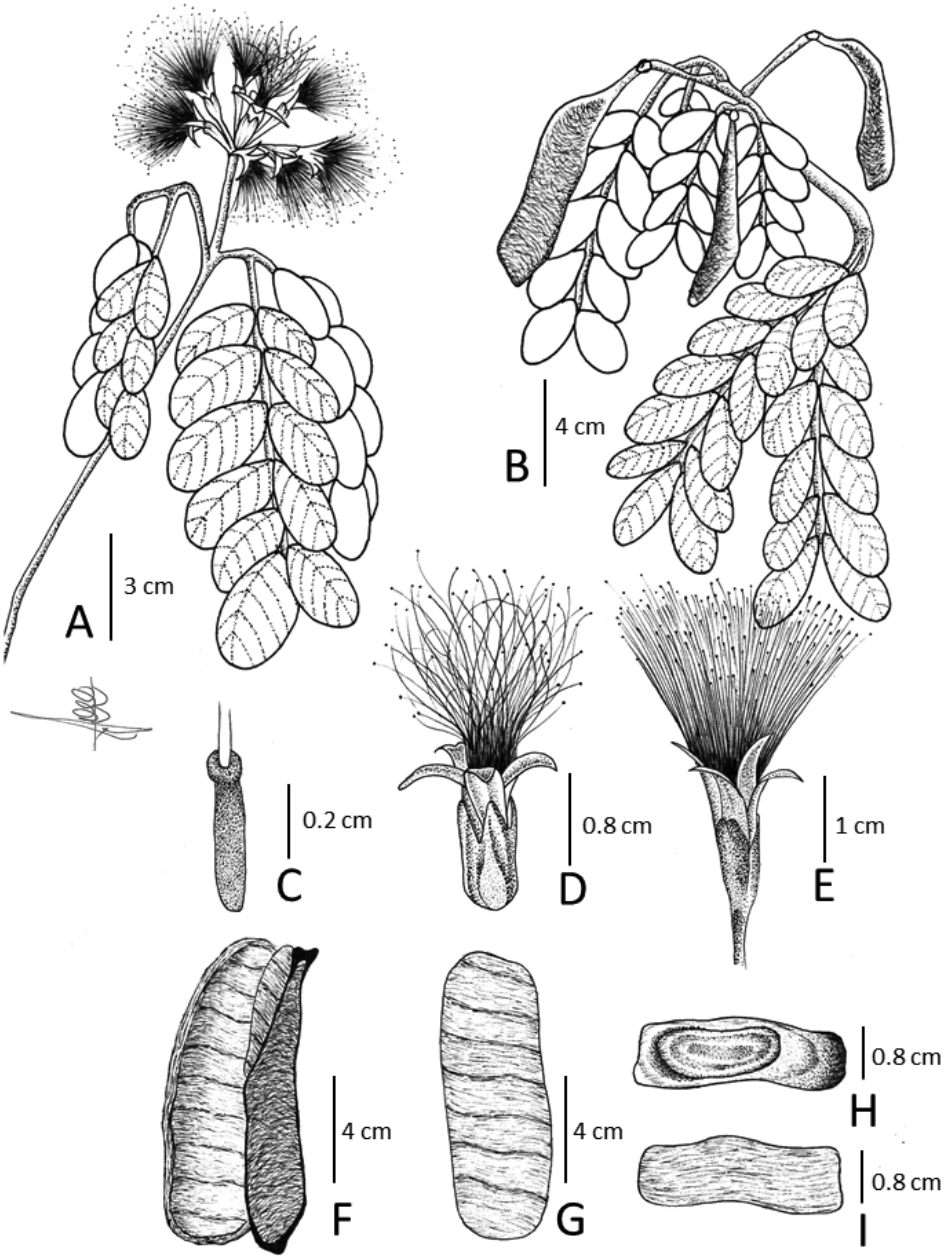

Figure 8. *Hydrochorea uaupensis* M.P. Morim, Iganci & E.J.M. Koenen **A** branch with inflorescences **B** branch with fruits **C** ovary **D** terminal flower **E** peripheral flower **F** dehisced fruit **G** detail of fruit endocarp forming 1-seeded articles **H, I** monospermous articles. **A–I** from *M.P. Morim et al. 577*. Illustration by João Augusto Castor Silva.

of which we have only seen an image, is here tentatively included under *H. uaupensis* because the fruit and leaves match the type material and the flowers are described as pink on the specimen label. Since these two occurrence records are close to the borders with Colombia and Venezuela, the species is to be expected in those two countries.

The phylogenetic position of *H. uaupensis*, as the sister lineage of the clade composed of *Hydrochorea* sensu Barneby and Grimes (1996) and the African *Hydrochorea* spp., provides ample support for this as a distinct taxon and a species new to science, as it does not form a sister pair with any other known species. Furthermore, this phylogenetic position is in line with the fruit morphology of the species being intermediate between *Balizia* and *Hydrochorea*, adding further support, along with the paraphyly of *Balizia*, for not maintaining these as distinct genera.

Conservation status. Data deficient. The species is known only from two adjacent localities in the Upper Rio Negro region of Amazonas state, Brazil. More collections are needed to assess the species' conservation status.

Conclusion

Our results provide significant advances in the generic delimitation of *Hydrochorea* and related taxa, as well as broadening our understanding of ongoing diversification in these taxa. The uncertain phylogenomic position of *Jupunba macradenia*, and other species of *Jupunba*, sharing a relatively large number of incompletely sorted genes with *Hydrochorea*, leads to further difficulties in our ability to delimit genera in a group where classification has been notoriously unstable. Nevertheless, given the complex evolutionary patterns across the genome presented by the Jupunba clade taxa, we decided to use morphology as our main guide for taxonomic decisions, re-circumscribing *Hydrochorea* to include ten species to account for the paraphyly of *Balizia*, while incomplete lineage sorting surrounding the divergence between *Hydrochorea* and *Jupunba* does not falsify these two genera as natural groups. Furthermore, not transferring all these species to *Jupunba*, although a cautious decision, avoids the publication of more new names while safeguarding morphological diagnosability. The species treated here as *Hydrochorea* form a morphologically homogeneous group in terms of vegetative and floral characters, although the fruits are variable as observed in other mimosoid genera (e.g., Aviles Peraza et al. 2022). Nevertheless, fruit type is useful for the identification of some species of *Hydrochorea*. Quantitative characters, such as the number of pinnae per leaf and number of leaflets per pinna, also can be useful for identification of some species, but we commonly observed overlap in these characters between species and even variation on the same individual.

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Appendix 1

Vouchers and European Nucleotide Archive (ENA, https://www.ebi.ac.uk/ena/) accession numbers for molecular phylogenetic data. Note that the taxonomy of *Albizia*

sect. *Arthrosamanea* is updated in this volume by Aviles Peraza et al. (2022), where new binomials in the genus *Pseudalbizzia* Britton & Rose are presented for the majority of the species of this section.

Acacia rostellifera Benth., *Murphy 466* (MEL): ERS11697109; *Afrocalliandra redacta* (J.H. Ross) E.R. Souza & L.P. Queiroz, *Germishuizen 5585* (PRE): ERS11697117; *Albizia adinocephala* Britton & Rose, *Hughes 1070* (FHO): ERS11697120; *Albizia burkartiana* Barneby & J.W. Grimes, *Stival-Santos 678* (RB): ERS4812854 ; *Albizia coripatensis* (Rusby) Schery, *Hughes 2433* (FHO): ERS11697123; *Albizia decandra* (Ducke) Barneby & J.W. Grimes, *Vilhena 231* (NY): ERS11697124; *Albizia edwallii* (Hoehne) Barneby & J.W. Grimes, *Dalmaso 272* (RB): ERS4812856 ; *Albizia glabripetala* (H.S. Irwin) G.P. Lewis & P.E. Owen, *Lewis 1652* (K): ERS11697125; *Albizia inundata* (Mart.) Barneby & J.W. Grimes, *Wood 26530* (K): ERS4812859; *Albizia multiflora* (Kunth) Barneby & J.W. Grimes, *Hughes 3090* (FHO): ERS11697127; *Albizia niopoides* (Spruce ex Benth.) Burkart, *Simon 1601* (CEN): ERS11697128; *Albizia sinaloensis* Britton & Rose, *Hughes 1576* (K): ERS11697130; *Albizia subdimidiata* var. *minor* Barneby & J.W. Grimes, *Gorts 341* (K): ERS11697131; *Albizia subdimidiata* (Splitg.) Barneby & J.W. Grimes var. *subdimidiata*, *Ferreira 210* (K): ERS11697129; *Albizia tomentella* Miq., *Leach & Dunlop 3801* (L): ERR9867596; *Albizia tomentosa* Standl., *Hughes 648* (K): ERS11697132; *Albizia xerophytica* J.Linares, *Hughes 1435* (K): ERS11697133; *Archidendron clypearia* (Jack) I.C. Nielsen, *Wieringa 1849* (WAG): ERS11697136; *Calliandra bella* Benth., *Queiroz 15696* (HUEFS): ERS11697156; *Enterolobium cyclocarpum* (Jacq.) Griseb., *Macqueen & Styles 75* (K): ERS11697204; *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes (1), *Bonadeu 655* (RB): ERS4812902 ; *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes (2), *Iganci 862* (RB): ERS4812903 ; *Hydrochorea elegans* (Ducke) Iganci, M.V.B. Soares & M.P. Morim, *Iganci 870* (RB): ERS11697146; *Hydrochorea gonggrijpii* (Kleinh.) Barneby & J.W. Grimes, *Tillett 45696* (K): ERS11697223; *Hydrochorea leucocalyx* (Britton & Rose) Iganci, M.V.B. Soares & M.P. Morim, *Aguilar 1939* (NY): ERS11697147; *Hydrochorea panurensis* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Morim 563* (NY): ERS11697224; *Hydrochorea obliquifoliolata* (De Wild.) E.J.M. Koenen, *Wieringa 6519* (WAG): ERS4812863 ; *Hydrochorea pedicellaris* (DC.) Iganci, M.V.B. Soares & M.P. Morim, *Queiroz 15529* (HUEFS): ERS4812877 ; *Hydrochorea rhombifolia* (Benth.) E.J.M. Koenen, *Deighton 3618* (K): ERS11697168; *Hydrochorea uaupensis* M.P. Morim, Iganci & E.J.M. Koenen, *Morim 577* (RB): ERS4812878 ; *Jupunba abbottii* Britton & Rose, *Zanoni 21220* (NY): ERS11697071; *Jupunba asplenifolia* Britton & Rose, *Ekman 6383* (NY): ERS11697072; *Jupunba barbouriana* (Standl.) M.V.B. Soares, M.P. Morim & Iganci, *Iganci 847* (RB): ERS11697073; *Jupunba brachystachya* (DC.) M.V.B. Soares, M.P. Morim & Iganci, *Lima 7438* (RB): ERS11697074; *Jupunba cochleata* (Willd.) M.V.B. Soares, M.P. Morim & Iganci, *Bonadeu 673* (RB): ERS11697076; *Jupunba commutata* (Barneby & J.W. Grimes) M.V.B. Soares, M.P. Morim & Iganci, *Maguire 46145* (NY): ERS11697077; *Jupunba filamentosa*, (Benth.) M.V.B. Soares, M.P. Morim & Iganci *Lima 7487* (RB): ERS11697079; *Jupunba floribunda* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Iganci*

883 (RB): ERS11697080; *Jupunba idiopoda* (S.F. Blake) M.V.B. Soares, M.P. Morim & Iganci, *Quesada 1718* (NY): ERS11697081; *Jupunba laeta* (Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Mori 25147* (NY): ERS11697083; *Jupunba langsdorfii* (Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Ribeiro 728* (RB): ERS11697084; *Jupunba leucophylla* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Iganci 839* (RB): ERS11697086; *Jupunba longipedunculata* (H.S. Irwin) M.V.B. Soares, M.P. Morim & Iganci, *Cardona 2682* (NY): ERS11697088; *Jupunba macradenia* (Pittier) M.V.B. Soares, M.P. Morim & Iganci, *Lourteig 3021* (NY): ERS11697089; *Jupunba microcalyx* (Spruce ex Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Iganci 855* (RB): ERS11697090; *Jupunba nipensis* Britton & Rose, *Mayo 19662* (NY): ERS11697091; *Jupunba oppositifolia* Britton & Rose, *Liegier 16014* (NY): ERS11697092; *Jupunba oxyphyllidia* (Barneby & J.W. Grimes) M.V.B. Soares, M.P. Morim & Iganci, *Yonker 6157* (NY): ERS11697093; *Jupunba rhombea* (Benth.) M.V.B. Soares, M.P. Morim & Iganci, *Iganci 261* (RB): ERS11697087; *Jupunba trapezifolia* Moldenke, *Simon 1600* (CEN): ERS4812839 ; *Jupunba villosa* (Iganci & M.P. Lima) M.V.B. Soares, M.P. Morim & Iganci, *Borges 423* (RB): ERS11697095; *Punjuba callejasii* (Barneby & J.W. Grimes) M.V.B. Soares, M.P. Morim & Iganci, *Daly 5935* (NY): ERS11697075; *Punjuba killipii* Britton & Rose, *Palodorios 6252* (NY): ERS11697082; *Punjuba lehmannii* Britton & Rose ex Britton & Killip, *Escobar 7465* (NY): ERS11697085; *Punjuba racemiflora* Britton & Rose, *Jimenez & Soares 3626* (USJ): ERS11697094.

Supplementary material 1

Supplementary data file S1

Authors: Marcos Vinicius Batista Soares, Erik Jozef Mathieu Koenen3, João Ricardo Vieira Iganci, Marli Pires Morim

Data type: zip. archiv.

Explanation note: Alignments of 560 nuclear loci in FASTA format (zipped).

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Supplementary material 2

Supplementary data file S2

Authors: Marcos Vinicius Batista Soares, Erik Jozef Mathieu Koenen3, João Ricardo Vieira Iganci, Marli Pires Morim

Data type: zip. archiv.

Explanation note: Gene trees of 560 nuclear loci in Newick format (zipped).

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Link: https://doi.org/10.3897/phytokeys.205.82775.suppl2

Supplementary material 3

Supplementary data file S3

Authors: Marcos Vinicius Batista Soares, Erik Jozef Mathieu Koenen3, João Ricardo Vieira Iganci, Marli Pires Morim

Data type: zip. archiv.

Explanation note: MI gene trees (one tip per accession) of 398 nuclear loci with nodes with < 10% bootstrap support collapsed, in Newick format.

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RESEARCH ARTICLE

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Boliviadendron, a new segregate genus of mimosoid legume (Leguminosae, Caesalpinioideae, mimosoid clade) narrowly endemic to the interior Andean valleys of Bolivia

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Abstract

Phylogenetic analyses of DNA sequence data sampling all species of *Leucochloron* alongside representatives of genera of the Inga and Albizia clades of the larger ingoid clade of mimosoid legumes (sensu Koenen et al. 2020) confirm the non-monophyly of the genus *Leucochloron*. We show that *Leucochloron bolivianum* is placed in the Albizia clade, while the remaining four species of *Leucochloron* are placed in the Inga clade, in line with previous results. To rectify this non-monophyly, *L. bolivianum* is segregated as the new genus, *Boliviadendron*, with a single species, *Boliviadendron bolivianum*, narrowly endemic to the interior Andean valleys of Bolivia. We illustrate this new segregate genus, present a map of its distribution and discuss the striking lack of morphological distinctions between *Boliviadendron* and *Leucochloron*, as well as the phylogenetic and morphological affinities of *Boliviadendron* to the genera *Enterolobium* and *Albizia*.

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Keywords
Fabaceae, generic delimitation, *Leucochloron*, monophyly, taxonomy

Introduction

The genus *Leucochloron* Barneby & J.W. Grimes was established by Barneby and Grimes (1996) as part of their generic system for the mimosoid legume tribe Ingeae in the New World, with four species, all of them native to Brazil: *L. incuriale* (Vell.) Barneby & J.W. Grimes, *L. limae* Barneby & J.W. Grimes, *L. minarum* (Glaz. ex Harms) Barneby & J.W. Grimes and *L. foederale* (Barneby & J.W. Grimes) Barneby & J.W. Grimes. Barneby and Grimes (1996) based their new genus on the combination of lack of armature, perulate resting buds, homomorphic flowers arranged in globose axillary capitula, broad plano-compressed stiffly papery or weakly coriaceous fruits and shiny discoid exareolate seeds, encircled by a marginal nerve or minute wing.

In May 2002, C.E. Hughes and collaborators collected material of an undescribed mimosoid legume tree from a single locality on the mid-elevation eastern flanks of the Bolivian Andes. A small number of additional collections from nearby localities have been made in subsequent years. This material shares the same combination of characters used by Barneby and Grimes (1996) to delimit *Leucochloron* and, hence, provided the basis for description of a fifth species, *Leucochloron bolivianum* C.E. Hughes & Atahuachi (Hughes and Atahuachi (2006, publ. 2007).

This apparently morphologically commodious generic home for *Leucochloron bolivianum* has been brought into question by phylogenetic evidence from Almeida (2014), LPWG (2017) and more recently generated DNA sequence data for 964 nuclear genes for two species of *Leucochloron*, *L. bolivianum* and *L. limae*, which showed that the genus *Leucochloron* is non-monophyletic (Koenen et al. 2020). Here, we further test this non-monophyly to ascertain where the remaining three species of *Leucochloron* are placed phylogenetically in relation to the two separate *Leucochloron* lineages identified by Koenen et al. (2020), with the aim of providing a solid basis for generic re-delimitation.

Materials and methods

Morpho-taxonomic analyses and sample selection for DNA extraction were based on field collections and herbarium specimens from BOLV, FHO, HUEFS, K, LPB, MBM, MEXU, NY, SP and VIC (acronyms follow Thiers 2022, [continuously updated]) collections and previous taxonomic literature (Hughes and Atahuachi 2006, publ. 2007; Almeida 2014).

We sampled 47 accessions (40 of them newly sequenced here and seven using sequences from GenBank) in 19 genera, including all genera of the Albizia and Inga

clades sensu Koenen et al. (2020), except *Abarema* s.s., plus a representative set of other lineages spanning the ingoid clade (see Suppl. material 1: Table S1, for GenBank accession numbers and voucher information). All five recognised species of *Leucochloron* were sampled, including seven accessions of *Leucochloron bolivianum*. *Acacia* Mill. (i.e. *Acacia* sensu stricto), which is also a member of the wider ingoid clade, was selected as outgroup.

Total genomic DNA was extracted from silica-dried or herbarium leaf tissue using a modified 2 × CTAB protocol (Doyle and Doyle 1987). DNA samples with low amplification were purified using Sepharose CL-6B (Sigma, St. Louis, Missouri, USA), following the manufacturer's protocol. We sequenced eight loci which have been used in previous phylogenetic studies of generic relationships in the ingoid clade (e.g., Souza et al. 2013): the nuclear ribosomal 5.8S subunit and flanking ITS1 and ITS2 spacers, the external transcribed spacer ETS and the plastid loci *rps16*, *psbA-trnH*, *rpL32-trnL*, *trnL intron*, *trnL-F* and *trnD-T* (see Suppl. material 1: Table S2 for primer sequences and amplification protocols). The ITS amplifications were performed with primers 17SE and 26SE or primers ITS92 and ITS4. The *trnD-T* region was amplified in two independent reactions combining primers: $trnD^{GUC}$ + $trnE^{UUC}$ and $trnY^{GUA}$ + $trnT^{GGU}$ (Shaw et al. 2007).

Polymerase Chain Reactions (PCR) were performed using TopTaq Master Mix Kit (QIAGEN GmbH, Hilden, Germany) according to the manufacturer's protocol, in 10–15 µl of final reaction volume. For the nrITS and ETS amplifications, 1.0 M betaine and 2% DMSO (dimethylsulphoxide; 2% of the preparation volume) were added. PCR products were purified by enzymatic treatments with Exonuclease I and Shrimp alkaline phosphatase (kit ExoSapIT, GE Healthcare Buckinghamshire, U.K.). Sequencing reactions were performed using the same primers used for PCR and Big Dye Terminator kit v.3.1 (Applied Biosystems, Foster City, California, U.S.A.), on the ABI3130XL Analyzer (Applied BioSystems), at the Laboratório de Sistemática Molecular de Plantas (LAMOL), of the Universidade Estadual de Feira de Santana (UEFS), Bahia, Brazil.

Electropherograms were assembled in Geneious 5.3.6 (Drummond et al. 2010) using default assembly settings. Consensus sequences were aligned in MUSCLE (Edgar 2004) using Geneious, with manual adjustments. We analysed three datasets: 1) the combined plastid loci, 2) combined nuclear loci and 3) combined plastid + nuclear loci. Incongruence between datasets was assessed via 1,000 replicates of the Homogeneity of Participation Test (Felsenstein 1985) using PAUP v. 4.0b10 for Windows (Swofford 2002).

Maximum Parsimony (MP) analyses were performed using PAUP v.4.0 (Swofford 2002), using Fitch parsimony (all characters unordered and equally weighted; Fitch 1971), 1,000 replications of taxon addition and resampling by tree bisection-reconnection (TBR) branch swapping, saving up to 15 trees per replication to prevent extensive searches in sub-optimal islands. Trees from the first search were used as a starting point for a second search using the same parameters retaining a maximum of 10,000 trees. Non-parametric bootstrapping (BS; Felsenstein 1985) was used to

estimate clade support, assessed through 1,000 replications, simple taxon-addition and the TBR algorithm, saving up to 15 trees per replicate.

Maximum Likelihood (ML) analyses were performed using RAxML v.8 (Stamatakis 2014), on the CIPRES Science Gateway v.3.3 (Miller et al. 2010), using the GTR + CAT evolutionary model and estimating GAMMA distribution during the run. Branch support was evaluated using 1,000 rapid bootstrap replicates.

Best-fitting substitution models for each data partition were selected using the Akaike Information Criterion (AIC) using MrModeltest v.2.3 (Nylander 2004) (Suppl. material 1: Table S2). Bayesian Inference (BI) analysis was performed on MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003; Ronquist et al. 2012), on the CIPRES Science Gateway v.3.3 (Miller et al. 2010). Two separate runs of a Metropolis-coupled Markov Chain Monte Carlo (MCMC) were initiated with random starting trees and four simultaneous chains set at default temperatures (Ronquist and Huelsenbeck 2003) for 30 million generations, sampling once every 10^3 generations. Convergence was assessed using Tracer v.1.6 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) ≥ 200. MrBayes was also used to summarise 75% post burn-in trees sampled from a 50% majority rule consensus tree that included posterior probabilities (PP) as branch support estimates. All trees from MP, BI and ML were visualised and edited in FigTree 1.4.4 (Rambaut 2018).

Results

While separate analyses of the nuclear ITS + ETS and plastid loci yielded gene trees that were, in many cases, poorly resolved (Suppl. material 1: Table S3, Suppl. material 2: Figs S1–S4), the combined nuclear + plastid analysis (Fig. 1) is sufficiently resolved to demonstrate that the genus *Leucochloron* is not monophyletic, with all seven accessions of *L. bolivianum* forming a robustly supported clade placed in a clade with *Albizia* Durazz., *Enterolobium* Mart. and *Samanea* (Benth.) Merr. and the other four species of *Leucochloron* forming a robustly supported clade that is placed in a clade with *Inga* Mill., *Zygia* P. Browne and *Macrosamanea* Britton & Rose ex Britton & Killip. (Fig. 1).

Discussion

The non-monophyly of the genus *Leucochloron* is supported by two independent phylogenetic studies, one presented here sampling all five species currently assigned to the genus, based on a small set of widely-used nrDNA and plastid DNA sequence loci (Fig. 1) and the other sampling just two species, but based on phylogenomic analyses of 964 nuclear gene sequences and a broad sample of genera across the whole mimosoid clade (Koenen et al. 2020). This non-monophyly is further confirmed in a more recent phylogeny constructed using a slightly expanded set of 997 nuclear genes, derived from a modified version of the *Mimobaits* gene set of Koenen et al. (2020),

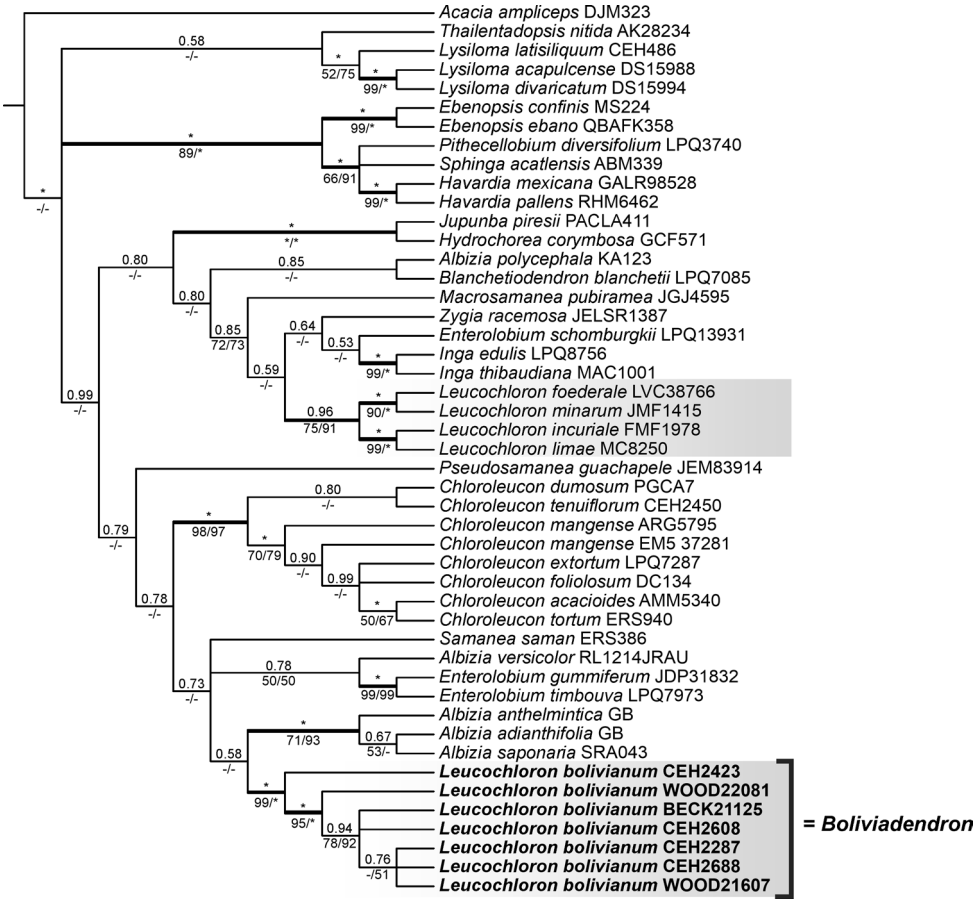

Figure 1. Majority-rule (50%) consensus tree from Bayesian analysis of the combined nuclear (ITS, ETS) and plastid (*psbA-trnH*, *rpL32*, *rps16*, *trnD-T*, *trnL-F*) data for *Boliviadendron* and related genera. Values above branches are Bayesian Posterior Probabilities (PP), below are Bootstrap Support (BS) percentages from the maximum parsimony (left) and Maximum Likelihood analyses (right). Branches supported by PP ≥ 95% are in bold. Only BS values ≥ 50% are shown; - indicates BS ≤ 50%; * indicates PP = 1.0 or BS = 100%.

which sampled all but five of the 151 genera of subfamily Caesalpinioideae (Ringelberg et al. 2022). This thorough sampling of both taxa and genes demonstrates beyond doubt that *Leucochloron* is indeed non-monophyletic, with *L. bolivianum* placed in the Albizia clade (sensu Koenen et al. 2020) and the remaining four species of *Leucochloron* forming a robustly-supported clade in the Inga clade (sensu Koenen et al. 2020; Fig. 1). These results provide strong evidence supporting segregation of *L. bolivianum* as a new genus, here named *Boliviadendron*.

This robustly-supported non-monophyly is unexpected, given the close morphological similarities between *L. bolivianum* and the other four species of *Leucochloron*. Indeed, there appear to be very few qualitative morphological differences

separating *Boliviadendron* (i.e., *L. bolivianum*) from *Leucochloron*, suggesting that the original combination of character states used by Barneby and Grimes (1996) to delimit *Leucochloron* has essentially been recapitulated in *Boliviadendron*. These striking morphological similarities between *Leucochloron* and *Boliviadendron* must, thus, be viewed as further evidence of the extensive morphological homoplasy evident across mimosoids which has frequently misled generic delimitation (Ringelberg et al. 2022). For example, the presence of minute wing-like rims of seeds, which was one of the characters supporting placement of *L. bolivianum* in the genus *Leucochloron* (Hughes and Atahuachi 2006, publ. 2007), have been documented across phylogenetically scattered mimosoid legume lineages, including the genera *Mimozyganthus* Burkart (Luckow et al. 2005), *Archidendropsis* I.C. Nielsen and *Leucochloron* and now here in the phylogenetically distinct lineage *Boliviadendron*. This suggests that this character, just like seeds with true wings which also occur across a disparate set of unrelated mimosoid genera, is homoplasious and evolutionarily labile.

Morphological characters which weakly separate *Boliviadendron* from *Leucochloron* s.s. are: (i) the leaflet base is more evidently asymmetrical in *Boliviadendron* than in the species of *Leucochloron* and the under-surface of *Boliviadendron* leaflets has 1–2 (–3) prominent primary veins, but otherwise the venation is not evident vs. the evident reticulate secondary and tertiary venation on the lower leaflet surface in *Leucochloron* species; (ii) in *Boliviadendron*, the upper leaflet surfaces are consistently blotched purple-black, while leaflets of *Leucochloron* s.s. species are strongly discolorous, with the upper surface drying dark brown and often glossy; (iii) the indumentum in *Boliviadendron* tends to be shorter and white, especially on the corollas and calyces which have fine white, appressed, silky trichomes vs. the generally more ferruginous and longer indumentum, occasionally with golden and/or white hairs intermixed, of *Leucochloron* species; (iv) the number of pollen grains per polyad is constant in *Boliviadendron* at 16 (counted on the isotype *Hughes 2423* and *Wood 21618* at K), while in *Leucochloron* s.s., it is variable (even within species) with 16, 18, 24 or 32 grains.

In the Koenen et al. (2020) phylogeny, *Boliviadendron* appeared as sister to a clade comprising *Enterolobium* and *Albizia* s.s. (i.e., Old World *Albizia*). In the phylogeny presented here, *Boliviadendron* is also placed in a clade with *Enterolobium* and *Albizia* s.s. (Fig. 1) in line with the findings of Koenen et al. (2020). This close relationship of *Boliviadendron* to *Enterolobium* is reflected in the closely similar leaf and flower morphologies of these two genera, including the asymmetrically displaced primary vein of the leaflets (which also characterises many species of *Albizia* s.s.), the blotched purple-black upper leaflet surfaces and superficially very similar globose axillary capitula of homomorphic flowers immersed amongst coevally developing leaves. However, in fruit, these two genera are immediately distinguishable by the characteristically thickened indehiscent curved 'ear-pod' fruits of *Enterolobium* vs. the plano-compressed, inertly dehiscent fruits with chartaceous valves of *Boliviadendron*. This means that material of *Boliviadendron* lacking fruits can be difficult to distinguish from *Enterolobium*. Indeed, one of the collections, cited as *L. bolivianum* by Hughes and Atahuachi (2006, publ. 2007) (*J.R.I. Wood 22134* at K, which has leaves and

flowers only), has since been correctly identified as *Enterolobium contortisiliquum* (Vell.) Morong. Closer examination of the inflorescences of these two taxa, which can occur in close geographical proximity in Bolivia, shows that the flowers of *Boliviadendron* are essentially sessile, while those of *Enterolobium contortisiliquum* are pedicellate, on more robust inflorescences. The plano-compressed fruits with stiffly papery chartaceous or weakly coriaceous valves dehiscing inertly along both sutures in *Boliviadendron* are strongly reminiscent of the fruits of the other closely related genus, *Albizia* s.s., but the marked lack of a pleurogram on the seeds in *Boliviadendron* clearly distinguishes the genus from *Albizia*. It is notable that polyads, like those of *Boliviadendron*, are also 16-celled in *Albizia* s.s. (although only few species of the genus have been studied for their pollen characteristics), but can be 16 or 32-celled in *Enterolobium*.

Taxonomy

Boliviadendron **E.R. Souza & C.E. Hughes, gen. nov.**
urn:lsid:ipni.org:names:77303834-1
Fig. 2

Type. *Boliviadendron bolivianum* (C.E. Hughes & Atahuachi) E.R. Souza & C.E. Hughes.

Diagnosis. *Boliviadendron* is similar in almost all respects to the genus *Leucochloron* and is segregated first and foremost because these two lineages are phylogenetically not closely related (Fig. 1; Koenen et al. 2020). *Boliviadendron* differs from *Leucochloron* in its more evidently asymmetrical leaflet bases, by having just 1–2 (–3) primary veins visible vs. the evident reticulate secondary and tertiary venation on the lower leaflet surface in *Leucochloron*, by the consistent purple-black blotches on the upper surface of the leaflets (sometimes the whole surface suffused purplish-black, but never glossy) vs. the strongly discolorous leaflets of *Leucochloron* where the upper surface dries dark brown and is often glossy and finally, by the shorter, white indumentum vs. the more generally ferruginous and longer indumentum of *Leucochloron* species.

Description. (modified from Hughes and Atahuachi 2006, publ. 2007). Small, unarmed multi-stemmed tree to 5–6 (–10) m tall and 20–35 cm dbh with an irregular spreading crown (Fig. 2A). Outer bark smooth, mid grey-brown, with horizontal lines of lenticels when young (Fig. 2B), becoming thick and corky and vertically fissured with age; inner bark reddish, then cream, gritty. Woody shoots glabrate, lenticellate, dull grey, lenticels round pustulate, the outer bark papery, slightly striate and sometimes slightly exfoliating. Young shoots, leaf stalks and peduncles minutely and sparsely to densely puberulent with whitish or dull golden 0.1– 0.2 mm hairs. **Resting buds** perulate, ovoid to 1.5 mm long and densely pilosulous (as for shoots), but these generally lacking. **Stipules** linear-triangular, 3 × 1.7–2 mm, caducous. **Leaves** bipinnate with 4–5 (–6) pairs of pinnae, leaf stalks canaliculate with two parallel longitudinal ridges, 7–11 cm long, ending in a 2 mm long mucro

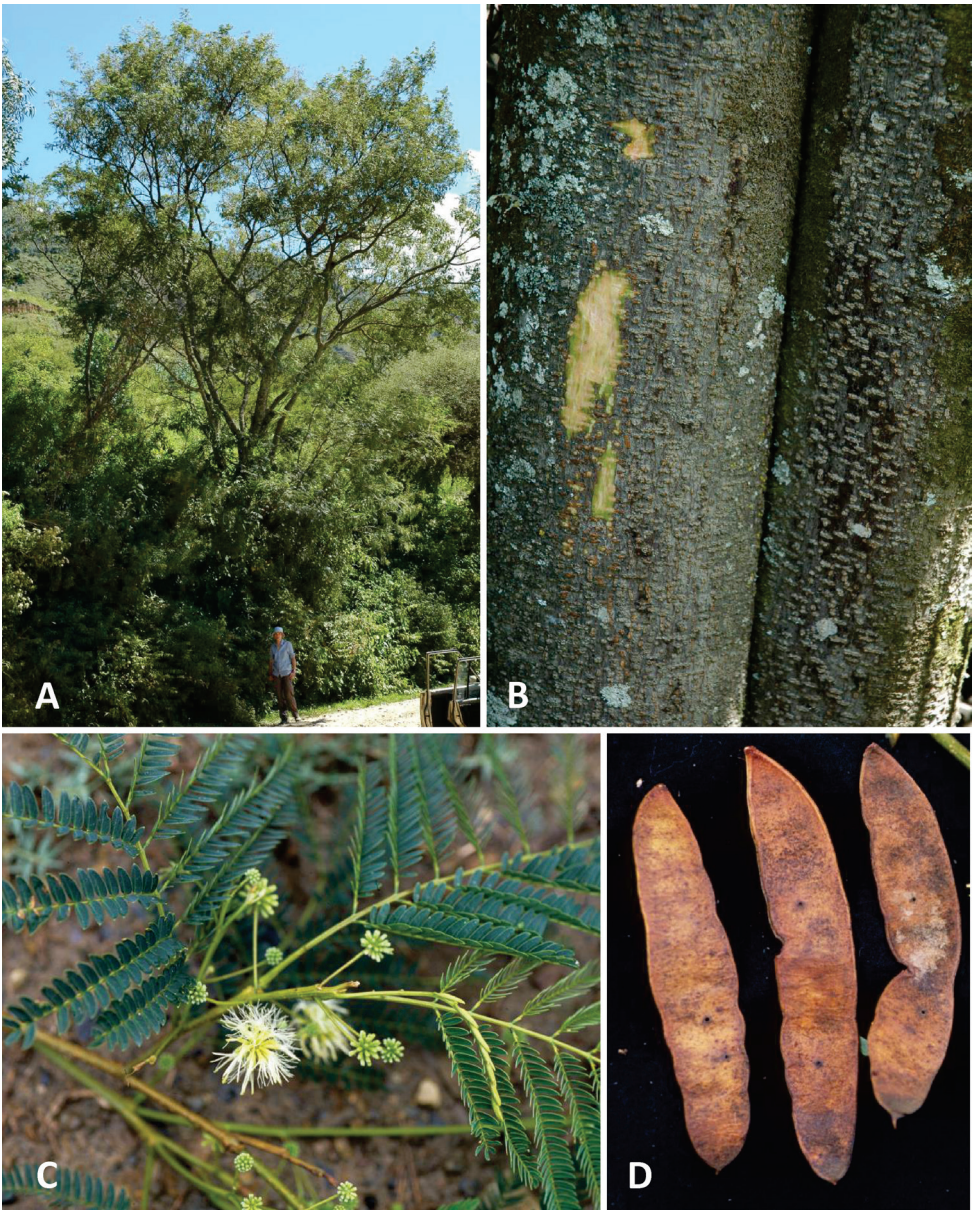

Figure 2. *Boliviadendron bolivianum* **A** habit **B** bark and slash **C** flowers and leaves **D** fruits **A, B** from *Hughes et al. 2608* **C,D** from *Hughes et al. 2423*. All photos Colin Hughes.

and including a 2.5–3.6 cm long petiole charged with a 1–1.3 mm diameter circular or weakly ellipsoid sessile or subsessile, thick-rimmed, cupular nectary at or slightly above mid-petiole position; similar smaller nectaries variably present between distal 1–2 pairs of pinnae or sometimes between all pinnae pairs. Longer interpinnal

segments 1.3–1.7 cm long, the rachis of longer pinnae 6–8 cm with 15–20 pairs of leaflets per pinna. Leaflets slightly decrescent proximally and distally, larger leaflets 7–10 × 2.1–3.0 (–3.2) mm, not strongly discolorous, nearly glabrous or very sparsely puberulent above, sparsely puberulent below, on small, ridged, transversely elliptic, asymmetric 3 × 0.6 mm pulvinules, the first anterior or first pair of leaflets reduced to 1.2–1.5 mm long paraphyllidia. Leaflets linear-oblong, obliquely truncate at base, obtuse at apex, the tip sometimes acute, venation indistinct, palmate-pinnate brochidodromous, with 1–2 (–weakly 3) primary veins at base, the main primary vein distinctly asymmetric, dividing the blade 1:2–2.5, giving rise on each side to 3–4 sinuous secondary veins, albeit these often indistinct or obscured by the indumentum, venation very faintly immersed or invisible above, the 1–2 (–3) primary veins clearly visible and weakly prominulous below. **Flowers** sessile, homomorphic and arranged in lax globose capitula (Fig. 2C) on 2.5–3 cm-long slender peduncles, moriform in bud, 12–13 mm in diameter (excluding the filaments), the receptacle 1.3 mm in diameter, each capitulum with 20–25 flowers, whitish-green in bud due to dense silky puberulent indumentum on calyx and corolla. The capitula immersed in new foliage, solitary or in fascicles of 2–3 in axils of coeval leaves. Bracts sessile, short spatulate, 0.2–0.4 mm long, puberulent. Calyx narrowly campanulate, 2.5 mm long, the triangular lobes 0.3–0.4 mm long. Corolla tubular, slightly funnel-shaped, 5–6 mm long, the free lobes 1 mm, slightly reflexed. Androecium of ca. 40 stamens to 10 mm long, fused basally into a 3–4 mm long tube that is not or hardly exserted beyond the corolla. Ovary 0.8 mm long, sessile, the style 2.5 mm, held below anthers of the stamens. **Pods** (Fig. 2D) 1 per capitulum, sessile, (6–) 7–10 × 1.7–2 (–2.7) cm, (3–) 4–6 (–8)-seeded, flat plano-compressed, linear-oblong or oblong, obtuse at each end, sometimes with a short apiculum at apex, the valves straight or with slightly undulate margins, stiff papery, pale whitish- or yellow-green when unripe, turning dull orange-brown when ripe, obscurely venulose, sparsely and minutely puberulent overall, internally dull stramineous, framed by plain sutures < 1 mm wide, tardily dehiscent along both sutures, opening narrowly to release seeds, the valves remaining attached after dehiscence. Seeds horizontal at middle of pod, flat disciform, broadly suborbicular, 11–13 mm in diameter, < 1 mm thick, the testa thin, lustrous, translucent castaneous, slightly wrinkled when dry, pleurogram lacking, surrounded by a narrow 0.4–0.6 mm dark marginal nerve or minute wing.

Geographic distribution. The monospecific genus *Boliviadendron* occupies a narrowly restricted distribution endemic to Bolivia and has been recorded from just a small number of localities on the eastern flanks of the Andes at mid-elevations in interior Andean valleys in the Departments of La Paz, Cochabamba and Santa Cruz (Fig. 3).

Habitat. Locally common in fence-lines and remnant patches of subhumid or seasonally dry Yungas forest and secondary thickets of *Baccharis dracunculifolia* DC., *Dasyphyllum brasiliense* (Spreng.) Cabrera (both Asteraceae), *Dodonaea viscosa* Jacq. (Sapindaceae) and *Tecoma stans* Juss. (Bignoniaceae). Other associated species include *Apurimacia michelii* Harms., *Coursetia brachyrhachis* Harms., *Erythrina falcata* Benth.,

Mimosa boliviana Benth., *M. woodii* Atahuachi & C.E. Hughes, *Parapiptadenia excelsa* (Griseb.) Burkart (all Leguminosae), *Schinopsis haenkeana* Engl. (Anacardiaceae), *Cordyline dracaenoides* Kunth (Asparagaceae), *Kageneckia lanceolata* Ruiz & Pav. (Rosaceae) and *Cleistocactus laniceps* (K. Schum.) Rol.-Goss (Cactaceae). *Boliviadendron* is known only from the slopes of interior valleys of Bolivia between 2150 and 2770 m alt., around the transition from seasonally-dry tropical inter-Andean valley forests to more moist mid-elevation montane Ceja de Monte Yungeña vegetation. Most collections (apart from two outlying localities in Dept. Santa Cruz) come from two nearby tributaries of the upper Río Cotacajes, in Prov. Ayopaya, Cochabamba and Prov. Inquisivi, La Paz, Bolivia, an area with several other narrowly-endemic plants, including *Justicia pluriformis* Wash. & J.R.I. Wood (Acanthaceae), *Philibertia fontellae* (Murillo) Goyder (Apocynaceae), *Solanum stellativelutinum* Bitter and *S. tunariense* Kuntze (Solanaceae) and *Mimosa woodii* (Leguminosae). *Boliviadendron* (as *Leucochloron bolivianum*) was assigned an IUCN threat category of Endangered (EN) B1ab(iii,iv) in 2011 (Atahuachi 2012) on account of its very limited extent of occurrence and threats from habitat destruction caused by agricultural expansion and fire which are continuing today.

Etymology. *Boliviadendron* is one of just two mimosoid legume genera known to be endemic to Bolivia (the other being *Pseudosenegalia* Seigler & Ebinger with two species) and that Bolivian endemism is highlighted here by the double-barrelled reference to that country in the name *Boliviadendron bolivianum*.

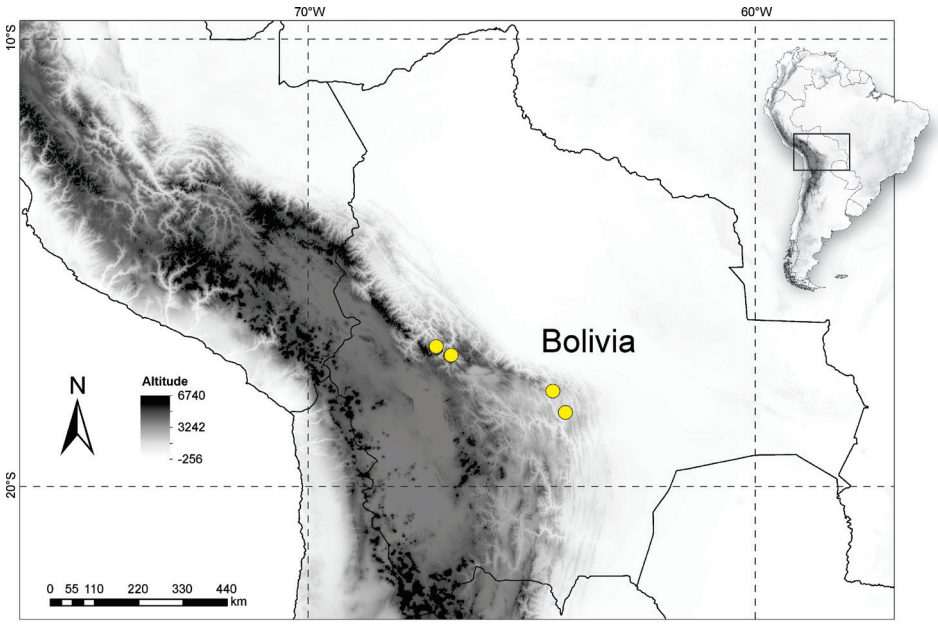

Figure 3. Distribution of *Boliviadendron bolivianum* endemic to the interior valleys on the eastern flanks of the Andes in Bolivia.

***Boliviadendron bolivianum* (C.E. Hughes & Atahuachi) E.R. Souza & C.E. Hughes, comb. nov.**
urn:lsid:ipni.org:names:77303835-1

Basionym. *Leucochloron bolivianum* C.E. Hughes & Atahuachi, Kew Bull. 61: 559. 2006, publ. 31 Jan 2007.

Type. Bolivia. La Paz, Prov. Inquisivi, 6 km N of Inquisivi, rd towards Cajuata, Circuata and Miguillas, 16°53'42"S, 67°08'23"W, 2385 m alt., 12 Dec 2003, *C.E. Hughes*, *T. Ortuño & M. Mendoza 2423* (holotype: LPB; isotypes: BOLV, FHO, K [K000532854], USZ).

Additional material examined. Bolivia. Cochabamba, Prov. Ayopaya, 1 km S of Independencia on rd to Pongo, 17°05'03"S, 66°48'53"W, 2630 m alt., 15 May 2002 (unripe fr.), *C.E. Hughes*, *J.R.I. Wood & R. Forrest 2287* (FHO!, K! [2 specimens], LPB!). Cochabamba, Ayopaya, 1 km above Independencia on road to Sailapata and La Mina, 17°04'S, 66°48'W, 2770 m, 18 Dec 2002 (fl.), *J.R.I. Wood*, *M. Mercado & M. Mendoza 18731* (K!). La Paz, Prov. Inquisivi, ca. 10 km N of Inquisivi, rd to Licoma and Circuata, 16°53'71"S, 67°08'35"W, 2300 m alt., 27 March 2007 (unripe fr.), *C.E. Hughes*, *T. Särkinen*, *A. Wortley & P. Duchen 2608* (FHO!, K! [2 specimens], LPB). La Paz, Prov. Inquisivi, 6 km N of Inquisivi, rd towards Cajuata, 16°53'43"S, 67°08'23"W, 2379 m alt., 12 Feb 2005 (ripe fr.), *J.R.I. Wood*, *M. Atahuachi & T. Ortuño 21607* (BOLV, FHO!, K! [2 specimens], LPB). La Paz, Prov. Inquisivi, 0.5 km above Sica rd from Inquisivi to Cajuata, 16°52'32"S, 67°08'04"W, 2565 m alt., 12 Feb 2005 (fl.), *J.R.I. Wood*, *M. Atahuachi & T. Ortuño 21618* (BOLV, FHO!, K! [2 specimens], LPB). La Paz, Prov. Inquisivi, 13 km from Inquisivi towards Licoma, crossing the Río Quime, 2150 m alt., 24 April 1992 (unripe fr.), *St.G. Beck 21125* (K! [2 specimens]). La Paz, Prov. Inquisivi, along slopes E of Communidad Micayani to the Rio Khokhoni more or less to the junction with a fork flowing down from Communidad Yamora and following the Rio Khokhoni upstream 1 km from this point, ca. 4 km SE from Inquisivi, 16°55'S, 67°06'W, 2650 m alt., 14 Jan 1989 (fl.), *M. Lewis 35094* (K!, LPB, MO). Santa Cruz, Prov. M. Caballero, ascending from Comarapa towards Cerro Bravo, 17°52'25"S, 64°31'32"W, 20 Nov 2005 (fl.), *J.R.I. Wood & M. Mendoza 22081* (BOLV, FHO!, K! [2 specimens], LPB). Santa Cruz, Prov. Valle Grande, 14.2 km on the gravel road towards Moro Moro from the highway in the Trigal / Muyurina valley, 18°21'00"S, 64°14'27"W, 2335 m alt., 1 Jan 2011 (fl.), *M. Nee & J.M. Mendoza F 57498* (NY!).

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Supplementary material 1

Table S1–S3
Authors: Lamarck Rocha
Data type: Tables
Explanation note: Includes voucher information, primers and protocols and summary of phylogenetic analyses.
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Supplementary material 2

Figures S1–S9
Authors: Lamarck Rocha
Data type: Individual phylogenetic analyzes
Explanation note: Includes all trees derived from the BI, MP and ML with combined nuclear + plastidial loci, and individual analyses from nuclear, and plastidial loci.
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Osodendron gen. nov. (Leguminosae, Caesalpinioideae), a new genus of mimosoid legumes of tropical Africa

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Abstract

The genus *Osodendron* is here newly described to accommodate three species and one subspecies of African mimosoid legumes. These taxa have previously been included by several authors in *Albizia*, *Cathormion* and/or *Samanea*, but they have been shown to be phylogenetically unrelated to any of these, being instead the sister-group of the recently described Neotropical genus *Robrichia*, which is similar in vegetative morphology and especially its very similar indumentum, but is decidedly different in pod morphology. A taxonomic treatment of the three species in the genus is presented, with species descriptions, photographs, distribution maps and an identification key. The type species *Osodendron altissimum* (Hook. f.) E.J.M. Koenen occurs in swamp and riverine rainforest and gallery forests, with the typical subsp. *altissimum* widespread across tropical Africa, while *Osodendron altissimum* subsp. *busiraensis* (G.C.C. Gilbert) E.J.M. Koenen is only known from the Busira river catchment in the western part of the Democratic Republic of Congo. Of the other two species, *Osodendron dinklagei* (Harms) E.J.M. Koenen is a common tree of rainforest and the forest-savannah transition including semi-deciduous and secondary forest as well as gallery forest and is restricted to Upper Guinea and the similar, but vegetatively more variable *Osodendron leptophyllum* (Harms) E.J.M. Koenen occupies comparable vegetation types in Lower Guinea and extends marginally into the Sudanian and Zambezian savannahs in gallery forest.

Keywords

Albizia, *Cathormion*, ingoid clade, Fabaceae, *Samanea*, taxonomy

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Introduction

The taxonomy and classification of the mimosoid legumes has seen significant changes over the last 35 years, including the disintegration of *Acacia* Mill. (Pedley 1986; Luckow et al. 2003; Miller and Seigler 2012), multiple contentious reclassifications of the ingoid mimosoids by several authors (e.g. Nielsen 1981; Barneby and Grimes 1996, 1997; Lewis and Rico-Arce 2005; reviewed by Brown 2008), as well as the clade not being recognised as a subfamily (LPWG 2017) anymore, being instead subsumed into a recircumscribed Caesalpinioideae. Following phylogenetic (Luckow et al. 2003; Bouchenak-Khelladi et al. 2010) and phylogenomic (Koenen et al. 2020; Ringelberg et al. 2022) studies, several further changes have recently been proposed (e.g. Souza et al. 2013; Soares et al. 2021).

In all this turmoil, a number of African species that have variously been placed in *Albizia* Durazz., *Cathormion* Hassk. and/or *Samanea* Merr., have been somewhat neglected by most authors. While Barneby and Grimes (1996) mentioned the similarities of some of these species to South-American taxa and Nielsen (1992) excluded them from *Cathormion*, they have not been formally dealt with and, therefore, Lewis and Rico-Arce (2005) referred them to the 'dustbin' genus *Albizia* (see Koenen et al. 2020) pending further studies on that genus. This was clearly unsatisfying and botanists working on the African flora have continued treating these species in *Cathormion* and *Samanea* (e.g. Hawthorne and Jongkind 2006: see note on p. 860), but this is an equally poor solution. The phylogenomic studies of Koenen et al. (2020) and Ringelberg et al. (2022) have elucidated the evolutionary relationships of these species for the first time. First, the type species of *Cathormion* was shown to be nested in *Albizia* and the generic name has been synonymised with that genus by Koenen et al. (2020), while the African *Cathormion obliquifoliolatum* (De Wild.) G.C.C. Gilbert & Boutique and *Cathormion rhombifolium* (Benth.) Keay were shown to be closely related to South American *Hydrochorea* Barneby & J.W. Grimes and are transferred to that genus by Soares et al. (2022). This leaves us with three species, *Cathormion altissimum* (Hook. f.) Hutch. & Dandy, *Samanea dinklagei* (Harms) Keay and *Samanea leptophylla* (Harms) Brenan & Brummit that were placed in the Inga clade by Koenen et al. (2020), but which cannot be placed decisively in any existing mimosoid genus. These three species have since been resolved by Ringelberg et al. (2022) as the sister-group to the recently established South and Central American genus *Robrichia* (Barneby & J.W. Grimes) A.R.M. Luz & E.R. Souza (syn. *Enterolobium* sect. *Robrichia* Barneby & J.W. Grimes; Souza et al. 2022).

While these African species are clearly similar to *Robrichia* in sharing the same ferruginous pubescence on young parts, as well as having very similar inflorescence morphology, the African species display wider variation in leaf size, leaflet number and shape, but differ most notably in pod morphology. The species of *Robrichia* are characterised by contorted ("ear-shaped") indehiscent pods (Fig. 1G, H; Souza et al. 2022: Fig. 2D, E, J) which led them to be previously classified in *Enterolobium* Mart., while the related African species have twisted to coiled articulated lomentiform pods (*C. altissimum*, Figs 1A, 2G, H), straight to slightly curved woody pods (*S. dinklagei*, Figs 1C, 3F) or intermediate straight to slightly curved articulated pods (*S. leptophylla*/*C. eriorhachis*, Figs 1D, 3K). The woody pods were likened to *Samanea* and the articulated pods are superficially similar to *Cathormion* s.s.; hence, these species have been placed in either or both these genera in the past.

Given the similarities and sister-group relationship with *Robrichia*, one could argue that these species might be accommodated in that genus, perhaps as a separate section. However, the generic description of *Robrichia* would then have to be considerably expanded to include the greater variation in leaf morphology and especially to encompass the different pod types. Given that the pods of *Robrichia* are highly characteristic, adding these African taxa to that genus would be undesirable and these two groups are equally conveniently accommodated in two separate genera. Therefore, I establish the new genus *Osodendron* E.J.M. Koenen to accommodate these three African species.

Much confusion about relationships and generic classification in mimosoids (especially ingoids) has been caused by homoplasious fruit characters (Ringelberg et al. 2022) and the lomentiform pod type is one of the most intriguing because it has apparently evolved multiple times associated with repeated adaptations to periodically inundated areas and/or riparian habitats to facilitate hydrochorous seed dispersal (Aviles Peraza et al. 2022; Ringelberg et al. 2022; Soares et al. 2022). Indeed, when comparing the pods of *Osodendron* spp. to those of some *Albizia* species (Fig. 1B) or *Hydrochorea* (Fig. 1F), one can understand why these have all been previously included in a broadly circumscribed *Cathormion* and why a close relationship between *Osodendron* and *Robrichia* was not suspected (Fig. 1G, H), even though Barneby and Grimes (1996: p. 247) noted that *Robrichia schomburgkii* (Benth.) A.R.M. Luz & E.R. Souza and *Samanea dinklagei* are very similar and essentially only differ in their fruits. To aid understanding of the differences in fruit morphology amongst the genera that are either closely related to *Osodendron* or with which these species were thought to share affinities, the critical pod characters of these groups are summarised globally in Table 1. It is clear that *Osodendron* can be separated from the continental African species of *Albizia* and *Hydrochorea* by at least some of the features of the fruit, especially dehiscence, but it becomes more complicated when taking Madagascan, Asian, Australian and Pacific *Albizia* into account. Further studies

Table 1. Fruit characters of *Osodendron* and morphologically similar genera.

	fruit shape	**pod valve texture**	**septate between seeds**	**dehiscence**
Osodendron – Africa	straight, slightly curved, coiled and/or twisted	woody, papery to thinly ligneous or aerenchymous	yes	indehiscent or tardily breaking up into articles
Robrichia – Neotropics	contorted/ "ear-shaped"	woody	yes	indehiscent
Hydrochorea – African continent (sensu Soares et al. (2022))	straight to falcate or slightly curved	papery	yes	loment, seeds dispersed in 1-seeded articles
Hydrochorea – Neotropics (sensu Soares et al. (2022))	straight to falcate or slightly curved	papery or ligneous to woody	yes	loment, cryptoloment, follicular or indehiscent
Albizia – African continent	straight	papery	no	dehiscent
Albizia – Madagascar	straight or twisted	papery, thinly ligneous or woody	variable	dehiscent or indehiscent
Albizia – Asia, Australia and Oceania (incl. *Cathormion* s.s.)	straight, slightly curved or coiled/contorted	papery or woody	variable	dehiscent or tardily breaking up into articles
Albizia sect. *Arthrosamanea* (= *Pseudalbizzia*) – Neotropics	straight	papery, coriaceous or ligneous	variable	dehiscent, indehiscent, loment or cryptoloment
Samanea – Neotropics	straight to slightly curved	thick and ligneous and/or fleshy	yes	indehiscent

are required to understand the morphological differences between *Albizia* and its allies and segregates, but it is clear that the genus *Albizia*, under its current circumscription, with the inclusion of *Cathormion* s.s. and exclusion of the New World species (these being transferred to *Pseudalbizzia* Britton & Rose by Aviles Peraza et al. 2022) is monophyletic (Koenen et al. 2020; Ringelberg et al. 2022; Koenen et al. unpubl. data). Regardless of this wider global context, *Osodendron* can be readily separated from all other ingoid genera on the African continent, for which I include an identification key below.

Taxonomic treatment

Identification key to the continental African genera of ingoid mimosoids

(i.e. the ingoid clade sensu Koenen et al. (2020), which, apart from *Senegalia* Raf. and *Faidherbia* A. Chev., equates to all mimosoid genera native to the African continent with stamens fused into a tube):

1	Plants with prickles, stamens usually free or sometimes connate at base ..... ***Senegalia***
–	Plants usually unarmed, rarely with spinescent shoots or stipular spines, stamens fused into a tube or at least connate at base **2**
2	Shrubs with elastically dehiscent pods ..... ***Afrocalliandra*** **E.R. Souza & L.P. Queiroz**
–	Trees or rarely shrubs with indehiscent, non-elastically dehiscent or lomentiform pods **3**
3	Trees with stipular spines, inflorescence spicate ..... ***Faidherbia***
–	Usually unarmed trees or with spinescent shoots, but never stipular spines, inflorescences capitate **4**
4	Fruit non-septate, with papery valves, usually dehiscent ..... ***Albizia***
–	Fruit septate, with thin fibrous or thick woody valves, indehiscent or lomentiform **5**
5	Peripheral flowers of capitulum on pedicels at least 1 mm long, leaves with (1–)2–3 pairs of pinnae, fruit lomentaceous with seeds dispersed as 1-seeded articles ..... ***Hydrochorea***
–	Peripheral flowers on pedicels up to 0.5 mm long, leaves with (3–)5–30(–35) pairs of pinnae, fruit indehiscent or, if lomentiform, only tardily breaking up into articles ..... ***Osodendron***

Osodendron **E.J.M. Koenen, gen. nov.**
urn:lsid:ipni.org:names:77303836-1

Type. *Osodendron altissimum* (Hook. f.) E.J.M. Koenen.

Diagnosis. *Osodendron* differs from *Robrichia* by pods being either straight to twisted or coiled, but not contorted and ear-shaped.

Description. ***Trees***, or rarely ***shrubs***, unarmed or sometimes with spine-like projections on twigs or spine-like outgrowths on adventitious roots, resting buds perulate with scales distinctly different from stipules. ***Indumentum*** of usually dense ferruginous pubescence on twigs, petioles, rachis and pinna rachises, stipules, bud scales and peduncles. ***Leaves*** with (3–)5–30(–34) pairs of pinnae, opposite or sometimes (the lowermost pairs) sub-opposite, with a single petiolar nectary usually present, as well as nectaries between at least some of the pinna pairs on abaxial surface of the rachis and often also between the upper 1–many leaflet pairs on the pinna-rachises, the lowermost pair of pinnae usually distinctly shorter than others, pinnae with (7–)13–40(–48) leaflet pairs, one of the two leaflets of the lowermost pair usually reduced to a small paraphyllidium or lacking. ***Inflorescences*** sub-globose capitula, dimorphic, borne on peduncles arising from axillary fascicles, sometimes arranged in short compound pseudoracemes with the leaves suppressed (not fully developing) and caducous as apparent from the presence of leaf scars in the pseudoracemes, these pseudoracemes developing below the foliage. ***Flowers*** sessile or shortly stipitate, 4- or 5-merous, with fused calyx and corolla, androecium consisting of 10–25 stamens that are fused in the lower part to form a staminal tube, pollen compound in 32-celled polyads, central flowers more robust with a broader nectariferous base and longer staminal tube exserted beyond corolla tube. ***Fruits*** septate, indehiscent or tardily breaking up into articles, either lomentiform, twisted and strongly curved to coiled or weakly to not articulate and slightly curved to straight, seeds with a hard testa and open or closed pleurogram.

Distribution and habitat. Three species in tropical Africa, from Senegal in the west to the Democratic Republic of Congo in the east and Zambia and Angola in the south. Typically occurring in rainforest and extending into the savannah zone in gallery forest.

Etymology. The genus is named after "*Oso*", a food that is prepared in West Africa (Ghana and Nigeria) by fermenting the seeds of the type species *O. altissimum* and grinding them into a protein-rich paste that is subsequently cooked and eaten as either a main food, a delicacy or as a condiment to flavour soups and stews (Popoola et al. 2004; Jolaoso et al. 2014).

Notes. *Osodendron* is closely related to the Central and South American *Robrichia*, which was originally described as a section of *Enterolobium* by Barneby and Grimes (1996) and later segregated as a new genus by Souza et al. (2022). In the phylogeny of Ringelberg et al. (2022), the sampled species of both genera form sister-lineages. In habit, leaves and flowers, the two genera are very similar; however, the numbers of pinnae per leaf and leaflets per pinna and leaflet dimensions show greater variation in *Osodendron* with especially relatively large leaflets in the type species compared to *Robrichia.* The clearest difference between the two genera is to be found in the fruits, where those of *Robrichia* are contorted (or "ear-shaped") and indehiscent, while those of *Osodondron* are either straight to falcate and indehiscent or twisted to spirally-coiled and lomentiform, only tardily breaking up into articles.

Species of *Osodendron* can be easily distinguished from African *Albizia* species by the sub-opposite lower few pinna-pairs of which the lowermost is usually distinctly shorter (half or two thirds the length of the next few pairs of pinnae), as well as the strong reduction or lack of one of the two leaflets of the lowermost leaflet pair on each pinna (in *Albizia*, the lowermost pair of pinnae is only slightly shorter at most and the lowermost leaflet pair is not reduced or lacking one leaflet). The fruits are also notably different, with the inertly dehiscent pods of continental African *Albizia* spp. never woody nor articulate and always flat and papery (although in several Asian, Australian and Madagascan *Albizia* spp., indehiscent woody or tardily dehiscent articulate pods occur, for example, Fig. 1B; Table 1).

Identification key to the species of *Osodendron*

1 Leaves with fewer than 10 pairs of pinnae; fruits coiled or twisted, rarely only curved, flowers with 20–25 stamens..... **1. *Osodendron altissimum***

– Leaves with more than 10 pairs of pinnae; fruit straight or somewhat curved, but not coiled nor twisted, flowers with 10–14 stamens.....**2**

2 Leaves of mature individuals (not those on coppice shoots) lacking nectaries between upper leaflet pairs, fruit a thick woody indehiscent pod, with uniform flat valves, not distinctly swollen over the seeds and rectangular in cross-section – West Africa (Upper Guinea) ....**2. *Osodendron dinklagei***

– Leaves usually with nectaries between the upper 1–3 leaflet pairs, fruit usually a flat sub-lomentiform indehiscent pod or sometimes a thicker woody pod, articulately swollen around the seeds, elliptic to circular in cross-section – Central and East Africa (Lower Guinea, Congolia and gallery forests in adjacent savannahs).....**3. *Osodendron leptophyllum***

1. *Osodendron altissimum* (Hook. f.) E.J.M. Koenen, comb. nov.
urn:lsid:ipni.org:names:77303837-1
Figs 1A, 2

Pithecellobium altissimum (Hook. f.) Oliv., Fl. Trop. Afr. [Oliver et al.] 2: 364. 1871.

Feuilleea altissima (Hook. f.) Kuntze, Revis. Gen. Pl. 1: 187. 1891.

Pithecellobium stuhlmannii Taub., Pflanzenw. Ost-Afrikas C 193. 1895. Type material: Democratic Republic of Congo, Bataibo bei Duki, 850 m, *Stuhlmann 2773* (holotype: B†), neotype here designated: Democratic Republic of Congo, Irumu, *Bequaert 4887* (BR!).

Albizia passargei Harms, Bot. Jahrb. 26: 253. 1899. Type material: Cameroon, Ngaoundéré, *Passarge 164* (holotype: B†), neotype here designated: Cameroon, Bordure du Meng près des lacs de Boubala, *Letouzey 2562* (P [P03502143] digital image!).

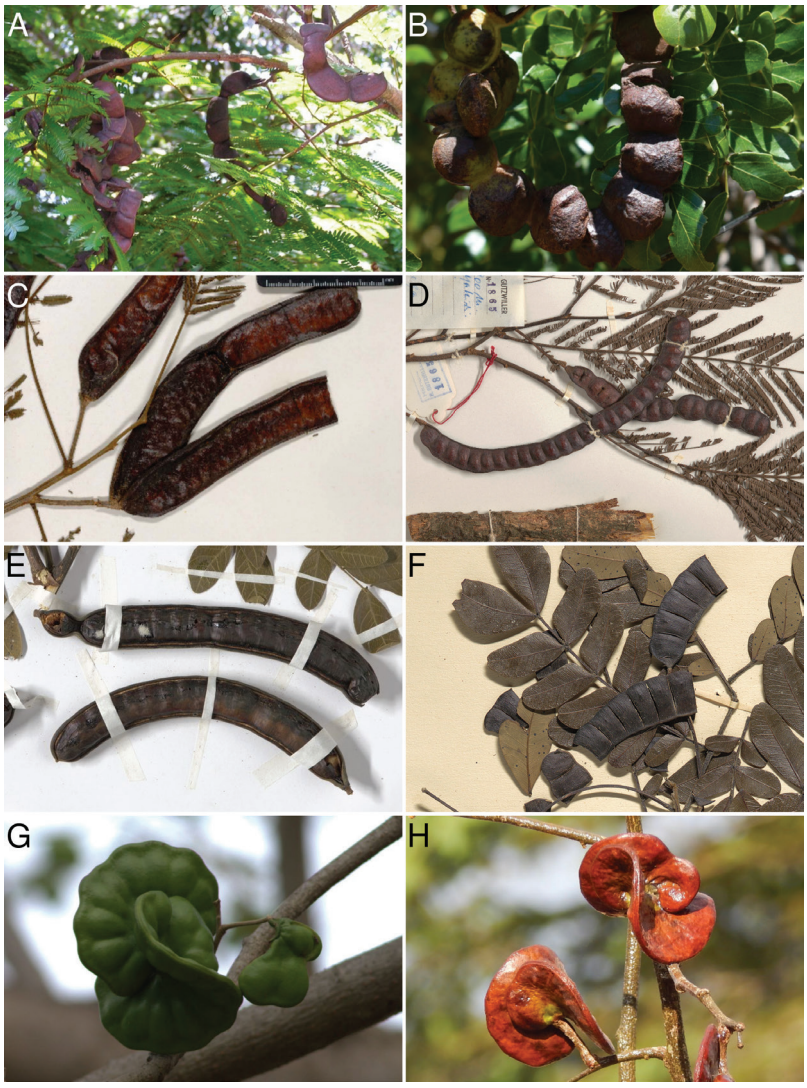

Figure 1. Confusing pods of *Cathormion* s.l. **A** pods of *Osodendron altissimum* that are very similar to **B** pods of the Australian species *Albizia moniliformis* (DC.) F. Muell. (syn. *Cathormion umbellatum* subsp. *moniliforme* (DC.) Brummit) **C** pods of *Osodendron dinklagei* and **D** pods of *Osodendron leptophyllum* that were likened to those of **E** *Samanea* (*S. saman* (Jacq.) Merr. is pictured here) and/or *Cathormion* **F** pods of *Hydrochorea obliquifoliolata* (De Wild.) E.J.M. Koenen (syn. *Cathormion obliquifoliolatum*) that are superficially similar to those of *O. leptophyllum* in particular; hence, this species having also been classified in a broadly circumscribed *Cathormion* in the past, but note that the pods become disarticulated while still on the tree rather than tardily as in *Osodendron* and *Albizia moniliformis* **G** and **H** pods of the closest relative of *Osodendron*, the Neotropical genus *Robrichia* (*R. schomburgkii* is pictured here). Images: **A** Jos Stevens, voucher unknown **B** Russel Cumming, voucher unknown **C** *J. Alves Pereira 2664* (MA) **D** *R. Gutzwiller 1865* (P) **E** *J.F. Maxwell 91-300* (L) **F** *B. Descoings 8278* (MPU) **G** Cristoph Moning, voucher unknown **H** José Benito Quezada Bonilla, *J.B. Quezada Bonilla 623* (HULE, MO). **A** from www.africanplants.senckenberg.de **B–H** from www.gbif.org **B–G** distributed under a Creative Commons BY-NC-SA 4.0 Licence **H** distributed under a Creative Commons BY-NC-SA 3.0 Licence.

Cathormion altissimum (Hook. f.) Hutch. & Dandy, Fl. W. Trop. Afr. [Hutchinson & Dalziel] 1: 364. 1928; Hutchinson & Dandy in Kew Bull. 1928 (10): 401. 1928.
Arthrosamanea altissima (Hook. f.) G.C.C. Gilbert & Boutique, Bull. Jard. Bot. État Bruxelles 22: 182. 1952.
Inga altissima (Hook.f.) Roberty, Bull. Inst. Franç. Afrique Noire, A. 16: 343. 1954.

Basionym. *Albizia altissima* Hook. f. Niger Fl. [W. J. Hooker]. 332. 1849.

Type material. Ghana, Cape Coast, 7/41, *T. Vogel 18* (lectotype here designated from amongst the syntypes: K!); Nigeria, Aboh, 8/41, *T. Vogel 28* (syntype: K!).

Description. ***Tree*** or rarely ***shrub***, unarmed or sometimes with blunt spine-like projections on young twigs (W. Hawthorne, personal communication), 5–35 m tall, stem to 40 cm in diameter. Branches covered with many minute round lenticels 0.1–0.2 mm, twigs, stipules, bud scales, all leaf axes and peduncles brown pubescent, often densely so. Foliage consisting of bipinnate leaves with opposite to sub-opposite pinnae with closely-spaced, distinctly discolourous leaflets, slightly wider in the middle with the apical pair distinctly distally projected, in the basal pair often one or both leaflets reduced to paraphyllidia. The inflorescences consisting of sub-spherical capitula emerging in axillary fascicles, often aggregated into pseudoracemes emerging from the perulate resting buds, with the leaves not fully developing and caducous. ***Stipules*** deltoid to linear, 2–8 ×1.0–1.8 mm, caducous, perulae deltoid, 2–4 × 1.8–3 mm. ***Leaves*** with (3–)5–7(–8) pairs of pinnae, apical pairs usually slightly longer and the basal pair sometimes much shorter with fewer leaflets, petiole 1.3–2.5 cm, pulvinate, adaxially shallowly canaliculate and often laterally and abaxially grooved, with a circular to elliptic sessile cupular nectary ca. 0.8–2.1 mm in diameter located ca. mid-petiole, rachis (1.8–)4.5–11(–14.5) cm, adaxially shallowly canaliculate and often laterally and abaxially grooved, with 2–5 circular to elliptic sessile cupular nectaries between or just below the distal pairs of pinnae ca. 0.5 mm in diameter, pinna-rachises (2.4–)3.5–8(–10.2) cm, proximally pulvinate, laterally compressed, with elliptic to circular sessile cupular nectaries of 0.2–0.8 × 0.2–0.5 mm between the upper 1–4(–15) leaflet pairs, pinnae with (7–)13–20(–25) leaflet pairs, very often the abaxial leaflet of the lowermost pair reduced to a paraphyllidium, leaflets sessile, pulvinate, inequilaterally hastate or weakly sigmoid, with acute or sometimes obtuse apex or (in subsp. *busiraensis*) weakly rhombic with oblique base and mostly obtuse apex or sometimes apiculate, (4–)7–14(–18) × (1.5–)3–4 mm, asymmetrically palmately-pinnate secondary venation with 7–10 veins starting from leaflet base next to the mid-rib and (7–)15–22 major and intercalary secondary veins laterally from the mid-rib, brochidodromous to craspedodromous, distinctly prominent on both surfaces when dry (or obscure on adaxial surface in subsp. *busiraensis*), tertiary venation finely reticulate, hardly visible on adaxial surface. ***Capitula*** ca. 35–50-flowered, on peduncles 1.8–3.2 cm, dimorphic with 3–9 central flowers with broader base and longer staminal tubes, bracts lanceolate to lanceolate-spatulate, ca. 0.9–1.2 × 0.1–0.2 mm, ciliate in upper half, caducous. Peripheral flowers slenderly campanulate

with pale green or greenish-white calyx and corolla, subsessile to shortly pedicellate, pedicel to ca. 0.5 mm, sparsely pubescent. Calyx 5-merous, 2–3.2 mm long, the deltoid lobes ca. 0.5 × 0.5 mm, ciliate at the apex and often also a few scattered short hairs on the outer surface of calyx tube and lobes, otherwise glabrous, corolla 5-merous, 5–7.5 mm long, glabrous, androecium of ca. 20–25 stamens, filaments white, ca. 12–17 mm long, fused into a tube at the base for ca. 2–3 mm, anthers yellow, basifixed, pollen aggregated into 32-celled flattened polyads. Pistil ca. 13–18 mm long, the ovary ca. 3 mm with a few scattered hairs on distal half and the funnel-shaped stigma extending ca. 1 mm beyond the anthers. Central flowers similar, but sessile, broadly campanulate and staminal tube ca. 5.5–8.5 mm long (i.e. the stamens are approximately the same length, but the fused tube is longer than in peripheral flowers), the tube exserted beyond the corolla. ***Fruit*** a spirally-curved, twisted or coiled lomentiform pod, usually articulate between the seeds, breaking up tardily after abscission in water or on the forest floor, often with arenchymous swollen mesocarp for flotation, (10–)18–29(–30) × (0.8–)1.1–1.7 × 0.2–0.6 cm, (3–)9–20(–23) seeded. Seeds plano-compressed, nearly round or slightly elliptic, ca. 5–7.5 × 4–6 × 1.5–2 mm, chestnut brown with a small 2.1–3.2 × 1–1.5 mm elliptic to obovate or oblong open pleurogram.

Notes. A specimen seen at Kew, of *Espírito Santo 1858*, collected in Guinée-Bissau, is doubtfully placed in this species. This specimen is highly unusual in the number of pairs of pinnae (13) and leaflet pairs (14–35) and the leaflets appear relatively small and elongate (even though they appear not fully expanded), while having the typical asymmetrical hastate shape. Furthermore, the fruit is not clearly articulate and also differs in being only somewhat curved rather than twisted or coiled. Brenan and Brummitt (1965) also cited this material as being unusual and speculated that it may be a distinct taxon. I do not share this opinion as I do not think it is sufficiently morphologically distinct. It is perhaps more likely of hybrid origin with *O. dinklagei*, which occurs sympatrically, as the other parent. However, this unusual specimen resembles *O. altissimum* much more closely than *O. dinklagei* and the number of pinnae and leaflets and dimensions of the leaflets clearly distinguish it from that species.

The holotype of *Pithecellobium stuhlmannii* was destroyed at B and no surviving isotypes are known. According to the Flora of East Tropical Africa (Brenan 1959), the original material was collected in the Democratic Republic of Congo, west of Lake Albert. The specimen of *Bequaert 4887* from BR is from the same region, includes leaves, flowers and immature fruit and matches the description in the protologue and is here selected as the neotype of *P. stuhlmannii*.

The holotype of *Albizia passargei* was also destroyed at B, but Villiers (1989) placed the name in synonymy with *C. altissimum*, based on the description in the protologue. A specimen of *Letouzey 2562* from P, comprising leaves and flowers, is here chosen as the neotype as it was collected in N Cameroon (ca. 150 km SW of the type locality) and matches the description in the protologue.

Key to subspecies of *O. altissimum*:

1 Leaflets typically asymmetrically hastate and weakly sigmoid, apex acute, usually > 3× as long as wide; fruits spirally-curved, coiled or twisted, 1-seeded articles (11–)13–17 mm wide and > (3–)4 mm thick when ripe – widespread in Lower and Upper Guinea.....**1.1. *Osodendron altissimum* subsp. *altissimum***

– Leaflets weakly rhombic with oblique base, apex obtuse, ≤ 3× as long as wide; fruits spirally-coiled, 1-seeded articles 8–11 mm wide and 2–3 mm thick when ripe – Local in west Democratic Republic of Congo..... .....**1.2. *Osodendron altissimum* subsp. *busiraensis***

1.1 *Osodendron altissimum* subsp. *altissimum*

Distribution. Widespread across Upper and Lower Guinea and Congolia, from Guinea-Bissau in the west to the Democratic Republic of Congo in the east and Angola in the south (Fig. 2A), also reported from Uganda and Zambia (Brenan 1959).

Ecology. Fresh-water swamp forest and along rivers in primary and secondary, evergreen or semi-deciduous rainforest.

Representative specimens studied. Guinée-Bissau: *Espírito Santo 3810* & *3832* (frts., BR); **Côte d'Ivoire:** *Oldeman 968* (fls, BR); **Cameroon**: *A.J.M. Leeuwenberg 8868* (fr., BR), *B. Sonké 5499* (fr., BR); **Gabon:** *N. Hallé 2119* (fls, frts, BR); **Democratic Republic of Congo:** *F. Seret 461* (fls, BR);

1.2. *Osodendron altissimum* subsp. *busiraensis* (G.C.C. Gilbert & Boutique) E.J.M. Koenen, stat. nov. et comb. nov.

urn:lsid:ipni.org:names:77303839-1

Basionym. *Arthrosamanea altissima* var. *busiraensis* G.C.C. Gilbert & Boutique, Fl. Congo Belge 3: 183. 1952.

Type material. Democratic Republic of Congo, Eala surroundings, Wangata-Watsiko, October 1943, *Germain 1604* (holotype: BR! [BR0000015846686], isotype: P [P00418269] digital image!).

Note. This subspecies was originally described as an infraspecific variety. I have considered treating it as a distinct species, but after studying material held at BR, I concluded it cannot be reliably separated from the typical subspecies across its entire range. The material stands out in its combination of slightly different leaf shape and smaller pods, but material outside the Busira river catchment in the Democratic Republic of Congo, as well as in other parts of Africa, is rather variable in leaf shape and pod size. Given that both these differences are consistently present in most of the material from that region, i.e. the variation is geographically structured within this variable and widespread species, subspecies is more appropriate than varietal rank and I treat it here as such.

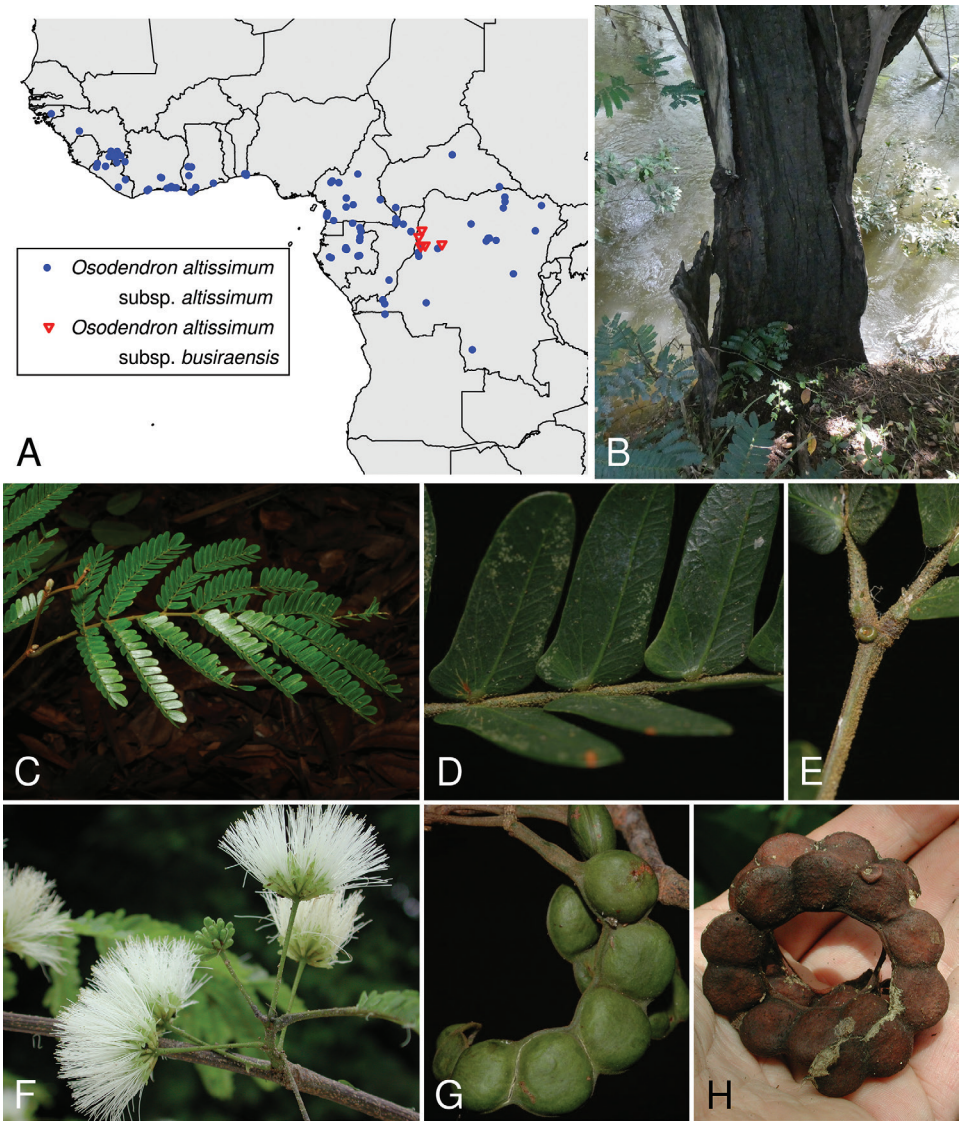

Figure 2. *Osodendron altissimum* **A** distribution of the two subspecies as per the legend, based on data from Gbif.org with the addition of occurrence records for *O. altissimum* subsp. *busiraensis* from specimens at BR **B** trunk on riverbank **C** bipinnate leaf **D** close-up of leaflets **E** close-up of rachis apex showing nectary **F** inflorescences **G** unripe pod **H** mature pod. Images: **B, F, H** William Hawthorne (FHO) **C–E, G** David Harris (E), from www.africanplants.senckenberg.de.

Distribution. Local to the Busira river catchment in the western Democratic Republic of Congo (Fig. 2A).

Ecology. As the typical subspecies.

Representative specimens studied. Democratic Republic of Congo: *Boyekoli Ebale Congo Expedition 2010 104* (fls, BR); *J. Louis 2052* (BR) & *13196* (BR); *Robyns 653* (BR); *Ghesquiere 2787* (BR); *G. Hulstaert 607* (BR).

2. *Osodendron dinklagei* (Harms) E.J.M. Koenen, comb. nov.
urn:lsid:ipni.org:names:77303840-1
Fig. 3A–F

Albizia dinklagei (Harms) Harms, Bot. Jahrb. Syst. 53(3–5): 455, in obs. 1915.
Pithecellobium dinklagei (Harms) Harms, Notizbl. Bot. Gart. Berlin-Dahlem 8: 145. 1922.
Cathormion dinklagei (Harms) Hutch. & Dandy, Fl. W. Trop. Afr. [Hutchinson & Dalziel] 1: 364. 1928; Hutchinson & Dandy in Kew Bull. 401. 1928.
Samanea dinklagei (Harms) Keay, Kew Bull. 8(4): 488. 1954.

Basionym. *Mimosa dinklagei* Harms, Bot. Jahrb. Syst. 26(3–4): 253. 1899.

Type material. Liberia, Grand Bassa, 21 May 1897, *Dinklage 1827* (holotype: B†, isotype: K! [K000044068]).

Description. ***Tree***, up to 30 m tall, twigs with rows of lenticels and becoming shallowly grooved with age. Twigs, stipules, perulate resting buds, all leaf-axes and peduncles covered in a densely villose ferruginous indumentum. Foliage consisting of very finely divided bipinnately compound leaves, the tiny leaflets ciliate and somewhat discolourous. The inflorescences consisting of sub-spherical capitula emerging from axillary fascicles of coeval leaves, sometimes in compound ramiflorous pseudoracemes with the leaves not fully developing and caducous. ***Stipules*** narrowly deltoid or lanceolate to linear 3.5–4.3(–9) × ca. 1 mm, caducous leaving conspicuous glabrous scars, perulae deltoid, ca. 2 × 1.5 mm. ***Leaves*** with 10–34 pairs of pinnae, often with one or a few much reduced pinnae at the base, petiole 5–11 mm, pulvinate and adaxially flattened at the base, usually with a sessile or shortly stipitate cupular nectary 0.5–0.7 mm in diameter just below the lowermost pinna pair, rachis grooved and adaxially canaliculate although obscured by dense indumentum, with a 1–1.5 mm long deciduous mucro, 6.5–16(–21) cm, with 3–8(–11) interpinnal subsessile cupular nectaries apically, these sometimes button-shaped and on a 0.7 mm long stipe, pinnae obscurely pulvinate, with an adaxial ridge and a tiny 0.3–0.4 mm long mucro at the apex, 1.0–2.5(–4.5) cm, usually without nectaries, except on larger leaves (of juveniles or coppice shoots) with cupular nectaries between the upper 1–3 leaflet pairs, pinnae with (9–)27–40(–48) leaflet pairs, the abaxial leaflet of the lowermost pair usually reduced to a paraphyllidium, leaflets inequilaterally linear, sessile and pulvinate, with strongly oblique base and acute apex, 0.8–3 × 0.2–0.8 mm, venation obscure on the adaxial surface, palmately-pinnate brochidodromous, with three secondary veins emerging from the base next to the clearly stronger mid-rib on the adaxial side, 2–3 further secondary veins on each side and sparse reticulate tertiary venation. ***Capitula*** 1–3 per leaf axil, ca. 40–60-flowered, on peduncles 1.8–3.5(–4.1) cm, dimorphic with 1(–3) central flower(s) that are more robust and with a longer, exserted staminal tube. Peripheral flowers ca. 0.7 mm broad at the base, the basal ones on a pedicel of ca. 0.4–0.6 mm, the others sub-sessile to sessile closer to the apex. Calyx slenderly campanulate, green, 5-merous, 1.6–3.1 mm long, densely puberulous on outer surface, the deltoid lobes ca. 0.4 × 0.4 mm, corolla green, 4- or 5-merous, 3–5.5 mm long, pubescent, the lobes 1.8–2 mm long, stamens 10–14, filaments white, 14 mm long,

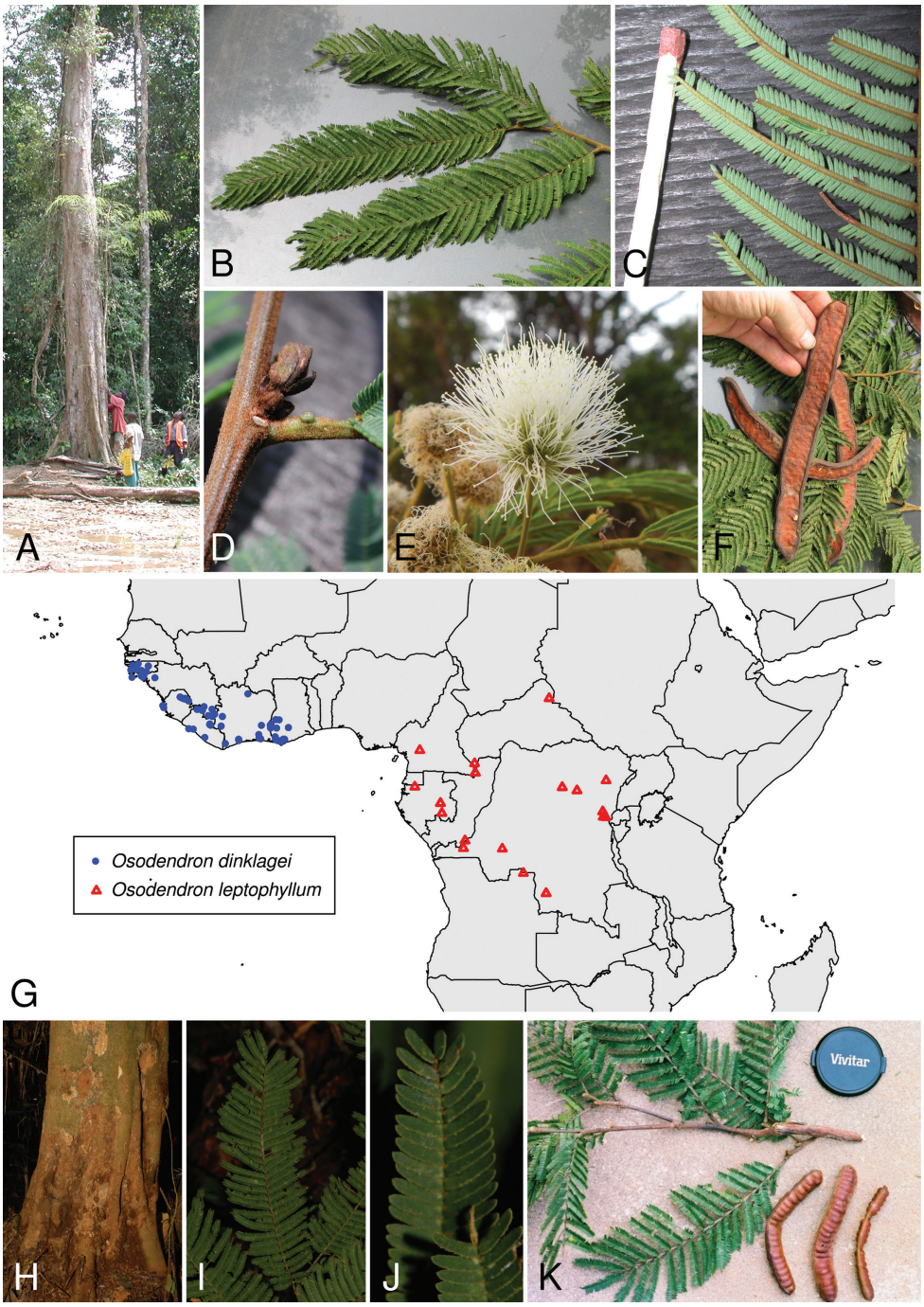

Figure 3. A–F *Osodendron dinklagei*: **A** trunk of adult specimen in terra firme forest **B** foliage **C** detail of pinnae **D** detail of resting bud and petiolar nectary **E** inflorescence **F** pods **G** distribution map of *O. dinklagei* and *O. leptophyllum* as per the legend based on data from Gbif.org **H–K** *O. leptophyllum*: **H** trunk **I** bipinnate leaf **J** close-up of leaflets **K** twig and pods. Images: **A–D, F** William Hawthorne (FHO) **E** Xander van der Burgt (K) **H–J** David Harris (E) **K** Paul Latham **H–K** from www.africanplants.senckenberg.de.

basally fused into a tube ca. 3 mm long, anthers light yellow, basifixed, pollen released in 32-celled polyads, pistil ca. 18 mm long with a sessile ovary ca. 2.5 mm long, puberulent on upper half with white hairs, stigma shallowly funnel-shaped. Central flower(s) similar to peripheral flowers, but ca. 1.8 mm broad at the base, calyx 2.0–2.4 mm long, corolla ca. 4.5 mm long, staminal tube ca. 6 mm long (i.e. the stamens are approximately the same length, but fused for a greater part than in peripheral flowers). ***Fruit*** an indehiscent woody pod up to 13–18 × 2–2.2(–2.5) × 0.3–0.6 cm, straight or slightly curved and with uniformly thick valves, except for the distinctly thickened margins, not swollen over the seeds, 16–24 seeded when well-fertilised, seeds rounded elliptical, only slightly laterally compressed, greenish light brown, 6–7.5 × 4–5 × 3–3.5 mm when dry, with a hard testa and an elongate closed pleurogram 5–6 × 2–2.5 mm.

Distribution. Upper Guinea, from Guinea-Bissau to Ghana (Fig. 3G).

Ecology. Rainforest, gallery forest, wooded grassland, edges of mangrove swamp.

Representative specimens examined. Guinée-Bissau: *Espírito Santo 1747* (K) & *1864* (K) & *1871* (K) & *2697* (K). **Sierra Leone:** *X. van der Burgt 1994* (K).

3. *Osodendron leptophyllum* (Harms) E.J.M. Koenen, comb. nov.

urn:lsid:ipni.org:names:77303841-1

Fig. 3H–K

Albizia eriorhachis Harms syn. nov., Bot. Jahrb. Syst. 53(3–5): 456. 1915. Type material: *Chevalier 7777* (lectotype here designated from amongst the syntypes: P [P00418361] digital image!, isolectotypes: P [P00418360] digital image!, P [P00418362] digital image!, L [L.1992190] digital image!).

Albizia flamignii De Wild., Pl. Bequaert. 3: 49. 1925. Type material: Democratic Republic of Congo, Kitobola, 12 Sept 1910, *Flamigni 265* (lectotype designated here: BR! [BR0000016145290], isolectotypes: BR! [BR0000016145283], BR! [BR0000016145306], P [P00418365], digital image!).

Cathormion eriorhachis (Harms) Dandy syn. nov., in F. W. Andrews, Fl. Pl. Anglo-Egypt. Sudan ii. 155. 1952. Type: Based on *Albizia eriorhachis* Harms.

Arthrosamanea leptophylla var. *guineensis* G.C.C. Gilbert & Boutique, Bull. Jard. Bot. État Bruxelles 22: 182. 1952. Type material: Democratic Republic of Congo, Yangambi, réserve flore Isalowe, févr. 1940, *Louis 16368* (BR!).

Samanea guineensis (G.C.C. Gilbert & Boutique) Brenan & Brummitt, Bol. Soc. Brot. sér. 2, 39: 202. 1965. Type: Based on *Arthrosamanea leptophylla* var. *guineensis* G.C.C. Gilbert & Boutique.

Basionym. *Albizia leptophylla* Harms, Bot. Jahrb. Syst. 53(3–5): 455. 1915.

Type material. Democratic Republic of Congo, Kimuenza, 17 km S of Leopoldville, August 1910, *Mildbread 3520* (lectotype (designated by Villiers (1989) as holotype, here corrected): HBG [HBG519160] digital image!, isolectotypes: HBG [HBG519161] digital image!, P [P00418364] digital image!).

Description. ***Tree*** or more rarely a ***shrub***, unarmed or with spine-like outgrowths near the base of the bole perhaps associated with adventitious roots (W. Hawthorne, personal communication), to 30 m tall and to 1.25 m in stem diameter, twigs dark with densely scattered small pustular lenticels or sometimes with lighter coloured corky bark. Twigs, stipules, perulate resting buds, all leaf-axes and peduncles covered in dense ferruginous villose indumentum. Foliage consisting of finely divided bipinnate leaves, the leaflets variably ciliate, sometimes with only very few hairs on the margins, the lamina usually glabrous, but sometimes also with a few scattered hairs along the mid-rib on lower surface or rarely pilose or with appressed long hairs on both surfaces especially in lower half, usually distinctly discolourous. The inflorescences consisting of sub-spherical capitula emerging from axillary fascicles of coeval leaves, usually a few below the leaves in the axils of caducous leaves on the same shoots or sometimes also with a few short ramiflorous pseudoracemes, with all leaves caducous, lower down on the branch. ***Stipules*** elliptically oblong to asymetrically oblanceolate or falcate, 5–8(–9) × 2–3 mm, more scarcely pubescent or nearly glabrous on adaxial surface, caducous leaving conspicuous scars, perulae deltoid to ovoid, ca. 1.5–5 × 1.5–3.5 mm. ***Leaves*** with (10–)12–30(–35) pairs of pinnae, the lower 1–2 pairs of pinnae often shorter with fewer leaflets, petiole pulvinate and flattened on adaxial side at the base, (0.5–)0.8–2.2(–3) cm long, petiolar nectary usually present, cupular and circular, sessile or shortly stipitate and 0.6–1 mm in diameter, in variable position ranging from just above the pulvinule to just below the basal pair of pinnae, rachis canaliculate although often obscured due to dense pubescence, 8–15(–22) cm long, with 1–4(–6) cupular nectaries between the upper pairs of pinnae, these 0.3–0.6 mm in diameter, pinnae pulvinate and with an adaxial ridge, (0.5–)2.5–5(–7.5) cm long, nearly always the abaxial leaflet of the lowermost pair reduced to a paraphyllidium and the adaxial one somewhat smaller than the other leaflets, with elliptical nectaries ca. 0.1–0.25 mm in diameter between the upper 1–3 leaflet pairs, pinnae with (17–)24–35(–42) leaflet pairs, leaflets sessile, pulvinate, asymmetrically oblong to oblanceolate, base oblique to sometimes hastate, apex rounded to acute, (2–)3–6(–9) × (0.3–)0.5–1.2(–2) mm, venation palmately-pinnate brochidodromous, with 2–4 basal veins adaxially next to the mid-rib and 5–8 further secondary veins on each side and reticulate tertiary venation, apart from the mid-rib, all venation often obscure in smaller leaves, otherwise the secondary venation prominent, sometimes only on the lower surface. ***Capitula*** 2–4 arranged in fascicles, on peduncles ca. 2.7–4.5 cm, dimorphic with ca. 50–70 peripheral flowers and a single elongated central flower. Bracteoles spatulate, ca. 0.5 mm long, pubescent on outer surface. Flowers white, the peripheral ones on pedicels 0.75–2.5 mm. Calyx slenderly campanulate, green, 5-merous, 2–2.5 mm long, densely puberulous on outer surface, the deltoid lobes ca. 0.25 mm long, corolla 4–4.5 mm long, pubescent on outer surface, the lobes 1.8–2 mm long, stamens 10–14, the filaments white, 11–14 mm long, basally fused into a tube 1.5–2.5 mm long, anthers basifixed, pollen released in 32-celled polyads, pistil on a ca. 0.25–0.75(–1.25) mm long stipe, ovary ca. 1–1.5 mm long, pubescent, style 12–16 mm long, stigma shallowly funnel-shaped. Central flower(s) similar to peripheral flowers, but sessile and longer, calyx ca. 2.5 mm long, corolla ca. 6–6.5 mm long,

staminal tube 4–6 mm long, exserted beyond corolla tube. ***Fruit*** a dark brown to black indehiscent pod that may tardily disintegrate into 1–multiple-seeded parts, the slightly thickened margins usually straight or also often articulate especially around aborted seeds, the valves papery and thin or with somewhat thickened mesocarp, but not really ligneous, when ripe, swollen over the seeds, when well-fertilised, 12–28(–32)-seeded, (4.5–)10–16(–20) × 0.9–1.3 × 0.4–0.7 cm. Seeds yellowish-brown, 5.5–7.5 × 3–4.5 × 2–3 mm with hard testa and a darker closed pleurogram of 4.5–5.5 × 1.2–1.5 mm.

Distribution. Lower Guinea and Congolia in Cameroon, Central African Republic, Gabon, Republic of the Congo, Democratic Republic of Congo, Angola (Fig. 3G).

Ecology. Forest edges and gallery forest.

Representative specimens examined. Cameroon: *J. Mildbread 8584* (K); **Democratic Republic of Congo:** Luidi, Thysville, Lusolo, 16 October 1959, *P. Compere 610* (BR), Isangi, 21 February 1950, *Callens 2363* (BR), Petite vallées d'affluente de la Belanzovi, près son confluent avec la Lubimbe, 26 January 1949, *A. Michelson 877* (BR, K).

Notes. *Osodendron leptophylla* is highly variable in number of pinnae per leaf, number and size of leaflets and density and length of the indumentum. No consistent correlations between any of these variations have been found suggesting that the material referred to two heterotypic synonyms is best included under *O. leptophyllum*. The first of these is *Albizia eriorhachis*, described by Harms in the same publication as *A. leptophylla*. Specimens from Cameroon, Central African Republic and Gabon, identified as *Cathormion eriorhachis*, appear to be similar to typical *O. leptophyllum*, but with relatively large leaflets and denser indumentum. However, the material is not distinct enough to merit recognition as a separate species, given the large variation in leaf dimensions and indumentum in *O. leptophyllum* across its range and is here placed in its synonymy.

The second is *Samanea guineensis*, which was originally described as a variety of *Arthrosamanea leptophylla*, based on more numerous pairs of pinnae and leaflets per leaf, but Brenan and Brummitt (1965) found it to be distinctive enough to recognise it at species rank. Apart from the difference in foliage, they noted differences in the indumentum of the calyx and corolla (glabrous to subglabrous, instead of densely puberulent) and a longer exserted staminal tube. I have observed material that fits their observations (e.g. *Jean Louis 10051*, BR), but in other collections with the leaf type of "guineensis", I have observed dense pubescence on the calyx (e.g. *Michelson 877*, BR) and vice versa specimens with ca. 15 pairs of pinnae and a subglabrous calyx (*Letouzey 9816*). Villiers (1989) also judged *S. guineensis* to be conspecific with *S. leptophylla*, having also seen numerous specimens with intermediate foliage. I follow Villiers (1989) and place this name in the synonymy of *O. leptophyllum*.

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This Special Issue – *Advances in Legume Systematics 14 Part 1* – presents 16 papers focused on generic delimitation across subfamily Caesalpinioideae (Leguminosae) which includes the mimosoid clade (former subfamily Mimosoideae). Caesalpinioideae is the second largest legume subfamily with ca. 4,600 species of trees, shrubs and lianas distributed pantropically across deserts, seasonally dry forests, savannas, and rain forests. Phylogenomic analyses presented in the introductory paper show that 22 of the 152 genera currently recognized are non-monophyletic or nested within another genus. The papers in this Special Issue address this extensive non-monophyly, reclassifying 15 of these 22 genera. Nine new genera are described (*Boliviadendron*, *Gretheria*, *Gwilymia*, *Heliodendron*, *Marlimorimia*, *Mezcala*, *Naiadendron*, *Osodendron*, *Ricoa*), five genera are reinstated (*Anonychium*, *Neltuma*, *Pseudalbizzia*, *Strombocarpa*, *Ticanto*), and three genera are subsumed into synonymy of other genera (*Balizia*, *Elephantorrhiza*, *Pseudopiptadenia*), bringing the number of Caesalpinioideae genera to 163. In total, 139 new name combinations are proposed. The generic re-circumscriptions include splitting of the large pantropical genus *Albizia* (the last 'dustbin' genus of mimosoid legumes), and the amphi-Atlantic *Prosopis*, one of the most important silvopastoral tree genera of tropical drylands. These taxonomic changes fundamentally re-shape the generic classification of Caesalpinioideae and lay foundations for a new higher-level classification of the subfamily.

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