

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 *Parapiptadenia* 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

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 folicles (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* (Benth 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

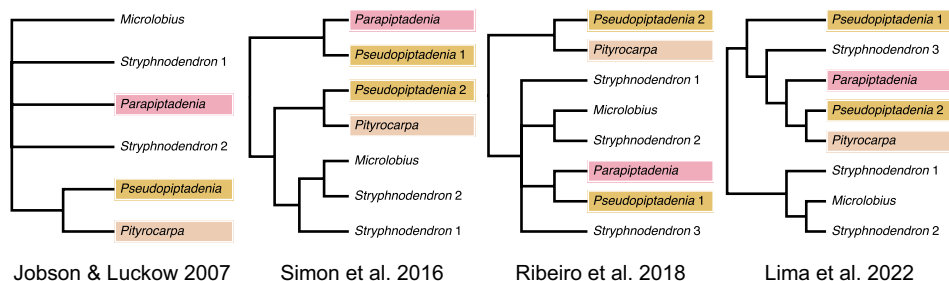


Figure 1. Topological differences amongst phylogenetic analyses of the Stryphnodendron clade.

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
<i>Inga edulis</i> Mart.	Queiroz 13797; Pennington 13282	HUEFS; K	JX870764	AF523078	JQ417383
<i>Lachesiodendron viridiflorum</i> (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow	Queiroz 13090	HUEFS	MG001274	MG001286	MG001305
<i>Microlobius foetidus</i> (Jacq.) M. Sousa & G. Andrade	Hughes 2150	FHO	KT364047	KT364172	FJ981976
<i>Microlobius foetidus</i> (Jacq.) M. Sousa & G. Andrade	Macqueen 432	FHO	AF458783	AF523095	(No data)
<i>Mimosa palmeri</i> Rose	Simon 823	FHO	KT364059	KT364212	FJ982142
<i>Mimosa pignu</i> L.	Hughes 2414	FHO	KT364060	KT364213	FJ982148
<i>Mimosa ursina</i> Mart.	Simon 704	CEN	KT364061	KT364210	FJ982217
<i>Parapiptadenia blanchetii</i> (Benth.) Vaz & M.P. Lima	Queiroz 15358	HUEFS	OM575100	ON409904	ON409927
<i>Parapiptadenia blanchetii</i> (Benth.) Vaz & M.P. Lima	Thomas 12372	NY	OM575099	ON409905	(No data)
<i>Parapiptadenia excelsa</i> (Griseb.) Burkart	Hughes 2425	FHO	KT364062	KT364160	FJ982235
<i>Parapiptadenia ilheusana</i> G.P. Lewis	Neves 1659	RB	OM575101	KY046081	ON409928
<i>Parapiptadenia pterosperma</i> (Benth.) Brenan	Cardoso 2359	HUEFS	OM575102	ON409906	ON409929
<i>Parapiptadenia pterosperma</i> (Benth.) Brenan	Ribeiro 902	HUEFS	MG001260	ON409910	MG001292
<i>Parapiptadenia rigida</i> (Benth.) Brenan	Marestoni 26	HUEFS	MG001261	ON409909	(No data)
<i>Parapiptadenia zehntneri</i> (Harms) M.P. Lima & H.C. Lima	Cotarelli 2029	HUEFS	OM575104	ON409907	(No data)
<i>Parapiptadenia zehntneri</i> (Harms) M.P. Lima & H.C. Lima	Pereira-Silva 3102	CEN	KT364063	KT364063	KT364108
<i>Parapiptadenia zehntneri</i> (Harms) M.P. Lima & H.C. Lima	Queiroz 10974	HUEFS	OM575105	ON409908	(No data)
<i>Parapiptadenia zehntneri</i> (Harms) M.P. Lima & H.C. Lima	Queiroz 15692	HUEFS	OM575106	KX302341	(No data)
<i>Piptadenia gonoacantha</i> (Mart.) J.F. Macbr.	Simon 735	FHO	KT364065	DQ790620	FJ982238
<i>Piptadenia stipulacea</i> (Benth.) Ducke	Simon 702; Queiroz 3115	CEN; HUEFS	KT386296	DQ790634	FJ982239
<i>Pityrocarpa leucacylon</i> (Barneby & J.W. Grimes) Luckow & R.W. Jobson	Fernandez 2909	NY	(No data)	DQ790622	(No data)
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W. Jobson	Melo 7518	HUEFS	(No data)	ON409911	ON409936
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W. Jobson	Queiroz 9084	HUEFS	ON191501	ON409912	(No data)
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W. Jobson	Way 2449	K	KT364067	KT364162	FJ982242
<i>Pityrocarpa obliqua</i> (Pers.) Brenan subsp. <i>brasilienis</i> (G.P. Lewis) Luckow & R.W. Jobson	Queiroz 12903	HUEFS	ON191500	ON409920	(No data)
<i>Pityrocarpa obliqua</i> (Pers.) Brenan subsp. <i>obliqua</i>	Macqueen 439	FHO	KT364068	KT364206	FJ982243
<i>Pseudopiptadenia babiana</i> G.P. Lewis & M.P. Lima	Melo 138	HUEFS	OM575115	ON409916	ON409930
<i>Pseudopiptadenia babiana</i> G.P. Lewis & M.P. Lima	Queiroz 15381	HUEFS	MG001277	MG001290	ON409931
<i>Pseudopiptadenia babiana</i> G.P. Lewis & M.P. Lima	Queiroz 15504	HUEFS	OM575114	ON409917	ON409932
<i>Pseudopiptadenia brenanii</i> G.P. Lewis & M.P. Lima	Borges 680	SPF	KT364069	(No data)	KT364111
<i>Pseudopiptadenia brenanii</i> G.P. Lewis & M.P. Lima	Cardoso 2807	HUEFS	OM575108	ON409914	ON409937
<i>Pseudopiptadenia brenanii</i> G.P. Lewis & M.P. Lima	Harley 56005	HUEFS	OM575109	ON409915	(No data)
<i>Pseudopiptadenia brenanii</i> G.P. Lewis & M.P. Lima	Queiroz 15585	HUEFS	MG001278	ON409913	ON409938
<i>Pseudopiptadenia contorta</i> (DC.) G.P. Lewis & M.P. Lima	Queiroz 15507	HUEFS	(No data)	KT364155	KT364113
<i>Pseudopiptadenia contorta</i> (DC.) G.P. Lewis & M.P. Lima	Queiroz 15582	HUEFS	MG001279	KX302348	MG001308
<i>Pseudopiptadenia inaequalis</i> (Benth.) Rauschert	Lima 7790	RB	OM575111	ON409921	ON409939
<i>Pseudopiptadenia leptostachya</i> (Benth.) Rauschert	Lima 8231	RB	OM575113	ON409922	ON409940
<i>Pseudopiptadenia leptostachya</i> (Benth.) Rauschert	Lima 8326	RB	OM575112	ON409923	ON409941
<i>Pseudopiptadenia psilotachya</i> (DC.) G.P. Lewis & M.P. Lima	Simon 1245	CEN	KT364070	KT364170	KT364114
<i>Pseudopiptadenia schumanniana</i> (Taub.) G.P. Lewis & M.P. Lima	Lima 7938	RB	OM575110	ON409924	ON409942
<i>Pseudopiptadenia</i> sp.	Neves 1675	RB	OM575116	ON409918	ON409933
<i>Pseudopiptadenia</i> sp.	Ribeiro 351	HUEFS	OM575117	ON409919	(No data)
<i>Pseudopiptadenia suaveolens</i> (Miq.) J.W. Grimes = <i>P. psilotachya</i>	Moacir & Clovis sn	IAN	OM575119	ON409925	ON409934
<i>Pseudopiptadenia warmingii</i> (Benth.) G.P. Lewis & M.P. Lima	Queiroz 12761	HUEFS	OM575118	ON409926	ON409935
<i>Senegalia macrostachya</i> (Rchb. ex DC.) Kyal. & Boatwr.	Miller 1322	CANB	KY688790	KY688920	(No data)
<i>Senegalia nigrescens</i> (Oliv.) P.J.H. Hurter	Maurin 255	JRAL	JQ265858	GQ872237	(No data)
<i>Stryphnodendron adstringens</i> (Mart.) Coville	Souza 29702	ESA	KT364072	KT364198	KT364116
<i>Stryphnodendron coriaceum</i> Benth.	Scalon 718	ESA	(No data)	KT364200	KT364120
<i>Stryphnodendron duckeanum</i> Occhioni	Simon 1343	CEN	KT364076	(No data)	KT364122
<i>Stryphnodendron fissuratum</i> E.M.O. Martins	Ivanaukas sn	ESA	KT364077	KT364175	KT364124
<i>Stryphnodendron foreroi</i> E.M.O. Martins	Asis 1143	SPF	KT364079	KT364201	KT364126
<i>Stryphnodendron gracile</i> Rizzini & Heringer	Scalon 458	ESA	KT364080	KT364177	KT364127
<i>Stryphnodendron obovatum</i> Benth.	Scalon 712	ESA	KT364081	KT364182	KT364130
<i>Stryphnodendron occhionianum</i> E.M.O. Martins	Simon 1597	CEN	KT364083	(No data)	KT364132

Taxon	Voucher	Herbarium	nrITS	matK	trnD-trnT
<i>Stryphnodendron paniculatum</i> Poepp.	Simon 1058	CEN	KT364084	(No data)	KT364133
<i>Stryphnodendron polyphyllum</i> Mart.	Mello-Silva 2659	SPF	KT364086	KT364184	KT364136
<i>Stryphnodendron pulcherrimum</i> (Willd.) Hochr.	Simon 980	CEN	KT364087	(No data)	KT364137
<i>Stryphnodendron roseiflorum</i> (Ducke) Ducke	Scalon 728	ESA	KT364090	KT364193	KT364143
<i>Stryphnodendron rotundifolium</i> Mart.	Scalon 715	ESA	KT364094	KT364194	KT364147
<i>Stryphnodendron velutinum</i> Scalon	Scalon 719	ESA	KT364101	KT364187	KT364153

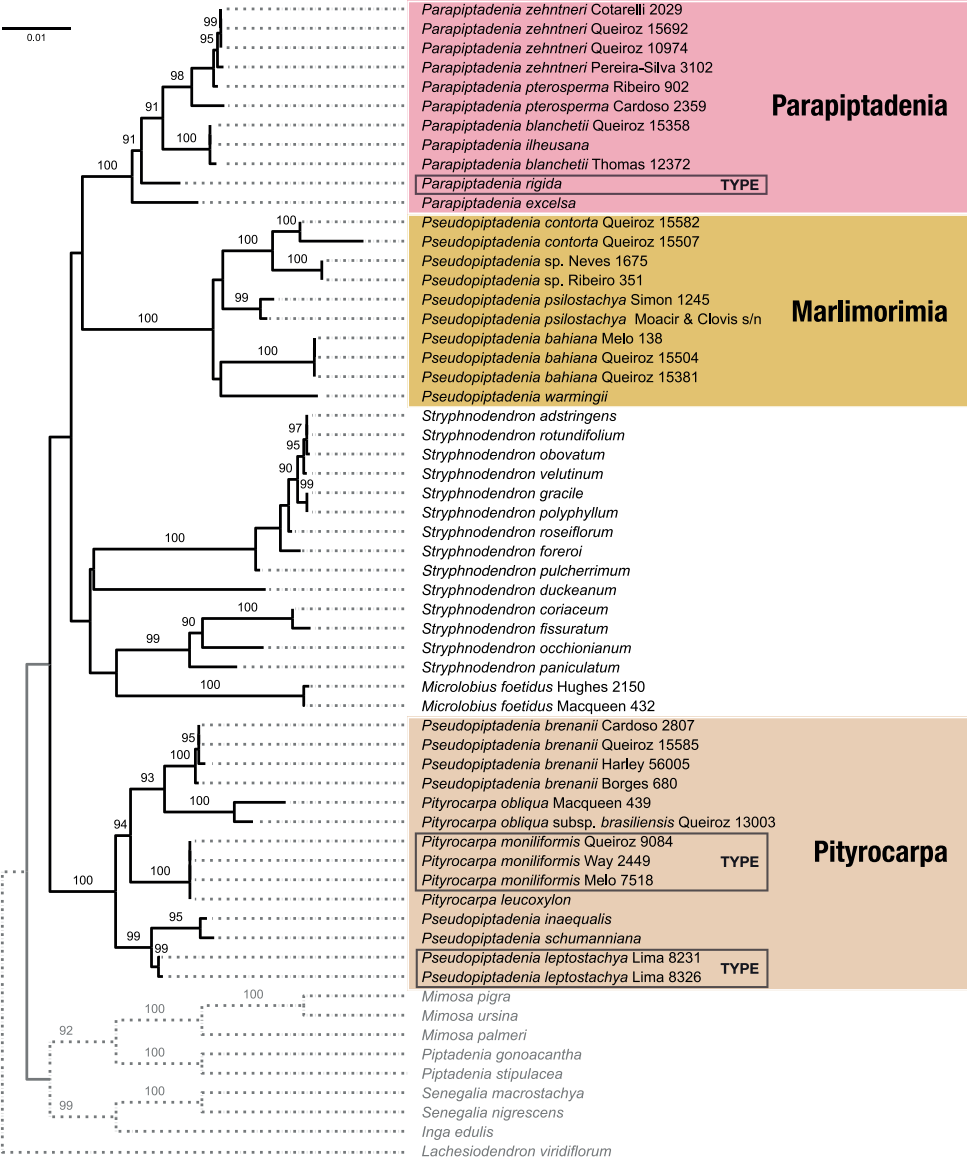


Figure 2. Phylogeny of the *Stryphnodendron* clade, based on Maximum Likelihood analysis of the concatenated nrITS, *matK* and *trnD-trnT* data. Significant ultrafast bootstrap values (> 90%) are given above branches. The tree was rooted using *Lachesiodendron viridiflorum*. Scale bar: expected number 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

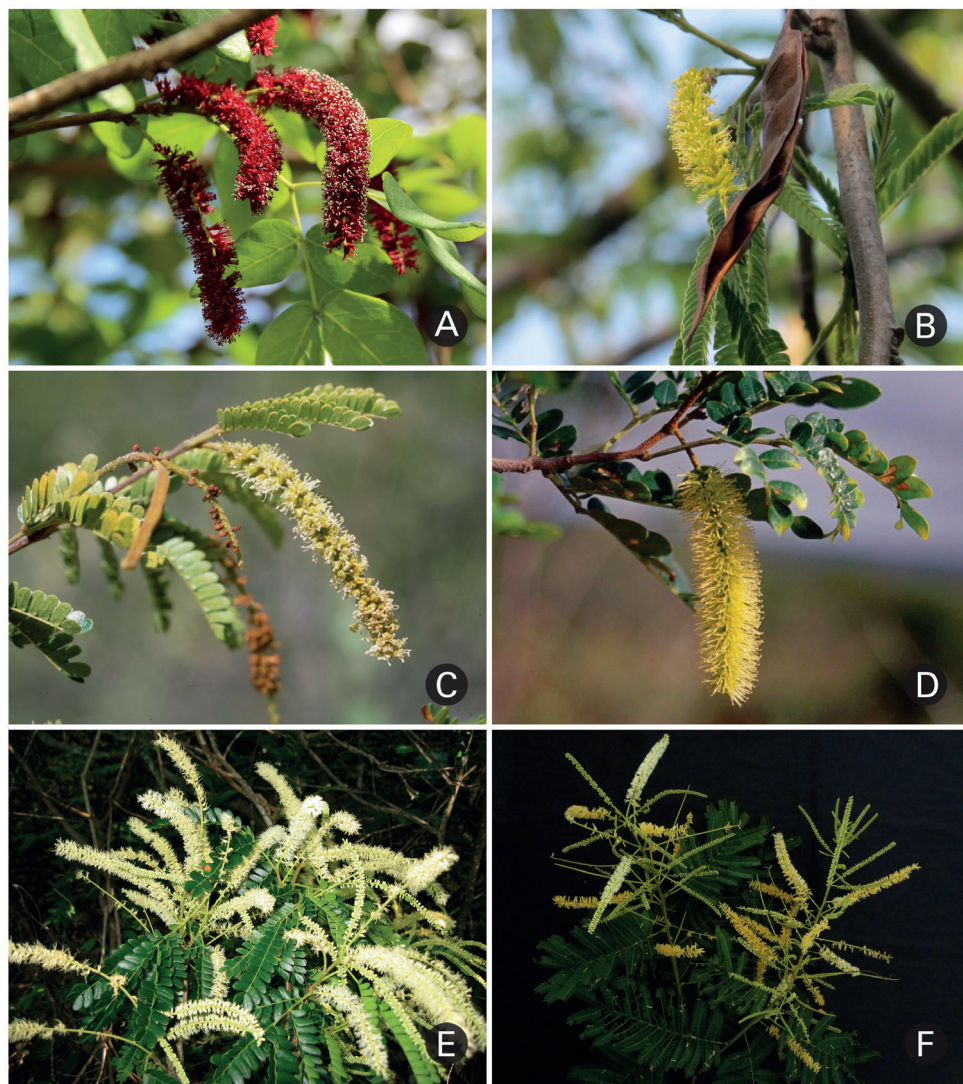


Figure 3. Inflorescences of *Parapiptadenia*, *Pityrocarpa* and *Marlimorimia* **A** *Parapiptadenia pterosperma* (Benth.) Brenan showing reddish inflorescences in the axils of coeval leaves **B** *Pa. rigida* (Benth.) Brenan showing yellowish inflorescences and fruits with valves plicate above the seeds **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 babiana* (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.

	<i>Parapiptadenia</i>	<i>Pityrocarpa</i>	<i>Marlimorimia</i>
Pinnae number	1–8	1–4 (rarely to 5 in <i>Pi. brenanii</i>)	5–10 or more (2–5 in <i>M. babiana</i> and <i>M. colombiana</i>)
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 <i>Pi. moniliformis</i>), 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 <i>Pa. excelsa</i> and <i>Pa. rigida</i>); united at the base (free in <i>Pa. rigida</i>)	White to yellowish or greenish; free and glabrous (united in <i>Pi. leucoxylon</i>)	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 <i>Pa. excelsa</i>)	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 <i>P. brenanii</i>).	Straight, (shallowly and irregularly sinuous in <i>M. babiana</i>, <i>M. colombiana</i> and <i>M. warmingii</i>), sometimes constricted where seeds abort
Valve consistency and indumentum	Thin, chartaceous, glabrous	Thick, coriaceous, mostly pubescent	Thin, coriaceous (thicker and harder in <i>M. warmingii</i>), glabrous
Embryo plumule	Developed and multifid	Rudimentary (developed and multifid in <i>P. brenanii</i>)	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. babiana* 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 [$\equiv$ *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 exerted 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 bifoliate 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

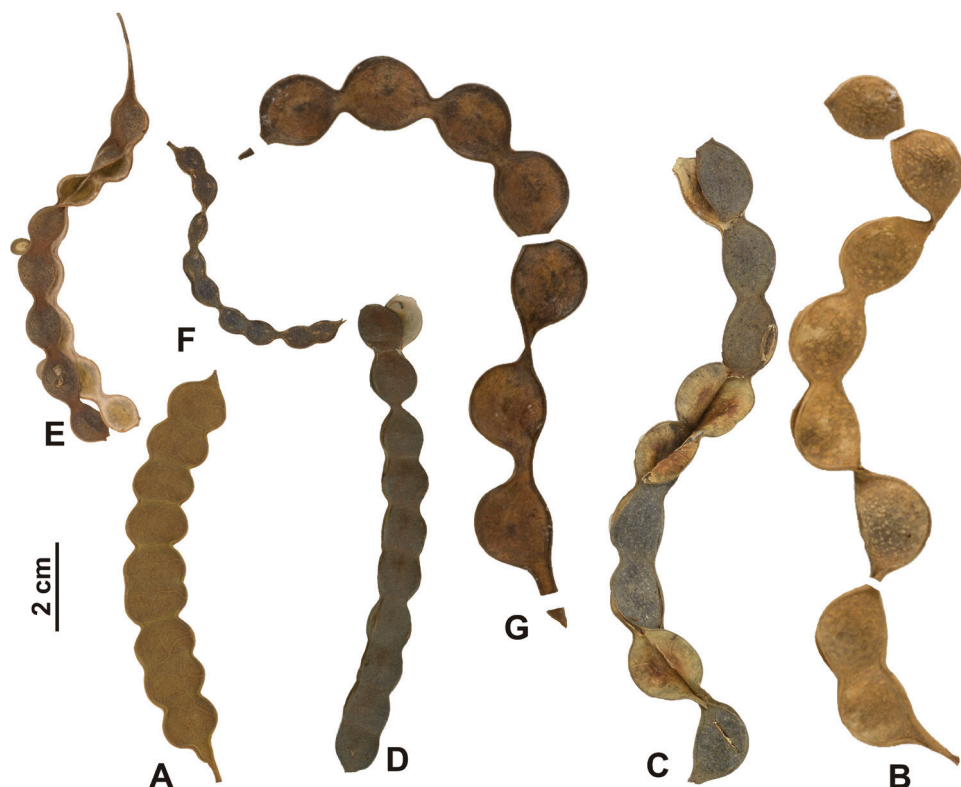


Figure 4. Fruits of *Pityrocarpa* species **A** *Pi. brenanii* (from Lewis *et al.* 1899, NY) **B** *Pi. inaequalis* (from Moreira *et al.* 3, F) **C** *Pi. leptostachya* (from Baez *et al.* 1174, NY) **D** *Pi. leucoxydon* (from de Bruijn 1750, NY) **E** *Pi. moniliformis* (from Nunes 597, HUEFS) **F** *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. leucoxydon* 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](https://nomenclature.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](https://nomenclature.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](https://nomenclature.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; isoelectotypes 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; isoelectotypes 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. Pl.* 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. Johnson, 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](https://nomenclature.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; isoelectotypes 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](https://nomenclature.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 exerted 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).

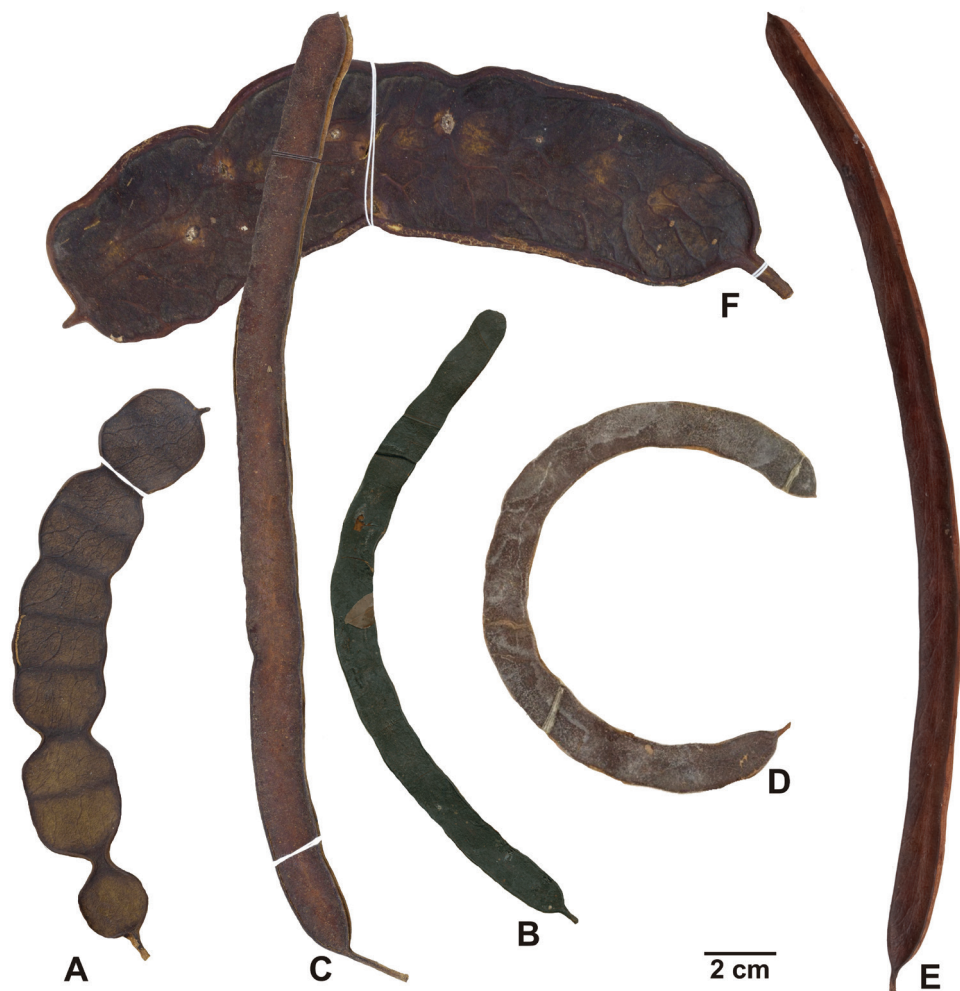


Figure 5. Fruits of *Marlimorimia* species **A** *Marlimorimia bahiana* (from Amorim 1009, NY) **B** *Marlimorimia colombiana* (from Killip 16268, NY) **C** *Marlimorimia contorta* (from Gomes 257, NY) **D** *Marlimorimia pittieri* (from Guevara 1264, F) **E** *Marlimorimia psilostachya* (from Rabelo 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](https://nomenclature.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; isoelectotypes 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; isoelectotype 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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References

- Barneby RC, Grimes JW (1984) Two new mimosaceous trees from the American Tropics. *Brittonia* 36(3): 236–240. <https://doi.org/10.2307/2806514>
- Bentham G (1842) Notes on Mimoseae, with a synopsis of species. *Journal of Botany* (Hooker) 4: 323–418.
- Brenan JPM (1955) Notes on Mimosoideae: I. *Kew Bulletin* 10(2): 161–192. <https://doi.org/10.2307/4108864>
- Brenan JPM (1963) Notes on Mimosoideae: VIII. *Kew Bulletin* 17(2): 227–228. <https://doi.org/10.2307/4118943>
- Britton NL, Rose JN (1928) Mimosaceae. *North American Flora* 23: 1–194.
- Grimes JW (1993) *Calliandra anthoniae* (Leguminosae, Mimosoideae, Ingeae), a new species, and a new combination in *Pseudopiptadenia* Rauschert (Leguminosae, Mimosoidae, Mimoseae). *Brittonia* 45(1): 25–27. <https://doi.org/10.2307/2806854>
- Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>
- Hughes CE, Bailey CD, Krosnick S, Luckow MA (2003) Relationships among genera of the informal *Dichrostachys* and *Leucaena* groups (Mimosoideae) inferred from nuclear ribosomal ITS sequences. In: Klitgaard BB, Bruneau A (Eds) *Advances in Legume Systematics Part 10. Higher Level Systematics*. Royal Botanic Gardens, Kew, 221–238.
- Inglis PW, Pappas M de CR, Resende LV, Grattapaglia D (2018a) Fast and inexpensive protocols for consistent extraction of high quality DNA and RNA from challenging plant and fungal samples for high-throughput SNP genotyping and sequencing applications. *PLoS ONE* 13(10): e0206085. <https://doi.org/10.1371/journal.pone.0206085>
- Inglis PW, Mata LR, da Silva MJ, Vieira RF, Alves R de BN, Silva DB, Azevedo VCR (2018b) DNA Barcoding for the identification of *Phyllanthus* taxa used medicinally in Brazil. *Planta Medica* 84(17): 1300–1310. <https://doi.org/10.1055/a-0644-2688>
- Jobson RW, Luckow M (2007) Phylogenetic study of the genus *Piptadenia* (Mimosoideae: Leguminosae) using plastid trnL-F and trnK/matK sequence data. *Systematic Botany* 32(3): 569–575. <https://doi.org/10.1600/036364407782250544>
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6): 587–589. <https://doi.org/10.1038/nmeth.4285>

- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Koenen EJM, Kidner C, Souza ER, Simon MF, Iganci JR, Nicholls JA, Brown GK, de Queiroz LP, Luckow M, Lewis GP, Pennington RT, Hughes CE (2020) Hybrid capture of 964 nuclear genes resolves evolutionary relationships in the mimosoid legumes and reveals the polytomous origins of a large pantropical radiation. *American Journal of Botany* 107(12): 1710–1735. <https://doi.org/10.1002/ajb2.1568>
- Lewis GP, Elias TS (1981) *Mimoseae* Bronn (1822). In: Polhill RM, Raven PH (Eds) *Advances in Legume Systematics, Part 1*. Royal Botanic Gardens Kew, 155–169.
- Lewis GP, Lima MPM (1991) *Pseudopiptadenia* Rauschert no Brasil (Leguminosae-Mimosoideae). *Arquivos do Jardim Botânico do Rio de Janeiro* 30: 43–67.
- de Lima AG, de Paula-Souza J, Ringelberg JJ, Simon MF, de Queiroz LP, Borges LM, de Freitas Mansano V, Souza VC, Scalon VR (2022) New segregates from the Neotropical genus *Stryphnodendron* (Leguminosae, Caesalpinoideae, mimosoid clade). In: Hughes CE, de Queiroz LP, Lewis GP (Eds) *Advances in Legume Systematics 14. Classification of Caesalpinoideae Part 1: New generic delimitations*. *PhytoKeys* 205: 203–238. <https://doi.org/10.3897/phytokeys.205.82220>
- Lima MPM (1985) Morfologia dos frutos e sementes dos gêneros da tribo *Mimoseae* (Leguminosae-Mimosoideae) aplicada à sistemática. *Rodriguésia* 37(62): 53–78. <https://doi.org/10.1590/2175-78601985376206>
- Lima MPM, Lima HC (1984) *Parapiptadenia* Brenan (Leguminosae-Mimosoideae) - Estudo taxonômico das espécies brasileiras. *Rodriguésia* 36(60): 23–30. <https://doi.org/10.1590/2175-78601984366004>
- LPWG [Legume Phylogeny Working Group] (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66(1): 44–77. <https://doi.org/10.12705/661.3>
- Luckow M (2005) Tribe *Mimoseae*. In: Lewis GP, Schrire B, Mackinder B, Lock M (Eds) *Legumes of the World*. Royal Botanic Gardens, Kew, 163–183.
- Luckow M, Miller JT, Murphy DJ, Livshultz T (2003) A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data. In: Klitgaard BB, Bruneau A (Eds) *Advances in Legume Systematics, Part 10. Higher Level Systematics*. Royal Botanic Gardens, Kew, 197–220.
- Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32(1): 268–274. <https://doi.org/10.1093/molbev/msu300>
- Queiroz LP (2009) *Leguminosae da Caatinga*. Universidade Estadual de Feira de Santana.
- Queiroz LP, Cardoso D, Fernandes MF, Moro MF (2017) Diversity and evolution of the flowering plants of the Caatinga Domain. In: Silva JMC, Leal I, Tabarelli M (Eds) *Caatinga: The largest Tropical Dry Forest Region in South America*. Springer, Cham, 23–63. https://doi.org/10.1007/978-3-319-68339-3_2
- Rauschert S (1982) *Nomina nova generica et combinationes novae Spermatophytorum et Pteridophytorum*. *Taxon* 31(3): 554–563. <https://doi.org/10.2307/1220694>

- Ribeiro PG, Luckow M, Lewis GP, Simon MF, Cardoso D, Souza ER, Silva APC, Jesus MC, dos Santos FAR, Azevedo V, de Queiroz LP (2018) *Lachesiodendron*, a new monospecific genus segregated from *Piptadenia* (Leguminosae: Caesalpinioideae: mimosoid clade): Evidence from morphology and molecules. *Taxon* 67(1): 37–54. <https://doi.org/10.12705/671.3>
- Ringelberg JJ, Koenen EJM, Iganci JR, de Queiroz LP, Murphy DJ, Gaudeul M, Bruneau A, Luckow M, Lewis GP, Hughes CE (2022) Phylogenomic analysis of 997 nuclear genes reveals the need for extensive generic re-delimitation in Caesalpinioideae (Leguminosae). In: Hughes CE, de Queiroz LP, Lewis GP (Eds) *Advances in Legume Systematics* 14. Classification of Caesalpinioideae Part 1: New generic delimitations. *PhytoKeys* 205: 3–58. <https://doi.org/10.3897/phytokeys.205.85866>
- Simon MF, Grether R, Queiroz LP, Skema C, Pennington RT, Hughes CE (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America* 106(48): 20359–20364. <https://doi.org/10.1073/pnas.0903410106>
- Simon MF, Pastore JFB, Souza AF, Borges LM, Scaloni VR, Ribeiro PG, Santos-Silva J, Souza VC, Queiroz LP (2016) Molecular phylogeny of *Stryphnodendron* (Mimosoideae, Leguminosae) and generic delimitations in the *Piptadenia* group. *International Journal of Plant Sciences* 177(1): 44–59. <https://doi.org/10.1086/684077>
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, et al. (2018) International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Koeltz Botanical Books. <https://doi.org/10.12705/Code.2018>

Supplementary material I

Voucher information and GenBank accession numbers (internal transcribed spacer-ITS sequences) for taxa used in this study

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Data type: excel file

Explanation note: Voucher information and GenBank accession numbers for taxa used in this study.

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