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MOLECULAR PHYLOGENY OF *STRYPHNODEDRON* (MIMOSOIDEAE, LEGUMINOSAE) AND GENERIC DELIMITATIONS IN THE *PIPTADENIA* GROUP

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Premise of research. Despite recent progress on the systematics of the Leguminosae, the relationships between some genera, as well as their circumscriptions, remain uncertain. Here we investigate the relationships between *Stryphnodendron* and closely related genera in the *Piptadenia* group, a clade of problematic taxonomy for which a robust phylogenetic hypothesis is still lacking.

Methodology. Taxonomic sampling included 23 species of *Stryphnodendron* (77% of the genus) and representatives of genera of the *Piptadenia* group. DNA (*matK/trnK*, *trnD-trnT*, *trnL-trnF*, and ITS) sequences constituting a data set with 6798 bp and 94 terminals were used in parsimony and Bayesian analyses. A set of 17 morphological characters were optimized on the estimated phylogeny to evaluate clade synapomorphies and character evolution.

Pivotal results. Our increased molecular and taxonomic sampling improved the resolution of a previously largely unresolved clade that included *Microlobius*, *Parapiptadenia*, *Pityrocarpa*, *Pseudopiptadenia*, and *Stryphnodendron*. Major lineages within this clade are an early-diverging clade containing the sister genera *Parapiptadenia* and *Pseudopiptadenia*; the genus *Pityrocarpa*, with *Pseudopiptadenia brenanii* nested within it; and a *Stryphnodendron* clade including the monospecific genus *Microlobius*. Samples of *Stryphnodendron* grouped into three strongly supported clades: a group of seven species bearing large leaflets and relatively few pairs of pinnae, sister to *Microlobius foetidus*; a clade containing samples of *Stryphnodendron duckeanum*; and a large and poorly resolved clade containing the remaining species of *Stryphnodendron*, including species with small leaflets and higher number of pinnae and highly specialized dwarf shrubs adapted to savanna fire regimes. Lack of resolution within this clade suggests rapid and recent diversification in both savannas and rain forests in the Neotropics.

Conclusions. Our findings highlight the importance of densely sampled phylogenies to rigorously test the monophyly of genera. Key morphological characters are proposed to assist generic delimitations in the *Piptadenia* group. New taxonomic rearrangements are needed in order to accommodate the results presented here.

Keywords: Amazon, Cerrado, diagnosability, diversification, monophyly, Neotropics.

Online enhancement: appendix figures.

Introduction

Despite recent progress on the molecular systematics of the Leguminosae (Lavin et al. 2005; Lewis et al. 2005; Cardoso et al.

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2012; LPWG 2013), the monophyly of many genera and relationships between a number of clades remain uncertain. Among the mimosoid legumes, one group where generic relationships are problematic is the *Piptadenia* group, an informal assemblage that includes the following genera: *Anadenanthera* Speg., *Microlobius* C. Presl, *Mimosa* L., *Parapiptadenia* Brenan, *Piptadenia* Benth., *Pseudopiptadenia* Rauschert, and *Stryphnodendron* Mart. The group was defined by Lewis and Elias (1981)

on the basis of the shared presence of compound pollen (polyads) and a small porate stigma at the end of a narrowing style. Those features are not exclusive to the *Piptadenia* group, but other Mimosoideae taxa where they occur have very dissimilar flower morphology (Lewis and Elias 1981).

The taxonomy within the *Piptadenia* group has been rather unstable because of a series of nomenclatural changes at the generic level, most notably within the genus *Piptadenia*, which has been subject to a number of generic realignments based on morphological studies (Brenan 1955, 1963, 1986; Lima and Lima 1984; Lewis 1991a, 1991b; Lewis and Lima 1991), leading to the recognition of segregate genera such as *Parapiptadenia* and *Pseudopiptadenia*. More recently, a molecular-based phylogenetic study focused on *Piptadenia* found the genus to be polyphyletic, resulting in a reclassification of the genus that rendered a monophyletic *Piptadenia* sensu stricto with 23 species, the resurrection of *Pityrocarpa* (Benth.) Britton & Rose, currently with three species, and the recognition of *Piptadenia viridiflora* as an isolated lineage for which a new genus name is still pending (Jobson and Luckow 2007). Such rearrangements are supported by a combination of morphological character states, namely, the occurrence of stipular spines, inflorescence organization, and flower morphology (Jobson and Luckow 2007). Further insights into the relationships and circumscription of genera within the *Piptadenia* group were provided by molecular phylogenetic studies based on plastid loci (Luckow et al. 2003; Jobson and Luckow 2007), although the relationships between most genera are still unclear. Within the *Piptadenia* group, some genera, such as *Piptadenia* and *Mimosa*, have been the subject of molecular phylogenetic studies (Jobson and Luckow 2007; Bessega et al. 2008; Simon et al. 2011), whereas detailed molecular studies focused on other genera, such as *Stryphnodendron*, *Parapiptadenia*, and *Pseudopiptadenia*, are still lacking.

The genus *Stryphnodendron* has approximately 30 species confined to the Neotropics, ranging from Costa Rica to southern Brazil (Occhioni 1990; Luckow 2005), although there are a number of new species yet to be formally described as well as new synonyms to be proposed (Scalon 2007). Early work on *Stryphnodendron* included the description of the genus (von Martius 1837, p. 117), followed by a taxonomic treatment and an increase in the number of species (Bentham 1842, 1875). More recent contributions included new species descriptions (Forero 1972; Occhioni-Martins and Martins 1972; Occhioni-Martins 1974, 1975, 1981; Barneby and Grimes 1984; Occhioni 1985; Neill and Occhioni 1989) and new morphological data, such as from pollen (Guinet and Caccavari 1992), as well as refinement of geographic distributions (Ducke 1949; Occhioni 1990). Key morphological features (fig. 1) of the genus are a lack of prickles or spines, reddish granular trichomes on young branches, leaves bearing extrafloral nectaries, spicate inflorescences, flowers with 5 petals and 10 free stamens, the presence of bark exudates, and pollen grains arranged predominantly in 16-grain polyads. Although those character states are not unique to *Stryphnodendron*, their combined occurrence differentiates the genus from other members of the *Piptadenia* group as well as from other mimosoid genera. Although some *Stryphnodendron* species have been included in phylogenetic studies, lack of resolution, as well as sparse and unequal taxon sampling, precluded any conclusion regarding the monophyly of the genus (Jobson and Luckow 2007; Simon et al. 2009).

Ecological preference and habit in the genus range from rain forest canopy trees (e.g., *S. excelsum*, *S. moricolor*, and *S. paniculatum*) to smaller trees that colonize disturbed areas (e.g., *S. foreroi* and *S. pulcherrimum*), savanna trees (e.g., *S. adstringens* and *S. coriaceum*), and dwarf geoxylic shrubs (e.g., *S. gracile*, *S. heringeri*, and *S. pumilum*) that grow in fire-prone savannas of the Cerrado in central Brazil (Rizzini and Heringer 1987; fig. 1). Medicinal qualities of the bark of *S. adstringens* have been described in the literature (Audi et al. 1999; Fernandes et al. 2010), and the high concentration of tannins provides the basis of anti-inflammatory, analgesic, and healing properties. An ointment based on the bark extract of *S. adstringens*, a species that has been extensively used in the traditional medicine in Brazil, has been developed for treatment of skin wounds (Minatel et al. 2010) and is now being commercialized by a Brazilian pharmaceutical company.

The most comprehensive phylogenetic study that focused on the *Piptadenia* group (Jobson and Luckow 2007) presented a substantial contribution to the understanding of relationships within the group. However, there are still open questions regarding generic delimitations, mainly because of a lack of resolution in the phylogeny and limited taxon sampling. The aim of this study was to produce a phylogenetic hypothesis for the *Piptadenia* group based on plastid and nuclear loci, as well as to test the monophyly of genera previously undersampled in phylogenetic studies, with emphasis on the genus *Stryphnodendron*.

Material and Methods

Taxonomic Sampling

Taxon sampling included 48 accessions of *Stryphnodendron* comprising 23 species (ca. 77% of the genus), encompassing both morphological and geographical variation within the genus. For some widespread taxa, multiple accessions representative of the geographic range of the species have been included. In addition, a number of representatives of the *Piptadenia* group that have been shown to be closely related to *Stryphnodendron* (Jobson and Luckow 2007) were sampled (42 samples, 38 species), including a comprehensive sample of *Parapiptadenia* (4 out of 6 species), *Pityrocarpa* (all 3 species), *Pseudopiptadenia* (5 out of 11 species), and *Microlobius* (monospecific genus, multiple samples), many of them included in a molecular phylogenetic analysis for the first time. In addition, five samples of mimosoid genera were used as outgroups, on the basis of published phylogenies focused on different groups (Hughes et al. 2003; Luckow et al. 2003; Kyalangalilwa et al. 2013).

Molecular Sampling

Total genomic DNA was extracted from silica-dried leaves or from herbarium specimens with the modified CTAB (cetyltrimethylammonium bromide) protocol (Doyle and Doyle 1987) or the DNeasy plant mini kit (Qiagen). Amplification of the *matK/trnK* locus was performed in two reactions with the set of primers trnK685F/1159R and matK1100L/trnK2R (Hu et al. 2000; Wojciechowski et al. 2004). The amplification of the *trnD-trnT* region (Shaw et al. 2005) used primers trnD2, trnE, trnT, and trnY as described in Simon et al. (2011). The *trnL-trnF* region (including the *trnL* intron and the *trnL-trnF* intergenic spacer) was amplified with primers “C” and “F” (Taberlet

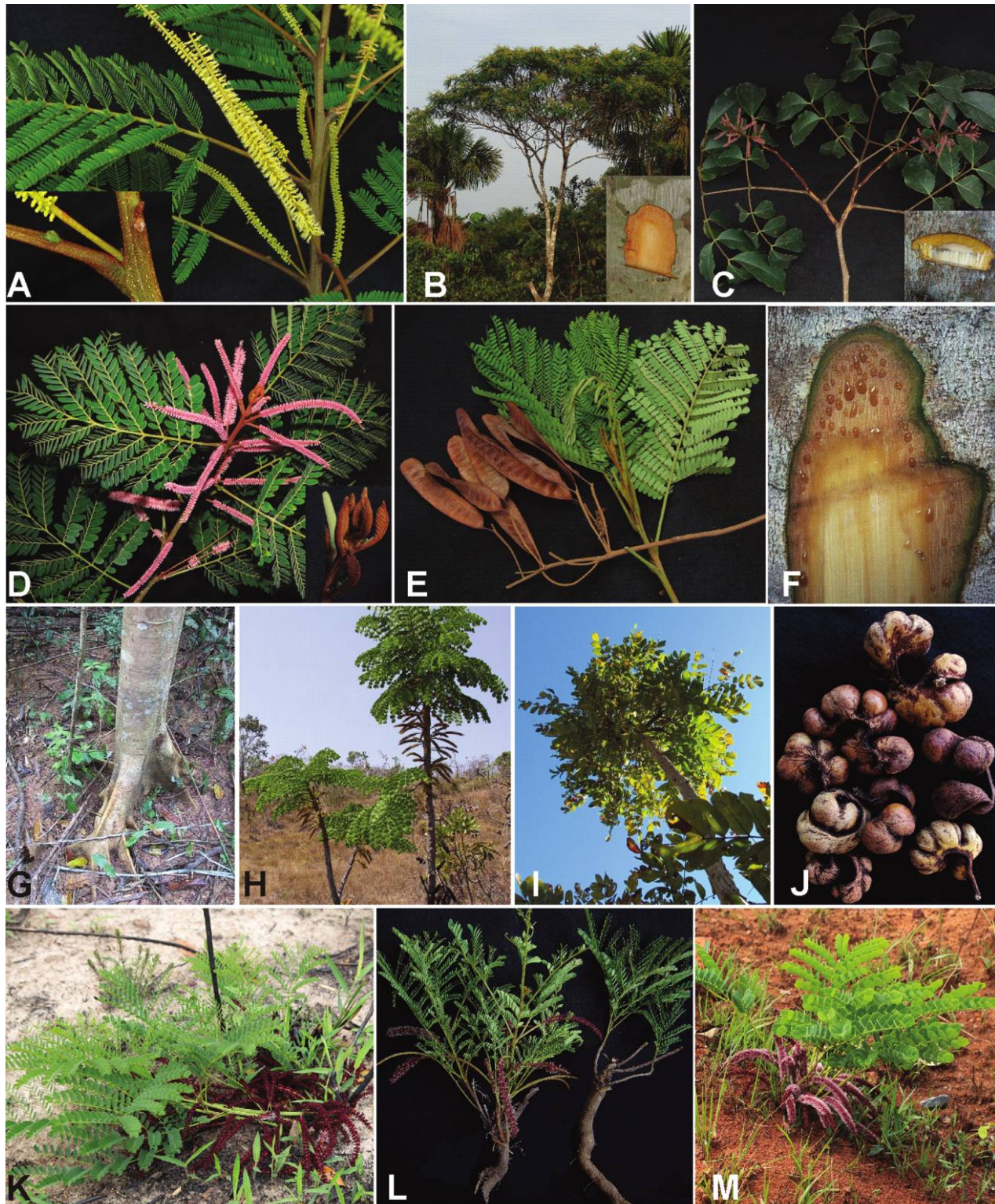


Fig. 1 General overview of the Neotropical genus *Stryphnodendron*. A, B: *S. pulcherrimum*. A, Flowering branch and extrafloral nectary (*inset*). B, Habit and bark slash (*inset*). C, *S. paniculatum* flowering branch and bark slash (*inset*). D, *S. foreroi* flowering branch and ferruginous indumentum on young leaves (*inset*). E–G, *S. duckeanum*. E, Leaves and plano-compressed fruits. F, Bark slash showing brown exudate droplets. G, Trunk base with small buttress. H, *S. adstringens* habit. I, J, *S. fissuratum*. I, Habit. J, Cochleate fruits. K–M, Savanna shrubs growing from underground woody organs. K, *S. gracilis*. L, *S. heringeri*. M, *S. pumilum*. Photos by Marcelo Simon (A–D, F, G, J, L, M), Glocimar Pereira-Silva (E), Henrique Moreira (H, K), and Ricardo Haidar (I).

et al. 1991). All plastid loci were sequenced with the same set of primers used for amplification. The nuclear ribosomal ITS region (internal transcribed spacer region, including ITS1 and ITS2 and the intervening 5.8S) was amplified with a nested PCR method. The first primers used in the nested PCR were ITS5p and ITS8p (Möller and Cronk 1997), followed by a second PCR using primers ITS1 and ITS4 (White et al. 1990). All PCR amplification reactions were performed in a final volume of 10 μ L containing 5 μ L of TopTaq master mix kit (Qiagen), 2.25 ρ Mol of each primer, 5–10 η g of genomic DNA, and ultrapure H₂O (q.s.p. 10 μ L). For the ITS amplification, DMSO (dimethyl sulfoxide; 2% of the preparation volume) was added in order to avoid secondary conformations. The amplification program used an initial denaturation at 94°C for 5 min, followed by 30–35 cycles of denaturation at 94°C for 1 min, annealing at 52°C (ITS) or 55°C (plastid loci) for 1 min, and elongation at 72°C for 2 min and a final elongation step at 72°C for 5 min. Amplified products were purified with 20% solution of polyethylene glycol 6000 macrogol. Sequencing reactions in both directions were performed with a Big Dye Terminator kit (ver. 3.1; Applied Biosystems).

Some sequences used in the analysis have been downloaded from GenBank from previous studies on mimosoids (Hughes et al. 2003; Luckow et al. 2003; Jobson and Luckow 2007; Simon et al. 2011). Two species of *Stryphnodendron* (*S. microstachyum* and *S. moricolor*) were represented only by partial sequences of the *matK-trnK* locus generated as part of barcoding studies (International Barcode of Life project [iBOL]; Baraloto et al. 2012). Voucher information, taxon authority, and GenBank accession numbers of sequences newly generated, as well as that of sequences published in other studies used in our phylogenetic analyses, are provided in appendix A.

Phylogenetic Analysis

Original electropherograms were assembled into final contigs with the Geneious, version 6.1.6, platform (Drummond et al. 2012). Sequences were automatically aligned in MUSCLE with default settings (Edgar 2004) and then manually adjusted in Geneious. Unambiguous indels were coded with the program SeqState (Müller 2005), following the simple gap-coding method of Simmons and Ochoterena (2000). Informative indels were used in parsimony analysis and also in Bayesian analysis under a binary model (Ronquist et al. 2012). Parsimony analysis was carried out in PAUP, version 4.0b10 (Swofford 2002), with a heuristic search with 1000 random-taxon additions and tree bisection-reconnection (TBR) branch swapping, saving 15 trees per replicate. Trees saved in the first round were used as starting trees in a second search using the same parameters, keeping a maximum of 10,000 trees. Nonparametric bootstrap resampling (BS) was used to estimate clade support through 10,000 bootstrap replicates using the heuristic search parameters mentioned above and with 15 trees retained per replicate.

A model of molecular evolution was selected for each partition (plastid, ITS1+ITS2, and 5.8S) with the Akaike information criterion implemented in jModelTest 2 (Darriba et al. 2012). The GTR+I+G model was selected for all partitions, except for the 5.8S ribosomal (K80+G model). Bayesian analyses were carried out with MrBayes, version 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012), through the Cyber-

infrastructure for Phylogenetic Research (Cipres Science Gateway; Miller et al. 2010). We performed two runs in parallel of four Markov chain Monte Carlo for 10⁷ generations, with trees sampled every thousandth generation. Permutation of parameters was initiated with a random tree and four simultaneous chains set at default temperatures (Huelsenbeck and Ronquist 2001). Convergence of runs was assessed by inspecting whether the standard deviation of split frequencies of runs was less than 0.01, and the first 10⁵ trees were discarded as burn-in. We then used MrBayes, version 3.1.2, to summarize trees sampled from post-burn-in into a 50% majority-rule consensus tree that included posterior probabilities (PP) as branch-support estimates.

Reconstruction of Ancestral State for Selected Morphological Characters

Specimens stored at the NY and SPF herbaria (acronyms according to Thiers 2015; see app. B for vouchers) were examined for the occurrence of 17 morphological characters (table 1). Character and character state definitions follow the general guidelines of Sereno (2007), but a distinction between neomorphic and transformational characters was not strictly adopted here. States were scored on the basis of their presence in specimens, complemented, when available and reliable, by data from the literature (Macbride 1943; Lima and Lima 1984; Barneby 1986, 1991; Lewis and Lima 1991; Scalon 2007). Terminology follows Harris and Harris (2001), Radford et al. (1976), and Weberling (1989). We have also adopted here the strict definition of fruit types of Barroso et al. (1999), who limit the use of “legume” to only a dry fruit derived from a superior unicarpellar ovary that opens along its two sutures (see also Spjut 1994). According to Barroso et al. (1999), a superior unicarpellar ovary can also give rise to a bacoid legume (an indehiscent fruit with a fleshy mesocarp), a nucoid legume (an indehiscent or tardily dehiscent fruit with a fibrous mesocarp), or a follicle (a dry fruit that opens along only one suture). Morphological data matrices were built with Mesquite, version 3.03 (Maddison and Maddison 2015). Initially, a specimen-versus-characters matrix was made, and subsequently, a new taxon-versus-characters matrix was produced by merging specimens belonging to the same taxon. At this point information obtained from the literature was added. Finally, the taxon matrix was adjusted to include all terminals sampled in the molecular phylogeny. The final taxon and specimen matrices are available in Morphobank (<http://morphobank.org/permalink/?P2220>). Character ancestral states were reconstructed with YBYRÁ (Machado 2015), which runs the command “APO” of TNT (Goloboff et al. 2008) to place unambiguous synapomorphies, and also with the unordered parsimony method implemented in Mesquite (Maddison and Maddison 2015), which shows predictions for missing and inapplicable data. Both analyses were conducted with the 50% majority-rule consensus tree obtained in the Bayesian analysis, with terminals pruned in order to keep one accession per taxon.

Results

The cpDNA data set, including sequences of three loci (*matK/trnK*, *trnD-T*, and *trnL-F*), contained 94 terminals and 5901 bp

Table 1

Morphological characters sampled in this study and their character states

| Character | States | Comments |
|---|--|--|
| 1. Habit, type | (0) tree; (1) shrub; (2) geoxylic shrub; (3) liana; (4) prostrate shrub | |
| 2. Prickles | (0) absent; (1) present | Prickles are considered here only as nonvascular epidermal projections; hence, the spines present in <i>Vachellia farnesiana</i> and <i>Piptadenia viridiflora</i> are not treated in this character |
| 3. Indumentum, granular reddish trichomes | (0) absent; (1) present | The typical ferruginous indumentum observed on younger branches of most <i>Stryphnodendron</i> species is formed by the agglomerated presence of granular reddish trichomes. Here we have chosen to code it as a distinct character, but it is possible that it is a variation of the glandular trichomes observed in most taxa of the <i>Piptadenia</i> group. A better assessment of this relationship must be done through a more detailed morphological study. |
| 4. Leaf, leaflets, arrangement | (0) opposite; (1) alternate | Leaflets are considered as the laminar structures of bipinnate leaves. In the case of <i>Inga</i> , which has once-pinnate leaves, all characters dealing with leaflet morphology were scored as inapplicable. |
| 5. Leaf, leaflet, tuft of trichomes near the midrib | (0) absent; (1) present on acroscopic side of midrib; (2) present on basioscopic side of midrib; (3) present on both sides of midrib | |
| 6. Leaf, leaflet, size | (0) microphyllidious; (1) macrophyllidious | The distinction between micro and macrophyllidia is usually contextual. Here we apply microphyllidious to plants with small to medium leaflets, as seen in <i>Stryphnodendron polyphyllum</i> and <i>Piptadenia paniculata</i> , respectively. Macrophyllidious is restricted to taxa with larger leaflets, as seen in <i>S. moricolor</i> , for instance. |
| 7. Inflorescence, peduncle, prophylla | (0) absent; (1) free from each other; (2) fused | Prophylla are laminate projections that usually subtend the portion of the inflorescence axis that bears the flowers. They usually occur in alternate or opposed pairs and can be free from each other, or fused. |
| 8. Flower, stamens, anther, gland | (0) absent; (1) present | |
| 9. Flower, petals, base, degree of fusion | (0) free almost to base; (1) cohered; (2) fused | Within the Mimosoideae, flowers may have petals free or united at the base forming a tube. Character state 0 is applied to the first condition but also to some cases in which the petals are slightly united at the very base. Character states 1 and 2 are applied only to flowers with tubes. "Cohered" is used here to describe the attachment of the petals, but without apparent epidermal fusion. This condition is recognized by the presence of a clear suture line between the petals. "Fused" is applied when epidermal fusion is inferred. This condition is recognized by the lack of a suture line between petals. |
| 10. Fruit, type | (0) legume; (1) follicle; (2) nuroid legume; (3) craspedium; (4) bacoid legume; (5) unjointed craspedium | |
| 11. Fruits, valves, orientation | (0) straight; (1) curved; (2) coiled | |
| 12. Fruit, margins | (0) straight; (1) undulate; (2) constricted between seeds | When the fruit margin showed a depression between each seed, no matter the degree, it was considered as constricted; undulate margins are the ones with irregular and usually of lower-degree depressions |
| 13. Seed, shape | (0) lenticular; (1) plano-compressed | Lenticular seed are compressed but with biconvex faces, while plano-compressed seeds have plane faces |
| 14. Seed, endosperm | (0) absent; (1) present | Compiled from Gunn 1984 |
| 15. Seed, pleurogram | (0) absent; (1) present | The seed testa of <i>Inga</i> species may be fused with the endocarp, so this character was scored as inapplicable for the genus |
| 16. Seed, wing | (0) absent; (1) present | Scored as inapplicable for <i>Inga</i> ; see character 15 |
| 17. Seed, testa, color | (0) brown; (1) whitish | Scored as inapplicable for <i>Inga</i> ; see character 15 |

(including 235 indels). The ITS data set was smaller (55 terminals and 897 bp, including 137 indels) because of difficulties in amplifying DNA from some samples and because only a few sequences for this locus were available in GenBank. Proportionally, the nuclear data set rendered a larger number of parsimony-informative characters (32.1%) compared to the chloroplast DNA data set (9.4%). Analysis of individual plastid (*matK/trnK*, *trnD-T*, and *trnL-F*) and nuclear (ITS) data sets produced highly similar topologies (figs. C1, C2; figs. C1–C19 available online), and therefore the two data sets were concatenated into a single matrix, which comprised an alignment of 6798 bp (including 372 coded indels). In the combined data set, missing data were most frequent in the ITS (42%) and *trnD-T* (27%) loci (app. A).

Analysis of the combined data set recovered a clade containing representatives of the *Piptadenia* group (*Microlobius*, *Mimosa*, *Parapiptadenia*, *Piptadenia*, *Pityrocarpa*, *Pseudopiptadenia*, and *Stryphnodendron*) plus one member of the tribe Ingeae and also one sample of *Senegalia* (clade A; fig. 2); this whole clade is sister to the genus *Vachellia*. *Anadenanthera*, which was previously assigned to the *Piptadenia* group sensu Lewis and Elias (1981), was placed outside this clade and appeared more closely related to *Parkia*.

Overall, the analysis recovered a well-resolved topology with well-defined lineages, although some of the relationships received low support from both parsimony and Bayesian analyses. *Mimosa*, *Piptadenia* (excluding *Piptadenia viridiflora*), *Parapiptadenia*, *Pseudopiptadenia*, *Pityrocarpa*, and *Stryphnodendron* have been recovered as strongly supported clades, although the last three are not monophyletic. Accessions of *Pseudopiptadenia brenanii*, included for the first time in a molecular-based phylogenetic study, are nested within a strongly supported clade containing samples of the genus *Pityrocarpa*, whereas samples of *Microlobius foetidus* grouped among the *Stryphnodendron* species. Within *Stryphnodendron*, three strongly supported clades were found: (1) a clade formed by seven species bearing large leaflets and relatively few pairs of pinnae, comprising five taxa from the Amazon and two from savannas and seasonally dry forests (fig. 2, clade H)—this group is sister to *M. foetidus*; (2) a clade including samples of *S. duckeanum* (fig. 2, clade I), which appears as a somewhat isolated lineage within the genus; and (3) a large but poorly resolved clade containing the remaining species of *Stryphnodendron*, including the type species of the genus (*S. adstringens*), dwarf fire-adapted Cerrado species, and savanna trees, as well as a number of rain forest taxa (fig. 2, clade J). All species in this group have small, alternate leaflets and more pinnae per leaf. Relationships within this clade are unclear because of short branch lengths (fig. 2), and multiple accessions of a species generally did not coalesce as monophyletic. Although *S. microstachyum* and *S. moricolor* were represented only by partial sequences of the *matK/trnK* locus, the placement of these species was consistent with morphological affinities. Other species not sampled here that would probably fall within this large clade are *S. confertum* Rizzini & Heringer, *S. excelsum* Harms, *S. guianense* (Aubl.) Benth., and *S. levelli* R.S. Cowan.

Ancestral character state reconstruction provided some putative unambiguous morphological synapomorphies for the clades inferred with the molecular data, all of them homoplastic (fig. 3). All characters, except presence of prickles (character 2),

showed at least one state with unambiguous reconstructions. Figure 3 shows only unambiguous optimizations. Reconstructions for each character individually, which also include the ambiguous optimizations, are presented in appendix C, available online.

The relationship between *Parkia timoriana* and *Anadenanthera colubrina* is supported by the presence of anther glands (character 8: state 1; see table 1). This character state is also a synapomorphy for the clade containing all samples of *Piptadenia*, excluding *P. viridiflora*, and also for clade B (fig. 2). This latter clade and the *Piptadenia* clade have cohered petals (9:1) as another synapomorphy, even though there are reversals within *Piptadenia*. The genus *Mimosa* is supported by the presence of craspedia (10:3), and its sister-group relationship with *Piptadenia* could be supported by the shared presence of prickles (2:1), but the optimization of this character state is ambiguous (fig. C4). The synapomorphy supporting clade C (fig. 2) is fruits with undulate margins (12:1), although there are multiple shifts from this state within the group (fig. C14). The change to fruits with constricted margins (12:2) supports the relationship between *Ps. brenanii* and *Pityrocarpa*. The latter genus has as its synapomorphy seeds with a white testa (17:1), a homoplastic character also found in *M. foetidus*. The relationship between *Parapiptadenia* and *Pseudopiptadenia* (clade E) is supported by plano-compressed (13:1), winged (16:1) seeds lacking a pleurogram (15:0). Some of these character states are shared in different combinations by convergence with *Anadenanthera* and *Piptadenia paniculata*. Petals almost free from each other (9:0) and the absence of endosperm in seeds (14:0) are the synapomorphies for the group with most *Pseudopiptadenia* species. Clade D is supported by the presence of granular reddish trichomes (3:1). Large leaflets (6:1) is the synapomorphy for *Stryphnodendron* clade H. No putative morphological synapomorphies support the relationship between *Microlobius* and clade H or the clustering of *S. duckeanum* (clade I) and the remaining *Stryphnodendron* species (clade J), which are placed in a group that has alternate leaflets (4:1) as its synapomorphy. *Stryphnodendron cristaliniae* and *S. heringeri* share the geoxylic habit (1:2), absence of a tuft of trichomes at the base of the leaflets (5:0), and follicles (10:1). It is not clear whether fused prophylla are a synapomorphy for clade D (fig. C9). Optimization of fruit type showed that the legume is apparently the plesiomorphic condition within the *Piptadenia* group (fig. C12), whereas follicles (10:1) and nuroid legumes (10:2) have probably evolved multiple times.

Discussion

Our results cast doubt on the monophyly of the informal *Piptadenia* group (sensu Lewis and Elias 1981), considering that *Anadenanthera* seems to be more closely related to *Parkia*. Furthermore, *Vachellia* and a clade containing the whole tribe Ingeae plus some of the segregates of *Acacia* sensu lato (the clade represented here by *Inga edulis* and *Senegalia nigrescens*) appear as closely related to members of the *Piptadenia* group, a topology also recovered in previous studies (Jobson and Luckow 2007; Kyalangalilwa et al. 2013). The poorly supported sister-group relationship between *Mimosa* and *Piptadenia* found in Jobson and Luckow (2007) was also recovered here, again

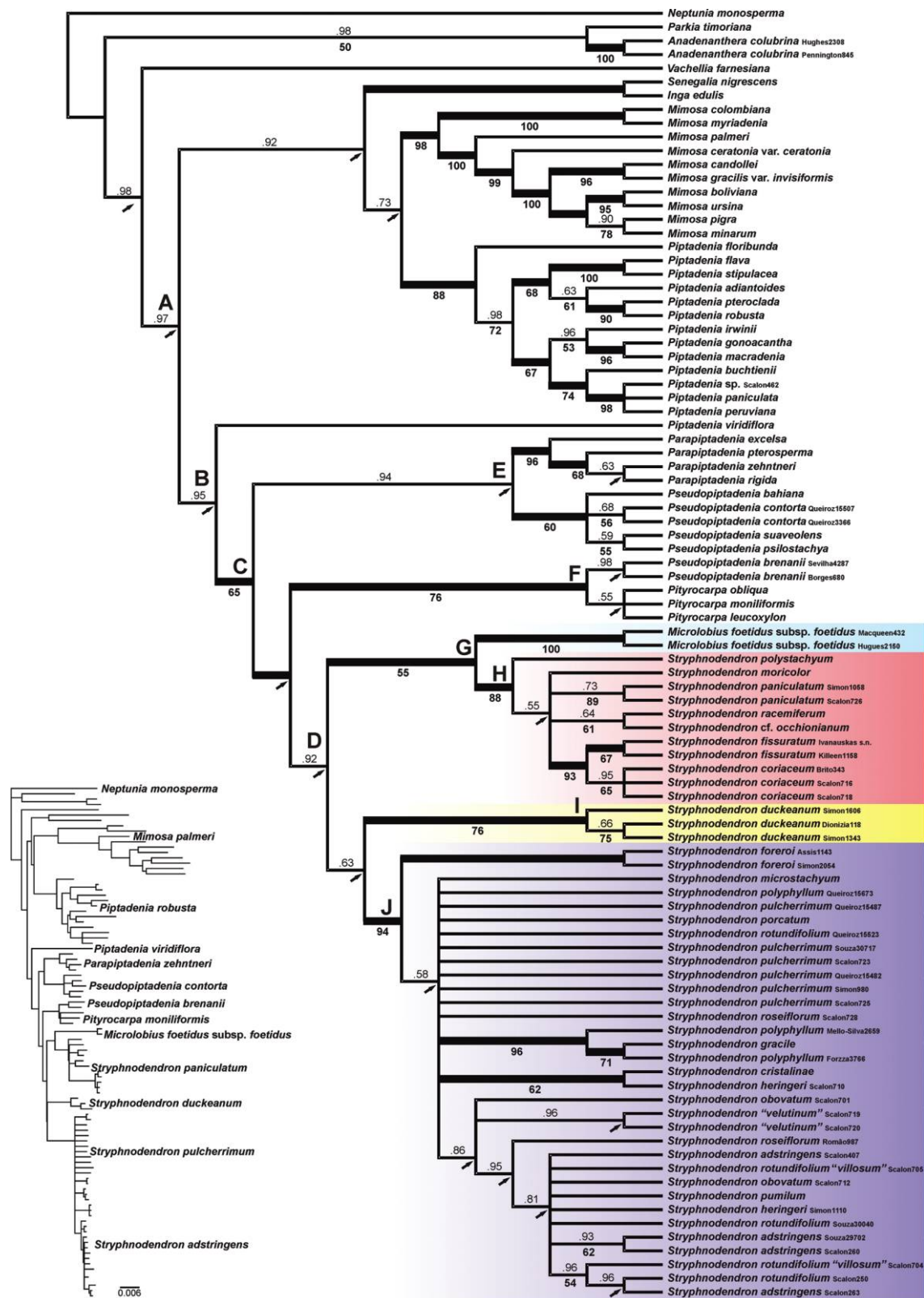


Fig. 2 Phylogeny of *Stryphnodendron* and related genera in the *Piptadenia* group, based on plastid (*matK/trnK*, *trnD-trnT*, *trnL-trnF*) and nuclear (ITS) DNA sequences and coded indels: the 50% majority-rule consensus tree and posterior probability values (PP; above nodes) from trees sampled in posterior of Bayesian analysis. Thickened branches have PP = 1.0. Numbers below branches are bootstrap support (BS) values from parsimony analysis. Nodes marked with an arrowhead have BS < 50. Unpublished species names are presented in quotation marks. Voucher information is provided to differentiate multiple accessions of the same species (see app. A for a full list of vouchers). Letters next to nodes correspond to clades discussed in the text. A phylogram derived from the Bayesian analysis with corresponding branch lengths is shown (*inset*). Scale bar is in substitutions per site.

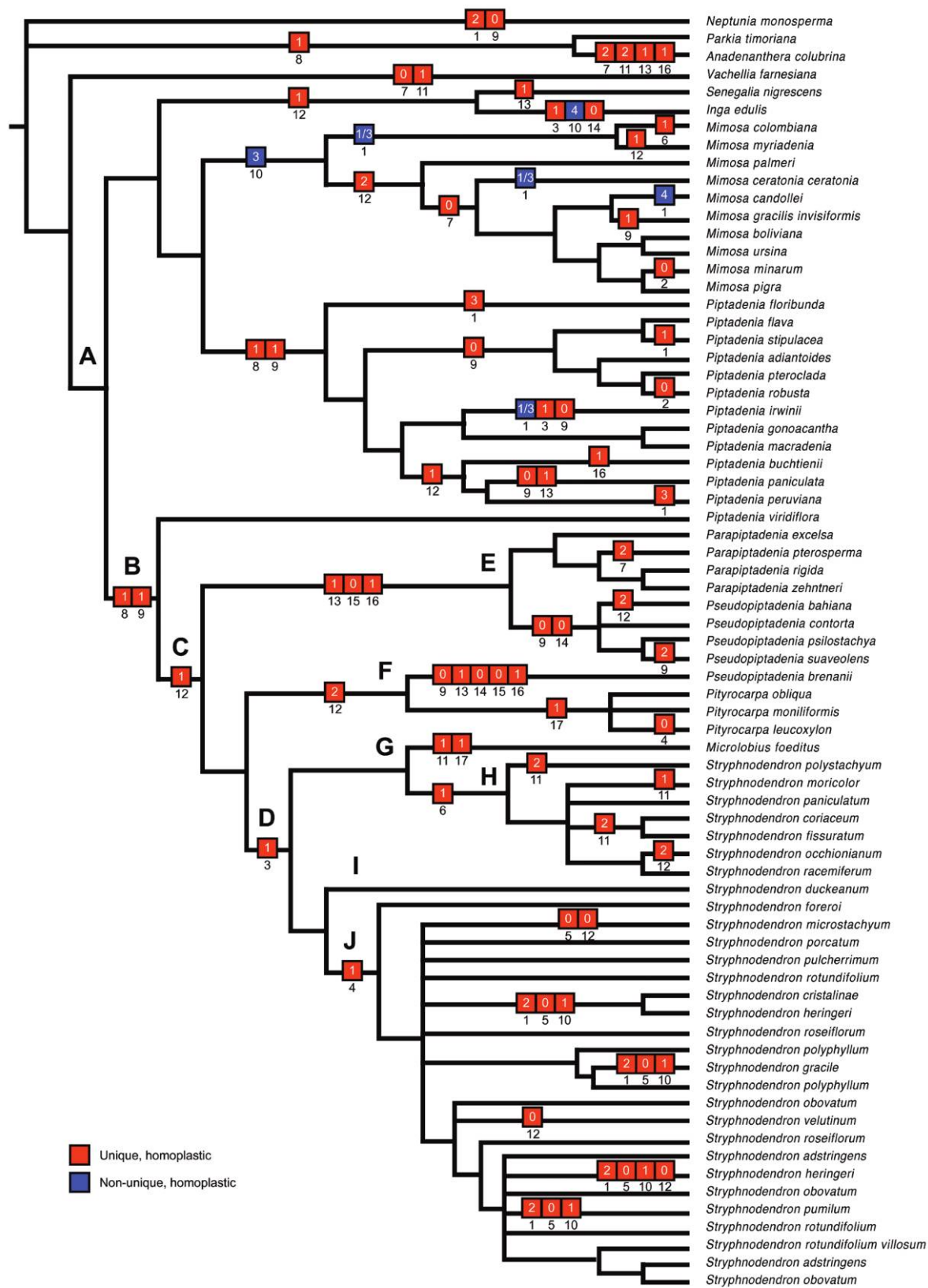


Fig. 3 Optimization of morphological character states over the 50% majority-rule consensus tree obtained in Bayesian analysis of molecular data. Only unambiguous optimizations are shown. See appendix C, available online, for ambiguous character states. Numbers in and below boxes correspond to characters and states listed in table 1.

with low support. *Piptadenia viridiflora*, which clearly does not belong to the genus *Piptadenia*, would be better placed in another genus or assigned to its own genus, as previously pointed out (Jobson and Luckow 2007). Sequences of the genus *Adenopodia* (a putative close relative of *Piptadenia* [Brenan 1986] still to be included in any molecular-based study) would be required to complete the picture of the *Piptadenia* group depicted here.

Despite an increase in character and taxon sampling relative to previous studies (Jobson and Luckow 2007; Simon et al. 2009), relationships between some clades are still unclear, most notably along the backbone of the phylogeny. Such persistent lack of resolution may be due to the well-documented low rates of nucleotide substitution of mimosoids when compared to other legumes (Lavin et al. 2005). Nevertheless, the monophyly of genera such as *Mimosa*, *Piptadenia* (except for *P. viridiflora*), and *Parapiptadenia* has been confirmed, corroborating previous findings (Jobson and Luckow 2007; Simon et al. 2011). In addition, generic rearrangements concerning *Piptadenia* based on morphology (Brenan 1955, 1963; Lima and Lima 1984; Lewis 1991a, 1991b; Lewis and Lima 1991) and molecular data (Jobson and Luckow 2007) are largely supported by our results. Our increased molecular sampling improved the resolution of a largely unresolved clade reported by Jobson and Luckow (2007) that included *Microlobius*, *Parapiptadenia*, *Pityrocarpa*, *Pseudopiptadenia*, and *Stryphnodendron* (clade C, fig. 2), improving our knowledge about the relationships between genera. Unexpectedly, *Ps. brenanii* grouped with *Pityrocarpa*, a relationship recovered in both nuclear and plastid individual analyses (figs. C1, C2). New relationships unveiled here also include *Parapiptadenia* as sister to *Pseudopiptadenia* and *Microlobius* as nested within *Stryphnodendron*. Some of the main clades are discussed below.

Mimosa and *Piptadenia*

The low branch support found for the clade comprising *Mimosa* and *Piptadenia* (PP = 0.73; BS < 50) reflects uncertainty about the relationship between the two genera, as does the ancestral character state reconstruction of morphological features at this node. The presence of prickles could be a synapomorphy uniting both genera, but it could also be a shared plesiomorphy. More samples of both Ingeae and *Acacia* sensu lato segregates, as well as an improved phylogenetic hypothesis, are necessary to ascertain more accurately the evolution of this character. Barneby (1991) indicated that the most distinguishing feature of *Mimosa* was its particular fruit type. We have shown here that he was correct and that the craspedium is a synapomorphy for the genus, even though it is homoplastic within it. Both synapomorphies of *Piptadenia* are also homoplastic. One, the presence of anther glands, is shared with the clade comprising *Parkia* and *Anadenanthera* and also with clade B (fig. C9). Anther glands in *Anadenanthera* and other members of the *Piptadenia* group have been considered developmentally homologous because of their extreme morphological similarity (Luckow and Grimes 1997; see also Barros and Teixeira 2016). We have shown, however, that the anther glands of *Piptadenia* probably do not share the same evolutionary history as those in other genera of the *Piptadenia* group. This character is also homoplastic within both *Anadenanthera*, with one of its two species lacking anther glands (Altschul 1964), and *Parkia*, for

which multiple losses of anther glands have been hypothesized (Luckow and Hopkins 1995). The other synapomorphy of *Piptadenia*, cohered (not fused; see table 1 for a precise differentiation between those states) petals, is shared with clade B. Interestingly, this character state is apomorphic with respect to corollas with fused parts.

Parapiptadenia and *Pseudopiptadenia*

Parapiptadenia and *Pseudopiptadenia* were recovered as sister groups, and, despite the low support obtained for this relationship (PP = 0.94; BS < 0.50), it is strengthened by the presence in both genera of compressed, winged seeds that lack a pleurogram, which contrasts with most genera of the *Piptadenia* group (table 2). *Parapiptadenia* is a small genus, with six species (Lima and Lima 1984; Luckow 2005), that was first described by Brenan (1963) in order to accommodate two species with typical legumes (dehiscing down both sutures) and compressed, winged seeds lacking endosperm, both formerly belonging to *Piptadenia* (Brenan 1955, 1963; Lima and Lima 1984). Later additions were made by Burkart (1969), Vaz and Lima (1980), Lima and Lima (1984), and Lewis (1993). All species of the genus are trees that occur in tropical and subtropical seasonally dry forests in South America. Although the clade containing *Parapiptadenia* species does not have its own apomorphy, the lack of endosperm in seeds and flowers with petals almost completely free are apomorphic for the *Pseudopiptadenia* clade and may be used to distinguish between those closely related genera (see table 2).

Pseudopiptadenia includes species that were previously treated as belonging to *Piptadenia* but have winged and plano-compressed seeds in follicular fruits (dehiscing along one suture; Brenan 1955; as *Monoschisma* Brenan). It also includes the former American species of *Newtonia* Baill., a genus now restricted to Africa (Lewis and Lima 1991), which has been shown to be distantly related to the *Piptadenia* group (Luckow et al. 2003; Luckow 2005). The 11 species currently assigned to *Pseudopiptadenia* are predominantly rain forest trees (rarely shrubs) that occur in Atlantic and Amazon rain forests, with only a few species occurring in seasonally dry forests in the Caatinga in northeast Brazil (e.g., *Ps. bahiana*).

Sampling of members of these two genera has been sparse in previous phylogenetic studies and included at most three species of *Parapiptadenia* and two species of *Pseudopiptadenia* (Luckow et al. 2003; Jobson and Luckow 2007; Simon et al. 2009). In these studies, both *Parapiptadenia* and *Pseudopiptadenia* grouped in a clade containing *Microlobius*, *Pityrocarpa*, and *Stryphnodendron*, but the lack of resolution in the phylogenies obtained precluded any conclusion about the affinity between these genera. Our results reinforce the previous segregation of *Parapiptadenia* and *Pseudopiptadenia* from *Piptadenia* based on fruit and seed morphology and also indicate that both genera, as currently circumscribed, represent monophyletic and morphologically well-defined lineages, with the exception of *Ps. brenanii* (see below).

Pityrocarpa and the True Identity of *Ps. brenanii*

The genus *Pityrocarpa*, which was first segregated from *Piptadenia* by Brenan (1955), is characterized by unarmed species

Table 2
Key morphological characters that differentiate selected genera/lineages of the *Piptadenia* group as recovered in the phylogeny displayed in figure 2

| Genus/lineage | Armature | Reddish granular trichomes | Fruit | Seed |
|--|-------------------------|----------------------------|--|--|
| <i>Microlobius</i> | Unarmed | Present | Follicle (dehiscing down one suture only) | Not winged, thick testa; endosperm and pleurogram present |
| <i>Mimosa</i> | Armed/unarmed | Absent | Craspedium | Not winged, thick testa; endosperm and pleurogram present |
| <i>Parapiptadenia</i> | Unarmed | Absent | Legume (dehiscing down both sutures) | Winged with a thin testa; endosperm present; pleurogram absent |
| <i>Piptadenia</i> | Armed (prickles) | Absent ^a | Legume (dehiscing down both sutures) | Not winged, thick testa; endosperm and pleurogram present |
| <i>Piptadenia viridiflora</i> | Armed (stipular spines) | Absent | Legume (dehiscing down both sutures) | Not winged, thick testa; endosperm and pleurogram present |
| <i>Pityrocarpa</i> (including <i>Pseudopiptadenia brenanii</i>) | Unarmed | Absent | Moniliform follicle (dehiscing down one suture only) | Not winged, thick testa; endosperm and pleurogram present ^b |
| <i>Pseudopiptadenia</i> | Unarmed | Absent | Follicle (dehiscing down one suture only) | Winged with a thin testa; endosperm and pleurogram absent |
| <i>Stryphnodendron</i> | Unarmed | Present | Indehiscent nuroid legume, follicle (dehiscing down one suture), legume (dehiscing down both sutures; only <i>S. duckeanum</i>) | Not winged, thick testa; endosperm and pleurogram present |

^a Present in *P. irwinii*.

^b *Pseudopiptadenia brenanii*, which grouped with *Pityrocarpa* in the phylogeny, has seed morphology similar to other species of *Pseudopiptadenia*.

with moniliform legumes covered in lepidote pubescence and with endospermous, wingless seeds having a white testa and a pleurogram (Jobson and Luckow 2007). The fact that multiple accessions of *Ps. brenanii*, a tree endemic to seasonally dry tropical forest in northeast Brazil, grouped within a strongly supported *Pityrocarpa* clade (clade E) provides evidence that *Ps. brenanii* should be transferred to *Pityrocarpa*, increasing the size of this genus to four species. Although many morphological features of *Ps. brenanii* suggest a relationship to *Pseudopiptadenia* (winged and compressed seeds lacking both endosperm and pleurogram), those are inferred here as homoplastic. On the other hand, the topology inferred in our phylogeny received morphological support from the presence of pendent inflorescences (not evaluated here) and fruits with constricted margins (although this is less pronounced in *Ps. brenanii*), the latter a synapomorphy for clade F (fig. 3). At the same time, the three species currently assigned to *Pityrocarpa* share the presence of white seeds, while *Ps. brenanii* has brown seeds. Apparently, compression of seeds is related to the appearance of wings and absence of pleurogram and/or endosperm, since the first character state is always present in taxa that have at least one of the others (e.g., *Anadenanthera*, *Piptadena paniculata*, *Piptadenia buchtienii*, *Ps. brenanii* and clade E; fig. 3). Also, winged seeds without a pleurogram and/or endosperm are not seen in genera of the *Piptadenia* group with noncompressed seeds (table 2; Gunn 1984; Luckow et al. 2003).

Our analyses support multiple origins of winged seeds in the *Piptadenia* group, a feature that is present in *Pseudopiptadenia* and *Parapiptadenia* but absent in all other genera within the *Piptadenia* group, except *Anadenanthera*. As a consequence, the circumscription of *Pityrocarpa* should be revised in order to accommodate the morphological features of *Ps. brenanii* that

are not present in other species of *Pityrocarpa*. Nevertheless, this genus remains ecologically coherent, with all species (including *Ps. brenanii*) restricted to seasonally dry forests in the Neotropics.

Unsurprisingly, a relationship between *Pseudopiptadenia* and *Pityrocarpa* was suggested by Bentham (1875), who considered in his section *Pityrocarpa* three taxa that are now included within *Pseudopiptadenia* (Brenan 1955; Lewis and Lima 1991). Of those, two were not sampled here (*Ps. inaequalis* and *Ps. leptostachya*), and since they also have constricted fruits, it remains to be verified whether they belong to *Pseudopiptadenia* or to *Pityrocarpa*. It is important to bear in mind, however, that constricted margins are not restricted to *Pityrocarpa* (e.g., *Ps. bahiana*; fig. 3).

Stryphnodendron Clade

A clade containing all samples of *Stryphnodendron* was recovered with low support (clade D; PP = 0.92, BS < 50). Despite the lack of support, the clade has as its putative morphological synapomorphy the presence of granular reddish trichomes, which confer a ferruginous aspect to the apex of young branches on *Stryphnodendron* species (fig. 1D). The presence of an abaxial tuft of trichomes on leaflets and nuroid legumes, typical features of most *Stryphnodendron* species, were not recovered here as synapomorphic for the clade. Reconstruction of the ancestral character state for both features is uncertain, and the trichome tuft could even be a synapomorphy for clade B (fig. C7), while the nuroid legume is apparently homoplastic between clades A and C (fig. C12). It is interesting that the lack of trichome tufts could support clade G, but polymorphism for this character in *Microlobius foetidus* prevents its recognition as

a synapomorphy. Although reconstruction of fruit-type ancestral states is dubious for clade C and uncertainty is also present within it (fig. C12), apparently at this node of the phylogeny there is a shift from fruits with dehiscence along both margins to follicular or completely indehiscent fruits, with a reversal to a true legume in *Stryphnodendron duckeanum*. Since branch support at the backbone of clade C is not high, it remains to be seen whether changes in the topology will shed light on the understanding of fruit evolution or whether this will remain an open question within the *Piptadenia* group.

Lewis and Elias (1981, p. 164) indicated in their key to genera within the *Piptadenia* group that *Stryphnodendron* is recognized by its alternate leaflets and an “involucel on peduncle completely covering young inflorescence.” Alternate leaflets, however, are restricted only to clade J and are not a synapomorphy for the whole genus (fig. 3). The involucel covering the young inflorescence was here interpreted as fused prophylla, which split at the apex with inflorescence elongation and may fall by detachment of the base (character 7; see table 1). Fused prophylla are not restricted to *Stryphnodendron*, but even though they occur in all species of the genus, it is not possible to know whether they are a synapomorphy of clade D or are homoplastic between clade H and the group including clades I and J (see fig. C9). Uncertainty here is related to the placement of *Microlobius*, which has free prophylla, as sister to clade H.

Some of the relationships within clade D are not clear, but three strongly supported and morphologically well-defined clades were found, with the monospecific genus *Microlobius* sister to clade H. Although it was not possible to infer the monophyly of *Stryphnodendron* in previous studies because of a lack of resolution, the three well-supported subclades found here were previously recovered as three independent lineages (Jobson and Luckow 2007). In addition, a study investigating pollen morphology and correlating it to leaf morphology and inflorescence branching patterns in *Stryphnodendron* (Guinet and Caccavari 1992) has also highlighted the differences between groups within the genus, which broadly coincide with the clades recovered here.

One of the three lineages, which appeared as sister to the rest of *Stryphnodendron*, contains a clade composed of seven species of the genus, sharing a sister-group relationship to *Microlobius* (clade G; fig. 2). This lineage has as its putative morphological synapomorphy large (at least 4 × 2-cm) leaflets (fig. 3). This clade may also be characterized by other morphological characters (not evaluated here), such as paucifoliate leaves with relatively few (1–4) pairs of pinnae. *Stryphnodendron* species within clade H also have branched inflorescences (paniculate or racemose spikes forming a compound thyrse, except in *S. coriaceum* and *S. fissuratum*). Coiled or cochleate fruits that may be deeply spiraled (fig. 1J) occur within this clade (fig. C13), although straight or slightly curved pods also occur within clade H (e.g., *S. ochchonianum* and *S. paniculatum*; Scalon 2007). Species in this group are predominantly rain forest trees (*S. moricolor*, *S. ochchonianum*, *S. paniculatum*, *S. polystachyum*, and *S. racemiferum*), but there are also species that occur in the Cerrado and occasionally in semideciduous forests in Brazil and Bolivia (*S. coriaceum* and *S. fissuratum*).

An unexpected result was the position of the monospecific genus *Microlobius*, nested within *Stryphnodendron* (clade G). *Microlobius foetidus*, which has previously been considered

as belonging to the genera *Goldmania* and *Piptadenia* (Sousa and Andrade 1992), shows some morphological affinities with *Stryphnodendron*, such as lack of aculei, flowers arranged in spikes, and curved pods (table 2). Except for the latter, these characters are plesiomorphic within the *Piptadenia* group as shown here (fig. 3). However, *Microlobius* shares with *Stryphnodendron* the synapomorphic presence of granular reddish trichomes. In *Microlobius*, granular trichomes are sparsely distributed along the leaves, whereas in *Stryphnodendron* they are densely concentrated on young leaves. The lack of abundant ferruginous indumentum on young leaves of *Microlobius* may be related to the origin of those organs from brachyblasts. Moreover, *Microlobius* has leaves with 1–4 pinnae bearing a single pair of opposite leaflets, lacks bark exudate, and is recognized in the field by its strong smell, known in Brazil (subspecies *paraguensis* (Benth.) M. Sousa & G. Andrade) as *pau-alho* (“garlic tree”), features that are not present in *Stryphnodendron* species. Another striking difference between these genera is their ecological preference, since *M. foetidus* occurs in dry forests in both North (subsp. *foetidus*) and South America (subsp. *paraguensis*), whereas *Stryphnodendron* grows predominantly in rain forests or mesic savannas. This relationship was strongly supported in the combined Bayesian analysis (but not in the ITS analysis; fig. C2) but received limited support from the morphological analysis. Therefore, any taxonomic rearrangement regarding *Microlobius* would be premature, since it could still be maintained as a segregate genus that is sister to *Stryphnodendron*, a possibility that is not completely contradicted by our data. Given the topological uncertainties regarding the position of *Microlobius* with respect to *Stryphnodendron*, further investigations are needed in order to confirm the results presented here.

Another strongly supported lineage within *Stryphnodendron* included multiple samples of *S. duckeanum*, a rain forest species restricted to southwest Amazonia. This species was considered morphologically dissimilar to other species of *Stryphnodendron* because of the presence of a large and concave petiolar nectary and stipitate pods with glabrous, papery valves that separate at maturity (fig. 1E), features that would suggest an affinity with some species of *Piptadenia* (Scalon 2007). However, our results suggest that *S. duckeanum*, although being a somewhat morphologically discrepant lineage, should be retained within *Stryphnodendron*. Leaves of *S. duckeanum* are microphyllidious, with opposite leaflets (fig. 1), and would therefore be intermediate between the large opposed leaflets of clade H and the small alternate leaflets of clade J.

A third clade within *Stryphnodendron* (clade J) received high support in all analyses and encompasses almost three-quarters of the species in the genus. Alternate leaflets, though not a synapomorphy for the whole genus, are inferred as a putative synapomorphy for this clade (fig. 3). Lack of resolution within clade J obscures inference about the origin of the geoxylic habit, but this is clearly a derived condition within *Stryphnodendron* (figs. 3, C3). In the context of *Stryphnodendron*, this clade may also be characterized by the presence of microphyllidious leaves with 3–18 pairs of pinnae and relatively small (mostly less than 3.5 × 2.5-cm) and numerous (5–32 pairs per pinnae) leaflets, as well as unbranched inflorescences (axillary spikes forming a simple thyrse) and straight, not curved, pods (Scalon 2007).

The most derived and largest lineage within *Stryphnodendron* has very short internal branches (fig. 2), which suggests rapid evolution of a morphologically diverse group that includes rain forest trees (e.g., *S. foreroi*, *S. microstachyum*, *S. polyphyllum*, *S. porcatum*, *S. pulcherrimum*, and *S. roseiflorum*) and thick-barked savanna trees (e.g., *S. adstringens* and *S. rotundifolium*) as well as dwarf shrubs with enlarged underground woody organs (xylopodia; *S. cristalinae*, *S. gracile*, *S. heringeri*, and *S. pumilum*; fig. 1K–1M). This clade comprises most of the diversity of the genus, representing a radiation in both rain forest and fire-prone savanna environments. The evolution of a number of fire-tolerant species in the genus, including some xylopodium-bearing dwarf life forms, from a predominantly rain forest lineage (species in early-diverging *Stryphnodendron* lineages are mostly from Amazonia) is in line with the growing evidence that Cerrado lineages are of recent origin (Simon and Pennington 2012). Therefore, *Stryphnodendron* would represent another example of a plant lineage that has undergone an ecological transition from the rain forest into the savanna, followed by a reduction in life form from tree to geoxylic subshrub or acquisition of thick bark in fire-tolerant savanna trees. Examples of rapid diversification and associated low nucleotide variation in highly diverse Neotropical groups, as inferred here for *Stryphnodendron*, have been documented in other plant lineages in both Amazonian rain forest (Erkens et al. 2007; Torke and Schaal 2008) and the Cerrado (Simon et al. 2009).

Conclusion

Many of the results shown here represent new relationships between members of the *Piptadenia* group, whereas other findings confirm previously hypothesized relationships and generic circumscriptions based on morphological and plastid DNA sequences. Despite some improvement in the phylogenetic hypothesis, which was supported by a nuclear data set for the first time in the study group, some uncertainties remain. Tackling some persistent issues related to lack of resolution on some parts of the phylogeny of the *Piptadenia* group and also within particularly problematic clades (e.g., *Stryphnodendron* clade J)

will depend on the use of much larger DNA sequence data sets, such as those generated in next-generation sequencing approaches (e.g., Stephens et al. 2015).

Our findings highlight that densely sampled phylogenies are needed to rigorously test the monophyly of genera, since poor taxon sampling can lead to misleading conclusions about taxonomic circumscriptions. New taxonomic decisions should search for generic circumscriptions based on monophyly coupled with coherent morphological delimitations using characters evaluated in a cladistic context. This way, misleading circumscriptions based on homoplastic characters or relying on features subjectively chosen, a common practice in the classification of many plant groups, may be avoided. In line with that, new rearrangements at the generic level of the *Piptadenia* group and a reevaluation of the circumscription of the group itself are necessary to accommodate the results obtained in this study and will be proposed in forthcoming studies.

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Appendix A

Taxa Sampled for Molecular Data

For each taxon, we show voucher information, herbarium, country, and GenBank accession numbers for *matK/trnK*, *trnD-T*, *trnL-F*, and ITS. Herbarium acronyms follow Thiers (2015). Unpublished names are presented in quotation marks.

Anadenanthera colubrina (Vell.) Brenan, Hughes 2308 (FHO), Bolivia, KT364207, FJ981975, KT363985, —; Pennington 845 (E), AF521813, —, AF278481, JQ910930. *Inga edulis* Mart., —, —, AF523078, JQ417383, JX870880, JX870764. *Microlobius foetidus* (Jacq.) M. Sousa & G. Andrade subsp. *foetidus*, Hughes 2150 (FHO), Mexico, KT364172, FJ981976, KT363986, KT364047; Macqueen 432 (FHO), Mexico, AF523095, —, AF278506, AF458783. *Mimosa boliviana* Benth., Hughes 2426 (FHO), Bolivia, KT364209, FJ982009, KT363987, KT364049. *Mimosa candollei* R. Grether, Hughes 2324 (FHO), Bolivia, KT364211, FJ982020, KT363988, KT364050. *Mimosa ceratonia* L. var. *ceratonia*, Grimes 3223 (NY), Puerto Rico, KT364208, JF694259, KT363989, KT364051. *Mimosa colombiana* Britton & Killip, Davidse 15198 (NY)/Torres 21343 (K), Colombia, DQ790603, FJ982027, DQ784646, KT386295. *Mimosa gracilis* Benth. var. *invisiformis* Barneby, Simon 762 (FHO), Brazil, KT364214, FJ982073, KT363990, KT364053. *Mimosa minarum* Barneby, Nascimento 495 (HUEFS), Brazil, KT364215, FJ982120, KT363991, KT364057. *Mimosa myriadenia* (Benth.) Benth., Acevedo-Rdgz 7483 (K)/Balslev 10611 (NY), Ecuador, DQ790605, FJ982127, DQ784648, KT364058. *Mimosa palmeri* Rose, Simon 823 (MEXU), Mexico, KT364212, FJ982142, KT363993, KT364059. *Mimosa pigra* L., Hughes 2414 (FHO), Bolivia, KT364213, FJ982148, KT363994, KT364060. *Mimosa ursina* Mart., Simon 704 (FHO), Brazil, KT364210, FJ982217, KT363995, KT364061. *Neptunia monosperma* F. Muell. ex

Benth., —, —, EU812005, —, AF278495, AF458789. *Parapiptadenia excelsa* (Griseb.) Burkart, Hughes 2425 (FHO), Bolivia, KT364160, FJ982235, KT363996, KT364062. *Parapiptadenia pterosperma* (Benth.) Brenan, Tameirão-Neto 2458 (NY), Brazil, DQ790608, —, DQ784651, —. *Parapiptadenia rigida* (Benth.) Brenan, Silva 1890 (NY), Brazil, DQ790609, —, DQ784652, —. *Parapiptadenia zehntneri* (Harms) M.P. Lima & H.C. Lima, Pereira-Silva 3102 (CEN), Brazil, KT364161, KT364108, KT363997, KT364063. *Parkia timoriana* (DC.) Merr., —, —, AF523091, —, AF195682/AF195701, AF360729. *Piptadenia adiantoides* (Spreng.) J.F. Macbr., Simon 726 (FHO), Brazil, KT364158, FJ982236, KT363998, KT364064. *Piptadenia buchtienii* Barneby, Hughes 2427 (FHO), Bolivia, DQ790614, FJ982237, KT386299, —. *Piptadenia flava* (Spreng. ex DC.) Benth., Salas 2415 (NY), Mexico, DQ790617, —, DQ784660, —. *Piptadenia floribunda* Kleinhoonte, Mori 20836 (NY), French Guiana, DQ790619, —, DQ784662, —. *Piptadenia gonoacantha* (Mart.) J.F. Macbr., Nee 36338 (NY)/Simon 735 (FHO), Bolivia/Brazil, DQ790620, FJ982238, KT363999, KT364065. *Piptadenia irwinii* G.P. Lewis, Queiroz 3500 (NY), Brazil, DQ790621, —, DQ784664, —. *Piptadenia macradenia* Benth., Nee 48772 (NY), Bolivia, DQ790623, —, DQ784666, —. *Piptadenia paniculata* Benth., Thomas 11101 (NY), Brazil, DQ790626, —, DQ784669, —. *Piptadenia peruviana* (J.F. Macbr.) Barneby, Nee 38898 (NY), Bolivia, DQ790627, —, DQ784670, —. *Piptadenia pteroclada* Benth., Prance 24672 (NY), Peru, DQ790629, —, DQ784672, —. *Piptadenia robusta* Pittier, Arroyo 850 (NY), Bolivia, DQ790632, —, DQ784674, —. *Piptadenia* sp., Scalon 462 (ESA), Brazil, KT364196, KT364109, KT364000, —. *Piptadenia stipulacea* (Benth.) Ducke, Harley 18962 (NY)/Simon 702 (FHO), Brazil, DQ790635, FJ982239, DQ784675, KT386296. *Piptadenia viridiflora* (Kunth) Benth., Hughes 1681 (FHO), Mexico, KT364173, FJ982241, KT364001, KT364066. *Pityrocarpa leucoxydon* (Barneby & J.W. Grimes) Luckow & R.W. Jobson, Fernandez 2909 (NY), Venezuela, DQ790622, —, DQ784665, —. *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson, Way SWM2449 (K), Brazil, KT364162, FJ982242, KT364002, KT364067. *Pityrocarpa obliqua* (Pers.) Brenan, Macqueen 439 (K), Mexico, KT364206, FJ982243, KT364003, KT364068. *Pseudopiptadenia bahiana* G.P. Lewis & M.P. Lima, Coradin 8580 (CEN), Brazil, —, KT364110, —, —. *Pseudopiptadenia brenanii* G.P. Lewis & M.P. Lima, Borges 680 (SPF), Brazil, KT364163, KT364111, KT364004, KT364069; Sevilha 4287 (CEN), Brazil, KT364216, KT364112, —, —. *Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima, Queiroz 3366 (NY), Brazil, DQ790636, —, DQ784676, —; Queiroz 15507 (HUEFS), Brazil, KT364155, KT364113, KT364005, —. *Pseudopiptadenia psilostachya* (DC.) G.P. Lewis & M.P. Lima, Simon 1245 (CEN), Brazil, KT364170, KT364114, KT364006, KT364070. *Pseudopiptadenia suaveolens* (Miq.) J.W. Grimes,¹ Mori 24790 (NY), French Guiana, DQ790637, —, DQ784677, —. *Senegalia nigrescens* (Oliv.) P.J.H. Hurter, —, —, GQ872237, —, GQ872282, JQ265858. *Stryphnodendron adstringens* (Mart.) Coville, Scalon 260 (ESA), Brazil, KT364188, KT364118, KT364010, KT364074; Scalon 263 (ESA), Brazil, KT364165, KT364117, KT364009, KT364073; Scalon 407 (ESA), Brazil, KT364197, KT364115, KT364007, KT364071; Souza 29702 (ESA), Brazil, KT364198, KT364116, KT364008, KT364072. *Stryphnodendron coriaceum* Benth., Brito 343 (NY), Brazil, DQ790639, —, DQ784679, —; Scalon 716 (ESA), Brazil, KT364199, KT364119, KT364011, —; Scalon 718 (ESA), Brazil, KT364200, KT364120, KT364012, KT364075. *Stryphnodendron cristalinae* Heringer ex Rizzini & A. Mattos, Scalon 706 (ESA), Brazil, KT364189, KT364121, KT364013, —. *Stryphnodendron duckeanum* Occhioni, Dionizia 118 (NY), Brazil, DQ790615, —, DQ784658, —; Simon 1343 (CEN), Brazil, KT364166, KT364122, KT364014, KT364076; Simon 1606 (CEN), Brazil, —, KT364123, KT364015, —. *Stryphnodendron fissuratum* E.M.O. Martins, Ivanauskas s.n. (ESA), Brazil, KT364175, KT364124, KT364016, KT364077; Killeen 1158 (NY), Bolivia, DQ790640, —, DQ784680, —. *Stryphnodendron foreroi* E.M.O. Martins, Assis 1143 (SPF), Brazil, KT364201, KT364126, KT364018, KT364079; Simon 2054 (CEN), Brazil, KT364164, KT364125, KT364017, KT364078. *Stryphnodendron gracile* Rizzini & Heringer, Scalon 458 (ESA), Brazil, KT364177, KT364127, KT364019, KT364080. *Stryphnodendron heringeri* Occhioni f., Scalon 710 (ESA), Brazil, KT364190, KT364129, KT364021, —; Simon 1110 (CEN), Brazil, KT364159, KT364128, KT364020. *Stryphnodendron microstachyum* Poepp., Hernandez BioBot06450, Costa Rica, JQ587856, —, —, —. *Stryphnodendron moricolor* Barneby & J.W. Grimes, Baraloto s.n. (CAY), French Guiana, JQ626465, —, —, —. *Stryphnodendron obovatum* Benth., Scalon 701 (ESA), Brazil, KT364183, KT364131, KT364023, KT364082; Scalon 712 (ESA), Brazil, KT364182, KT364130, KT364022, KT364081. *Stryphnodendron* cf. *occhionianum* E.M.O. Martins, Simon 1597 (CEN), Brazil, KT364157, KT364132, KT364024, KT364083. *Stryphnodendron paniculatum* Poepp., Scalon 726 (ESA), Brazil, KT364174, KT364134, KT364026, KT364085; Simon 1058 (CEN), Brazil, KT364156, KT364133, KT364025, KT364084. *Stryphnodendron polyphyllum* Mart., Forzza 3766 (RB), Brazil, KT364202, KT364135, KT364027, —; Mello-Silva 2659 (SPF), Brazil, KT364184, KT364136, KT364028, KT364086; Queiroz 15673 (HUEFS), Brazil, KT364204, KT364149, KT364041, —. *Stryphnodendron polystachyum* (Miq.) Kleinhoonte, Sabatier 3758 (NY), French Guiana, DQ790641, —, DQ784681, —. *Stryphnodendron porcatum* D.A. Neill & Occhioni f., Neill 14001 (MO), Ecuador, AY944564, —, DQ784682, —. *Stryphnodendron pulcherrimum* (Willd.) Hochr., Queiroz 15482 (HUEFS), Brazil, KT364186, KT364150, KT364042, —; Queiroz 15487 (HUEFS), Brazil, KT364205, KT364151, KT364043, —; Scalon 723 (ESA), Brazil, KT364191, KT364139, KT364031, KT364088; Scalon 725 (ESA), Brazil, KT364192, KT364140, KT364032, KT364089; Simon 980 (CEN), Brazil, KT364167, KT364137, KT364029, KT364087; Souza 30717 (ESA), Brazil, KT364203, KT364138, KT364030, —. *Stryphnodendron pumilum* Glaz., Scalon 709 (ESA), Brazil, KT364178, KT364141, KT364033, —. *Stryphnodendron racemiferum* (Ducke) W.A. Rodrigues, Scalon 727 (ESA), Brazil, KT364176, KT364142, KT364034, —. *Stryphnodendron roseiflorum* (Ducke) Ducke, Romão 987 (ESA), Brazil, KT364179, KT364144, KT364036, KT364091; Scalon 728 (ESA), Brazil, KT364193, KT364143, KT364035, KT364090. *Stryphnodendron rotundifolium* Mart., Queiroz 15523 (HUEFS), Brazil, KT364180, KT364145, KT364037, —; Scalon 250

¹ Cited as *Pseudopiptadenia psilostachya* in Jobson and Luckow (2007) but appears as *Ps. suaveolens* in GenBank.

(ESA), Brazil, KT364168, KT364148, KT364040, KT364095; Souza 30040 (ESA), Brazil, KT386297, KT386298, KT386300, KT364096. *Stryphnodendron rotundifolium* Mart. “villosum,” Scalon 704 (ESA), Brazil, KT364185, KT364146, KT364038, KT364092; Scalon 715 (ESA), Brazil, KT364194, KT364147, KT364039, KT364094. *Stryphnodendron* “velutinum,” Scalon 719 (ESA), Brazil, KT364187, KT364153, KT364045, KT364101; Scalon 720 (ESA), Brazil, KT364181, KT364154, KT364046, KT364102. *Vachellia farnesiana* (L.) Wight & Arn., —, AF523115, —, AY574119, AF360728.

Appendix B

Specimens Sampled for Morphological Characters

Species shown in figure 3 not represented here had states scored on the basis of the literature. Herbarium acronyms follow Thiers (2015).

Anadenanthera colubrina: Calatayud 1970 (NY), Killeen 6654 (NY), Lewis 40660 (NY), Arroyo 3245 (NY), Beck St.G. 29510 (NY), Jardim 451 (NY); *Inga edulis*: Thomas 12778 (NY), Carvalho 4348 (NY), Miranda 385 (NY), Jardim 1005 (NY), Vargas 5010 (NY), Daly 1652 (NY); *Microlobius foetidus* subsp. *foetidus*: Hughes 1219 (NY), Hughes 1719 (NY), Gereau 1923 (NY), Leavenworth 1751 (NY), Hinton 3811 (NY); *Mimosa boliviana*: Beck 4950 (NY), Beck 12086 (NY), Solomon 11913 (NY), Dorr 6897 (NY); *Mimosa candollei*: Ekman 1627 (NY), Rimachi 3035 (NY), Krapovickas 35034 (NY), Krapovickas 45821 (NY), Baldwin Jr. 4520 (NY), Simon 1412 (NY); *Mimosa colombiana*: Hermann 11111 (NY), Marulanda 1713 (NY), Wurdack 40906 (NY), Davidse 13931 (NY), Davidse 15198 (NY); *Mimosa gracilis* var. *invisiformis*: Irwin 33129 (NY), Anderson 6684 (NY), Anderson 6734 (NY), Anderson 11492 (NY); *Mimosa minarum*: Hatschbach 54985 (NY), Hatschbach 64179 (NY), Hatschbach 64357 (NY), Irwin 23022 (NY); *Mimosa myriadenia*: Callejas 4 406 (NY), Blanco 319 (NY), Curran 351 (NY), Johnson 4738 (NY); *Mimosa palmeri*: Montes 442 (NY), Gentry 4779 (NY), Van Devender 97–1000 (NY), Soto Núñez 9147 (NY); *Mimosa pigra*: Schessl 100/1–3 (NY), Hatschbach 37456 (NY), Hatschbach 56095 (NY), Hatschbach 62394 (NY), Silva 4576 (NY); *Mimosa ursina*: Pinto 94/86 (NY), Lewis 1921 (NY), Hatschbach 56573 (NY), Hatschbach 60307 (NY), Hatschbach 64096 (NY); *Parapiptadenia excelsa*: Killeen 4151 (NY), Michel 465 (NY), Vargas 4569 (NY), Vargas 5419 (NY), Nee 50286 (NY), Nee 50651 (NY); *Parapiptadenia pterosperma*: Tameirão-Neto 1807 (NY), Lima 2796 (NY), Martinelli 11678 (NY), Kuhlmann 6578 (NY), Mori 13048 (NY); *Parapiptadenia rigida*: Hatschbach 21534 (NY), Hatschbach 48543 (NY), Smith 13845 (NY), Hahn 1837 (NY), Hoehne (NY 00459086), Pereira 5917 (NY); *Parapiptadenia zebntneri*: Harley 16198 (NY), Silva 3102 (NY), Gomes 80 (NY), Gomes 155 (NY), Orlandi 453 (NY); *Parkia timoriana*: Merrill 604 (NY), Merrill 689 (NY), Elmer 6888 (NY), Barnes 89 (NY); *Piptadenia adiantoides*: Irwin 27772 (NY), Irwin 27971 (NY), Trinta 826 (NY), Hatschbach 46303 (NY), Lombardi 920 (NY); *Piptadenia buchtienii*: Thomas 5533 (NY), Uslar 226 (NY), Nee 49473 (NY), Beck 12053 (NY); *Piptadenia flava*: Lewis 2334 (NY), Kirkbride 2638 (NY), Hitchcock 20143 (NY); *Piptadenia floribunda*: Rabelo 3097 (NY), Pruski 3308 (NY), Ek 1782 (NY), Mori 20836 (NY); *Piptadenia gonoacantha*: Lage (NY 00459197), Sucre 3397 (NY), Handro 30843 (NY); *Piptadenia irwinii*: Amorim 986 (NY), Thomas 10213 (NY); *Piptadenia macradenia*: Heringer 5148 (NY), Irwin 21743 (NY); *Piptadenia paniculata*: Kuhlmann 2745 (NY), Jardim 1221 (NY), Thomas 11101 (NY), Lima 2992 (NY), Lima 3015 (NY), Lima 3020 (NY); *Piptadenia peruviana*: Saldias 1460a (NY), Beck 13271 (NY), Nee 38898 (NY), Nee 48865 (NY); *Piptadenia robusta*: Arroyo 838 (NY), Nee 38618 (NY), Nee 38620 (NY), Nee 48636 (NY), Nee 55004 (NY), Nee 55017 (NY); *Piptadenia stipulacea*: Queiroz 3115 (NY), Queiroz 3883 (NY); *Piptadenia viridiflora*: Nunes 646 (SPF), Salino 3306 (SPF), Tameirão-Neto 914 (SPF), Moraes 1158 (NY); *Pityrocarpa leucoxylo*: Marcano-Berti 724 (NY), Gillespie 1688 (NY), Liesner 11128 (NY), Liesner 11200 (NY), Jansen-Jacobs 4005 (NY), Aymard 8841 (NY), Aymard 7600 (NY), Huber 2909 (NY); *Pityrocarpa moniliformis*: Carvalho 3896 (NY), Fonseca 397 (NY), Harley 16147 (NY), Nunes 597 (NY), Tamayo 3552 (NY); *Pseudopiptadenia bahiana*: Amorim 1009 (NY), Pinheiro 379 (NY), Pereira 2001 (NY), Hatschbach 68438 (NY); *Pseudopiptadenia brenanii*: Silva 1455 (NY), Pirani H51382 (NY), Ganey 2555 (NY), Irwin 31172 (NY), Pereira 9652 (NY), Lewis 1899 (NY), Lewis CFCR 7101 (NY); *Pseudopiptadenia contorta*: Heringer 16019 (NY), Heringer 2856 (NY), Heringer 3489 (NY), dos Santos 3478 (NY); *Pseudopiptadenia psilostachya*: Irwin 54449 (NY), Kuhlmann 147 (NY), Steward 55 (NY), Ducke 957 (NY), R.Oldeman 2435 (NY), Marinho 330 (NY); *Pseudopiptadenia suaveolens*: Boom 5366 (NY), Silva 1160 (NY), Silva 1322 (NY), Villiers 2229 (NY); *Senegalia nigrescens*: Balaka 1042 (NY), Tinley 1056 (NY), Plowe 34777 (NY), Brass 17951 (NY), Chase 29365 (NY); *Stryphnodendron adstringens*: Eiten 7793 (NY), Machado (NY 00934640), Fonseca 377 (NY), Hatschbach 27984 (NY), Irwin 5118 (NY), FEPP 205 (NY), Anderson 8638 (NY), Ganey 1237 (NY); *Stryphnodendron coriaceum*: Pires 51915 (NY), Silva 57858 (NY), Pereira 2988 (NY), Irwin 14431 (NY), Britto 343 (NY); *Stryphnodendron cristalinae*: Esteves CFCR 15489 (NY), Castro (NY 00934844), Irwin 9770 (NY), Irwin 20430 (NY), Anderson 8086 (NY); *Stryphnodendron duckeanum*: Teixeira 587 (NY), Teixeira 1115 (NY), Cid 10245 (NY), Thomas 5039 (NY), Simon 1457 (NY), Dionizia 118 (NY); *Stryphnodendron fissuratum*: Harley 10273 (NY), Pennington 913 (NY), Souza 1631 (NY), Killeen 1158 (NY), Killeen 1909 (NY); *Stryphnodendron foreroi*: Schunke 5462 (NY), Prance 3465 (NY), Prance 5623 (NY), Prance 6004 (NY), Prance 6243 (NY); *Stryphnodendron gracile*: Hatschbach 35285 (SPF), Salimena-Pires CFSC 11420 (SPF), Pirani 12218 (SPF), Borges 193 (SPF); *Stryphnodendron beringeri*: Anderson 7682 (NY), Heringer 2636 (NY), Hatschbach 60218 (NY); *Stryphnodendron microstachyum*: Moraga 888 (NY), Salas 195 (NY); *Stryphnodendron moricolor*: Mori 15236 (NY); *Stryphnodendron obovatum*: Dubs 498 (NY), Eiten 9621 (NY), Hatschbach 33180 (NY), Hatschbach 65532 (NY), Maguire 56258 (NY), Krapovickas 32876 (NY), Vargas 3458 (NY); *Stryphnodendron ochionianum*: Oliveira 4040 (NY), Mori 16130

(NY), Silva 2567 (NY); *Stryphnodendron paniculatum*: Krukoff 6441 (NY), Krukoff 8538 (NY); *Stryphnodendron polyphyllum*: Duarte 7973 (NY), Mello-Silva 2659 (NY), Davide 11444 (NY), Irwin 22306 (NY), Irwin 30292 (NY); *Stryphnodendron polystachyum*: Irwin 48381 (NY), Irwin 55179 (NY), Irwin 48381 (NY), Blanco 285 (NY), Blanco 287 (NY), Sabatier 3758 (NY), Emden (NY 01476792), Silva 3126 (NY); *Stryphnodendron porcatum*: Palacios 8019 (NY), Palacios 8908 (NY), Dorr 5821 (NY); *Stryphnodendron pulcherrimum*: Mori 11315 (NY), Eupunino 332 (NY), Pirani 2662 (NY), Nee 43030 (NY), Ferreira 6503 (NY), Ferraz 368 (NY); *Stryphnodendron racemiferum*: Santos 135 (NY), Costa INPA/WWF 1202.3570 (NY), Rodrigues (NY 01204054), Pacheco 77 (NY), Oliveira 74 (NY), Oliveira 226 (NY); *Stryphnodendron rotundifolium*: Fonseca 512 (NY), Walter 2913 (NY), Pereira 9499 (NY), Violatti 104 (NY); *Vachellia farnesiana*: Hill 27179 (NY), Irwin 15870 (NY), Carvalho 3857 (NY), Pires 58153 (NY), Sarmento 758 (NY).

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