

Phylogeny of *Calliandra* (Leguminosae: Mimosoideae) based on nuclear and plastid molecular markers

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Abstract We reconstructed phylogenetic relationships in Leguminosae subfam. Mimosoideae tribe Ingeae using 135 sequences from the nuclear (ITS) and 119 from the plastid (*trnL-F*) genome, representing 23 of the 36 currently recognized genera in the tribe with newly generated sequences of *Blanchetiodendron*, *Guinetia*, *Macrosamanea*, *Thailentadopsis* and *Viguieranthus* and an extensive sampling of *Calliandra*. Only two of the five Neotropical generic alliances of Barneby & Grimes (1996) were supported as monophyletic. *Calliandra* is resolved as monophyletic with the inclusion of *Guinetia*. The five previously proposed sections within *Calliandra* were not supported by our study. Nevertheless, based on these results, a new infrageneric classification is proposed for *Calliandra*, and the African species of the genus are assigned to a new genus, *Afrocalliandra*. Three new sections are proposed for *Calliandra*: (1) sect. *Tsugoideae* based on *C.* ser. *Tsugoideae*, with four species from northwestern South America; (2) sect. *Septentrionales*, with six species distributed in dry areas from the United States to Mexico and (3) sect. *Monticola*, which consists of species restricted to the Espinhaço range of Brazil; these latter species form a clade with low levels of sequence variation, a potential indicator of the recent diversification of this group.

Keywords Ingeae; phylogenetic analyses and dating; pollen morphology; taxonomy

Supplementary Material The Electronic Supplement (Table S1; Fig. S1) is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

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■ INTRODUCTION

Larger genera of Leguminosae subfam. Mimosoideae have a long history of taxonomic complexity and nomenclatural instability. The attention devoted to unravel the non-monophyly of *Acacia* Mill. s.l. (e.g., Miller & Bayer, 2001, 2003; Brown & al., 2008; Murphy & al., 2010; Miller & Seigler, 2012) is such an example. Nevertheless, recent studies of the phylogeny of particular groups demonstrated that several genera, as traditionally delimited, are not monophyletic and/or require significant taxonomic adjustments, for example: *Piptadenia* Benth. (Jobson & Luckow, 2007), *Prosopis* L. (Burghardt & Espert, 2007; Catalano & al., 2008), *Mimosa* L. (Bessega & al., 2008; Simon & al., 2011), *Albizia* Durazz. (Brown & al., 2008), and *Paraserianthes* I.C. Nielsen (Brown & al., 2011).

The taxonomic history of *Calliandra* Benth. (tribe Ingeae) mirrors that of other large mimosoid genera such as *Mimosa* and *Acacia*. The genus was established by Bentham (1840) based on the combination of a monadelphous and polystemonous androecium and a fruit with thick margins that dehisces elastically from the apex and is usually held erect. Eighteen New World species were included in *Calliandra* in Bentham's treatment. Later, Bentham (1844) presented a more detailed account of the genus, recognizing 60 species in five series (*C.* ser.

Macrophyllae Benth., ser. *Laetevirentes* Benth., ser. *Pedunculatae* Benth., ser. *Nitidae* Benth., ser. *Racemosae* Benth.), based on characters of the leaves and inflorescences. The geographic range of the genus was expanded to the Old World by Bentham (1875) with the inclusion of four Asian species (*C. cynometroides* Beddome, *C. geminata* Benth., *C. griffithii* Benth., *C. umbrosa* Benth.) because of similar fruit morphology. New species were later proposed from Madagascar (*C. amblyphylla* Harms; Harms, 1921) and continental Africa (*C. gilbertii* Thulin & Asfaw, *C. redacta* (J.H. Ross) Thulin & Asfaw; Thulin & al., 1981).

This increase in size of the genus was somewhat counteracted by the work of Hernández (1986) who segregated the species of *C.* ser. *Laetevirentes* and two species of ser. *Macrophyllae* (*C. amazonica* Benth., *C. aculeata* Spruce ex Benth.) to the new genus *Zapoteca* H.M. Hern. Barneby (1998) published a monographic account of *Calliandra*, described 36 new taxa and recognized a total of 133 species. *Calliandra* was kept as distinct from *Zapoteca* and restricted to the New World. As a consequence, 18 Old World species were excluded from *Calliandra* but not ascribed to any other genus by Barneby (1998). Subsequently, nine species endemic to Madagascar were included in the new genus *Viguieranthus* Villiers (Villiers, 2002); *C. geminata* Benth., from India, was considered as a

synonym of *Thailentadopsis nitida* (Vahl) G.P. Lewis & Schrire (Lewis & Schrire, 2003). Six species formerly described as *Calliandra* remained without a definite taxonomic position. To accommodate these different concepts of *Calliandra*, we here refer to *Calliandra* s.l. as representing the widest historical circumscription of the genus (i.e., including *Zapoteca*, *Viguieranthus* and *Thailentadopsis* Kostermans) and *Calliandra* s.str. to represent the delimitation proposed by Barneby (1998).

Hernández (1986) highlighted the importance of polyad structure in the taxonomy of *Calliandra* and allied genera. He segregated *Zapoteca* because it has acalymmate polyads (i.e., the constituent pollen grains do not have a common exine). In contrast, the polyads of *Calliandra* are calymmate, having a common exine to all eight pollen grains and a viscous appendix in the basal cell that adheres the polyad to a stigmatic surface during pollination (Greissl, 2006). Besides this polyad structure, *Calliandra* s.str. has other morphological features atypical in tribe Ingeae; for example, the basic chromosome number is 8 or 11 (vs. 13 in the remaining Ingeae; Hernández, 1986), calyx lobes with imbricate aestivation and unidirectional initiation of the sepals (vs. valvate aestivation and helicoid initiation; Prenner, 2004; Prenner & Teppner, 2005) and stamens with helicoid initiation (vs. simultaneous in other Mimosoideae; Prenner, 2004; Prenner & Teppner, 2005).

The most recent classification of *Calliandra* was proposed by Barneby (1998) who recognized five sections and fourteen series and put strong emphasis on inflorescence architecture in defining sections: a terminal pseudoraceme of heads or umbels in *C.* sect. *Calliandra* (Fig. 1B, F–L) and sect. *Microcallis* Barneby (further differentiated by dimension of the perianth—Fig. 1N); isolated heads or umbels arising from lateral specialized short branches in *C.* sect. *Androcallis* Barneby (Fig. 1A, C–E, M, O); an isolated terminal umbel in *C.* sect. *Acroscias* Barneby; and lateral inflorescences associated with stipular spicules in sect. *Acistegia* Barneby.

Phylogenetic relationships of *Calliandra* in tribe Ingeae have not yet been well established. In some phylogenetic studies based on morphological data (Grimes, 1995; Barneby & Grimes, 1996) and on the plastid region *trnL-F* (Luckow & al., 2000), *Zapoteca* appeared as sister to *Calliandra*. A wider analysis of Mimosoideae, based on *trnL-F*, *trnK* introns, and *matK*, including five species of *Calliandra*, found *Cedrelinga* Ducke as sister of *Calliandra*, but with low support (Luckow & al., 2003). In more recent phylogenetic studies (Brown & al., 2008) based on the nuclear ITS and ETS regions, *Calliandra* appeared in an unresolved position (in the ITS and combined ITS+ETS data) or as sister group to *Zapoteca* (in the ETS analysis). Lewis & Rico-Arce (2005) included *Calliandra* in the “Inga Alliance” of Barneby & Grimes (1996) together with *Archidendron* F. Muell., *Cedrelinga*, *Cojoba* Britton & Rose, *Guinetia* L. Rico & M. Sousa, *Macrosamanea* Britton & Rose, *Marmaroxylon* Killip, *Inga* Mill., *Viguieranthus*, *Zapoteca* and *Zygia* P. Brown. *Viguieranthus*, *Guinetia* and *Thailentadopsis* have not been included in any published phylogenetic study of the group to date.

As currently circumscribed by Barneby (1998), *Calliandra* occurs mostly in seasonally dry tropical forests (SDTFs),

savannas and campos rupestres (open rocky fields) and less commonly in wet forests and subtropical grasslands, known as Pampas in southern South America. The region of the Chapada Diamantina in the Brazilian State of Bahia is the main center of diversity of the genus, with a total of 46 species of which 36 are restricted to this region. The other major centers of diversity are in North America (southern United States and Mexico to Central America) with 35 species, and northwestern South America (Colombia, Venezuela) with 29 species (Barneby, 1998; Souza & Queiroz, 2004; Hernández, 2008; Souza, 2010). All of these centers of diversity occur in areas with strong climatic seasonality.

In this paper, we present a phylogenetic study of *Calliandra* based on the nuclear ribosomal ITS region, the plastid *trnL* intron and the *trnL-trnF* spacer. We also used a wide sampling from tribe Ingeae in order to (1) test the monophyly of *Calliandra* and its relationship with other ingoid genera, especially those formerly included in *Calliandra*; (2) test the monophyly of the sections and series proposed by Barneby (1998); (3) investigate the evolution of morphological characters within the genus and their diagnostic importance within a proposed new classification system; and (4) investigate the biogeographical history of the genus.

■ MATERIALS AND METHODS

Taxon and DNA region sampling. — Leaf tissues were dehydrated in silica-gel from field-collected material in five Brazilian states and in the state of Guerrero in Mexico. Voucher specimens are housed in the herbaria of Feira de Santana State University (HUEFS) and the Universidad Nacional Autónoma de México (MEXU). Additional samples were taken, with permission, from herbarium sheets at BM, BR, HUEFS, INPA, K, MEXU, P and W.

The dataset includes 95 of the 141 recognised species of *Calliandra* s.str. including three undescribed species (Souza, ined.). All five sections and twelve of the fourteen series proposed by Barneby were included. The ingroup also includes representatives of the genera segregated from *Calliandra* s.l.: *Thailentadopsis* (2 of 3 species), *Viguieranthus* (6/23), *Zapoteca* (7/17), as well as the two species of *Calliandra* from continental Africa (*C. redacta*, *C. gilbertii*) excluded from *Calliandra* by Barneby (1998) but not yet positioned in any other genus. It was not possible to include in the analyses some species (e.g., *C. cynometroides* and *C. umbrosa*, both Indo-Burmese species) formerly classified in *Calliandra* because we could not obtain good-quality DNA.

Also included in our study were representatives of all remaining genera of the “Inga Alliance” except for *Marmaroxylon* and *Archidendron*. Genera included were: *Cedrelinga* (monospecific), *Cojoba* (3 of 12 species), *Guinetia* (1/1), *Inga* (2/300), *Macrosamanea* (1/11) and *Zygia* (1/50). Because all published phylogenetic studies of tribe Ingeae did not identify well-resolved topologies or well-supported clades, we also sampled representatives of other genera of Ingeae not included in the Ingeae Alliance: *Abarema* Pittier (2 of 46 species), *Balizia*

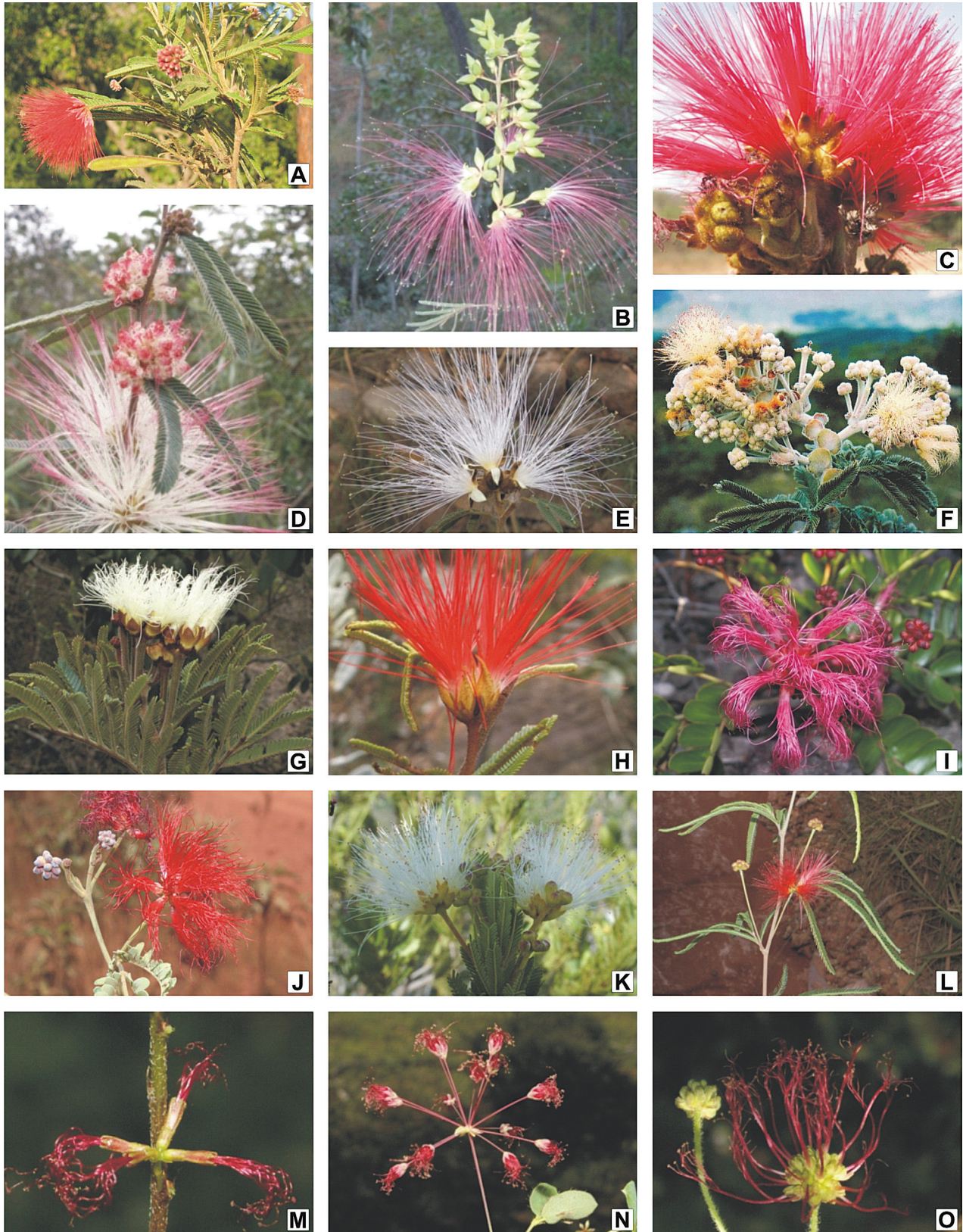


Fig. 1. Inflorescences in *Calliandra*. **A**, *C. dolichopoda* H.M. Hern.; **B**, *C. physocalyx* H.M. Hern. & M. Sousa; **C**, *C. dysantha* Benth.; **D**, *C. sessilis* Benth.; **E**, *C. macrocalyx* Harms; **F**, *C. lanata* Benth.; **G**, *C. bahiana* Renvoize; **H**, *C. coccinea* Renvoize; **I**, *C. semiseputa* Barneby; **J**, *C. stelligera* Barneby; **K**, *C. calycina* Benth.; **L**, *C. longipinna* Benth.; **M**, *C. depauperata* Benth.; **N**, *C. leptopoda* Benth.; **O**, *C. aeschynomenoides* Benth. — Photos: A–L, E.R. Souza; M–O, L.P. Queiroz.

Barneby & J.W. Grimes (1/3), *Blanchetiodendron* Barneby & J.W. Grimes (monospecific), *Ebenopsis* Britton & Rose (1/3), *Enterolobium* Mart. (1/11), *Havardia* Small (1/5), *Hesperalbizia* Barneby & J.W. Grimes (monospecific), *Hydrochorea* Barneby & J.W. Grimes (1/3), *Leucochloron* Barneby & J.W. Grimes (1/5), *Pithecellobium* Mart. (1/18), *Pseudosamanea* Harms (1/2), *Samanea* (Benth.) Merr. (1/3) and *Sphinga* Barneby & J.W. Grimes (1/3). As outgroup we used *Acacia spinescens* Benth. as a taxon phylogenetically distant from the Inga Alliance (Miller & al. 2003; Brown & al., 2008). Voucher details and sequences downloaded from GenBank (<http://www.ncbi.nlm.nih.gov>) are listed in Appendix 1.

We tested eight potential molecular markers for variation in the group, following information from previous phylogenetic studies in Mimosoideae (Luckow & al., 2000, 2003) and those suggested by Shaw & al. (2005, 2007): the nuclear ITS/5.8S region (including ITS1 and ITS2 regions, hereafter referred to as ITS) and the plastid *matK*, *trnL-F*, *trnS-G*, *rps16*, *trnD-T*, *psbA-trnH*, *rpl32-trnL*. We selected the ITS and the *trnL-F* regions (both *trnL* intron and *trnL-trnF* spacer) because they had higher substitution rates and proved to be more easily amplified in the study group than the other regions. In total, 254 sequences were used in this study, 247 of which were newly generated. For ITS, 135 taxa were sampled and 119 for *trnL-F*, with 76 covering the *trnL* intron and the *trnL-trnF* spacer and 43 for the *trnL* intron only.

Primers for the ITS region were 17SE and 26SE (Sun & al., 1994) for most accessions. For the most difficult materials we used primers ITS4 and ITS5 (White & al., 1990) and ITS75 and ITS92 (Desfeux & Lejeune, 1996). A combination of primers 17SE and 26SE with ITS2 and ITS3 (White & al., 1990) was used when it was necessary to amplify this region in two separate reactions. The *trnL* intron and *trnL-trnF* spacer were amplified in two reactions, using a combination of the universal primers “c” and “d”, and “e” and “f” (Taberlet & al., 1991), respectively.

DNA extraction, amplification and sequencing. — Laboratory procedures were performed at the Plant Molecular Systematics Laboratory (LAMOL) of Feira de Santana State University (UEFS) and at the Jodrell Laboratory of the Royal Botanic Gardens, Kew. Total DNA was extracted from silica-gel dried leaves and herbarium material using a modified 2× CTAB protocol (Doyle & Doyle, 1987).

Polymerase chain reactions were carried out using two different procedures. In the first approach, the reactions consisted of 22.5 µL of ReddyMix Master Mix (ABgene, Surrey, U.K.), 5 pmol of each primer, 2% DMSO and 1 µL of total DNA. Amplifications were carried out as follows: 2 min initial denaturation at 94°C followed by 35 to 40 cycles of 30 s denaturation at 94°C, 1 min annealing at 48°C–50°C and 1.5 min extension at 72°C, and completed by a final extension of 4 min at 72°C. The second approach used 50 µL reactions comprising PCR reaction buffer 1×, 2.5 mM MgCl₂, 1 mM dNTPs, 7.5 pmol of each primer, 0.5 µM BSA, 2% DMSO, 1 M betaine and 1.25 units of *Taq* DNA polymerase (Phonetrria Ltda, Belo Horizonte, Brazil). For ITS, the number of cycles and the annealing temperature were slightly different depending on the primers

used, as follow: 40 cycles at 48°C–50°C for ITS4 and ITS5, 28 cycles at 54°C–56°C for 17SE and 26SE, and 40 cycles at 58°C for ITS92 and ITS75. All reactions were carried out in a 9700 GeneAmp Thermocycler (Applied Biosystems, Singapore).

PCR products were purified using the QIAquick kit (Qiagen, Hilden, Germany) or by enzymatic treatment with Exonuclease I and shrimp phosphatase alkaline (kit ExoSapIT, GE Healthcare, Buckinghamshire, U.K.). Sequencing reactions were carried out with the same primers as used for amplifications and using the Big Dye Terminator kit version 3.1 (Applied Biosystems, Foster City, California, U.S.A.). Complementary strands for each region were sequenced using the automatic sequencers Spectrumedix SCE9624 and ABI3130XL at LAMOL and ABI3100 at the Jodrell. All sequences were deposited in GenBank (Appendix 1). Aligned data matrices are available in TreeBase (<http://treebase.org>, study no. S14957).

Alignment and phylogenetic analyses. — Complementary strands were combined and base-calling verified with the Staden package (Staden & al., 2003) or Sequencher v.4.1 (Gene Codes Corp., Ann Arbor, Michigan, U.S.A.). Alignments were performed by eye in PAUP* v.4.0b10 (Swofford, 2002). Gaps were considered as missing data; most gaps were autapomorphic and for this reason were not coded as additional characters. A total of 231 characters at the ends of the sequences and in regions of ambiguous alignment were excluded (118 from ITS and 113 from *trnL-F*).

The combined data matrix was constructed using 130 taxa, for the majority of which both nuclear and plastid markers (ITS+*trnL-F*) could be obtained. Taxa with only one marker were included in order to sample the morphological variation and full biogeographical range of *Calliandra*. These were: *C. belizensis* Standl., *C. californica* Benth., *C. dolichopoda* H.M. Hern., *C. eriophylla* Benth., *C. gilbertii*, *C. hirsuta* Benth., *C. humilis* Benth., *C. palmeri* S. Watson, *C. physocalyx* H.M. Hern. & M. Sousa, *C. rhodocephala* Donn. Sm., *C. riparia* Pittier, *C. trinervia* Benth., *C. tsugoides* R.S. Cowan, and *C. tweedii* Benth.

Maximum parsimony (MP) analyses were carried out in PAUP* v.4.0b10 for Windows (Swofford, 2002) using Fitch parsimony (all characters unordered and equally weighted; Fitch, 1971). The search for the most parsimonious trees (MPTs) was carried out using a heuristic search, 1000 random taxon-addition, and tree bisection-reconnection (TBR) branch swapping, saving 15 trees per replicate. Trees saved in this first round were used as starting trees in a second search using the same parameters, but saving a maximum of 10,000 trees. Clade support was estimated with non-parametric bootstrapping (Felsenstein, 1985) with 1000 pseudoreplications, simple taxon-addition and TBR branch swapping, saving 15 trees per pseudoreplicate.

Maximum likelihood (ML) analyses were carried out using RAxML (Stamatakis, 2006) as implemented on the CIPRES v.2.0 gateway (<http://www.phylo.org>). We used the model GTR + CAT for both the ITS and *trnL-F* regions; both regions were treated a separate partitions. Support was assessed using 1000 replicates and the rapid bootstrap option.

Bayesian analyses were carried out using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003). Best-fit substitution models

Table 1. Geographical distribution and morphological characters examined.

Characters	States
1 Distribution	1 Amazonia 2 Andes 3 Continental Africa 4 Asia 5 Madagascar 6 NE Brazil without Espinhaço 7 Espinhaço mountain range 8 Central Brazil 9 Subtropical South America 10 North/central Mexico & U.S.A. 11 Central America & Caribbean 12 Australia 13 Northern South America without Amazonia
2 Habitat	1 Dry Forests 2 Wet Forests 3 Savannas 4 Subtropical grasslands 5 “Campos rupestres”
3 Armament	1 absent 2 present
4 Extrafloral nectaries	1 present 2 absent
5 Number of pinnae per leaf	1 1–2 2 3–10 3 >10
6 Number of leaflets per pinna	1 ≤10 2 11–20 3 >20
7 Leaflet length	1 ≤10 mm 2 11–20 mm 3 >20 mm
8 Inflorescence position	1 lateral 2 terminal
9 Inflorescence aggregation	1 compound 2 simple
10 Synflorescence type	1 fascicle 2 pseudoraceme 3 pseudopanicule
11 Partial inflorescence	1 globose capitulum 2 spicate 3 umbelliform 4 raceme
12 Corolla length	1 3–7 mm 2 8–10 mm 3 >10 mm
13 Glandular trichomes	1 absent 2 present
14 Fruit dehiscence	1 elastically from apex to base 2 not elastically dehiscent 3 indehiscent
15 Polyad type	1 7-celled, acalymmate 2 16–32-celled, acalymmate 3 8-celled, calymmate

were selected using MrModeltest v.2.3 (Nylander, 2004). Model GTR+ Γ was selected for the *trnL*, *trnL-F* and 5.8S regions and model GTR+I+ Γ for ITS1 and ITS2. The analyses were performed with uniform priors and a random starting tree. Two simultaneous Monte Carlo Markov Chains (MCMC) were run for 13,000,000 generations sampling one tree each 1000 generations. Stability of the chains was reached near the beginning of the analysis and trees from the initial 25% of the runs were discarded as burn-in, as assessed in Tracer v.1.5. (Rambaut & Drummond, 2003). Remaining trees were used to compute a 50% majority-rule consensus tree in PAUP* v.4.0b10 (Swofford, 2002), and the frequencies of clades were taken as estimates of posterior probabilities.

Phylogenetic congruence between the ITS and *trnL-F* region datasets was assessed using the partition homogeneity test (PHT; Felsenstein, 1985). Topological conflicts between trees resulting from different analyses were checked by eye in case of significant differences in PHT, and by the use of split networks with the supernet algorithm in Splits Tree v.4.11.3 (Huson & Bryant, 2006) using 50% majority-rule consensus trees of the BI and ML analyses.

The possible presence of ITS pseudogenes was investigated through comparison of length and substitution rates in fast-evolving (ITS 1–2) and conserved (5.8S) regions and the presence of polymorphic specimens, following the recommendation of Bailey & al. (2003).

Molecular divergence time estimates. — Divergence time estimates were obtained using an uncorrelated relaxed molecular clock as implemented in BEAST v.1.7.2. (Drummond & al., 2012) based on the combined nuclear and plastid data. Two calibration points were used in the analysis: the crown node of *Ingeae* and *Acacia* s.str. was set to 23.9 ± 3.1 million years ago (Ma) based on the results of a previous analysis (Lavin & al., 2005) assuming a normal prior distribution. A second calibration point assuming a lognormal prior distribution was based on a fossil polyad from the Miocene of Argentina, consisting of eight pollen grains in a monopolar, calymmate arrangement (Caccavari & Barreda, 2000), unequivocally belonging to *Calliandra*. This fossil has an estimated age of 16 ± 1 Ma based on radiometric dating, and this value was used as the minimum age constraint for the most recent common ancestor (MRCA) which represents the stem node of *Calliandra* with calymmate polyads.

The analysis was carried out using three partitions for ITS and substitution models GTR+ Γ for 5.8S, *trnL* and *trnL-F* and GTR+I+ Γ for ITS1 and ITS2. Convergence of all parameters was evaluated in Tracer v.1.5. (Rambaut & Drummond, 2003). The maximum clade credibility tree with annotation of posterior probability, mean age, substitution rates and respective standard deviations was compiled using TreeAnnotator v.1.4.8 (Drummond & Rambaut, 2007). The nodes are named according to the majority consensus of 10,000 trees derived from the Bayesian analysis of the combined dataset.

Biogeography and evolution of morphological characters. — Thirteen morphological characters (Table 1) were selected to assess potential synapomorphies and provide diagnostic characters for well-supported clades recovered in the molecular phylogenetic reconstruction. Most characters selected were

used by Barneby (1998) as diagnostic traits of infrageneric groups of *Calliandra*. In addition, we assessed the evolution of pollen traits as these have been used previously to differentiate generic entities. Ancestral character state reconstructions were performed using the parsimony criterion in Mesquite v.2.01 (Maddison & Maddison, 2007), and using trees derived from the Bayesian analysis of the combined dataset. All characters were coded as unordered and optimized using the ACCTRAN algorithm on the majority consensus tree of 10,000 trees derived from the Bayesian analysis of the combined dataset using the option “Trace over Trees” to account for topological uncertainty (Electr. Suppl.: Table S1).

Geographical areas and habitat were optimized using the same parameters as used to reconstruct the evolution of morphological traits. Based on the distribution range of the American species of *Calliandra* as provided by Barneby (1998), thirteen major geographical areas were coded: Amazonia; Andes; Asia; Australia; continental Africa; Central America & Caribbean; central Brazil; Espinhaço mountain range; Madagascar; northeast Brazil without Espinhaço; north/central Mexico & U.S.A.; northern South America without Amazonia; and subtropical South America. For the Old World taxa, major continental areas were used, i.e., continental Africa, Madagascar, Asia and Australia. Four major habitats were selected based mostly on the work of Schrire & al. (2005) who identified the major global biomes relevant for the diversification history of the legume family: tropical wet forests, savanna (the “grass rich biome”), seasonally dry tropical forests (hereinafter SDTF, part of the global “succulent rich biome”) and subtropical grasslands (included in the “temperate biome”). Besides these major biomes, we added another particular habitat where *Calliandra* is particularly rich, the campos rupestres (upland rocky fields) of the Espinhaço mountain range in the eastern Brazilian states of Bahia and Minas Gerais.

Pollen morphology. — Pollen samples were obtained from dried herbarium specimens deposited in the herbaria HUEFS, K and MEXU. We sampled three species of *Calliandra* s.str.: *C. debilis* Renvoize, *C. houstoniana* (Miller) Standl. and *C. parviflora* Benth.; three Old World species traditionally included in the genus: *C. cynometroides*, *C. gilbertii* and *C. umbrosa*, and three species of genera segregated from *Calliandra* s.l.: *Thailentadopsis nitida*, *Viguieranthus umbilicus* Villiers and *Zapoteca formosa* (Kunth) H.M. Hern. It was not possible to include a sample of *Guinetia* because flowers are available only on the type specimen.

Pollen samples were acetolysed according to Erdtman (1960) and then dehydrated in an ethanol series of 50%, 70%,

90% and 100%, for five minutes in each solution. The pollen grains were then placed on “stubs”, dried at room temperature and coated with gold (using a Balzers SCD 050). Electron micrographs were taken on a LEO 1430VP scanning electron microscope.

Additional data on pollen morphology was taken from the literature; for *Calliandra* from Souza (2007), Santos & Romão (2008), Guinet & Hernandez (1989), Niezgodá & al. (1983), and Guinet (1965); for *Guinetia* from Rico Arce & al. (1999); for *Zapoteca* from Guinet & Hernandez (1989), Niezgodá & al. (1983), and Guinet (1965); for *Thailentadopsis* from Souza (2007).

■ RESULTS

Phylogenetic reconstructions. — The aligned ITS region for 135 accessions comprised 970 characters of which 852 were used in the analyses; 284 were parsimony-informative (33.3%). The aligned *trnL-F* region for 119 accessions comprised 1477 characters, of which 1380 were included in the analyses; 169 of these were parsimony-informative (12.2%). The concatenated matrix of 130 accessions contained 2430 characters, with 2,170 included in the analyses; 412 were potentially parsimony informative (19.1%) (Table 2).

The majority consensus of 10,000 trees derived from the Bayesian analysis of the combined dataset, ITS+*trnL-F*, is shown in Fig. 2. The clades with posterior probabilities equal to or higher than 0.95 (BI, Bayesian inference) and/or bootstrap values equal to or higher than 0.75 (MP, maximum parsimony; ML, maximum likelihood) are indicated on the majority consensus tree and are discussed later.

The trees generated from the ITS and *trnL-F* datasets are significantly different in the MP analysis based on the PHT test ($P < 0.01$). However, the trees generated from the MP, ML and BI analyses were not significantly different based on split networks with the supernet algorithm. Clades C, E and F appeared in all analyses of the individual and combined datasets, with topological differences occurring in clades G to K, which were recovered only from the nuclear and combined datasets (Fig. 3).

Relationships within tribe Ingeae. — The “Inga alliance” (sensu Barneby & Grimes, 1996; Lewis & Rico Arce, 2005) was not recovered as monophyletic in any analysis (e.g., Fig. 2). Interestingly, with the exception of *Calliandra* and *Abarema*, all genera represented by more than one species were strongly supported as monophyletic (Fig. 2). *Inga*, *Macrosamanea*,

Table 2. Characteristics of each DNA sequence region used.

DNA region	Alignment length	Variable characters	Parsimony-informative characters	MP tree length	Consistency index	Retention index
<i>trnL-F</i>	1477	405	169	594	0.77	0.90
ITS	970	422	284	1378	0.50	0.83
Combined data	2430	745	412	1866	0.56	0.84

Zygia and *Leucochloron* formed one clade (PP 0.98). The remaining genera of the “Inga alliance” (*Calliandra*, *Cojoba*, *Guinetia*, *Viguieranthus*, *Zapoteca*) were placed together in clade B with *Thaileadopsis* and with high support only in the Bayesian analysis based on combined nuclear and plastid data (PP 0.98, Fig. 2). The monophyly of the “Abarema alliance” and of the “Pithecellobium alliance” is supported by our analyses (PP 1.0, BS ML 1.0, BS MP 1.0 and PP 1.0, BS ML 1.0, BS MP < 0.75, respectively; Fig. 2).

Infrageneric classification of *Calliandra* s.str. — *Calliandra* s.str., as circumscribed by Barneby (1998), was paraphyletic because of the inclusion of *Guinetia tehuantepecensis* L. Rico & M. Sousa. The sections of *Calliandra* proposed by Barneby (1998) were not supported as monophyletic with the exception of *C.* sect. *Acistegia*, which includes only two species, *C. haematomma* (DC.) Benth., *C. pedicellata* Benth. (Fig. 2). Species of Barneby’s *C.* sect. *Calliandra* appeared in four clades: (1) in clade F, composed of species restricted to the Espinhaço Mountain range in eastern Brazil; (2) in clade G that includes species from the southern United States to Central America (including *C. houstoniana* (Miller) Standley, the type species of the genus) and species of *C.* sect. *Acistegia*; (3) in clade H comprising *C. vaupesiana* and *C. tsugoides* only, and (4) in clade K, which includes only one species of *C.* sect. *Calliandra*, *C. vir-*

gata, and this species was nested in the large *C.* sect. *Androcallis* (plus sect. *Acroscias* and *Guinetia tehuantepecensis*). Clade I (PP 1.0; BS ML 1.0; BS MP 1.0) comprised species from the United States to Mexico of Barneby’s *C.* sect. *Androcallis*. Clade J (PP 0.99; BS ML 0.79; BS MP < 0.75) was a mixture of four species of Barneby’s sect. *Androcallis* and two species of sect. *Microcallis* (*C. parviflora* Benth., *C. leptopoda* Benth.). Clade K (PP 1.0; BS ML 0.85; BS MP < 0.75), which is widely distributed from the southern United States to northern Argentina, includes most representatives of Barneby’s *C.* sect. *Androcallis* together with *Guinetia tehuantepecensis*, *C. brevicaulis* (sect. *Acroscias*) and *C. virgata* (sect. *Calliandra*).

Of the twelve series (of a total of fourteen) proposed by Barneby (1998) included in this study, seven are monospecific (*C.* ser. *Biflorae*, ser. *Chilensis*, ser. *Hymenaeoides*, ser. *Lep-topodae*, ser. *Longipedes*, ser. *Microcallis*, ser. *Virgatae*), four were shown to be non-monophyletic (*C.* ser. *Ambivalente*, ser. *Androcallis*, ser. *Calliandra*, ser. *Macrophyllae*) and only ser. *Tsugoideae* was recovered as monophyletic.

Relationships of *Calliandra* s.str. to other groups of Ingeae were not well resolved. A well-supported group of two species from continental Africa (*Calliandra gilbertii* and *C. redacta*) was recovered as sister to *Calliandra* s.str. (Fig. 2) with *Cojoba arborea* as sister group of this clade, but always with low

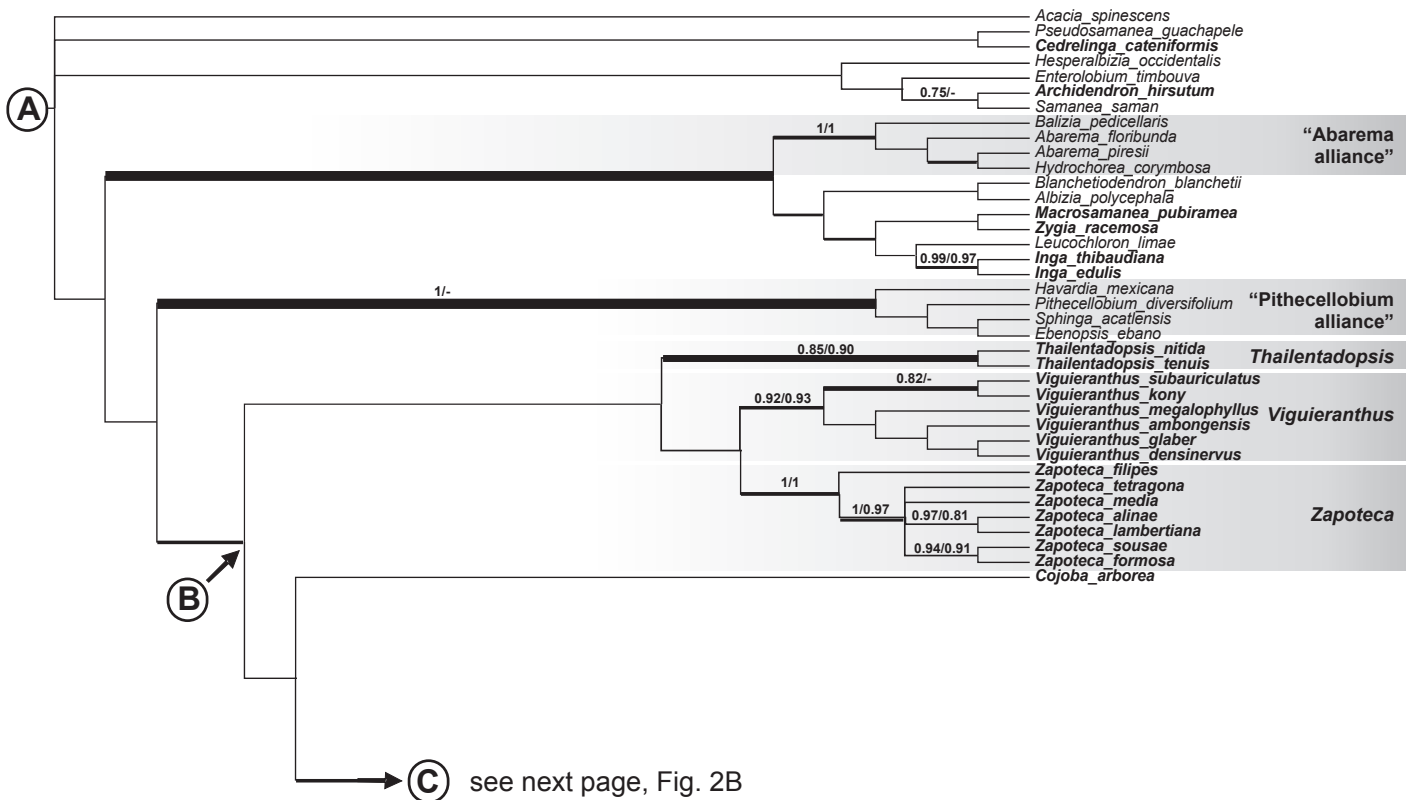


Fig. 2A–B. Majority-rule (50%) consensus tree of 10,000 trees sampled at stationarity from the Bayesian analysis of the combined data (ITS+trnL/trnL-F) of *Calliandra* and related genera. Thick lines indicate clades supported by posterior probabilities (PP) ≥ 0.90. Numbers on the branches indicate bootstrap values (≥ 0.75) of the maximum likelihood (ML) and of the maximum parsimony (MP) analyses, respectively. Color of names of taxa indicate sectional assignment of species in *Calliandra* sensu Barneby (1998). The new infrageneric classification presented in this study is represented by gray boxes. Letters on nodes refer to clades discussed in the text. Taxa in bold belong to the “Inga alliance” (sensu Barneby & Grimes, 1996; Lewis & Rico-Arce, 2005). In the inset in Fig. 2B is the same tree depicted as a phylogram to show the branch lengths.

support. Most of the morphological characters used by Ben-
tham (1844) and Barneby (1998) to characterize infrageneric
groups of *Calliandra* were recovered as homoplastic (e.g., in-
florescence architecture, number of pairs of pinnae and number
of leaflets per pinna; Electr. Suppl.: Fig. S1).

Molecular divergence time estimates. — All estimated
parameters had sufficient effective sample size, in most cases
well above the minimum of 200. Age estimates for relevant
crown nodes (mean and 95% credibility intervals) are shown in
Table 3. The mean ages of stem and crown group of *Calliandra*

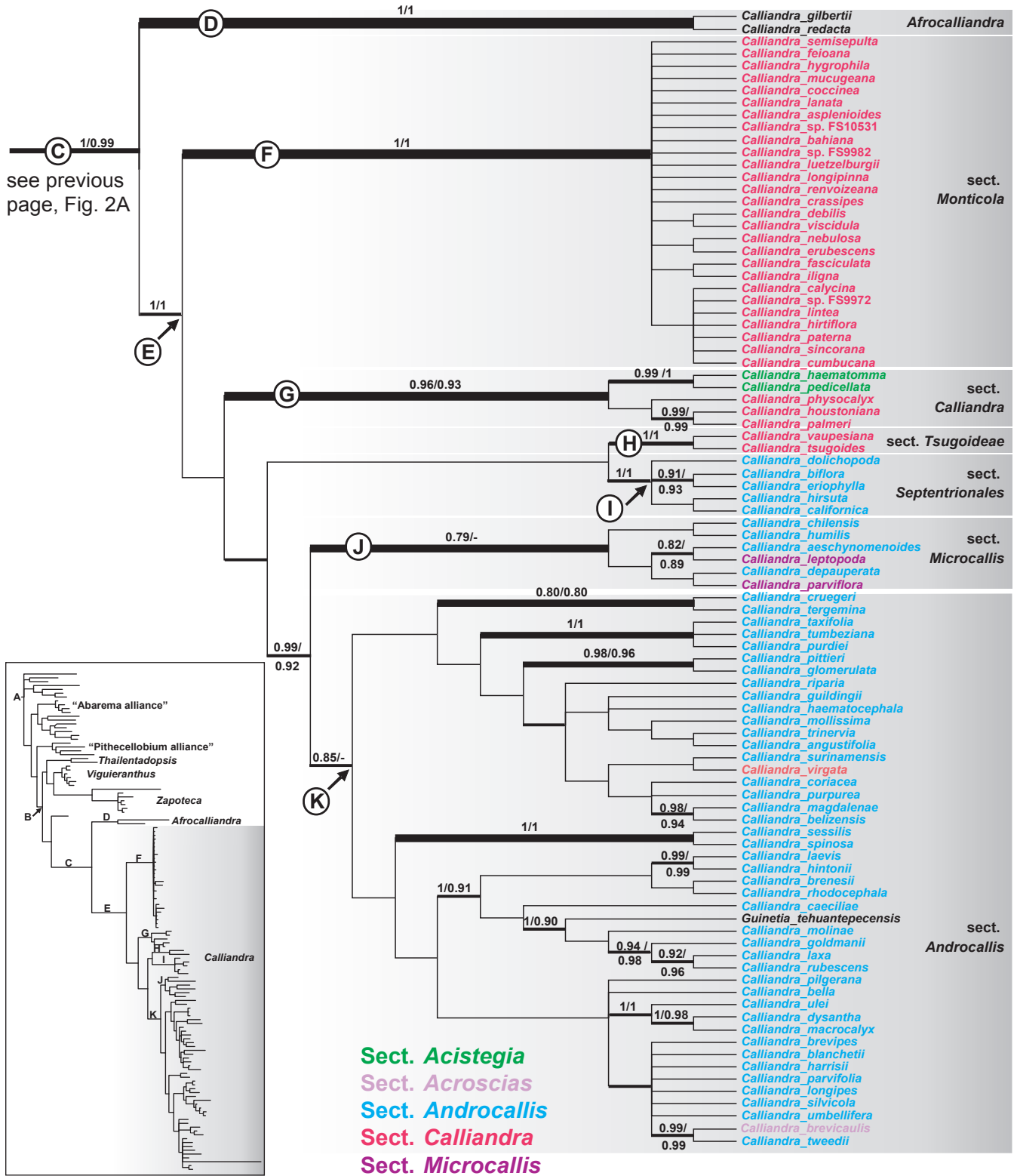
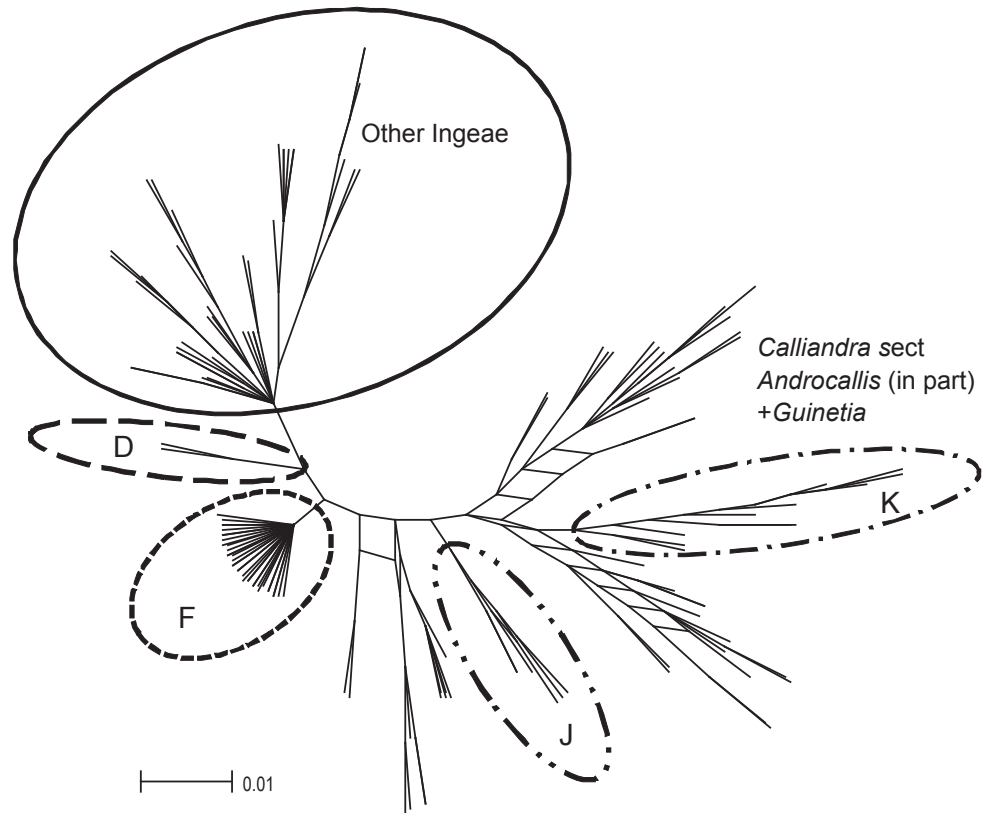


Fig. 3. Supernetwork obtained from the majority-rule consensus tree of the Bayesian analysis illustrating the incongruence between ITS and *trnL* trees. Clades are named according as in Fig. 2.



were estimated at 14.74 Ma (clade C) and 11.36 Ma (clade E), respectively (Fig. 4). Crown ages of the major clades are presented in Table 3.

The topological differences found in the tree obtained in the dating analysis with BEAST were: (1) clade G sister group of clade F and (2) a clade composed of *Cojoba*, *Thailentadopsis*,

Viguieranthus and *Zapoteca*. These differences (in comparison with the Bayesian analysis of MrBayes) are not supported and probably reflect differences in the model used, since BEAST estimates molecular rates for each branch with a more complex model than MrBayes (probably at the expense of topological precision) (Drummond & al., 2012).

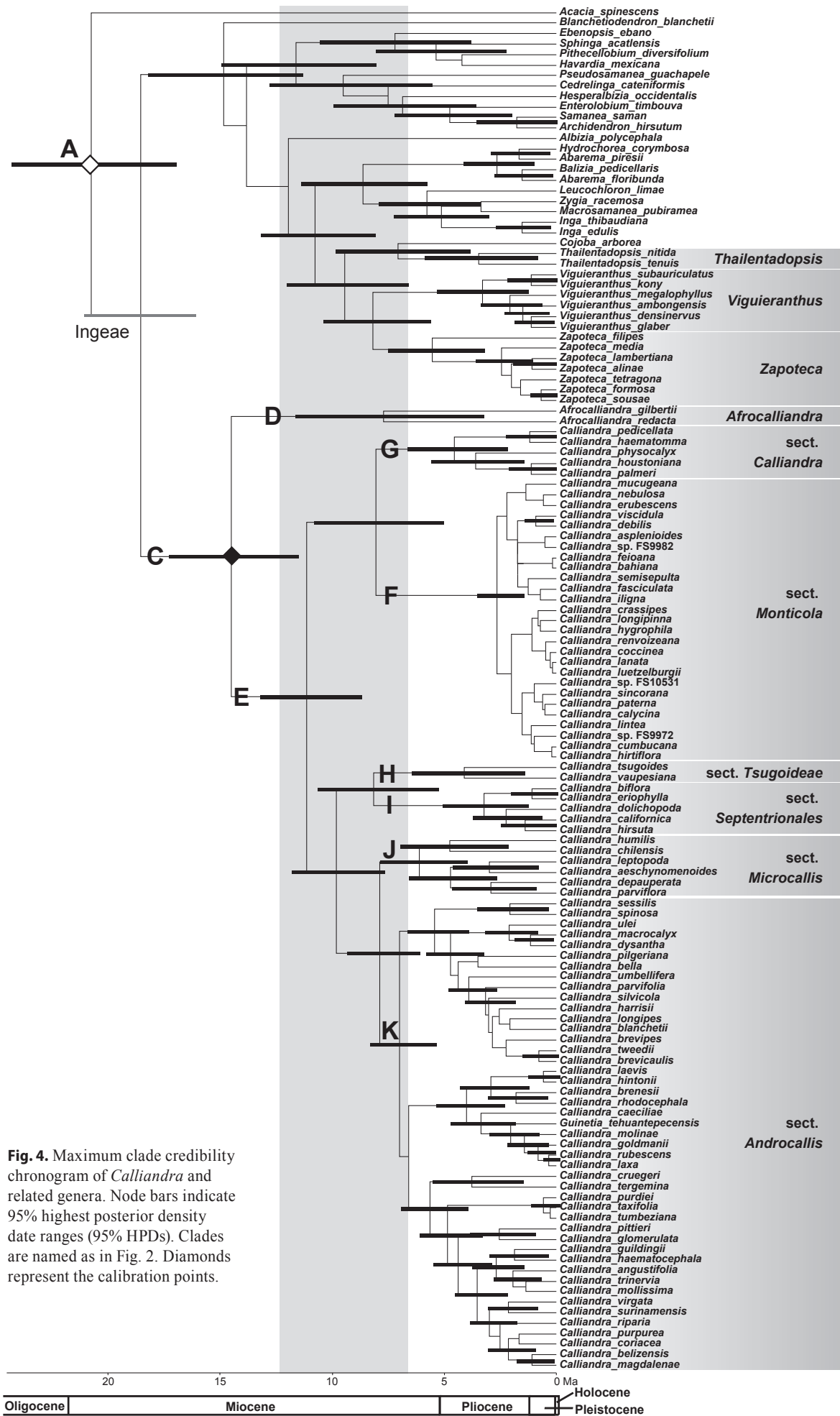
Pollen morphology. — Palynological studies carried out on the two African species (Guinet, 1965; Thulin & al., 1981; Souza, 2007; Souza & al., in prep.), two Asian species (Guinet, 1965; Souza, 2007; Souza & al., in prep.) and 66 American species (Guinet, 1965; Niezgodá & al., 1983; Guinet & Hernández, 1989; Souza, 2007; Santos & Romão, 2008; Souza & al., in prep.), representing all sections and series recognized by Barneby (1998), showed that calymmate and ellipsoid polyads are an exclusive trait of the American taxa of *Calliandra*, whereas, in contrast, the paleotropical species have acalymmate polyads. *Calliandra cynometroides* (Fig. 5B) and *C. umbrosa* (Fig. 5C), both Asian, have radially symmetrical, 16-celled polyads, whereas *C. redacta* and *C. gilbertii* (Fig. 5A), the two African species, have bilateral, 7-celled polyads.

Table 3. Molecular divergence time (crown age) estimates (for names of nodes see Fig. 4).

Most recent common ancestor of	Mean [Ma]	Minimum [Ma]	Maximum [Ma]
Clade A (Ingeae+Acacieae)	20.98	17.18	24.54
Ingeae	18.76	16.27	21.29
Clade C	14.74	11.75	17.52
Clade D (<i>Afrocalliandra</i>)	7.94	3.44	11.87
Clade E (<i>Calliandra</i> s.str.)	11.36	8.90	13.42
Clade F (sect. <i>Monticola</i>)	2.88	1.65	3.78
Clade G (sect. <i>Calliandra</i>)	4.77	2.41	6.88
Clade H (sect. <i>Tsugoideae</i>)	4.34	1.62	6.67
Clade I (sect. <i>Septentrionales</i>)	3.47	1.47	5.30
Clade J (sect. <i>Microcallis</i>)	6.31	4.17	8.07
Clade K (sect. <i>Androcallis</i>)	7.21	5.56	8.51
<i>Thailentadopsis</i>	3.64	1.05	6.12
<i>Viguieranthus</i>	3.51	1.49	5.55
<i>Zapoteca</i>	5.75	3.42	7.73

DISCUSSION

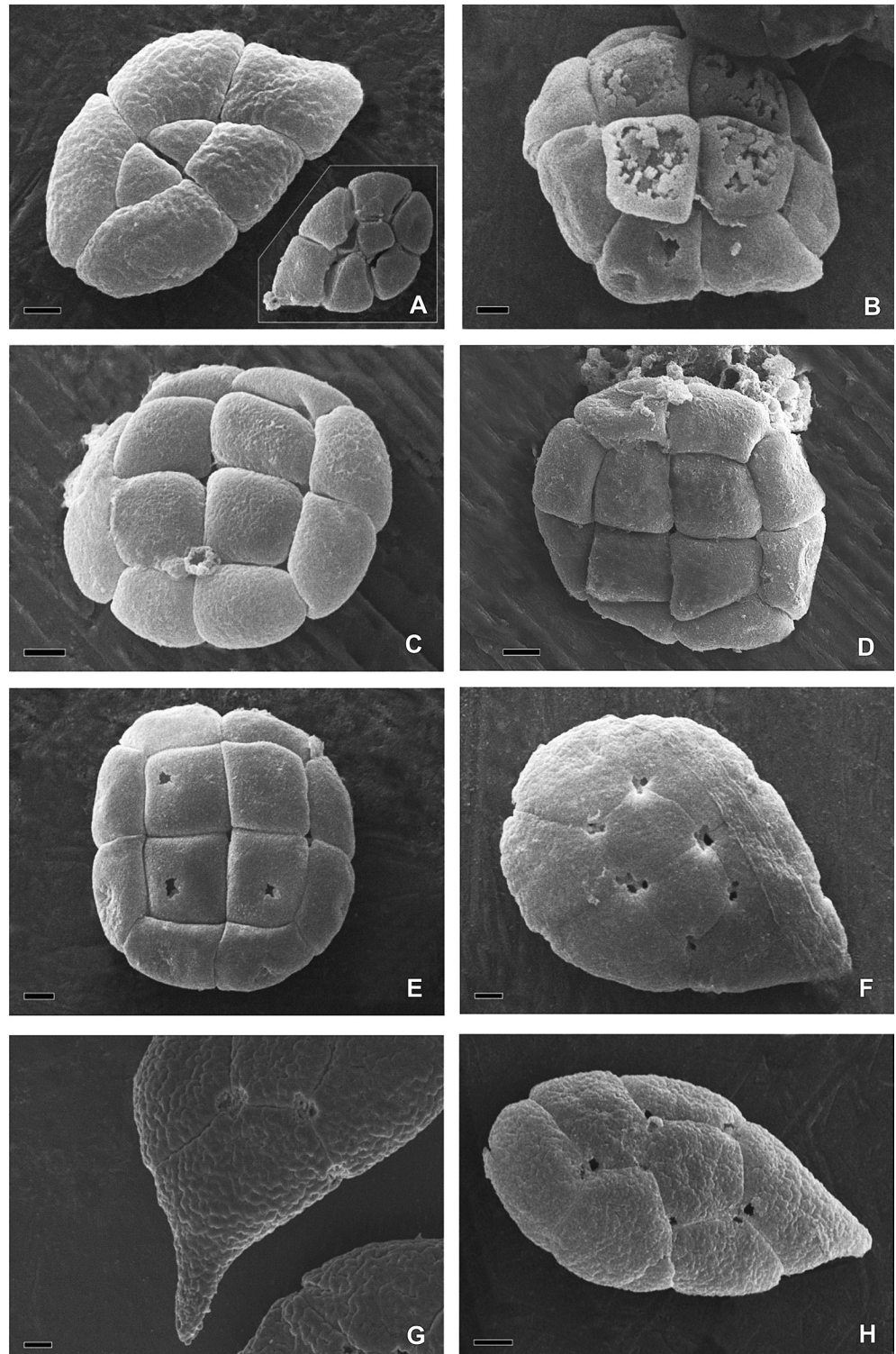
Most phylogenetic studies in Mimosoideae have revealed a relatively low substitution rate in plastid markers (e.g., Lavin & al., 2005) which resulted in a persistent lack of resolution in many areas of the mimosoid phylogeny (Luckow & al., 2000, 2003; Lavin & al., 2005; Jobson & Luckow, 2007). One



exception is the *trnD-trnT* region that contained enough variation to uncover major clades in *Mimosa* (Simon & al., 2011). The evolutionary rates of both the ITS and *trnL-F* regions observed in our study are similar to those found in other Mimosoideae (Murphy & al., 2003; Ariati & al., 2006; Brown & al., 2008; Govindarajulu & al., 2011). However, potentially

non-functional pseudogene copies of ITS have been identified in some mimosoid groups (Bailey & al., 2003), including *Leucaena* (Hughes & al., 2002) and *Inga* (Richardson & al., 2001). ITS pseudogenes, unlike functional copies, are not subject to functional constraints and, therefore, can have similar substitution rates in the 5.8S gene region and the ITS spacers (Bailey

Fig. 5. SEM micrographs of polyads. **A**, *Afrocalliandra gilbertii* (Thulin & Hunder) E.R. Souza & L.P. Queiroz (*Powys 493*, K) with detail showing polyad with only one central grain (*Tardelli 161*, K); **B**, *Calliandra cynometroides* Bedd. (*Sasidharan 10003*, K); **C**, *C. umbrosa* Benth. (*Clarke 44932*, K); **D**, *Viguieranthus umbiliscus* Villiers (*Capuro 796*, P); **E**, *Zapoteca formosa* (Kunth) H.M. Hern. (*Wood 8782*, K); **F**, *C. houstoniana* (Mill.) Standl. (*Colin 16765*, MEXU); **G**, *C. debilis* Renvoize, basal grain showing the appendix (*Harley 18676*, HUEFS); **H**, *C. parviflora* (Hook. & Arn.) Speg. (*Wood 19934*, K). — Scale bars: A–F, H = 10 μ m; G = 20 μ m.



& al., 2003). We did not find evidence for pseudogenes in our data because the 5.8S gene region did not contain indels and had a much lower substitution rate than the two ITS regions across the sampled taxa. Also, taxa represented by multiple accessions did not reveal polymorphic sites in ITS sequences.

The topological conflicts between trees generated from the ITS and *trnL-F* data probably arose from: (1) different taxonomic sampling between the two datasets: *Calliandra belizensis*, *C. californica*, *C. chilensis*, *C. dolichopoda*, *C. eriophylla*, *C. hirsuta*, *C. humilis*, *C. palmeri*, *C. tsugoides* are present only in the nuclear dataset, whereas *C. gardnerii*, *C. glyphoxylon*, *C. juzepczukii*, *C. peninsularis*, *C. trinervia*, and *Thailentadopsis tenuis* were included only in the plastid dataset; (2) lack of inclusion of the plastid spacer (*trnL-F*) in some taxa such as *C. brevicaulis*, *C. goldmanii*, *C. guildingii*, *C. hintoni* and *C. houstoniana*.

Relationships within tribe Ingeae.— The “Inga alliance” was not recovered as monophyletic in any analysis. This group was proposed by Grimes (1995, 1999) and Barneby & Grimes (1996) based on a morphological phylogenetic analysis and characterized by persistent axillary reproductive meristems (ramiflory). It is heterogeneous with respect to habit and habitat since it includes arboreal genera typical of humid and riparian forests (e.g., *Archidendron*, *Cedrelinga*, *Cojoba*, *Inga*, *Macrosamanea*, *Marmaroxylon*, *Zygia*), as well as small trees, shrubs, and subshrubs typical of STDfs (e.g., *Calliandra*, *Guinetia*, *Viguieranthus*, *Zapoteca*). Relationships amongst these genera were not well resolved in our study, except within the clade comprising *Inga*, *Macrosamanea* and *Zygia* with *Leucochloron* (“Chloroleucon alliance”) nested within it, and the clade containing *Calliandra*, with *Guinetia* nested within it, *Cojoba*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca*. In previous molecular analyses (Luckow & al., 2000, 2003; Brown & al., 2008), the “Inga alliance” also was not supported as monophyletic.

The “Abarema alliance” as circumscribed by Barneby & Grimes (1996) and Lewis & Rico-Arce (2005) was recovered as monophyletic in all analyses. It includes genera typical of humid forests that are differentiated mainly by fruit type (Barneby & Grimes, 1996). Rico Arce (1999) considered *Balizia* as a synonym of *Albizia*, which was maintained by Lewis & Rico Arce (2005). However, our study indicated that *Balizia* is independent of *Albizia* and placed within the “Abarema alliance” as proposed by Barneby & Grimes (1996).

The “Pithecellobium alliance” comprises genera typical of STDfs: *Havardia*, *Sphinga*, *Pithecellobium*, *Ebenopsis* and *Painteria*, distributed in Mexico, the Caribbean region and surrounding areas (e.g., Honduras and Nicaragua in Central America; Colombia and Venezuela in South America), with only *Pithecellobium* occurring in eastern South America. Of the genera belonging to this alliance, only *Painteria* was not included in our analyses, and so far has not been included in any other molecular study. The group is highly supported as monophyletic in all analyses except the maximum parsimony analysis and is diagnosed by new growth developing from both standard vegetative branches and brachyblasts, the presence of separate vegetative and reproductive brachyblasts, and

spinescent stipules as morphological synapomorphies (Grimes, 1995; Barneby & Grimes, 1996).

Monophyly and generic relationships of *Calliandra*.— The phylogenetic position of the two African species of *Calliandra* had not been evaluated until now. According to palynological studies, the two species were deemed to be early diverging lineages that probably represent a genus distinct from *Calliandra* (Thulin & al., 1981; Guinet & Hernandez, 1989). Barneby (1998) subsequently circumscribed *Calliandra* to be restricted to the New World. The two African species differ from *Calliandra* s.str. by their acalymmate polyads (Fig. 5A) and the presence of extrafloral nectaries. Our results strongly support the two African species as a monophyletic group sister to an American *Calliandra* s.str. clade, itself also strongly supported. Based on the reciprocal monophyly of these sister clades, different taxonomic status could be ascribed to the African clade without violating the principle of monophyly. We have chosen to recognize the African clade as a new genus, sister to *Calliandra*, based on the criterion of morphological diagnosability. If we had chosen to include the species of the African clade in a more broadly circumscribed *Calliandra*, this would have rendered *Calliandra* to lack any clear-cut synapomorphy and virtually lacking diagnostic characters with respect to *Zapoteca*, *Viguieranthus* and *Thailentadopsis*. Recognizing the two African species as a distinct genus is supported by their different pollen characters (8-celled polyads with a calymmate exine in *Calliandra* vs. 7-celled acalymmate polyads in *Afrocalliandra*), the absence of extrafloral nectaries (vs. absent or present in *Afrocalliandra*), and spines or thorns which are absent in *Calliandra*, in addition to the continental disjunction.

The Asian *C. cynometroides* and *C. umbrosa* (Fig. 5B, C, respectively) also have polyad morphologies different from those found in *Calliandra* s.str. and might be better placed in a new genus, but such an action would be premature because these two species have not yet been included in any molecular study.

Higher-level relationships of the *Calliandra* s.str.–*Afrocalliandra* clade with other genera formerly included in *Calliandra* s.l., as well as with other genera of Ingeae, were unresolved, although each genus (*Zapoteca*, *Viguieranthus*, *Thailentadopsis*) is supported as monophyletic both in the ITS and the combined ITS+*trnL-F* analyses and each has a pollen morphology distinct from *Calliandra* (Fig. 5). These results add support to the current generic circumscriptions in the *Calliandra* s.l. group, that is, keeping *Calliandra* s.str. (with the inclusion of *Guinetia*) as distinct from *Zapoteca*, *Viguieranthus* and *Thailentadopsis* as well as supporting each of these as distinct genera, as proposed by several authors (Hernández, 1986; Barneby, 1998; Villiers, 2002; Lewis & Schrire, 2003).

The transfer of *Guinetia* to *Calliandra* s.str. renders the latter monophyletic with robust support in all analyses (Fig. 2). *Guinetia* is placed in the clade of Neotropical *Calliandra* species along with the species of *C.* sect. *Androcallis* (Fig. 2, clade K). These species and *Guinetia* have in common the axillary inflorescences arising from brachyblasts, and the majority of them have heteromorphic inflorescences, although this character is not mentioned in the original description of *Guinetia* (Rico Arce & al., 1999). This clade (*Calliandra* s.str.+*Guinetia*)

is diagnosed by the following morphological synapomorphies: absence of a petiolar nectary (Electr. Suppl.: Fig. S1D) and calymmate polyads composed of eight pollen grains (Fig. 5F–H; Electr. Suppl.: Fig. S1K).

The clade (*Zapoteca* (*Afrocalliandra*+ [*Calliandra* s.str. + *Guinetia*])) is characterized by fruits elastically dehiscent from the apex (with a reversal in *Guinetia* that does not possess this kind of dehiscence but instead opens along one margin). *Zapoteca* was regarded as the sister group of *Calliandra* s.str. in the analyses of Grimes (1995), Barneby & Grimes (1996), Luckow & al. (2000) and the ETS analysis of Brown & al. (2008), although there was low support for this relationship in our analyses.

In the molecular analyses of Luckow & al. (2003), *Cedrelinga* was supported as the probable sister group to *Calliandra* s.str., but in our study this position was not confirmed and *Cedrelinga* was placed as sister to *Pseudosamanea guachapele*. *Cedrelinga* was not included in the analyses of Brown & al. (2008).

Habitat evolution in *Calliandra*. — Divergence time analyses indicated that *Calliandra* s.str. and *Afrocalliandra* split from each other at about 14.74 Ma (mean age; clade C) in the Miocene (Fig. 4; Table 3). Modern *Calliandra* s.str. diversified from 11.36 Ma (clade E) forming two major groups: (1) The radiation of the first group seems to have started at about 10 Ma in the Miocene, and contains the majority of the species included in this study. These species are resolved in four distinct clades: clade H, from 4.34 Ma, which contains only two species distributed in the Guianas, Venezuela, the Colombian Amazon and the northern state of Amazonas, Brazil; clade I, from 3.47 Ma, which includes species that grow in the desert and semi-desert regions of the Mexican highlands, extending to the southern United States; clade J, 6.31 Ma, which comprises species restricted to the arid and semi-arid regions of northeastern Brazil, Chile, southwestern United States (Arizona) to Mexico and extra-Amazonian Brazil, Paraguay and Bolivia, and clade K, from 7.21 Ma, which includes species widely distributed from the southern United States to Argentina; (2) The second group may have split about 8 Ma. These species are resolved into two distinct clades: clade G, which diversified from 4.77 Ma, includes species distributed from Mexico to Central America; clade F, which diversified within the past 2.88 Ma, in the Pleistocene. This clade comprises species restricted to the Espinhaço mountain range in Brazil.

Calliandra is more diverse in STDfS, savannas and campos rupestres with a few species in wet forests and subtropical grasslands (Electr. Suppl.: Fig. S1B). Our results indicate that the STDf is the most probable ancestral habitat of the genus and the stage of the major diversification events. As in other dry forest specialists (e.g., *Coursetia*, Lavin & al., 2001; Queiroz & Lavin, 2011; *Indigofera*, Schrire & al., 2009; *Mimosa*, Simon & al., 2011), the STDf clades of *Calliandra* show strong geographical and phylogenetic coherence, as exemplified by the dry forest clades G, I and some subclades of clade K distributed from Mexico to northwestern South America, and the *C. aeschynomoides*–*C. parviflora* clade of clade J, distributed only in the Caatinga vegetation of northeastern Brazil. This suggests niche

conservatism and limited dispersal in STDf lineages (Lavin, 2006, Queiroz & Lavin, 2011).

Habitat shifts to savanna vegetation have occurred several times. Most of these transitions occurred independently to the Cerrado vegetation of central Brazil corroborating the finding of Simon & al. (2009) that most of the Cerrado flora had a recent origin and evolved from different surrounding biomes. In sharp contrast with this Cerrado diversification pattern, the campos rupestres, another area also dominated by similar fire-prone savanna-like vegetation, harbours a spectacular radiation of *Calliandra*, comprising 46 of the 142 species of the genus. These 46 species are concentrated in the northern part of the Chapada Diamantina mountain range, and 36 of them are narrowly restricted to this region, paralleling the rapid species diversification also observed in other montane regions for other legume genera, such as the Andean clade of *Lupinus* L. (Hughes & Eastwood, 2006).

One important aspect of this endemism in the Chapada Diamantina is that it is not distributed uniformly among the infrageneric groups of *Calliandra* (Souza, 2001). Of the 36 species of *Calliandra* restricted to the Chapada, one belongs to the *Androcallis* clade (*C. pilgerana* Harms) and 35 to the *Monticola* clade. In addition, we observed no habitat shifts between Cerrado and campos rupestres clades of *Calliandra* despite striking environmental similarities and the geographical proximity of these two vegetation types. This pattern suggests that there is strong dispersal barrier between the Chapada Diamantina region and the remaining areas of campos rupestres of the Espinhaço range, as well as to other areas of Cerrado in central Brazil. This high level of taxonomically unbalanced endemism may indicate that much of the floristic diversity observed in the campos rupestres vegetation may be the result of a relatively recent and rapid adaptive radiation, as suggested by Harley (1988) for *Eriope* Humb. & Bonpl. ex Benth. (Labiatae). This hypothesis predicts that relatively isolated areas should have floras that are composed of similar taxa, but with distinct local patterns of diversity (high beta diversity). This is exactly the pattern seen in the distribution of *Calliandra*, which is concentrated in the southern region of the Chapada Diamantina. This recent and rapid radiation can be observed in an analysis of the diversity of the two main blocks of the Espinhaço mountain range: the Espinhaço Mountains (in Minas Gerais State) and the Chapada Diamantina (in Bahia). While some groups show an explosive diversification in Minas Gerais, with relatively few species in Bahia (e.g. *Leiothrix* Ruhland (Eriocaulaceae), *Pseudotrimezia* R.C. Foster (Iridaceae), *Senna* Mill. (Leguminosae), Barbaceñoideae (Velloziaceae); Giulietti & Pirani, 1988 and *Minaria* T.U.P. Konno & Rapini (Apocynaceae); Rapini & al., 2002, 2007; Ribeiro & al., 2012), other groups show the exact opposite, with their greatest diversity in the Chapada Diamantina (e.g. *Calliandra*, *Marcetia* DC. (Melastomataceae); Giulietti & al., 1996; Santos, 2009).

Apart from the proposed taxonomic changes presented below, our results also demonstrate the importance of delimiting conservation areas within the main centers of diversity of *Calliandra* where the largest number of species and the greatest number of endemics occur. On the one hand, the significant

diversity and endemism encountered in a number of areas represents a high level of beta diversity, while on the other hand it raises the question of the fragility of these ecosystems and the urgent need for their conservation, for example, in the Chapada Diamantina where the endemic species are narrowly restricted, often with populations composed of very few individuals.

■ TAXONOMIC TREATMENT

Based on the analyses presented here, we propose a new circumscription of *Calliandra* with the inclusion of the Mexican genus *Guinetia*. We also propose a new infrageneric classification for *Calliandra* based on the well-supported clades identified in our study, describe two new sections and give sectional status to *C.* ser. *Tsugoideae*. Optimization of morphological traits defines *Calliandra* by three uniquely derived apomorphic characters: the 8-celled calymmate polyads, with an entire exine covering all grains (Fig. 5F–H; Electr. Suppl.: Fig. S1K), and the loss of foliar nectaries. The two African species excluded from *Calliandra* by Barneby (1998) are here assigned to a new genus. Besides its wide geographical disjunction, this new genus is defined by the 7-celled acalymmate polyads (Fig. 5A; Electr. Suppl.: Fig. S1K) and the presence of thorns derived from axillary branches or modified stipules.

Afrocalliandra E.R. Souza & L.P. Queiroz, **gen. nov.** – Type: *Afrocalliandra redacta* (J.H. Ross) E.R. Souza & L.P. Queiroz.

Similar to *Calliandra* in having elastically dehiscent pods with thick margins and ellipsoid polyads, but differing by the presence of thorns derived from axillary branches or modified stipules, acalymmate polyads which are 7-celled with each cell provided with internal proximal pores.

Densely branched subshrubs, branches with brachyblasts from which leaves and inflorescences emerge, axillary branches modified (or not) into thorns. Stipules herbaceous or modified into thorns. Leaves bipinnate with one pair of pinnae, extrafloral nectaries present or absent on the petiole. Inflorescences lateral, pedunculate, few-flowered heads. Flowers homomorphic, small, 8–15 mm long, sessile or with a short pedicel, filaments whitish cream, fused at the base into an included (within the corolla) or slightly exerted tube, pollen grains in 7-celled acalymmate polyads. Pods erect, oblanceolate, compressed, margins thickened, elastically dehiscent from the apex.

Two species in tropical Africa.

Afrocalliandra gilbertii (Thulin & Asfaw) E.R. Souza & L.P. Queiroz, **comb. nov.** ≡ *Calliandra gilbertii* Thulin & Asfaw in *Nordic J. Bot.* 1: 27. 1981 – Holotype: KENYA. Mandera District, War Gedud, 1 May 1978, *M.G. Gilbert & M. Thulin 1288* (UPS; isotypes: BR!, C, EA, FT, K!, MO, P!, PRE!, WAG).

Afrocalliandra redacta (J.H. Ross) E.R. Souza & L.P. Queiroz, **comb. nov.** ≡ *Acacia redacta* J.H. Ross in *Bothalia* 11: 231.

1974 ≡ *Calliandra redacta* (J.H. Ross) Thulin & Asfaw in *Nordic J. Bot.* 1: 29. 1981 – Holotype: SOUTH AFRICA. Cape Province, 22.4 km N of Sunkfontein on the way to Jenkinkop, 15 Nov. 1971, *M.J.A. Werger 1518* (PRE!; isotype: K!).

Calliandra Benth. in *J. Bot. (Hooker)* 2(11): 138. 1840, nom. cons. – Type: *C. houstoniana* (Mill.) Standl. [≡ *Mimosa houstoniana* Mill. ≡ *C. houstonii* Benth. (“*houstonii*”), nom. superfl. et illeg. ≡ *M. houstonii* L’Her. (“*houstonii*”) nom. superfl. et illeg.], typ. cons. (see Hernández & Nicolson in *Taxon* 35: 747–748. 1986).

=? *Anneslia* Salisb., *Parad. Lond.*: ad t. 64. 1807, nom. rej., non *Anneslea* Wall., *Pl. Asiat. Rar.* 1: 5. 1829, nom. cons. – Type: *A. falcifolia* Salisb., nom. superfl. et illeg. [≡ *Gleditsia inermis* L. ≡ *Calliandra inermis* (L.) Druce].

= *Clelia* Casar., *Nov. Stirp. Bras.*: 83. 1845 – Type: *C. ornata* Casar.

= *Codonandra* H. Karst., *Fl. Columb.* 2: 43. 1863 – Type: *Codonandra purpurea* H. Karst. ≡ *Calliandra codonandra* Benth.

Shrubs, treelets or subshrubs, branches with or without lateral brachyblasts. Stipules herbaceous, rarely modified into thorns. Leaves bipinnate with one to many pairs of pinnae, extrafloral nectaries absent. Inflorescences pedunculate or sessile obconical heads, lateral on brachyblasts or terminal in pseudoracemes. Flowers homomorphic or heteromorphic, sessile or with a short pedicel, filaments white, red or bicolor, rarely yellow, fused at the base into an included (within the corolla) to exerted tube, pollen grains in 8-celled calymmate polyads. Pods erect, oblanceolate, compressed, margins thickened, elastically dehiscent from the apex.

142 species (three undescribed) from America.

Anneslia and *Calliandra* were treated as homotypic synonyms (e.g., Barneby, 1998), based on *C. houstoniana*. However, Salisbury (1807) cited *Gleditsia inermis* L. as a synonym of *Anneslia falcifolia* Salisb., which makes it a superfluous and illegitimate name. The basis for the name *Gleditsia inermis* L. is a Plukenet illustration of a single leaf, the identification of which is uncertain but that is possibly a species of *Acacia* (Jarvis, 2007). Thus, *Calliandra* and *Anneslia* are heterotypic and it is not sure that they should be synonyms.

Calliandra* sect. *Calliandra

= *Calliandra* ser. *Comosae* Barneby in *Mem. New York Bot. Gard.* 74(3): 196. 1998 – Type: *C. comosa* (Sw.) Benth.

= *Calliandra* sect. *Acistegia* Barneby in *Mem. New York Bot. Gard.* 74(3): 139. 1998 – Type: *C. haematomma* (DC.) Benth.

Shrubs or subshrubs, armed or not; heads grouped in elongate, exerted, terminal pseudoracemes or a panicle of pseudoracemes or in axillary fascicles. Mexico, Guatemala, Cuba, Bahamas, Haiti, Jamaica, Porto Rico and Dominican Republic.

1. *C. comosa* (Sw.) Benth.
2. *C. houstoniana* (Mill.) Standl.
3. *C. haematomma* (DC.) Benth.
4. *C. juzepczukii* Standl.

5. *C. palmeri* S. Watson
6. *C. paniculata* C.D. Adams
7. *C. pedicellata* Benth.
8. *C. physocalyx* H.M. Hern. & M. Sousa (Fig. 1B)
9. *C. quetzal* (Donn. Sm.) Donn. Sm.
10. *C. wendlandii* Benth.

Calliandra* sect. *Septentrionales E.R. Souza & L.P. Queiroz, **sect. nov.** – Type: *C. californica* Benth., Bot. Voy. Sulphur: 14, t. 11. 1844.

= *Calliandra* ser. *Biflorae* Barneby in Mem. New York Bot. Gard. 74(3): 98. 1998 – Type: *C. biflora* Tharp.

Shrubs or densely branched subshrubs; heads grouped in axillary fascicles. United States to Mexico.

11. *C. biflora* Tharp
12. *C. californica* Benth.
13. *C. cualensis* H.M. Hern.
14. *C. dolichopoda* H.M. Hern. (Fig. 1A)
15. *C. eriophylla* Benth.
16. *C. hirsuta* Benth.

Calliandra* sect. *Androcallis Barneby in Mem. New York Bot. Gard. 74(3): 21. 1998 – Type: *C. laxa* (Willd.) Benth.

= *Calliandra* ser. *Macrophyllae* (Benth.) Barneby in Mem. New York Bot. Gard. 74(3): 111. 1998 – Type: *C. trinervia* Benth.

= *Calliandra* ser. *Pauciflorae* Barneby in Mem. New York Bot. Gard. 74(3): 101. 1998 – Type: *C. pauciflora* (A. Rich.) Griseb.

= *Calliandra* ser. *Ambivalentes* Barneby in Mem. New York Bot. Gard. 74(3): 103. 1998 – Type: *C. guildingii* Benth.

= *Calliandra* ser. *Hymenaeodeae* Barneby in Mem. New York Bot. Gard. 74(3): 134. 1998 – Type: *C. hymenaeodes* (Pers.) Benth.

= *Calliandra* ser. *Longipedes* Barneby in Mem. New York Bot. Gard. 74(3): 137. 1998 – Type: *C. longipes* Benth.

= *Calliandra* ser. *Virgatae* Barneby in Mem. New York Bot. Gard. 74(3): 189. 1998 – Type: *C. virgata* Benth.

= *Calliandra* sect. *Acroscias* Barneby in Mem. New York Bot. Gard. 74(3): 146. 1998 – Type: *C. brevicaulis* Micheli.

= *Guinetia* L. Rico & M. Sousa in Kew Bull. 54: 977. 1999, **syn. nov.** – Type: *G. tehuantepecensis* L. Rico & M. Sousa. Shrubs, treelets or subshrubs, sometimes rhizomatous; inflorescences lateral on brachyblasts or in terminal umbels (*C. brevicaulis*), the units never assembled into a terminal efoliate pseudoraceme. Distribution almost the same as for the genus, United States to Uruguay.

17. *C. angustifolia* Spruce ex Benth.
18. *C. antioquiae* Barneby
19. *C. belizensis* (Britton & Rose) Standl.
20. *C. bella* Benth.
21. *C. bijuga* Rose
22. *C. blanchetii* Benth.
23. *C. bombycina* Spruce ex Benth.
24. *C. brenesii* Standl.
25. *C. brevicaulis* Micheli
26. *C. brevipes* Benth.

27. *C. caeciliae* Harms
28. *C. carcereae* Standl. & Steyererm.
29. *C. carrascano* Barneby
30. *C. chulumania* Barneby
31. *C. colimae* Barneby
32. *C. conferta* Benth.
33. *C. coriacea* (Humb. & Bonpl. ex Willd.) Benth.
34. *C. cruegeri* Griseb.
35. *C. duckei* Barneby
36. *C. dysantha* Benth. (Fig. 1C)
37. *C. enervis* (Britton) Urb.
38. *C. erythrocephala* H.M. Hern. & M. Sousa
39. *C. falcata* Benth.
40. *C. fernandesii* Barneby
41. *C. foliolosa* Benth.
42. *C. gardneri* Benth.
43. *C. glaziovii* Taub.
44. *C. glomerulata* H. Karst.
45. *C. glyphoxylon* Spruce ex Benth.
46. *C. goldmanii* Rose ex Barneby
47. *C. guildingii* Benth.
48. *C. haematocephala* Hassk.
49. *C. harrisii* (Lindl.) Benth.
50. *C. hintonii* Barneby
51. *C. hymenaeodes* (Pers.) Benth.
52. *C. imperialis* Barneby
53. *C. jariensis* Barneby
54. *C. laevis* Rose
55. *C. laxa* (Willd.) Barneby
56. *C. longipes* Benth.
57. *C. macqueenii* Barneby
58. *C. macrocalyx* Harms
59. *C. magdalenae* (DC.) Benth.
60. *C. medellinensis* Britton & Rose ex Britton & Killip
61. *C. molinae* Standl.
62. *C. mollissima* (Humb. & Bonpl. ex Willd.) Benth.
63. *C. parvifolia* (Hook. & Arn.) Speg.
64. *C. pauciflora* (A. Rich.) Griseb.
65. *C. peninsularis* Rose
66. *C. pilgerana* Harms
67. *C. pittieri* Standl.
68. *C. pityophila* Barneby
69. *C. purdiei* Benth.
70. *C. purpurea* (L.) Benth.
71. *C. rhodocephala* Donn. Sm.
72. *C. riparia* Pittier
73. *C. rubescens* (Martens & Galeotti) Standl.
74. *C. samik* Barneby
75. *C. sesquipedalis* McVaugh
76. *C. sessilis* Benth. (Fig. 1D)
77. *C. silvicola* Taub.
78. *C. spinosa* Ducke
79. *C. squarrosa* Benth.
80. *C. staminea* (Thunb.) Barneby
81. *C. subspicata* Benth.
82. *C. surinamensis* Benth.
83. *C. taxifolia* (Kunth) Benth.

84. *Calliandra tehuantepecensis* (L. Rico & M. Sousa) E.R. Souza & L.P. Queiroz, **comb. nov.** ≡ *Guinetia tehuantepecensis* L. Rico & M. Sousa in Kew Bull. 54: 977. 1999 – Holotype: MEXICO. Oaxaca, 5 km W of Salina Cruz, *M. Sousa & al. 9117* (MEXU!; isotype K!).

85. *C. tergemina* (L.) Benth.

86. *C. tolimensis* Taub.

87. *C. trinervia* Benth.

88. *C. tumbeziana* J.F. Macbr

89. *C. tweedii* Benth.

90. *C. ulei* Harms

91. *C. umbellifera* Benth.

92. *C. virgata* Benth.

Calliandra sect. *Microcallis* Barneby in Mem. New York Bot. Gard. 74(3): 197. 1998 – Type: *C. parviflora* Benth.

= *Calliandra* ser. *Leptopodae* Barneby in Mem. New York Bot. Gard. 74(3): 199. 1998 – Type: *C. leptopoda* Benth.

= *Calliandra* ser. *Chilensis* Barneby in Mem. New York Bot. Gard. 74(3): 100. 1998 – Type: *C. chilensis* Benth.

Scandent to erect shrubs or subshrubs up to 2 m in height; phyllotaxy distichous (or exceptionally spiral in *C. chilensis*); small flowers in obconical heads or umbels terminal or in brachyblasts; perianth 3–7 mm; androecium small (from 7 to 23 mm in *C. aeschynomenoides*). The section comprises a small number of species restricted to the arid regions of northeastern Brazil: *C. aeschynomenoides*, *C. depauperata* and *C. leptopoda*; Chile: *C. chilensis*, northwestern United States (Arizona) to Mexico: *C. humilis*, and one widely distributed species in extra-Amazonian Brazil, Paraguay and Bolivia: *C. parviflora*.

93. *C. aeschynomenoides* Benth. (Fig. 1O)

94. *C. chilensis* Benth.

95. *C. depauperata* Benth. (Fig. 1M)

96. *C. humilis* Benth.

97. *C. leptopoda* Benth. (Fig. 1N)

98. *C. parviflora* Benth.

Calliandra sect. *Monticola* E.R. Souza & L.P. Queiroz, **sect. nov.** – Type: *C. calycina* Benth.

Treelets to densely branched shrubs or rhizomatous subshrubs; inflorescences of terminal pseudoracemes, never axillary, mostly inserted amongst the foliage; brachyblasts absent. Distributed in the Espinhaço mountain range (Bahia and Minas Gerais, Brazil), in mountainous regions, especially rocky fields (campos rupestres).

99. *C. asplenioides* (Nees) Renvoize

100. *C. bahiana* Renvoize (Fig. 1G)

101. *C. calycina* Benth. (Fig. 1K)

102. *C. coccinea* Renvoize (Fig. 1H)

103. *C. concinna* Barneby

104. *C. crassipes* Benth.

105. *C. cumbcana* Renvoize

106. *C. debilis* Renvoize

107. *C. elegans* Renvoize

108. *C. erubescens* Renvoize

109. *C. fasciculata* Benth.

110. *C. feioana* Renvoize

111. *C. fuscipila* Harms

112. *C. ganevii* Barneby

113. *C. geraisensis* E.R. Souza & L.P. Queiroz

114. *C. germana* Barneby

115. *C. hirsuticaulis* Harms

116. *C. hirtiflora* Benth.

117. *C. hygrophila* Mackinder & G.P. Lewis

118. *C. iligna* Barneby

119. *C. imbricata* E.R. Souza & L.P. Queiroz

120. *C. involuta* Mackinder & G.P. Lewis

121. *C. lanata* Benth. (Fig. 1F)

122. *C. linearis* Benth.

123. *C. lintea* Barneby

124. *C. longipinna* Benth. (Fig. 1L)

125. *C. luetzelburgii* Harms

126. *C. mucugeana* Renvoize

127. *C. nebulosa* Barneby

128. *C. paganuccii* E.R. Souza

129. *C. paterna* Barneby

130. *C. renvoizeana* Barneby

131. *C. santosiana* Glaz. ex Barneby

132. *C. semiseputa* Barneby (Fig. 1I)

133. *C. sincorana* Harms

134. *C. stelligera* Barneby (Fig. 1J)

135. *C. viscidula* Benth.

Calliandra sect. *Tsugoideae* (Barneby) E.R. Souza & L.P. Queiroz, **stat. nov.** ≡ *C.* ser. *Tsugoideae* Barneby in Mem. New York Bot. Gard. 74(3): 190. 1998 – Type: *C. tsugoides* R.S. Cowan.

Treelets or shrubs, similar to *C.* sect. *Calliandra* in having terminal (never axillary) pseudoracemose inflorescences (these sometimes only shortly exerted from the foliage), but distinguished from other species of the genus by the parallel primary venation of the leaflets; brachyblasts absent. Guayana Highland and sand savannas in the Guianas, Venezuela, the Colombian Amazon and the northern state of Amazonas, Brazil.

136. *C. pakaraimensis* R.S. Cowan

137. *C. rigida* Benth.

138. *C. tsugoides* R.S. Cowan

139. *C. vaupesiana* R.S. Cowan

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Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study. Voucher data is given for accessions for which DNA sequences were newly obtained, using the following format: Taxon name, country, largest political subdivision, collector and collector number, herbarium acronym, ITS, *trnL-trnF* GenBank accession numbers. –, missing data; *, newly generated sequences.

Abarema floribunda (Benth.) Barneby & J.W. Grimes, Brazil, Bahia, L.P. de Queiroz 13930 (HUEFS), JX870654*, JX870786*; *Abarema piresii* Barneby & J.W. Grimes, Brazil, Amazonas, P.A.C.L. Assunção 411 (INPA), JX870655*, –, *Abarema piresii* Barneby & J.W. Grimes, Brazil, Amazonas, L.P. de Queiroz 13911 (HUEFS), –, JX870787*; *Acacia spinescens* Benth., AF360700, AF19706; *Afrocalliandra gilbertii* (Thulin & Asfaw) E.R. Souza & L.P. Queiroz, Kenya, Mandara, M. Tardelli 67 (K), JX870690*, –, *Afrocalliandra redacta* (J.H. Ross) E.R. Souza & L.P. Queiroz, Africa, Cape Province, *Oliver* 338 (K), JX870732*, JX870853*; *Albizia polycephala* (Kunth) Killip, Brazil, Bahia, R.M. Harley 54554 (K), JX870656*, –, *Albizia polycephala* (Kunth) Killip, Brazil, Bahia, D. Cardoso 253 (HUEFS), –, JX870788*; *Archidendron hirsutum* I.C. Nielsen, –, AF365042.1; *Balizia pedicellaris* (DC.) Barneby & J.W. Grimes, Brazil, Bahia, E.R. de Souza 358 (HUEFS), JX870657*, JX870799*; *Blanchetiodendron blanchetii* (Benth.) Barneby & J.W. Grimes, Brazil, Bahia, L.P. de Queiroz 7085 (HUEFS), JX870658*, JX870790*; *Calliandra aeschynomoides* Benth., Brazil, Bahia, E.R. de Souza 390 (HUEFS), JX870659*, JX870790*; *Calliandra angustifolia* Spruce ex. Benth., Bolivia, Cochabamba, J.R.I. Wood 16132 (K), JX870660*, JX870792*; *Calliandra asplenoides* (Nees) Renvoize, Brazil, Bahia, E.R. de Souza 601 (HUEFS), JX870661*, JX870793*; *Calliandra bahiana* Renvoize, Brazil, Bahia, E.R. de Souza 562 (HUEFS), JX870664*, JX870796*; *Calliandra bahiana* Renvoize, Brazil, Bahia, L.P. de Queiroz 14550 (HUEFS), JX870662*, JX870795*; *Calliandra bahiana* Renvoize, Brazil, Bahia, A. Rapini 1047 (HUEFS), JX870663*, JX870794*; *Calliandra belizensis* (Britton & Rose) Standl., Honduras, Belize, C.L. Lundell 148 (K), JX870665*, –, *Calliandra bella* (Spreng.) Benth., Brazil, Bahia, M.L.C. Neves 16 (HUEFS), JX870666*, JX870797*; *Calliandra biflora* Tharp, Mexico, J.M. Aguilar P. 1111 (MEXU), JX870667*, JX870798*; *Calliandra blanchetii* Benth., Brazil, Bahia, E.R. de Souza 813 (HUEFS), JX870668*, JX870799*; *Calliandra brenesii* Standl., Costa Rica, Guanacaste, D.J. Macqueen 122 (K), –, JX870800*; *Calliandra brenesii* Standl., Costa Rica, Alajuelo, A. Estrada 2394 (K), JX870669*, –, *Calliandra brevicaulis* M. Micheli, S. Caceres 362 (K), JX870670*, JX870801*; *Calliandra brevipes* Benth., Brazil, Bahia, L.P. de Queiroz 12630 (HUEFS), JX870671*, JX870802*; *Calliandra caeciliae* Harms, Mexico, T.S. Cochrane 13160 (MEXU), JX870674*, JX870803*; *Calliandra californica* Benth., Mexico, Baja California, M.E. Jones 22440 (MEXU), JX870672*, –, *Calliandra calycina* Benth., Brazil, Bahia, E.R. de Souza 333 (HUEFS), JX870673*, JX870804*; *Calliandra chilensis* Benth., Chile, Huasco, M. Acosta BB 018 (K), JX870675*, –, *Calliandra coccinea* Renvoize, Brazil, Bahia, A. Rapini 1046 (HUEFS), JX870676*, JX870805*; *Calliandra coriacea* (Humb. & Bonpl. ex Willd.) Benth., Panama, D.J. Macqueen 623 (K), JX870677*, JX870806*; *Calliandra crassipes* Benth., Brazil, Bahia, E.R. de Souza 378 (HUEFS), JX870678*, JX870807*; *Calliandra cruegeri* Griseb., Trinidad, W. Johnson 927 (K), JX870679*, JX870808*; *Calliandra cubucana* Renvoize, Brazil, Bahia, E.R. de Souza 361 (HUEFS), JX870680*, JX870809*; *Calliandra debilis* Renvoize, Brazil, Bahia, L.P. de Queiroz 13734 (HUEFS), JX870681*, JX870810*; *Calliandra depauperata* Benth., Brazil, Bahia, E.R. de Souza 412 (HUEFS), JX870682*, JX870811*; *Calliandra dolichopoda* H.M. Hern., Mexico, Guerrero, R.T. Colin 16771 (MEXU), JX870683*, –, *Calliandra dysantha* Benth., Brazil, Bahia, E.R. de Souza 344 (HUEFS), JX870684*, JX870813*; *Calliandra eriophylla* Benth., Mexico, R.T. Colin 14773 (MEXU), JX870685*, –, *Calliandra erubescens* Renvoize, Brazil, Bahia, E.R. de Souza 338 (HUEFS), JX870686*, JX870812*; *Calliandra fasciculata* Benth., Brazil, Minas Gerais, E.R. de Souza 346 (HUEFS), JX870687*, JX870814*; *Calliandra feioana* Renvoize, Brazil, Bahia, E.R. de Souza 637 (HUEFS), JX870688*, –, *Calliandra gardneri* Benth., Brazil, Goiás, G. Hatschbach 60415 (HUEFS), –, JX870816*; *Calliandra glomerulata* H. Karst., Panama, Coclé, M.N. Stapf 368 (HUEFS), JX870691*, JX870817*;

Appendix 1. Continued.

Calliandra glyphoxylon Spruce ex Benth., Ecuador, Chimborazo, *W.H. Camp 3177* (K), –, JX870819*; *Calliandra goldmanii* Rose ex Barneby, Mexico, Chiapas, *C.E. Hughes 1493* (K), JX870692*, JX870818*; *Calliandra guildingii* Benth., Trinidad, Northern Hills, *D. Hollis M48* (K), JX870693*, JX870820*; *Calliandra haematocephala* Hassk., Bolivia, Santa Cruz, *D. Soto 1235* (USZ), JX870694*, JX870821*; *Calliandra haematomma* Benth., Dominican Republic, *M. Fuertes 1927*, P, JX870695*, JX870822*; *Calliandra harrisii* (Lindl.) Benth., Brazil, Bahia, *J.R.I. Wood 17334* (K), JX870696*, JX870823*; *Calliandra hintonii* Barneby, Mexico, Temascaltepec, *G.B. Hinton 4099* (K), JX870697*, JX870824*; *Calliandra hirsuta* Benth., Mexico, Guerrero, *A. Salinas T. 8203* (MEXU), JX870698*, –, *Calliandra hirtiflora* Benth., Brazil, Bahia, *E.R. de Souza 360* (HUEFS) JX870699*, JX870825*; *Calliandra houstoniana* (Mill.) Standl., Mexico, Guerrero, *R.T. Colin 16765* (MEXU), JX870700*, JX870826*; *Calliandra humilis* Benth., *P. Tenório L. 5970* (MEXU), JX870701*, –, *Calliandra hygrophila* Mackinder & G.P. Lewis, Brazil, Bahia, *E.R. de Souza 331* (HUEFS), JX870702*, JX870827*; *Calliandra iligna* Barneby, Brazil, Minas Gerais, *J.R. Pirani 4163* (HUEFS), JX870703*, JX870828*; *Calliandra juzepczukii* Standl., Mexico, Oaxaca, *M.T. Walter 2675* (HUEFS), JX870829*; *Calliandra laevis* Rose, Mexico, Jalisco, *D.J. Macqueen 617* (K), JX870704*, JX870830*; *Calliandra lanata* Benth., Brazil, Bahia, *A. Rapini 1045* (HUEFS), JX870705*, JX870831*; *Calliandra laxa* (Willd.) Benth., *S.M. Souza 13374* (MEXU), JX870707*, –, *Calliandra laxa* (Willd.) Benth., *G.T. Prance 29534* (MEXU), JX870706*, JX870832*; *Calliandra leptopoda* Benth., Brazil, Bahia, *G.P. Lewis 1884* (K), JX870708*, JX870833*; *Calliandra lintea* Barneby, Brazil, Bahia, *E.R. de Souza 350* (HUEFS), JX870709*, JX870834*; *Calliandra longipes* Benth., Brazil, Goiás, *B.M.T. Walter 2675* (HUEFS), JX870710*, JX870835*; *Calliandra longipinna* Benth., Brazil, Bahia, *E.R. de Souza 376* (HUEFS), JX870711*, JX870836*; *Calliandra luetzelburgii* Harms, Brazil, Bahia, *E.R. de Souza 340* (HUEFS), JX870712*, JX870837*; *Calliandra macrocalyx* Harms, Brazil, Bahia, *L.P. de Queiroz 9111* (HUEFS), JX870713*, –, *Calliandra macrocalyx* Harms, Brazil, Bahia, *E.R. de Souza 413* (HUEFS), –, JX870838*; *Calliandra magdalenae* (Bertero ex DC.) Benth., Costa Rica, San Jose, *Q. Jimenez 1883* (K), JX870714*, JX870839*; *Calliandra molinae* Standl., Honduras, Francisco Morazan, *M. Chorley 1* (BM), JX870715*, –, JX870840*; *Calliandra mollissima* (Humb. & Bonpl. ex Willd.) Benth., Peru, Amazonas, *T.D. Pennington 16851* (K), JX870716*, JX870841*; *Calliandra mucugeana* Renvoize, Brazil, Bahia, *E.R. de Souza 329* (HUEFS), JX870717*, JX870842*; *Calliandra nebulosa* Barneby, Brazil, Bahia, *E.R. de Souza 342* (HUEFS), JX870718*, JX870843*; *Calliandra paganuccii* E.R. Souza, Brazil, Bahia, *S. Leython 854* (HUEFS), JX870720*, –, *Calliandra paganuccii* E.R. Souza, Brazil, Bahia, *E.R. de Souza 524* (HUEFS), JX870719*, –, *Calliandra palmeri* S. Watson, Mexico, Jalisco, *D.J. Macqueen 200* (K), JX870721*, –, *Calliandra parviflora* Benth., Bolivia, Santa Cruz, *D. Soto 1195* (USZ), JX870723*, –, *Calliandra parviflora* Benth., Brazil, Bahia, *J.R.I. Wood 19934* (K), JX870722*, JX870844*; *Calliandra parvifolia* (Hook & Arn.) Speg., Brazil, Bahia, *E.R. de Souza 357* (HUEFS), JX870724*, JX870845*; *Calliandra paterna* Barneby, Brazil, Bahia, *E.R. de Souza 353* (HUEFS), JX870725*, JX870846*; *Calliandra pedicellata* Benth., Haiti, *E.L. Ekman 985* (K), JX870726*, JX870847*; *Calliandra peninsularis* Rose, Mexico, Baja California Sur, *C.E. Hughes 1493* (K), –, JX870848*; *Calliandra physocalyx* H.M. Hern. & M. Sousa, Mexico, Guerrero, *R.T. Colin 16773* (MEXU), JX870727*, –, *Calliandra pilgerana* Harms, Brazil, Bahia, *T.S. Nunes 980* (HUEFS), JX870728*, JX870849*; *Calliandra pittieri* Standl., *B.B. Klitgaard 649* (K), JX870729*, JX870850*; *Calliandra purdiei* Benth., Ecuador, Napo, *Spruce* (K), JX870730*, JX870851*; *Calliandra purpurea* (L.) Benth., Martinique, Cap Salomon, *D.C. Daly 5310* (K), JX870731*, JX870852*; *Calliandra renvoizeana* Barneby, Brazil, Bahia, *E.R. de Souza 383* (HUEFS), JX870733*, JX870854*; *Calliandra rhodocephala* Donn. Sm., Costa Rica, Alajuela, *W. Haber 11246* (K), JX870734*, –, *Calliandra riparia* Pittier, Brazil, Bahia, *J.L. Hage 1860* (HUEFS), JX870735*, –, *Calliandra rubescens* (M. Martens & Galeotti) Standl., *M. Sousa 8600* (MEXU), JX870736*, JX870855*; *Calliandra semisepulta* Benth., Brazil, Bahia, *E.R. de Souza 688* (HUEFS), –, JX870856*; *Calliandra semisepulta* Barneby, Brazil, Bahia, *E.R. de Souza 544* (HUEFS), JX870737*, –, *Calliandra sessilis* Benth., Brazil, Bahia, *C. Correia 105* (HUEFS), JX870738*, JX870857*; *Calliandra silvicola* Taub., Brazil, DF – Brasília, *H.S. Irwin 6204* (K), JX870739*, JX870858*; *Calliandra sincorana* Harms, Brazil, Bahia, *E.R. de Souza 359* (HUEFS), JX870740*, –, *Calliandra sincorana* Harms, Brazil, Bahia, *E.R. de Souza 355* (HUEFS), –, JX870859*; *Calliandra sp.*, Brazil, Bahia, *M.L.S. Guedes 14602* (ALCB), JX870742*, JX870861*; *Calliandra sp.*, Brazil, Bahia, *E.R. de Souza 548* (HUEFS), JX870743*, –, *Calliandra sp.*, Brazil, Bahia, *E.R. de Souza 558* (HUEFS), JX870744*, JX870863*; *Calliandra sp.*, Brazil, Bahia, *L.P. de Queiroz 9281* (HUEFS), JX870746*, JX870864*; *Calliandra sp.*, Brazil, Bahia, *E.R. de Souza 514* (HUEFS), JX870745*, JX870862*; *Calliandra spinosa* Ducke, Brazil, Bahia, *E.R. de Souza 138* (HUEFS), JX870741*, JX870860*; *Calliandra surinamensis* Benth., Brazil, Pará, *J. Jardim 4524* (HUEFS), JX870747*, JX870865*; *Calliandra taxifolia* (Kunth) Benth., Ecuador, Loja, *J.E. Madsen 8368-B* (K), JX870748*, JX870866*; *Calliandra tehuantepecensis* (L. Rico & M. Sousa) E.R. Souza & L.P. Queiroz, Mexico, Oaxaca, *M. Sousa 7433* (K), JX870761*, JX870877*; *Calliandra tergemina* (L.) Benth., *D. Neel 5513* (MEXU), JX870749*, JX870867*; *Calliandra trinervia* Benth., –, *AF365044.1*; *Calliandra trinervia* Benth., –, *AF278516*; *Calliandra tsgooides* R.S. Cowan, *G.T. Prance 28958* (MEXU), JX870750*, –, *Calliandra tumbeziana* J.F. Macbr., Peru, Piura, *R.J. Eastwood 119* (K), JX870751*, JX870868*; *Calliandra tweedii* Benth., Brazil, Rio Grande do Sul, *G. Hatschbach 61367* (HUEFS), JX870752*, –, *Calliandra ulei* Harms, Brazil, Piauí, *L.P. de Queiroz 14769* (HUEFS), JX870689*, JX870815*; *Calliandra umbellifera* Benth., Brazil, Piauí, *L.P. Félix 7825* (HUEFS), JX870753*, JX870869*; *Calliandra vaupesiana* R.S. Cowan, Colombia, Caquetá, *J. Duivenvoorden 271* (K), JX870754*, JX870870*; *Calliandra virgata* Benth., Brazil, Goiás, Luziânia, *G. Hatschbach 54373* (HUEFS), JX870755*, –, *Calliandra virgata* Benth., Brazil, Distrito Federal, Planaltina, *F.H.F. Oldenburger 1879* (K), –, JX870871*; *Calliandra viscidula* Benth., Brazil, Bahia, *E.R. de Souza 327* (HUEFS), –, JX870872*; *Calliandra viscidula* Benth., Brazil, Bahia, *E.R. de Souza 332* (HUEFS), JX870756*, –, *Cedrelinga cateniformis* (Ducke) Ducke, Brazil, Manaus, *J.R. Nascimento 674* (INPA), JX870757*, JX870873*; *Cajoba arborea* (L.) Britton & Rose, *M. Chase 8244* (K), JX870758*, JX870874*; *Cajoba catenata* (Donn.Sm.) Britton & Rose, –, *AY944538.1*; *Cajoba rufescens* (Benth.) Britton & Rose, *EF638187*, –, *Ebenopsis ebano* (Berland.) Barneby & J.W. Grimes, Mexico, *Q.B.A.F. Ku 358* (MEXU), JX870759*, JX870875*; *Enterolobium timbouva* Mart., Brazil, Bahia, *L.P. de Queiroz 7973* (HUEFS), JX870760*, JX870876*; *Havardia mexicana* Britton & Rose, Mexico, *E. Joyal 2019* (MEXU), JX870762*, JX870878*; *Hydrochorea corymbosa* (Rich.) Barneby & J.W. Grimes, Brazil, Pará, *G.C. Ferreira 571* (K), JX870763*, JX870879*; *Inga edulis* Mart., Brazil, Bahia, *L.P. de Queiroz 13797* (HUEFS), JX870764*, JX870880*; *Inga thibaudiana* DC., Brazil, Manaus, *M.A.S. Costa 1001* (INPA), JX870765*, JX870881*; *Leucochloron lima* Barneby & J.W. Grimes, Brazil, Bahia, *M. Chase 8250* (K), JX870766*, JX870882*; *Macrosamanea pubiramea* (Steud.) Barneby & J.W. Grimes, Venezuela, Amazonas, *J. Jardim 4595* (HUEFS), JX870767*, JX870883*; *Pithecellobium diversifolium* Benth., Brazil, Bahia, *L.P. de Queiroz 3740* (K), JX870768*, JX870884*; *Pseudosamanea guachapele* Harms, Ecuador, Guayas, *J.E. Madsen 83914* (K), JX870769*, JX870885*; *Samanea saman* (Jacq.) Merr., Brazil, Bahia, *E.R. de Souza 386* (HUEFS), JX870770*, JX870886*; *Sphinga acatlensis* (Benth.) Barneby & J.W. Grimes, Mexico, *A. Martinez B. 339* (MEXU), JX870771*, JX870887*; *Thailentadopsis nitida* (Vahl) G.P. Lewis & Schrire, Sri Lanka, Ceylon, *A. Kostermans 28234* (K), JX870772*, JX870888*; *Thailentadopsis tenuis* (Craib) Kosterm., Thailand, Kanchanaburi, *K & S.S. Larsen 33960* (K), –, JX870889*; *Viguieranthus ambongensis* (R. Vig.) Villiers, Africa, Madagascar, *J.N. Labat 2197* (K), JX870773*, JX870890*; *Viguieranthus densinervis* Villiers, Africa, Madagascar, *SF 12564* (K), JX870774*, JX870891*; *Viguieranthus glaber* Villiers, Africa, Madagascar, *D.J. Du Puy M247* (K), JX870775*, JX870892*; *Viguieranthus konyi* (R. Vig.) Villiers, Africa, Madagascar, *R. Rakoto 296* (P), JX870776*, –, *Viguieranthus megalophyllus* (R. Vig.) Villiers, Africa, Madagascar, *R. Rabehohitra 2354* (P), JX870777*, –, *Viguieranthus subauriculatus* Villiers, Africa, Madagascar, *D. Turk 107* (P), JX870778*, –, *Zapoteca alinae* H.M. Hern., Mexico, *G. Manzanero M. 1137* (MEXU), JX870779*, JX870893*; *Zapoteca filipes* (Benth.) H.M. Hern., Brazil, Minas Gerais, *E.R. de Souza 324* (HUEFS), JX870780*, JX870896*; *Zapoteca formosa* (Kunth) H.M. Hern., Mexico, *M. Sousa 9491* (HUEFS), JX870781*, JX870897*; *Zapoteca lambertiana* (G. Don) H.M. Hern., Mexico, *A.L.H. Mayfield 854* (MEXU), JX870782*, JX870894*; *Zapoteca media* (M. Martens & Galeotti) H.M. Hern., Mexico, *E. Torrecillas 68* (MEXU), –, JX870895*; *Zapoteca sousae* H.M. Hern. & A. Campos, Mexico, *A. Campos 5224* (MEXU), JX870783*, JX870898*; *Zapoteca tetragona* (Willd.) H.M. Hern., Mexico, *G. Flores F. 669* (MEXU), JX870784*, JX870899*; *Zygia racemosa* (Ducke) Barneby & J.W. Grimes, Brazil, Manaus, *J.E.L.S. Ribeiro 1383* (INPA), JX870785*, JX870900*.