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A molecular phylogeny of *Caesalpinia* sensu lato: Increased sampling reveals new insights and more genera than expected

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ABSTRACT

Caesalpinia sensu lato, in its broadest circumscription, is a pantropical group of c.150 species of trees, shrubs and lianas many of which grow in arid habitats of the Succulent Biome (sensu Schrire et al., 2005), and especially in the seasonally dry tropical forests of Central and South America and the Caribbean. As traditionally circumscribed, *Caesalpinia* s.l. was one of the largest genera in tribe Caesalpinieae, but seven generic segregates, namely *Coulteria*, *Erythrostemon*, *Guilandina*, *Libidibia*, *Mezoneuron*, *Poincianella* and *Tara* were reinstated by Lewis (2005), greatly reducing the number of species remaining in *Caesalpinia* sensu stricto. Nevertheless, doubts remain regarding the monophyly and delimitation of some of these segregate genera, which have not been thoroughly tested using molecular data, and this has hindered the establishment of a comprehensive generic classification of the broader *Caesalpinia* Group as a whole. Here we present a new phylogeny of the *Caesalpinia* Group, based on plastid *rps16* sequences and dense taxon sampling including 18 of the 21 genera of the *Caesalpinia* Group and 98 of the c.150 species of *Caesalpinia* s.l. Our results support the monophyly of five of the genera reinstated by Lewis, but the three other genera (including *Caesalpinia* s.s.) are non-monophyletic and need to be re-evaluated. Furthermore, three robustly supported newly discovered clades within *Caesalpinia* s.l. potentially merit recognition as distinct genera pending complete investigation of diagnostic morphological characters. Uncertainties concerning the delimitation of some clades are discussed especially in relation to the extensive morphological variation found within *Caesalpinia* s.l.

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1. Introduction

Caesalpinia sensu lato (Leguminosae subfamily Caesalpinioideae), as traditionally circumscribed, is a pantropical group of about 150 species of trees, shrubs and lianas that mostly grow in seasonally dry and semi-arid habitats of the Succulent biome (sensu Schrire et al., 2005) and especially in seasonally dry tropical forests (SDTF) in the Neotropics. The genus in its broadest sense not only needs taxonomic revision at the species level, but also reorganisation at the intra-generic level. While both morphological and molecular phylogenetic analyses (Bruneau et al., 2008; Lewis and Schrire, 1995; Manzanilla and Bruneau, 2012; Nores et al., 2012; Simpson and Miao, 1997; Simpson et al., 2003) have clearly demonstrated that *Caesalpinia* s.l. is not monophyletic, the lack of a densely sampled and robustly supported phylogeny has left many doubts about how many genera should be recognised and how they should be delimited.

Caesalpinia s.l. is part of the larger informal *Caesalpinia* Group of tribe Caesalpinieae, which has a long and complex taxonomic history (reviewed by Lewis, 1998, 2005). In brief, the number of genera in the *Caesalpinia* Group has been modulated by the varying size of the genus *Caesalpinia*, both in terms of its species and generic nomenclatural composition, with 25 generic names having been, at one time or another, placed in synonymy under a broadly circumscribed *Caesalpinia* s.l.

The informal *Caesalpinia* Group proposed by Polhill and Vidal (1981) originally comprised 16 genera, including the then broadly circumscribed genus *Caesalpinia*. This group was considered to be one of the most distinctive of the nine informal generic groups in the Caesalpinieae tribe, based on a set of morphological characters that included the presence of a lower cucullate sepal on the calyx, as well as the highest occurrence and diversity of spines, thorns, trichomes and secretory structures within the tribe. Based largely on these characters, Polhill and Vidal (1981) also included *Conzattia*, *Lemuropisum* and *Parkinsonia* in the *Caesalpinia* Group, but these three genera were subsequently shown to belong to the *Peltophorum* Group (Bruneau et al., 2001; Haston et al., 2005; Lewis and Schrire, 1995). Within their

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Caesalpinia Group, Polhill and Vidal (1981) also recognised a number of genera with consistently pinnate (rather than bipinnate) leaves, including *Cenostigma*, *Cordeauxia*, *Stahlia*, *Stuhlmannia*, and *Zuccagnia*.

More recently, Lewis (2005) proposed the reinstatement of eight genera, including *Caesalpinia* s.s. (Table 1 in bold) from within *Caesalpinia* s.l., bringing the number of recognised genera in the Caesalpinia Group to 21. As noted by Lewis (2005), the monophyly of these reinstated genera remains to be tested, firm generic boundaries must be determined to ensure correct generic placement of all species of *Caesalpinia* s.l., and morphological support and diagnosability need to be established for each genus. To date, no adequately sampled and robust molecular phylogeny has been available to test the proposed genus-level classification of the Caesalpinia Group. Furthermore, there are some 15 species, mainly Asian taxa, of uncertain generic affinities that are presently unassigned to any segregate genus. Lewis (2005) pointed out that it was critical for these Asian taxa to be included in molecular analyses before they could be assigned to any one genus with confidence, and before a comprehensive new generic system for the Caesalpinia group could be established.

Caesalpinia s.l. encapsulates the difficulties and dilemmas surrounding generic delimitation. To date it has been difficult, due to inadequate sampling of either morphological or molecular data, to establish stable groups that have predictive taxonomic value, in the sense that this permits reliable prediction of specific attributes for taxa that have not been characterised or formally described (Humphreys and Linder, 2009). This is one of the main difficulties in the classification of *Caesalpinia* s.l.: the apparent lack of obvious diagnostic morphological synapomorphies for some genera that would provide a clear basis for assigning to genera

species that have not been sampled in molecular phylogenies. This is partly due to high levels of homoplasy for many morphological characters in *Caesalpinia* s.l. As a result, certain authors, including Bentham (1865), considered *Caesalpinia* to be a single large polymorphic genus best divided at the infrageneric level into several sections. Others have argued that *Caesalpinia* should be separated into several genera based on specific subsets of morphological characters. For example, Britton and Rose (1930) recognised 16 genera from within *Caesalpinia* s.l. based mostly on fruit characters. A number of in-depth morphological, phytochemical and anatomical studies have presented diverse new evidence for phylogenetic analysis and generic delimitation, but none have achieved the comprehensive taxon sampling needed to definitively support the division of *Caesalpinia* s.l. These include studies on floral development and ontogeny (Kantz and Tucker, 1994; Kantz, 1996; Rudall et al., 1994), phytochemistry of non-protein amino acids in seeds (Kite and Lewis, 1994), leaf anatomy and secretory structures (Lersten and Curtis, 1994, 1996; Herendeen et al., 2003; Rudall et al., 1994), and wood anatomy (Gasson et al., 2009).

The other challenge is that species of the Caesalpinia Group and *Caesalpinia* s.l. occur on all five continents, and it has thus been difficult to obtain fresh leaf material or DNA samples of all relevant taxa. Furthermore, many species are locally abundant, but narrowly distributed endemics, particularly those that grow in SDTF (Linares-Palomino, 2006; Linares-Palomino et al., 2011; Pennington et al., 2009), some of them only described within the last decade (*Caesalpinia celendiniana*, *Caesalpinia pluviosa* var. *maraniona*, Lewis et al., 2010; *Caesalpinia oyamae*, Sotuyo and Lewis, 2007), requiring highly targeted fieldwork

Table 1
Generic delimitation of *Caesalpinia* s.l. proposed by Lewis (2005). In bold, genera reinstated by Lewis (2005). Geographic distribution: Africa (AF), Asia (AS), Caribbean, Central America (CA), North America (NA), South America (SA).

Generic names	# species	Synonyms	Geographic distribution
<i>Balsamocarpon</i> Clos.	1		SA
<i>Cenostigma</i> Tul.	2		SA
<i>Cordeauxia</i> Hemsl.	1		AF
<i>Hoffmannseggia</i> Cav.	24	<i>Larrea</i> Ortega <i>Larrea</i> auct. Cav. <i>Moparia</i> Britton & Rose	NA, SA
<i>Pomaria</i> Cav.	16	<i>Melanosticta</i> DC. <i>Cladotrichium</i> Vogel	NA, SA, AF
<i>Haematoxylum</i> L.	4	<i>Haematoxylon</i> L. <i>Cymbosepalum</i> Baker	CA, SA, AF
<i>Lophocarpinia</i> Burkart	1		SA
<i>Moullava</i> Adans.	1	<i>Watagea</i> Dalzell	AS
<i>Pterolobium</i> R.Br. ex Wight & Arn.	11	<i>Cantuffa</i> J.F.Gmel. <i>Reichardia</i> Roth	AF, AS
<i>Stenodrepanum</i> Harms	1		SA
<i>Stuhlmannia</i> Taub.	1		AF
<i>Stahlia</i> Bello	1		Caribbean
<i>Zuccagnia</i> Cav.	1		SA
<i>Coulteria</i> Kunth	9–10	<i>Guaymasia</i> Britton & Rose <i>Brasilettia</i> sensu Britton & Rose	CA
<i>Tara</i> Molina	3	<i>Russelodendron</i> Britton & Rose <i>Nicargo</i> Britton & Rose <i>Schrammia</i> Britton and Rose (1930)	SA
<i>Erythrostemon</i> (Hook.) Klotzsch	13		SA
<i>Poinciana</i> Britton & Rose	~35		CA
<i>Guilandina</i> L.	7–18	<i>Bonduc</i> Mill. <i>Caesalpinia</i> subgenus <i>Guilandina</i> (L.) Gillis & Proctor	Pantropical
<i>Libidibia</i> (DC.) Schltld.	6–8	<i>Caesalpinia</i> sect. <i>Libidibia</i> DC. (1825)	CA, SA
<i>Mezoneuron</i> Desf.	26	<i>Mezoneuron</i> DC. <i>Caesalpinia</i> subgenus <i>Mezoneuron</i> Desf. ex Herendeen & Zarucchi	AS
<i>Caesalpinia sensu stricto</i> L.	~25	<i>Poinciana</i> L. <i>Brasilettia</i> (DC.) Kuntze	CA, SA, Caribbean
Unplaced Old World Taxa	~15	<i>Biancaea</i> Tod. <i>Campecia</i> Adans. <i>Cinclidocarpus</i> Zoll. <i>Ticanto</i> Adans. <i>Caesalpinia</i> sect. <i>Sappania</i> DC. <i>Caesalpinia</i> sect. <i>Nugaria</i> DC. <i>Caesalpinia</i> sect. <i>Cinclidocarpus</i> (Zoll.) Benth. & Hook. f.	AS, AF

Table 2

Accessions included in this study. Species of the *Caesalpinia* group are classified sensu Lewis (2005), and the number of species sampled over the total number of species recognised in the genus is given in parentheses. Type species for genera in the *Caesalpinia* Group are preceded by an asterisk (*). Collector names and numbers (and herbarium acronym) of voucher specimens are listed for all material that was taken from herbarium specimens and for the voucher specimens of seed collections and silica-dried leaf samples, if known. Accession numbers are provided for published sequences downloaded directly from Genbank: Haston et al. (2005), Marazzi and Sanderson (2010) and Marazzi et al. (2006).

Genus (no. of species sampled/total no. species) Species	Voucher specimen (herbarium)	Collection locality	Genbank accession number
Outgroup			
<i>Acrocarpus fraxinifolius</i> Wight & Arn.	Faden 74/1314 (K: Krukoff), Haston V200301 (RNG)	Kenya	AY899741
<i>Acrocarpus fraxinifolius</i> Wight & Arn	Manos 1416 (DUKE)	China, cultivated	KF522306
<i>Arapatiella emarginata</i> R.S. Cowan	Thomas 10913 (K)	Brazil	AY899746
<i>Arcoa gonavensis</i> Urb.	Jiménez 3522 (JSBD)	Dominican Republic	KF522309
<i>Batesia floribunda</i> Spruce ex Benth.	Ricker et al. 11 (K)	Peru	AY899745
<i>Bussea sakalava</i> Du Puy & R. Rabev.	Capuron 23.331_SF (K)	Madagascar	AY899766
<i>Cassia javanica</i> L.	Fougère-Danezan 6 (MT)	Singapore, cultivated	KF522255
<i>Cassia fistula</i> L.	Marazzi & Flores BM177 (MEXU, Z)	Mexico, cultivated	AM086915
<i>Ceratonia oreoethauma</i> Hillc. & al.	Muntun 16 (K)	Oman	KF522310
<i>Ceratonia siliqua</i> L.	Wieringa & Janzen 3477 (WAG)	Greece	KF522311
<i>Cercidium andicola</i> Griseb.	Hughes & Forrest 2313 (K)	Bolivia	AY899779
<i>Chamaecrista acosmifolia</i> (Benth.) H.S.Irwin & Barneby	Conceição & Marazzi AC1129 (HUEFS, Z)	Brazil	AM086584
<i>Chamaecrista desvauxii</i> (Collad.) Killip	Marazzi et al. BM013 (Z, CTES, PY)	Paraguay	AM086911
<i>Chamaecrista nictitans</i> Moench	Klitgaard et al. 686 (K)	Ecuador	KF522254
<i>Chamaecrista nictitans</i> Moench	Marazzi et al. BM034 (Z, CTES, PY)	Paraguay	AM086912
<i>Chamaecrista serpens</i> Greene	Marazzi & Flores BM179 (Z, CTES, PY)	Mexico	AM086913
<i>Colvillea racemosa</i> Bojer ex Hook.	Haston V200302 (RNG)	Madagascar	KF522247
<i>Colvillea racemosa</i> Bojer ex Hook.	Lewis et al. 2147 (K)	Madagascar	AY899794
<i>Conzattia chiapensis</i> Miranda	López 7571 (MEXU)	Mexico	KF522249
<i>Conzattia multiflora</i> (B.L. Rob.) Standl.	Du 600 (K), Haston V200303 (RNG)	Mexico	AY899785
<i>Conzattia multiflora</i> (B.L. Rob.) Standl.	Hughes 1824 (MEXU)	Mexico	KF522244
<i>Conzattia multiflora</i> (B.L. Rob.) Standl.	Sahagun sn (RNG)	Mexico	AY899786
<i>Delonix baccal</i> (Chiov.) Baker f.	Gillett 13717 (K)	Kenya	AY899792
<i>Delonix brachycarpa</i> (R. Vig.) Capuron	Phillipson 3081 (FHO)	Madagascar	AY899790
<i>Delonix elata</i> (L.) Gamble	Wood Y/74/449 (BM)	Yemen	AY899787
<i>Delonix elata</i> (L.) Gamble	Friss et al. 8579 (K)	Ethiopia	KF522246
<i>Delonix floribunda</i> (Baill.) Capuron	Randriarimalala 16A (K)	Madagascar	AY899791
<i>Delonix pumila</i> Du Puy, Phillipson & R. Rabev.	Miller et al. 6147 (K)	Madagascar	AY899793
<i>Delonix regia</i> (Bojer ex Hook.) Raf.	du Puy et al. M578 (K)	Madagascar	AY899788
<i>Delonix regia</i> (Bojer ex Hook.) Raf.	Jodrell Acc. No. 06483 (K: Krukoff) Haston V200304 (RNG)	Mexico	AY899789
<i>Delonix regia</i> (Bojer ex Hook.) Raf.	Marazzi & Flores BM179 (MEXU, Z)	Mexico, cultivated	AM086916
<i>Delonix regia</i> (Bojer ex Hook.) Raf.	Phillipson et al. 3778 (K)	Madagascar, cultivated	KF522248
<i>Gleditsia sinensis</i> Lam.	Keith 58 (Hilliers Arboretum), Haston V200305 (RNG)	cultivated	AY899744
<i>Gleditsia sinensis</i> Lam.	Marazzi BM188 (Z)	Switzerland, cultivated	AM086917
<i>Gleditsia triacanthos</i> L.	Marazzi BM189 (Z)	Switzerland, cultivated	AM086918
<i>Gymnocladus chinensis</i> Baill.	Herendeen II-V-02-1 (US)	USA, cultivated	KF522308
<i>Gymnocladus dioica</i> (L.) Koch	P 495609 (USDA), Haston V200306 (RNG)	cultivated	AY899743
<i>Heteroflorum sclerocarpum</i> M. Sousa	Hughes 1845 (FHO)	Mexico	AY899784
<i>Heteroflorum sclerocarpum</i> M. Sousa	Hughes 1849 (FHO, MEXU)	Mexico	KF522245
<i>Jacqueshuberia lorentensis</i> R.S. Cowan	Rimachi Y 9050 (NY)	Peru	AY899761
<i>Jacqueshuberia purpurea</i> Ducke	de Lima 3273 (NY, INPA)	Brazil	AY899762
<i>Lemuropium edule</i> H. Perrier	Willings sn (K)	Madagascar	AY899795
<i>Melanoxydon brauna</i> Schott	Noscheler 10 (K)	Brazil	AY899757
<i>Moldenhawera brasiliensis</i> Yakovlev	de Carvalho sn (NY)	Brazil	AY899759
<i>Moldenhawera luschnathiana</i> Yakovlev	de Sant'Ana 595 (NY)	Brazil	AY899760
<i>Parkinsonia aculeata</i> L.	Hawkins 94/5 (FHO)	Mexico	AY899772
<i>Parkinsonia aculeata</i> L.	Contreras 1136 (FCME)	Mexico	KF522243
<i>Parkinsonia africana</i> Sond.	Kolberg sn (OFI)	South Africa	AY899780
<i>Parkinsonia anacantha</i> Brenan	Adamson EA12869 (FHO)	Kenya	AY899781
<i>Parkinsonia florida</i> (Benth. ex A. Gray) S. Watson	Hawkins 101 (FHO)	Mexico	AY899775
<i>Parkinsonia florida</i> (Benth. ex A. Gray) S. Watson	Hawkins 126 (FHO)	Mexico	AY899776
<i>Parkinsonia florida</i> (Benth. ex A. Gray) S. Watson	Hughes 1562 (FHO)	Mexico	AY899777
<i>Parkinsonia microphylla</i> Torr.	Hawkins 127 (FHO)	Mexico	KF522250
<i>Parkinsonia peruviana</i> C.E. Hughes, Daza & Hawkins	Hughes 2022 (FHO)	Peru	AY899771
<i>Parkinsonia praecox</i> (Ruiz & Pav.) Hawkins	Hawkins 36 (FHO)	Mexico	AY899778
<i>Parkinsonia raimondoi</i> Brenan	Thulin 4135 (FHO)	Somalia	AM089783
<i>Parkinsonia scioana</i> (Chiov.) Brenan	Hassan 63 (FHO)	Somalia	AY899782
<i>Parkinsonia texana</i> (A. Gray) S. Watson	Hawkins 151/152/153 (FHO)	Mexico	AY899774
<i>Peltophorum africanum</i> Sond.	Kornas 2861 (FHO)	Zambia	AY899768
<i>Peltophorum dubium</i> (Spreng.) Taub.	Hughes 1685 (FHO)	Mexico	AY899769
<i>Peltophorum pterocarpum</i> (DC.) Backer ex K. Heyne	Grierson & Long 2884 (E)	Bhutan	AY899770
<i>Peltophorum pterocarpum</i> (DC.) Backer ex K. Heyne	Goyder 3719 (K)	Australia	KF522242
<i>Poeppegia procera</i> Presl	Klitgaard 65 (K)	Brazil	AY899740
<i>Pterogyne nitens</i> Tul.	Pennington 244 (FHO)	Brazil	AY899747
<i>Recordoxylon speciosum</i> (R. Ben.) Normand & Mariaux	de Lima 3333 (NY)	Brazil	AY899756
<i>Schizolobium parahyba</i> (Vell.) S.F. Blake	Hughes 1880 (FHO)	Mexico	AY899767
<i>Senna covesii</i> (A. Gray) H.S. Irwin & Barneby	Marazzi BM297 (ARIZ)	USA, cultivated	HM236885
<i>Senna spectabilis</i> (DC.) H.S. Irwin & Barneby	Marazzi et al. BM029 (PY, CTES, Z)	Paraguay	AM086983
<i>Senna</i> sp.	Bruneau 1287 (MT)	Mexico	KF522256
<i>Tachigali densiflora</i> (Benth.) L.F.Gomes da Silva & H.C. Lima	de Carvalho 4095 (K)	Brazil	AY899763

(continued on next page)

Table 2 (continued)

Genus (no. of species sampled/total no. species) Species	Voucher specimen (herbarium)	Collection locality	Genbank accession number
Outgroup			
<i>Tachigali myrmecophila</i> Ducke	Cowan 38220 (K)	Brazil	AY899764
<i>Tetrapterocarpon geayi</i> Humbert	Noyes 1049 (K)	Madagascar	AY899742
<i>Umtiza listeriana</i> Sim.	Schrire 2602 (K)	South Africa	KF522307
<i>Vouacapoua macropetala</i> Sandwith	Breteler 13793 (WAG)	French Guiana	AF365110
Caesalpinia group			
<i>Balsamocarpon</i> Clos (1/1 species)			
* <i>Balsamocarpon brevifolium</i> Clos.	Baxter DCI 1869 (E)	Chile	KF522135
* <i>Balsamocarpon brevifolium</i> Clos.	Taylor 745 (K)	Chile	KF522136
<i>Caesalpinia</i> L. sensu stricto (18/~25 species)			
* <i>Caesalpinia brasiliensis</i> L.	Leonard & Leonard 13904 (US, K)	Haiti	KF522092
<i>Caesalpinia bahamensis</i> Lam.	Baker B27 (K)	Bahamas	KF522091
<i>Caesalpinia bahamensis</i> Lam.	Michael 8975 (MEXU)	Bahamas	KF522093
<i>Caesalpinia barahonensis</i> Urb.	Ekman 5965 (K)	Haiti	KF522094
<i>Caesalpinia bracteata</i> Germish.	Van Hoepen 2018 (K)	South Africa	KF522258
<i>Caesalpinia buchii</i> Urb.	Acevedo-Rodriguez et al. 8522 (US, K)	Dominican Republic	KF522115
<i>Caesalpinia cassioides</i> Willd.	Hughes et al. 2023 (FHO)	Peru	KF522097
<i>Caesalpinia cassioides</i> Willd.	Hughes et al. 2228 (FHO)	Peru	KF522098
<i>Caesalpinia cassioides</i> Willd.	Hughes et al. 2641 (FHO)	Peru	KF522095
<i>Caesalpinia cassioides</i> Willd.	Pennington et al. 789 (E)	Peru	KF522096
<i>Caesalpinia dauensis</i> Thulin	Gilbert et al. 7695 (K)	Ethiopia	KF522266
<i>Caesalpinia erianthera</i> Chiov.	Friis et al. 4698 (K)	Somalia	KF522123
<i>Caesalpinia erianthera</i> Chiov.	Radcliffe-Smith 5518 (K)	Oman	KF522122
<i>Caesalpinia erianthera</i> Chiov.	Thulin & Mohamed 6941 (K)	Somalia	KF522125
<i>Caesalpinia erianthera</i> Chiov.var. <i>erianthera</i>	Thulin 5557 (K)	Somalia	KF522118
<i>Caesalpinia erianthera</i> var. <i>pubescens</i> Brenan	Boulos et al. 17000 (K)	Yemen	KF522117
<i>Caesalpinia glandulopedicellata</i> R. Wilczek	Bamps & Malaisse 8647 (K)	Zaire	KF522261
<i>Caesalpinia madagascariensis</i> (R.Vig) Senesse	Bruneau 1348 (MT)	Madagascar	KF522119
<i>Caesalpinia madagascariensis</i> (R.Vig) Senesse	Lewis et al. 2158 (K)	Madagascar	KF522120
<i>Caesalpinia oligophylla</i> Harms.	Hassan 70 (FHO, K)	Somalia	KF522262
<i>Caesalpinia pauciflora</i> (Griseb.) C. Wright	Ekman 9703 (K)	Cuba	KF522124
<i>Caesalpinia pauciflora</i> (Griseb.) C. Wright	Liogier & Liogier 20521 (NY)	Hispaniola	KF522116
<i>Caesalpinia pulcherrima</i> (L.) Sw.	Cox 1, RBG Liv.Coll. 1975–3028 (K)	cultivated	KF522174
<i>Caesalpinia pulcherrima</i> (L.) Sw.	Fougère-Danezan 19 (MT)	Singapore, cultivated	KF522172
<i>Caesalpinia pulcherrima</i> (L.) Sw.	Lewis & Hughes 1715 (K)	Guatemala	KF522171
<i>Caesalpinia pulcherrima</i> (L.) Sw.	Montreal Botanical Garden 7089–92 (MT)	Canada, cultivated	KF522173
<i>Caesalpinia rubra</i> (Engl.) Brenan	de Winter 3164 (K)	South Africa	KF522260
<i>Caesalpinia rubra</i> (Engl.) Brenan	Oshikoto 1917BD (K)	Namibia	KF522259
<i>Caesalpinia sessilifolia</i> S. Watson	Hinton 24737 (MEXU)	Mexico	KF522121
<i>Caesalpinia stuckertii</i> Hassl.	Beck 9443 (NY)	Bolivia	KF522126
<i>Caesalpinia stuckertii</i> Hassl.	Kaprovickas 4626 (K)	Argentina	KF522127
<i>Caesalpinia trothae</i> subsp. <i>erlangeri</i> (Harms) Brenan	Beckett & White 1711 (K)	Somalia	KF522263
<i>Caesalpinia trothae</i> subsp. <i>erlangeri</i> (Harms) Brenan	Thulin & Warfa 5816 (K)	Somalia	KF522267
<i>Caesalpinia trothae</i> subsp. <i>erlangeri</i> (Harms) Brenan	Vollesen & Hassan 4873 (K)	Somalia	KF522264
<i>Caesalpinia trothae</i> subsp. <i>trothae</i> Harms	Bidgood et al. 559 (K)	Tanzania	KF522265
<i>Cenostigma</i> Tul. (2/2 species)			
* <i>Cenostigma macrophyllum</i> Tul.	Coradin et al. 6306 (K)	Brazil	KF522053
* <i>Cenostigma macrophyllum</i> Tul.	Thomas 9615 (K)	Brazil	KF522069
<i>Cenostigma macrophyllum</i> Tul.	de Queiroz 9147 (HUEFS)	Brazil	KF522037
<i>Cenostigma tocaninum</i> Ducke	Klitgaard & de Lima 88 (K)	Brazil, cultivated	KF522071
<i>Cenostigma tocaninum</i> Ducke	Klitgaard s.n. (INPA)	Brazil	KF522070
<i>Cordeauxia</i> Hemsl. (1/1 species)			
* <i>Cordeauxia edulis</i> Hemsl.	Gillett & Beckett 23305 (K)	Somalia	KF522083
* <i>Cordeauxia edulis</i> Hemsl.	Hassan 232 (FHO, K)	Somalia	AY899748
* <i>Cordeauxia edulis</i> Hemsl.	Kuchar 17803 (K)	Somalia	KF522084
<i>Coulteria</i> Kunth (7/9–10 species)			
* <i>Coulteria mollis</i> Kunth	Way NMLW 28 (K)	Venezuela	KF522187
<i>Coulteria platyloba</i> (S. Watson) N. Zamora	Gagnon & Marazzi, EG2010.007 (MT)	USA, cultivated	KF522175
<i>Coulteria platyloba</i> (S. Watson) N. Zamora	Lorea Lozada 685 (MEXU)	Mexico	KF522183
<i>Coulteria platyloba</i> (S. Watson) N. Zamora	MacQueen 178 (K)	Mexico	KF522178
<i>Coulteria platyloba</i> (S. Watson) N. Zamora	Steinmann 3199 (INIREB, K)	Mexico	KF522184
<i>Caesalpinia colimensis</i> F.J.Herm.	Sousa 6163 (K)	Mexico	KF522176
<i>Caesalpinia pringlei</i> (Britton & Rose) Standl.	Cruz Duran 926 (MEXU)	Mexico	KF522180
<i>Caesalpinia pumila</i> (Britton & Rose) F.J.Herm.	Gagnon & Marazzi EG 2010.014 (MT)	USA, cultivated	KF522182
<i>Caesalpinia pumila</i> (Britton & Rose) F.J.Herm.	Lewis et al. 2067 (K)	Mexico	KF522177
<i>Caesalpinia pumila</i> (Britton & Rose) F.J.Herm.	Nabhan et al. 1988 (MEXU)	Mexico	KF522185
<i>Caesalpinia velutina</i> (Britton & Rose) Standl.	Hughes et al. 2087 (FHO)	Mexico	KF522189
<i>Caesalpinia velutina</i> (Britton & Rose) Standl.	Lewis 1797 (NY)	Mexico	KF522179
<i>Caesalpinia velutina</i> (Britton & Rose) Standl.	Tenorio 296 (MEXU)	Mexico	KF522191
<i>Caesalpinia velutina</i> (Britton & Rose) Standl.	Torres 1590 (MEXU)	Mexico	KF522186
<i>Caesalpinia velutina</i> (Britton & Rose) Standl.	Way et al. JIC 22176 (K)	Mexico	KF522190
<i>Caesalpinia violacea</i> (Mill.) Standl.	Lewis et al. 1763 (NY)	Mexico	KF522188

Table 2 (continued)

Genus (no. of species sampled/total no. species) Species	Voucher specimen (herbarium)	Collection locality	Genbank accession number
<i>Caesalpinia violacea</i> (Mill.) Standl.	Tenorio 4442 (MEXU)	Mexico	KF522181
<i>Erythrostemon</i> (Hook.) Klotzsch (13/13 species)			
* <i>Erythrostemon gilliesii</i> Klotzsch	Marazzi et al. BM131 (CTES, Z)	Argentina	AM086914
* <i>Erythrostemon gilliesii</i> Klotzsch	Spellenberg 12701 (MT)	USA, cultivated	KF522296
<i>Erythrostemon calycina</i> (Benth) L.P.Queiroz	Giuletti 2045 (HUEFS)	Brazil	KF522304
<i>Erythrostemon calycina</i> (Benth) L.P.Queiroz	Lewis & Andrade 2003 (K)	Brazil	AY899749
<i>Erythrostemon calycina</i> (Benth) L.P.Queiroz	Lewis & Andrade 1885 (K)	Brazil	KF522303
<i>Caesalpinia ancashiana</i> Ulibarri	Hughes et al. 3021 (MT, Z)	Peru	KF522164
<i>Caesalpinia ancashiana</i> Ulibarri	Hughes et al. 3025 (MT, Z)	Peru	KF522166
<i>Caesalpinia ancashiana</i> Ulibarri	Hughes et al. 3026 (MT, Z)	Peru	KF522165
<i>Caesalpinia ancashiana</i> Ulibarri	Hughes et al. 3027 (MT, Z)	Peru	KF522169
<i>Caesalpinia ancashiana</i> Ulibarri	Hughes et al. 3065 (MT, Z)	Peru	KF522168
<i>Caesalpinia ancashiana</i> Ulibarri	Hughes et al. 3070 (MT, Z)	Peru	KF522167
<i>Caesalpinia ancashiana</i> Ulibarri	Lewis & Klitgaard 2266 (K)	Ecuador	KF522170
<i>Caesalpinia angulata</i> (Hook & Arn.) Baill.	Brownless et al. 591 (E)	Chile	KF522288
<i>Caesalpinia angulata</i> (Hook & Arn.) Baill.	Nee 37585 (K)	Chile	KF522287
<i>Caesalpinia argentina</i> Burkart	Hughes et al. 2460 (FHO)	Bolivia	KF522289
<i>Caesalpinia argentina</i> Burkart	Pennington et al. 13323 (K)	Bolivia	KF522290
<i>Caesalpinia caudata</i> (A. Gray) Fisher	Simpson I-IV-01-3 (TEX)	USA	KF522298
<i>Caesalpinia celendiniana</i> G.P. Lewis & C.E. Hughes	Hughes et al. 2210 (FHO)	Peru	KF522148
<i>Caesalpinia celendiniana</i> G. P. Lewis & C.E. Hughes	Hughes et al. 3097 (MT, Z)	Peru	KF522149
<i>Caesalpinia celendiniana</i> G.P. Lewis & C.E. Hughes	Hughes et al. 3102 (MT, Z)	Peru	KF522147
<i>Caesalpinia coluteifolia</i> Griseb.	Gagnon et al. EG207 (MT)	Argentina	KF522291
<i>Caesalpinia coluteifolia</i> Griseb.	Gagnon & Atchison EG223 (MT)	Argentina	KF522292
<i>Caesalpinia coulterioides</i> Griseb. Emend. Burkart	Gagnon & Atchison EG209 (MT)	Argentina	KF522285
<i>Caesalpinia exilifolia</i> Griseb.	Gagnon et al. EG201 (MT)	Argentina	KF522295
<i>Caesalpinia exilifolia</i> Griseb.	Gagnon et al. EG202 (MT)	Argentina	KF522294
<i>Caesalpinia exilifolia</i> Griseb.	Gagnon & Atchison EG219 (MT)	Argentina	KF522293
<i>Caesalpinia fimbriata</i> Tul.	Hughes et al. 2441 (FHO)	Bolivia	KF522284
<i>Caesalpinia fimbriata</i> Tul.	Hughes et al. 2466 (FHO)	Bolivia	KF522286
<i>Caesalpinia fimbriata</i> Tul.	Wood 10627 (K)	Bolivia	KF522211
<i>Caesalpinia fimbriata</i> Tul.	Solomon & Nee 16062 (NY)	Bolivia	KF522297
<i>Caesalpinia mimosifolia</i> Griseb.	Gagnon et al. EG203 (MT)	Argentina	KF522160
<i>Caesalpinia mimosifolia</i> Griseb.	Gagnon & Atchison EG211 (MT)	Argentina	KF522159
<i>Caesalpinia mimosifolia</i> Griseb.	Särkinen et al. 2006 (FHO)	Argentina	KF522161
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 2442 (FHO)	Bolivia	KF522162
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3041 (MT, Z)	Peru	KF522152
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3042 (MT, Z)	Peru	KF522154
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3047 (MT, Z)	Peru	KF522150
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3056 (MT, Z)	Peru	KF522158
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3057 (MT, Z)	Peru	KF522155
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3063 (MT, Z)	Peru	KF522157
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3155 (MT, Z)	Peru	KF522156
<i>Caesalpinia trichocarpa</i> Griseb.	Hughes et al. 3156 (MT, Z)	Peru	KF522153
<i>Caesalpinia trichocarpa</i> Griseb.	Lewis & Klitgaard 2166 (K)	Argentina	KF522163
<i>Caesalpinia trichocarpa</i> Griseb.	Särkinen et al. 2225 (FHO)	Peru	KF522151
<i>Guilandina</i> L. (5/7–18 species)			
* <i>Guilandina bonduc</i> L.	Bruneau 1342 (MT)	Madagascar	KF522062
* <i>Guilandina bonduc</i> L.	van Balooy s.n., Krukoff coll. (K)	Malaysia	KF522063
<i>Guilandina major</i> L.	Herendeen & Pooma 30-IV-1999-1 (US)	USA, cultivated	KF522253
<i>Caesalpinia minax</i> Hance	Li Shi Jin 802 (CAS, IBSC)	China	KF522131
<i>Caesalpinia minax</i> Hance	Living collection National Botanic Garden of Belgium 19645275(BR)	China, cultivated	KF522132
<i>Caesalpinia murifruca</i> Gillis & Proctor	Gillis 13096 (K)	Bahamas	KF522064
<i>Caesalpinia volkensii</i> Harms	Archbold 2861 (K)	Tanzania	KF522065
<i>Caesalpinia volkensii</i> Harms	Friis et al. 3516 (K)	Ethiopia	KF522066
<i>Caesalpinia volkensii</i> Harms	Somers s.n., RBG Liv.Coll. 1978–891 (K)	Kenya	KF522067
<i>Haematoxylum</i> L. (3/4 species)			
* <i>Haematoxylum campechianum</i> L.	Bruneau 1313 (MT)	Mexico	KF522200
* <i>Haematoxylum campechianum</i> L.	du Puy et al. M356 (K)	Madagascar	KF522208
* <i>Haematoxylum campechianum</i> L.	Hughes 1273 (FHO)	Guatemala	AY899754
* <i>Haematoxylum campechianum</i> L.	Miller & Morello 8849 (MO)	Dominica	KF522201
<i>Haematoxylum brasiletto</i> H. Karst.	Bernandes et al. 891 (MO)	Colombia	KF522209
<i>Haematoxylum brasiletto</i> H. Karst.	Gagnon & Marazzi EG2010.011 (MT)	USA, cultivated	KF522207
<i>Haematoxylum dinteri</i> Harms	Sucbeach s.n. (OFI), Haston V200308 (RNG)	Namibia	AY899755
<i>Haematoxylum brasiletto</i> H. Karst.	Gagnon & Marazzi EG2010.013 (MT)	USA, cultivated	KF522206
<i>Haematoxylum brasiletto</i> H. Karst.	Lewis et al. 2057 (FHO)	Mexico	AY899753
<i>Hoffmannseggia</i> Cav. (7/24 species)			
* <i>Hoffmannseggia glauca</i> (Ortega) Eifert	Gagnon & Marazzi EG2010.05 (MT)	USA	KF522214
* <i>Hoffmannseggia glauca</i> (Ortega) Eifert	Gagnon & Marazzi EG2010.19 (MT)	USA	KF522212
* <i>Hoffmannseggia glauca</i> (Ortega) Eifert	Spellenberg 12699 (MT)	USA	KF522213
<i>Hoffmannseggia aphylla</i> (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6503 (E)	Chile	KF522146

(continued on next page)

Table 2 (continued)

Genus (no. of species sampled/total no. species) Species	Voucher specimen (herbarium)	Collection locality	Genbank accession number
<i>Hoffmannseggia aphylla</i> (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6557 (E)	Chile	KF522144
<i>Hoffmannseggia microphylla</i> Torr.	Holmgren 6505 (NY)	USA	KF522145
<i>Hoffmannseggia miranda</i> Sandwith	FLSP 945 (NY)	Peru	KF522239
<i>Hoffmannseggia miranda</i> Sandwith	Hughes & Daza 2358 (FHO)	Peru	KF522240
<i>Hoffmannseggia prostrata</i> DC.	Hughes & Daza 2359 (FHO)	Peru	KF522241
<i>Hoffmannseggia viscosa</i> Hook.& Arn.	Eastwood et al. RJE35 (FHO)	Peru	KF522138
<i>Hoffmannseggia viscosa</i> Hook.& Arn.	Hughes et al. 2221 (FHO)	Peru	KF522137
<i>Hoffmannseggia viscosa</i> Hook.& Arn.	Simpson 22-II-00-3 (TEX)	Peru	KF522139
<i>Libidibia</i> (DC.) Schlttd. (6/6–8 species)			
* <i>Libidibia coriaria</i> (Jacq.) Schlttd.	Fougère-Danezan 20 (MT)	Singapore, cultivated	KF522109
* <i>Libidibia coriaria</i> (Jacq.) Schlttd.	Hughes 1495 (K)	Mexico	AY899750
* <i>Libidibia coriaria</i> (Jacq.) Schlttd.	Hughes et al. 2163 (FHO)	Mexico	KF522107
<i>Libidibia ferrea</i> (Mart. ex Tul.) L.P.Queiroz	Fougère-Danezan 21 (MT)	Singapore, cultivated	KF522105
<i>Libidibia ferrea</i> (Mart. ex Tul.) L.P.Queiroz G.P.Lewis	Lewis et al. 1623 (K)	Brazil	KF522114
<i>Libidibia glabrata</i> (Kunth) Castellanos & G.P. Lewis	Delgado 2097 (MEXU)	Peru	KF522103
<i>Libidibia glabrata</i> (Kunth) Castellanos & G.P. Lewis	Eastwood et al. RJE84 (FHO)	Peru	KF522102
<i>Libidibia glabrata</i> (Kunth) Castellanos & G.P. Lewis	Lewis & Lozano 3043 (K)	Ecuador	KF522101
<i>Libidibia glabrata</i> (Kunth) Castellanos & G.P. Lewis	Särkinen et al. 2151 (FHO)	Peru	KF522104
<i>Libidibia paraguariensis</i> (Parodi) G.P.Lewis	Hughes et al. 2307 (FHO)	Bolivia	KF522110
<i>Libidibia paraguariensis</i> (Parodi) G.P.Lewis	Hughes et al. 2475 (FHO)	Bolivia	KF522111
<i>Libidibia paraguariensis</i> (Parodi) G.P.Lewis	Lewis & Klitgaard 2170 (K)	Argentina	KF522112
<i>Libidibia paraguariensis</i> (Parodi) G.P.Lewis	Zardini & Velazquez 19907 (K)	Paraguay	KF522113
<i>Libidibia punctata</i> (Willd.) Britton	Cardenas 4071 (K)	Venezuela	KF522106
<i>Libidibia sclerocarpa</i> (Standl.) Britton & Rose	Lewis & Hughes 1778 (K)	Mexico	KF522108
<i>Mezoneuron</i> Desf. (11/26 species)			
<i>Mezoneuron andamanicum</i> Prain	Herendeen 29-IV-1999-1 (US)	Thailand	KF522305
<i>Mezoneuron benthamianum</i> Baill.	Ern 2602 (K)	Togo	KF522196
<i>Mezoneuron benthamianum</i> Baill.	Morton & Jarr SL3295 (K)	Sierra Leone	KF522195
<i>Mezoneuron benthamianum</i> Baill.	Vigne 3487 (FHO)	Ghana	KF522197
<i>Mezoneuron cucullatum</i> (Roxb.) Wight & Arn.	Grierson & Long 3623 (K)	Bhutan	KF522194
<i>Mezoneuron deverdiana</i> Guillaumin	McPherson 6211 (K)	New Caledonia	KF522078
<i>Mezoneuron hildebrandtii</i> Vatke	Lewis et al. 2137 (K)	Madagascar	KF522198
<i>Mezoneuron kavaiensis</i> (H. Mann) Hillbr.	Lorence & Wagner 8904 (NTBG)	Hawaii, U.S.A.	KF522192
<i>Mezoneuron scortechinii</i> F. Muell.	Wieringa et al. 4195 (WAG)	Australia	KF522077
<i>Mezoneuron sumatranum</i> (Roxb.) Wight & Arn.	Beaman 9642 (NY, MO)	Malaysia	KF522199
<i>Mezoneuron</i> sp.	Pullen 7619 (K)	New Guinea	KF522193
<i>Caesalpinia erythrocarpa</i> Pedley	Schodde 2246 (K)	New Guinea	KF522257
<i>Caesalpinia nitens</i> (F.Muell ex Benth.) Pedley	Bean 18033 (MO)	Australia	KF522076
<i>Moullava</i> Adans. (1/1 species)			
* <i>Moullava spicata</i> (Dalzell) Nicolson	Critchett 11/79 (K)	Zambia, cultivated	KF522252
<i>Poincianella</i> Britton & Rose (27/–35 species)			
* <i>Poincianella mexicana</i> (A. Gray) Britton & Rose	Hughes et al. 1606 (NY, FHO)	Mexico	KF522218
* <i>Poincianella mexicana</i> (A. Gray) Britton & Rose	Delgado 01–2114 (MEXU)	Mexico	KF522219
* <i>Poincianella mexicana</i> (A. Gray) Britton & Rose	Lewis s.n., Kew Living Coll. 1973–21714 (K)	Mexico	KF522215
* <i>Poincianella mexicana</i> (A. Gray) Britton & Rose	Gagnon & Marazzi EG2010.015 (MT)	USA, cultivated	KF522217
<i>Poincianella</i> aff. <i>mexicana</i>	Contreras s.n. (MEXU)	Mexico	KF522227
<i>Poincianella acapulcensis</i> (Standl.) Britton & Rose	Lott 3205 (K)	Mexico	KF522233
<i>Poincianella acapulcensis</i> (Standl.) Britton & Rose	MacQueen et al. 406 (K)	Mexico	KF522235
<i>Poincianella bracteosa</i> (Tul.) L.P. Queiroz	Carvalho-Sobrinho 218 (HUEFS)	Brazil	KF522035
<i>Poincianella bracteosa</i> (Tul.) L.P. Queiroz	de Queiroz 7845 (HUEFS)	Brazil	KF522036
<i>Poincianella bracteosa</i> (Tul.) L.P. Queiroz	de Queiroz 10085 (HUEFS)	Brazil	KF522079
<i>Poincianella caladenia</i> (Standl.) Britton & Rose	Contreras 2868 (MEXU)	Mexico	KF522234
<i>Poincianella caladenia</i> (Standl.) Britton & Rose	Lewis et al. 2072 (K)	Mexico	KF522228
<i>Poincianella eriostachys</i> (Benth.) Britton & Rose	Hughes 1832 (K)	Mexico	AY899751
<i>Poincianella eriostachys</i> (Benth.) Britton & Rose	Lewis et al. 1799 (K)	Mexico	KF522029
<i>Poincianella exostemma</i> (DC.) Britton & Rose	Contreras s.n. febrero 2000 (MEXU)	Mexico	KF522237
<i>Poincianella exostemma</i> (DC.) Britton & Rose subsp. <i>exostemma</i>	Bruneau 1317 (MT)	Mexico	KF522221
<i>Poincianella exostemma</i> (DC.) Britton & Rose subsp. <i>exostemma</i>	Lewis & Hughes 1712, RBG Liv.Coll. 1989–3073 (K)	Guatemala	KF522224
<i>Poincianella exostemma</i> (DC.) Britton & Rose subsp. <i>exostemma</i>	Lewis & Hughes 1753 (K)	Guatemala	KF522222
<i>Poincianella gaumeri</i> (Greenm.) Britton & Rose	Calzada 19333 (K, MEXU)	Mexico	KF522030
<i>Poincianella gaumeri</i> (Greenm.) Britton & Rose	Hughes 492 (K)	Mexico	KF522034
<i>Poincianella gaumeri</i> (Greenm.) Britton & Rose	Lewis & Hughes 1762 (K)	Mexico	KF522044
<i>Poincianella laxa</i> (Benth.) Britton & Rose	Delgado 2337 (MEXU)	Mexico	KF522274
<i>Poincianella laxiflora</i> (Tul.) L.P. Queiroz	de Queiroz 7063 (HUEFS)	Brazil	KF522051
<i>Poincianella melanadenia</i> (Rose) Britton & Rose	Hughes et al. 2074 (FHO)	Mexico	KF522276
<i>Poincianella melanadenia</i> (Rose) Britton & Rose	Hughes et al. 2091 (FHO)	Mexico	KF522275
<i>Poincianella melanadenia</i> (Rose) Britton & Rose	Contreras 7369 (MEXU)	Mexico	KF522277
<i>Poincianella microphylla</i> (Mart. ex G. Don) L.P. Queiroz	Coradin et al. 5941 (K)	Brazil	KF522040
<i>Poincianella microphylla</i> (Mart. ex G. Don) L.P. Queiroz	de Queiroz 9060 (HUEFS)	Brazil	KF522039
<i>Poincianella nelsonii</i> Britton & Rose	Contreras & Sotuyo s.n. (MEXU)	Mexico	KF522300
<i>Poincianella nelsonii</i> Britton & Rose	Sotuyo, s.n., RBG Liv.Coll. 2002-3577(K)	Mexico	KF522301
<i>Poincianella palmeri</i> (S. Watson) Britton & Rose	Gagnon et al. EG2010.010 (MT)	USA, cultivated	KF522230
<i>Poincianella palmeri</i> (S. Watson) Britton & Rose	Gagnon et al. EG2010.023 (MT)	USA, cultivated	KF522229

Table 2 (continued)

Genus (no. of species sampled/total no. species) Species	Voucher specimen (herbarium)	Collection locality	Genbank accession number
<i>Poincianella palmeri</i> (S. Watson) Britton & Rose	Lewis 2064 (K)	Mexico	KF522232
<i>Poincianella palmeri</i> (S. Watson) Britton & Rose	Lewis et al. 2065 (K)	Mexico	KF522231
<i>Poincianella pannosa</i> (Standl.) Britton & Rose	Gentry 4365 (MEXU)	Mexico	KF522283
<i>Poincianella pannosa</i> (Standl.) Britton & Rose	Lewis 2051 (K)	Mexico	KF522282
<i>Poincianella phyllanthoides</i> (Standl.) Britton & Rose	Nee 32666 (K)	Mexico	KF522220
<i>Poincianella phyllanthoides</i> (Standl.) Britton & Rose	Steinmann 3718 (INIREB, MEXU)	México	KF522216
<i>Poincianella placida</i> (Brandegee) Britton & Rose	Lewis et al. 2032 (K)	Mexico	KF522273
<i>Poincianella placida</i> (Brandegee) Britton & Rose	Lewis 2046 (K)	Mexico	KF522272
<i>Poincianella pluviosa</i> (DC.) L.P. Queiroz	de Queiroz 12795 (HUEFS)	Brazil	KF522049
<i>Poincianella pluviosa</i> (DC.) L.P. Queiroz	Wood et al. 26552 (K)	Bolivia	KF522047
<i>Poincianella pluviosa</i> (DC.) L.P. Queiroz var. <i>pluviosa</i>	Nee 40000 (K)	Bolivia	KF522054
<i>Poincianella pluviosa</i> (DC.) L.P. Queiroz var. <i>pluviosa</i>	Wood 8838 (K)	Bolivia	KF522052
<i>Poincianella pluviosa</i> var. <i>sanfranciscana</i> (G.P. Lewis) L.P. Queiroz	Lewis & Andrade 1896 (K)	Brazil	KF522050
<i>Poincianella pyramidalis</i> (Tul.) L.P. Queiroz	Dorea 117 (HUEFS)	Brazil	KF522041
<i>Poincianella pyramidalis</i> (Tul.) L.P. Queiroz	de Queiroz 9020 (HUEFS)	Brazil	KF522042
<i>Poincianella pyramidalis</i> (Tul.) L.P. Queiroz	Mori & Boom 14207 (K)	Brazil	KF522038
<i>Poincianella standleyi</i> Britton & Rose	Contreras 2745 (K)	Mexico	KF522236
<i>Poincianella yucatanensis</i> (Greenm.) Britton & Rose subsp. <i>yucatanensis</i>	Lewis 1765 (K)	Mexico	KF522280
<i>Poincianella yucatanensis</i> (Greenm.) Britton & Rose subsp. <i>yucatanensis</i>	Lewis & Hughes 1766 (NY, K)	Mexico	KF522281
<i>Caesalpinia coccinea</i> G.P. Lewis & J.L. Contr.	Lewis 1802 (K)	Mexico	KF522225
<i>Caesalpinia coccinea</i> G.P. Lewis & J.L. Contr.	Lewis 1803 (K)	Mexico	KF522226
<i>Caesalpinia echinata</i> Lam.	Filgueiras 3391 (NY)	Brazil, cultivated	KF522099
<i>Caesalpinia echinata</i> Lam.	Lewis et al. 1624 (K)	Brazil	KF522072
<i>Caesalpinia echinata</i> Lam.	Miranda 76 (HUEFS)	Brazil	KF522100
<i>Caesalpinia epifanioi</i> J.L. Contr.	Contreras 2309 (K)	Mexico	KF522278
<i>Caesalpinia epifanioi</i> J.L. Contr.	Sotuyo & Sotuyo 20 (MEXU)	Mexico	KF522279
<i>Caesalpinia hintonii</i> Sandwith.	Sotuyo 46 (MEXU)	Mexico	KF522270
<i>Caesalpinia hughesii</i> G.P. Lewis	Lewis et al. 1795 (K)	Mexico	KF522223
<i>Caesalpinia macvaughii</i> J.L. Contr. & G.P. Lewis	Sotuyo et al. 8 (MEXU)	Mexico	KF522299
<i>Caesalpinia macvaughii</i> J.L. Contr. & G.P. Lewis	Sotuyo et al. 54 (MEXU)	Mexico	KF522269
<i>Caesalpinia macvaughii</i> J.L. Contr. & G.P. Lewis	Steinmann 3175 (INIREB, K, MEXU)	Mexico	KF522268
<i>Caesalpinia marginata</i> Tul.	Dubs 1746 (K)	Brazil	KF522045
<i>Caesalpinia marginata</i> Tul.	Wood et al. 26514 (K)	Bolivia	KF522048
<i>Caesalpinia marginata</i> Tul.	Wood et al. 26561 (K)	Bolivia	KF522046
<i>Caesalpinia nicaraguensis</i> G.P. Lewis	Hawkins & Hughes 4 (K)	Nicaragua	KF522302
<i>Caesalpinia oyamae</i> Sotuyo & G.P. Lewis	Hawkins & Hughes 23 (FHO, MEXU)	Mexico	KF522210
<i>Caesalpinia pluviosa</i> var. <i>maraniona</i> G.P. Lewis & C.E. Hughes	Hughes et al. 2215 (FHO)	Peru	KF522033
<i>Caesalpinia pluviosa</i> var. <i>maraniona</i> G.P. Lewis & C.E. Hughes	Hughes et al. 3105 (MT)	Peru	KF522032
<i>Caesalpinia pluviosa</i> var. <i>maraniona</i> G.P. Lewis & C.E. Hughes	Pennington et al. 793 (E, K)	Peru	KF522031
<i>Caesalpinia pluviosa</i> var. <i>maraniona</i> G.P. Lewis & C.E. Hughes	Särkinen et al. 2191 (FHO)	Peru	KF522043
<i>Caesalpinia yucatanensis</i> subsp. <i>chiapensis</i> G.P. Lewis	Hughes 1353 (FHO)	Mexico	KF522271
<i>Pomaria</i> Cav. (4/16 species)			
* <i>Pomaria glandulosa</i> Cav.	Ventura & López 9294 (TEX)	Mexico	KF522088
<i>Pomaria jamesii</i> (Torr. & A. Gray) Walp.	Gagnon & Marazzi EG2010.020 (MT)	USA	KF522089
<i>Pomaria jamesii</i> (Torr. & A. Gray) Walp.	Higgins 17628 (NY)	USA	KF522090
<i>Pomaria rubicunda</i> (Vogel) B.B. Simpson & G.P. Lewis	Biganzoli et al. s.n. (NY)	Argentina	KF522085
<i>Pomaria rubicunda</i> var. <i>hauthallii</i> (Harms) B.B. Simpson & G.P. Lewis	Ibarrola 1750 (US)	Argentina	KF522087
<i>Pomaria stipularis</i> (Vogel) B.B. Simpson & G.P. Lewis	Jonsson 1002a (A)	Brazil	KF522086
<i>Pterolobium</i> (1/11 species)			
* <i>Pterolobium stellatum</i> (Forssk.) Brenan	Herendeen 17-XII-97-9 (US)	Tanzania	KF522238
<i>Tara</i> Molina (3/3 species)			
* <i>Tara spinosa</i> (Molina) Britton & Rose	Eastwood et al. RJ36 (FHO)	Peru	KF522128
* <i>Tara spinosa</i> (Molina) Britton & Rose	Hughes 2360 (FHO)	Peru	KF522129
* <i>Tara spinosa</i> (Molina) Britton & Rose	Nee 45494 (MO)	Australia, cultivated	KF522130
<i>Caesalpinia cacalaco</i> Humb. & Bonpl.	Gagnon & Marazzi EG2010.022 (MT)	USA, cultivated	KF522202
<i>Caesalpinia cacalaco</i> Humb. & Bonpl.	Soto Nuñez 13682 (MEXU)	Mexico	KF522312
<i>Caesalpinia cacalaco</i> Humb. & Bonpl.	Walker s.n., RBG Liv. Coll. 1986–6481 (K)	Mexico	KF522203
<i>Caesalpinia vesicaria</i> L.	Hawkins & Hughes 11 (FHO)	Nicaragua	KF522204
<i>Caesalpinia vesicaria</i> L.	Lewis & Hughes 1768 (K)	Mexico	KF522205
<i>Stuhlmannia</i> Taub. (1/1 species)			
* <i>Stuhlmannia moavi</i> Taub.	Keraudren-Aymonin & Aymonin 25628 (MO)	Madagascar	KF522060
* <i>Stuhlmannia moavi</i> Taub.	Luke 3710 (MO, K)	Tanzania	KF522061
* <i>Stuhlmannia moavi</i> Taub.	Luke & Robertson 2336 (K)	Kenya	KF522058
* <i>Stuhlmannia moavi</i> Taub.	Robertson 7509 (K)	Kenya	KF522059
* <i>Stuhlmannia moavi</i> Taub.	Tanner 3167 (K)	Tanzania	AY899765
<i>Zuccagnia</i> Cav. (1/1 species)			
* <i>Zuccagnia punctata</i> Cav.	Fortunato 5545 (MO)	Argentina	KF522142
* <i>Zuccagnia punctata</i> Cav.	Galletto et al. 171 (CORD)	Argentina	KF522141
* <i>Zuccagnia punctata</i> Cav.	Guglianone et al. 1668 (K, SI)	Argentina	KF522143

(continued on next page)

Table 2 (continued)

Genus (no. of species sampled/total no. species) Species	Voucher specimen (herbarium)	Collection locality	Genbank accession number
* <i>Zuccagnia punctata</i> Cav.	Lutz 136 (NY)	Argentina	KF522140
Unassigned Old World taxa (6/~15 species)			
<i>Caesalpinia crista</i> L.	Herendeen 1-V-99-3 (US)	Thailand	KF522073
<i>Caesalpinia crista</i> L.	Wieringa et al. 4199 (WAG)	Australia, cultivated	KF522074
<i>Caesalpinia decapetala</i> (Roth) Alston	Marazzi BM137 (Z)	Switzerland, cultivated	AM086910
<i>Caesalpinia decapetala</i> (Roth) Alston	Hughes et al. 2227 (FHO)	Peru, cultivated	KF522081
<i>Caesalpinia decapetala</i> (Roth) Alston	Hooper & Gandhi 2429 (US)	India, cultivated	KF522080
<i>Caesalpinia decapetala</i> (Roth) Alston	Herendeen & Mbago 19-XII-97-1 (US)	Tanzania	KF522082
<i>Caesalpinia mimosoides</i> Lam.	Larsen et al. 44653 (MO)	Thailand	KF522251
<i>Caesalpinia oppositifolia</i> Hattink	Lugas 607 (K)	Malaysia	KF522056
<i>Caesalpinia oppositifolia</i> Hattink	Lugas 921 (K)	Malaysia	KF522055
<i>Caesalpinia parviflora</i> Prain	van Beusekom et al. 3977 (K)	Thailand	KF522057
<i>Caesalpinia vernalis</i> Benth.	Li Shi Jin 787 (CAS, IBSC)	China	KF522075
<i>Caesalpinia welwitschiana</i> (Oliv.) Brenan	Bidgood et al. 2913 (K)	Tanzania	KF522133
<i>Caesalpinia welwitschiana</i> (Oliv.) Brenan	Malaisse 13658 (K)	Zaire	KF522134

to obtain material. Previous molecular and morphological phylogenetic studies have focused either on higher-level relationships and employed sparse species-level sampling (Bruneau et al., 2008; Haston et al., 2005; Lewis and Schrire, 1995; Manzanilla and Bruneau, 2012; Nores et al., 2012; Simpson and Miao, 1997), or have focused on particular segregates by producing phylogenies with denser species-level sampling either within *Caesalpinia* s.l. or the broader *Caesalpinia* Group (e.g., Hoffmannseggia, Simpson et al., 2004, 2005; Pomaria, Simpson et al., 2006). The recent phylogenetic study by Nores et al. (2012), based on sequences from the plastid regions *trnL-trnF* and *matK*, as well as morphology, included representatives of all genera of the informal *Caesalpinia* Group (sensu Lewis, 2005), and established the placements of the four monospecific genera, *Balsamocarpon*, *Lophocarpinia*, *Stenodrepanum* and *Zuccagnia*. They also compiled a more extensive sampling of *Caesalpinia* s.l. (51 species) based on plastid *trnL-trnF* region sequences from Genbank. However, even this denser taxon sampling remains insufficient to address generic delimitation issues across *Caesalpinia* s.l. as a whole. Furthermore, no previous phylogenetic studies have sampled the type species of *Caesalpinia* sensu stricto, *Caesalpinia brasiliensis* L., nor the types of other genera proposed for reinstatement by Lewis (2005), making it difficult to ascertain to what extent clades that have been recovered truly correspond to the proposed classification.

The overall objective of this study is to clarify phylogenetic relationships within *Caesalpinia* s.l. and the higher level informal *Caesalpinia* Group as a whole, and specifically to test the monophyly of the Lewis (2005) segregate genera and evaluate whether other well-supported clades within *Caesalpinia* s.l. merit recognition as distinct genera. Given the remarkable morphological variation across *Caesalpinia* s.l., it is essential to sample specimens as widely as possible, both taxonomically and geographically. We use the densely sampled molecular phylogenetic hypothesis based upon a variable plastid marker to discuss possible morphological synapomorphies or sets of diagnostic characters for the robustly supported clades recovered in our analyses.

2. Materials and methods

2.1. Taxonomic sampling

In this study, we sample 276 accessions representing 120 species (98 from *Caesalpinia* s.l.) from 18 of the 21 genera belonging to the informal *Caesalpinia* Group (sensu Lewis, 2005). The phylogenetic positions of three monospecific genera missing from our sampling, *Lophocarpinia*, *Stahlia*, and *Stenodrepanum*, were previously investigated by Nores

et al. (2012) and Simpson et al. (2003). Our sample includes type species for all the genera sampled from the *Caesalpinia* Group (Table 2; type species marked *) except *Mezoneuron* (*Mezoneuron glabrum* Desf.) As far as possible, multiple accessions from different localities per species were included. Material was sampled from herbarium specimens or field-collected silica-dried leaf samples from wild and cultivated plants. Locality details, herbarium vouchers and GenBank numbers for all accessions are listed in Table 2. An additional 11 sequences from Haston et al. (2005) and Marazzi et al. (2006) were downloaded from Genbank.

As outgroup, we included 56 sequences from Genbank (Haston et al., 2005; Marazzi et al., 2006; Marazzi and Sanderson, 2010) and 17 new sequences that were generated *de novo*, that encompassed the tribe *Caesalpinieae* (28 genera), as well as the more distantly related *Poepiggia procera* (Dialiinae clade), which was used to root the trees (Table 2). This extensive outgroup was included to verify if all species hypothesized to belong to *Caesalpinia* s.l. fall within the *Caesalpinia* Group rather than elsewhere in tribe *Caesalpinieae*, as suggested for example for *Cenostigma* (Simpson et al., 2003).

2.2. Molecular methods

DNA was extracted using: (1) a modified CTAB protocol (Joly and Bruneau, 2006); (2) QIAGEN DNeasy Plant Mini Kit (Mississauga, ON, Canada), following the manufacturer's instructions; or (3) a 4% MATAB protocol (Ky et al., 2000).

The plastid region *rps16* was selected based on screening for ease of amplification and adequate phylogenetic resolution of the ten most variable chloroplast markers from Shaw et al. (2005, 2007) in an initial sample of ten *Caesalpinia* s.l. species (Babineau et al., in this issue). The locus was amplified using primers *rps16F* and *rps2R* (Oxelman et al., 1997) in reaction volumes of 50 µl, with 1 × *Taq* DNA polymerase buffer without MgCl₂ (Roche Diagnostics, Indianapolis, IN, USA), 3.0 mM MgCl₂, 200 µM of each dNTP (Fermentas, Burlington, ON, Canada), 0.4 µM of each primer, 3 µg bovine serum albumin (New England Biolabs, Ipswich, MA, USA), 0.03% tween-20, 3% pure DMSO, one unit of *Taq* polymerase, and 50–300 ng of genomic DNA. The PCR consisted of an initial denaturing step of 5 min at 80 °C, followed by 35 cycles of these three steps: a denaturing step of 45 s at 94 °C, an annealing step of 45 s at 53 °C, and an elongation step of 60 s at 72 °C. The final elongation step was 7 min at 72 °C.

For more difficult samples, we used a nested PCR with a second amplification of a 1/10 dilution of the original PCR product, identical PCR

conditions, and replacing the primers with R851 and F68 (Babineau, 2013).

All PCR amplification products were submitted to Genome Quebec (Montreal, Canada), where they were purified and sequenced with Big Dye Terminator 3.1 chemistry on an ABI 3730x1 DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA). Chromatograms were assembled and visually inspected using Geneious (version 5.6-6.0.1-5, Biomatters, Auckland, New Zealand). Because the nested PCR technique can sometimes lead to non-specific amplification, sequences were submitted to a BLAST search (Altschul et al., 1990) and eliminated if they did not correspond to Leguminosae sequences in Genbank.

2.3. Phylogenetic analyses

Sequences were aligned, inspected and manually adjusted in Geneious. Gaps were coded using simple indel coding (SIC; Simmons and Ochoterena, 2000), implemented in SeqState 1.4.1 (Müller, 2005). Only indels that did not represent autapomorphies were retained.

Both maximum parsimony and Bayesian phylogenetic analyses were performed and the resulting trees compared. Maximum parsimony analysis was performed in PAUP* (Swofford, 2003) using a two-step analysis procedure (Davis et al., 2004) with an initial 1000 replicates of random addition sequence, with tree bisection-reconnection branch swapping, retaining the five most parsimonious trees at each replicate, followed by a second heuristic search with the same settings, starting from the trees in memory, retaining a maximum of 100,000 trees. To assess branch support, 10,000 bootstrap replicates were performed, with one tree retained per replicate.

Bayesian analysis was conducted in MrBayes3.2 (Ronquist et al., 2012), with the data partitioned between the DNA sequence matrix and SIC gap matrix. Jmodeltest 2 (Darriba et al., 2012) was used to estimate the best evolutionary model for the DNA matrix, which was identified as the GTR + I + G model according to the Aikake Criterion. The F81 model was specified for the indel matrix. The analysis was run on a server (Réseau Québécois de Calcul de Haute Performance (RQCHP), Université de Montréal, Canada) with two parallel runs of eight Markov Chain Monte Carlo (MCMC) chains each, four swaps per swapping cycle, and trees sampled every 1000 generations. The stop criterion was set to an average standard deviation of split frequencies that dropped to below the critical value 0.01. After observing results with Tracer v. 1.5 (Rambaut and Drummond, 2007) and ensuring that effective sample sizes were sufficient, the burn-in fraction was set to 10%.

3. Results

The aligned *rps16* matrix of 349 sequences had a total length of 1138 base pairs. Missing characters at the ends of sequences, caused by the nested PCR, were coded as missing, and represented 2.59% of the data. Within the Caesalpinia Group, sequence lengths varied from 378 to 834 bp, resulting in the inferences of 73 indels. A total of 64 characters were removed due to alignment ambiguities resulting from polymorphic nucleotide repeats making a final combined matrix of 1147 characters. A total of 564 characters were constant, 196 characters were variable but uninformative, and 387 (33.74%) were parsimony-informative.

The parsimony analysis resulted in the maximum 100,000 equally most parsimonious trees (length 1536 steps, CI 0.43, RI 0.86). The Bayesian analysis reached an average standard deviation of split frequencies of 0.009967 after 5,200,000 generations.

In both the strict consensus parsimony tree and the Bayesian majority rule consensus, the Caesalpinia Group is supported as monophyletic within the tribe Caesalpinieae (results not shown, BS: 74%, PP: 1.0), while *Caesalpinia* s.l. is clearly non-monophyletic (Fig. 1). While almost all clades corresponding to genera or putative genera were identical and had moderate to good support from the Bayesian and parsimony analyses, there is a lack of resolution and support for the backbone of the tree, which thus reveals very little about inter-clade relationships within the

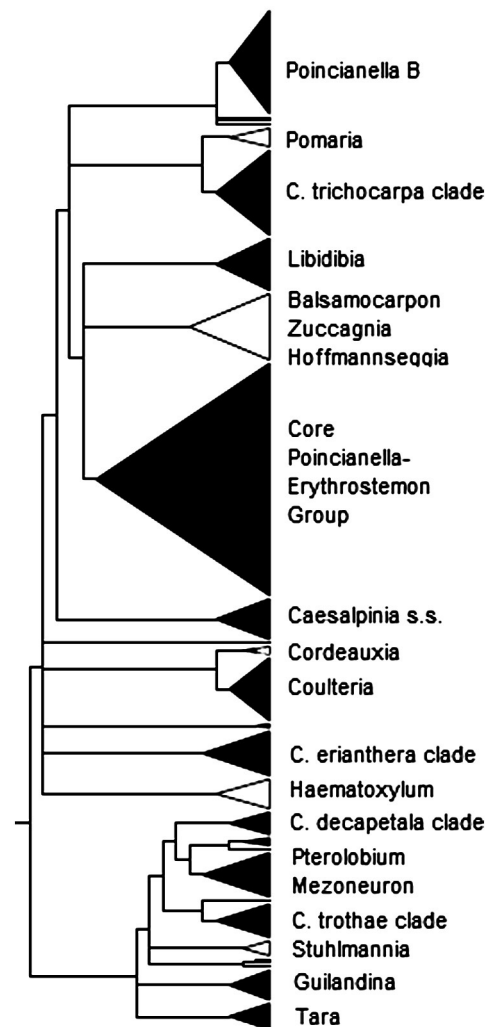


Fig. 1. Summary phylogeny of the Caesalpinia Group, based on the parsimony strict consensus tree. Clades coloured in black contain only members of *Caesalpinia* s.l. Clades in white represent genera that are part of the Caesalpinia Group, but not *Caesalpinia* s.l. Size of triangles reflects size of clades and sampling efforts.

Caesalpinia Group. Nonetheless, the recovered topologies from the Bayesian and parsimony consensus trees were highly congruent, the only major difference being that *Tara* is supported as sister to *Coulteria* in the Bayesian phylogeny (albeit with very weak support, PP 0.53), whereas these two groups do not occur together in the parsimony analysis. Other minor differences in topology also lack support (e.g. *Caesalpinia* s.s. forms a polytomy with the *Cenostigma*-*Poincianella* B and *Pomaria*-*Caesalpinia trichocarpa* clades in the Bayesian tree, whereas in the parsimony tree it is sister to these two clades, plus *Libidibia*, *Balsamocarpon* and the core P-E Group; one accession of *Cenostigma* (*Cenostigma macrophyllum*, Thomas 9615, K) falls outside of the *Cenostigma*-*Poincianella* B group in the Bayesian tree). Given the high congruence between the two trees, we present the strict consensus parsimony topology, but show both bootstrap and Bayesian posterior probability support values on branches (Fig. 2). It is interesting to note that although the parsimony strict consensus tree is more resolved than the Bayesian consensus, for certain nodes deeper in the phylogeny, which lack bootstrap support in the parsimony strict consensus, Bayesian support is high.

Of the eight genera (including *Caesalpinia* s.s.) proposed by Lewis (2005), five are monophyletic: *Coulteria* (BS:73%, PP:0.99), *Tara* (BS:84%, PP:1.0), *Libidibia* (BS:95%, PP:1.0), *Guilandina* (BS:54%, PP:1.0), and *Mezoneuron* (BS:72%, PP:1.0). The remaining three genera, *Poincianella*, *Erythrostemon* and *Caesalpinia* s.s. are not supported as

monophyletic. While a core *Poincianella*-*Erythrostemon* Group is recovered, part of *Erythrostemon* (here designated the *C. trichocarpa* clade, BS:98%, PP: 1.0) forms a distinct clade, sister to *Pomaria*, and part of *Poincianella* is nested within *Cenostigma*, albeit with low BS and PP. *Caesalpinia echinata*, tentatively placed in the *Poincianella*-*Erythrostemon* Group by Lewis (2005), is not placed in this clade, but its position is unresolved. Species of *Caesalpinia* s.s. (as circumscribed by Lewis, 2005) are placed in three distinct and highly supported monophyletic groups: *Caesalpinia* s.s., amended here to include a reduced number of species (BS:78%, PP:1.0); the *Caesalpinia trothae* clade (BS:100%, PP:1.0); and the *Caesalpinia erianthera* clade (BS:96%, PP:1.0; Figs. 1 & 2). Two previously unassigned Old World species are placed within a clade comprising the genus *Pterolobium*; three species form a distinct clade, here designated the *Caesalpinia decapetala* clade (BS: 74%, PP: 1.0), which is sister to

the clade comprising *Pterolobium* plus *Mezoneuron*; and three species (*Caesalpinia welwitschiana*, *Caesalpinia mimosoides* and *Moullava spicata*) remain unresolved within a large polytomy.

4. Discussion

Here we present the most comprehensively sampled and well-resolved phylogeny of the informal *Caesalpinia* Group published to date. Wide and representative taxon sampling, combined with use of a more variable plastid DNA sequence locus, has yielded better phylogenetic resolution than in previous studies (e.g. Bruneau et al., 2001, 2008; Manzanilla and Bruneau, 2012; Nores et al., 2012; Simpson et al., 2003). Despite the general lack of resolution and support across

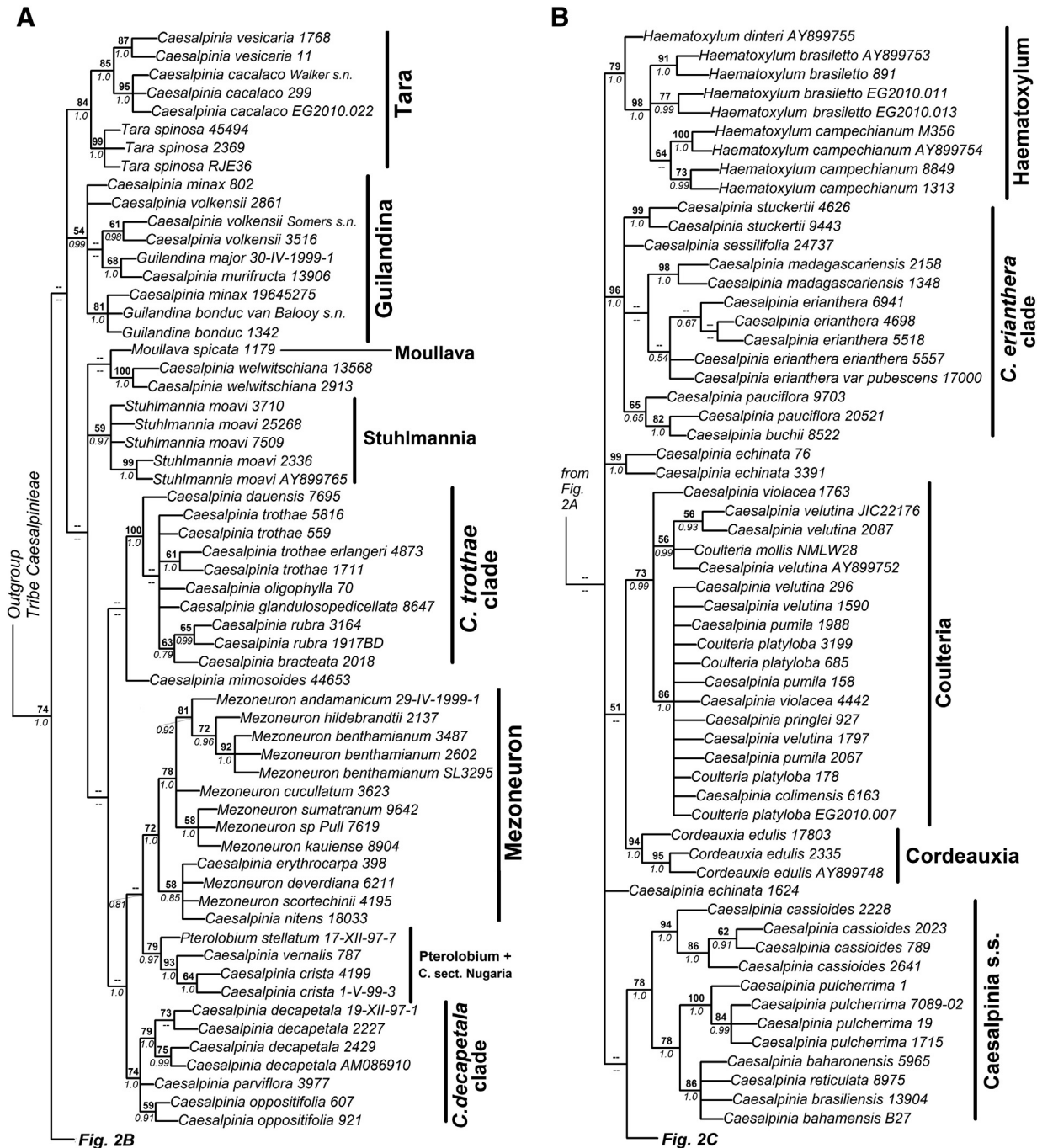


Fig. 2. A–D. Phylogeny of the informal *Caesalpinia* Group. Strict consensus of 100,000 equally parsimonious trees based on rps16 plastid sequences. Bootstrap support is shown in bold above branches, and posterior probability values are shown italicized, below the branch. Values below 50% or 0.5 are not shown, and are indicated by two dashed lines.

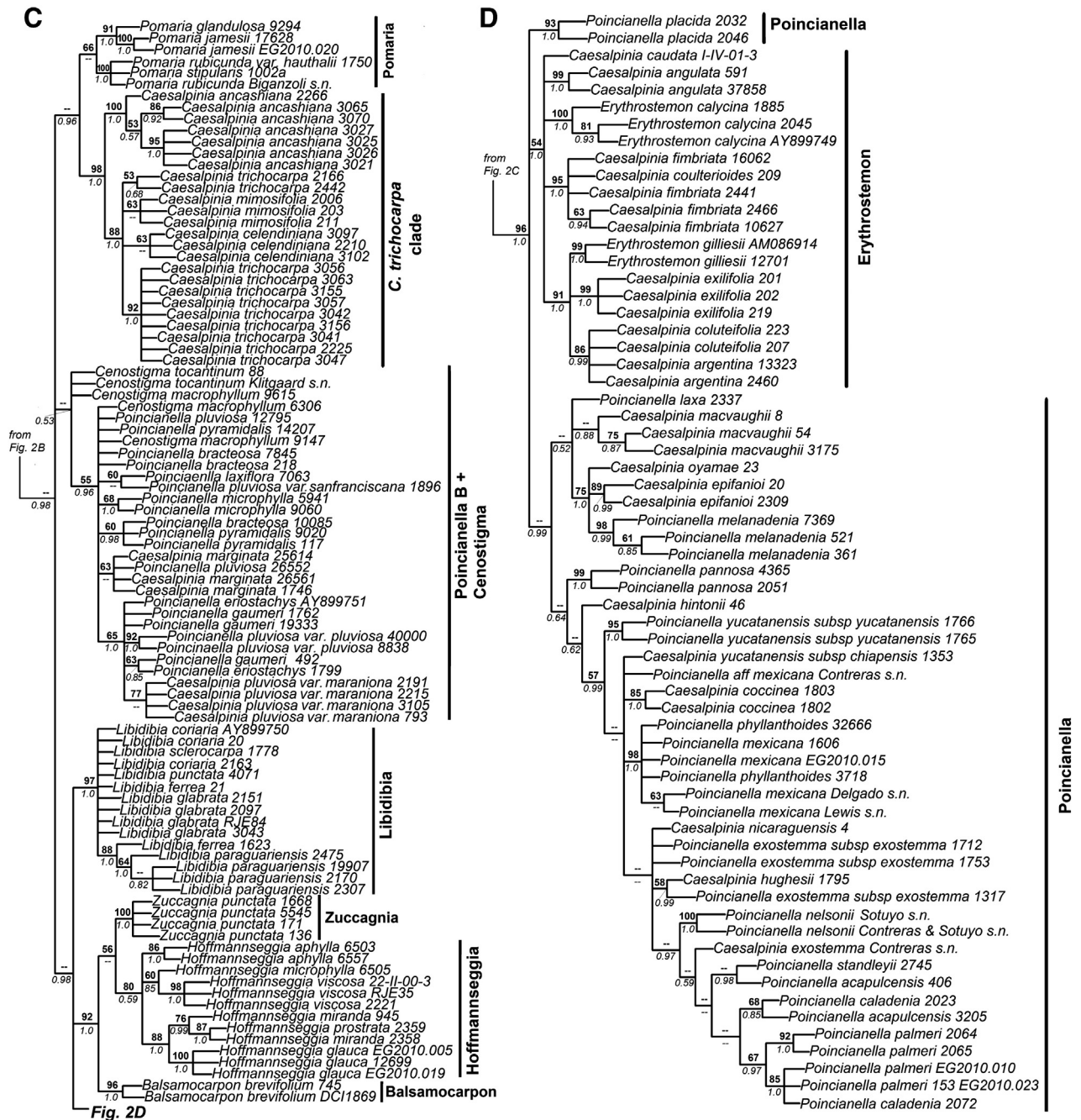


Fig. 2 (continued).

the backbone of the phylogeny, it is clear that *Caesalpinia* s.l. is not supported as monophyletic (Fig. 1).

While relationships amongst the major clades remain largely unresolved or weakly supported in our analyses, precluding detailed inferences about sister group relationships, our expanded phylogeny suggests that there are potentially many more genera in the *Caesalpinia* group. Previous studies looking at character evolution within the *Caesalpinia* Group need to be reconsidered. For example, the recent phylogenetic analysis by Nores et al. (2012), with one representative of each of the genera of the *Caesalpinia* Group sensu Lewis (2005) (with the exception of *Guilandina* (see Section 4.3 below)), based on an analysis of *trnL-trnF* and *matK* sequences, as well as morphological data, supported the idea that species with idioblasts form a clade distinct from species that lack idioblasts and commonly have glandular secretory structures. This observation was first made by Lersten and Curtis (1994,

1996), who noted that external glandular trichomes and internal secretory cavities were found predominantly in leaflets of specific Neotropical genera (*Balsamocarpon*, *Cenostigma*, *Erythrostemon*, *Hoffmannseggia*, *Libidibia*, *Poincianella*, *Pomaria*), whereas idioblasts were mainly present in the other groups (*Caesalpinia* s.s., *Coulteria*, *Cordeauxia*, *Haematoxylum*, *Guilandina*, *Mezoneuron*, *Moullava*, *Pterolobium*, *Stuhlmannia*, *Tara*). Future analyses with stronger resolution of the backbone will need to re-examine if the inclusion of the new clades found here upholds this pattern of mutually exclusive clades with distinct leaf anatomical structures.

Our analyses support the monophyly of three genera that are clearly distinct from *Caesalpinia* s.l.: *Haematoxylum*, *Pomaria*, and *Hoffmannseggia*. Four monospecific genera *Zuccagnia*, *Balsamocarpon*, *Cordeauxia*, and *Stuhlmannia*, for which we sampled multiple individuals, also formed distinct clades, which did not nest in other genera of *Caesalpinia* s.l. Contrary to Simpson et al. (2003), we find that the two

species of *Cenostigma* are placed in the *Caesalpinia* Group, as found by *Manzanilla and Bruneau* (2012), but in a clade with *Poincianella pro parte* (*Poincianella* B), rather than nested within *Mezoneuron* (see Section 4.6.3). *Nores et al.* (2012) found strong support for the monospecific *Lophocarpinia* as sister to *Haematoxylum*, and for *Stenodrepanum* as sister to *Hoffmannseggia* within a *Balsamocarpon-Hoffmannseggia-Zuccagnia* clade, the latter also supported in our analyses.

Here we review in detail all clades containing species from the eight genera reinstated from within *Caesalpinia* s.l. by *Lewis* (2005), including the five genera that are clearly supported as monophyletic in our analyses, as well as a set of nine new clades arising from the non-monophyly of three of the genera (*Caesalpinia* s.s., *Poincianella*, and *Erythrostemon*) recognised by *Lewis* (2005) and the inclusion of previously unsampled Old World taxa. We provide a discussion of diagnostic morphological characters for each clade, whether these newly discovered clades should be considered as distinct genera, and whether they require new genus names.

4.1. *Tara* and *Coulteria*

Previous phylogenetic studies based on morphological, molecular and phytochemical data have suggested that *Tara* and *Coulteria* are closely related and potentially sister groups (*Bruneau et al.*, 2008; *Kite and Lewis*, 1994; *Manzanilla and Bruneau*, 2012; *Nores et al.*, 2012; *Simpson et al.*, 2003). Although both *Tara* and *Coulteria* form strongly supported monophyletic groups in our analysis (Fig. 2A, B), thus supporting the re-segregation of these genera by *Lewis* (2005), lack of resolution and support preclude making any firm inferences about their relationships to each other. Both genera have a distinctive cucullate lower sepal with a fimbriate margin, suggesting a pseudocopulatory insect pollination syndrome. However, the fruits of *Tara* are thick and indehiscent, and seeds are subglobose to globose, while *Coulteria* has thin, laterally compressed, subchartaceous fruits and laterally compressed seeds. In addition, certain species of *Coulteria* are known to be dioecious (*G.P. Lewis*, pers. obs., *J.L. Contreras*, pers. comm.). The wood anatomy of the three species of *Tara* is distinctive, characterised by non-storied, heterocellular rays and axial parenchyma and indistinct growth rings (*Gasson et al.*, 2009). Although species of *Coulteria* have a more variable wood anatomy, of the five species investigated to date (from a total of eight), all share the presence of prismatic crystals in ray cells and chambered axial parenchyma.

4.2. *Libidibia*

As found in other studies (*Bruneau et al.*, 2008; *Manzanilla and Bruneau*, 2012; *Nores et al.*, 2012), *Libidibia* forms a robustly supported (BS: 97%, PP: 1.0) monophyletic group, supporting the reinstatement of the genus by *Lewis* (2005). Species of *Libidibia* are unarmed trees, with impari-bipinnate leaves, and terminal paniculate or racemose inflorescences, and occur in disjunct areas of seasonally dry tropical forest across the Neotropics, from Mexico and the Antilles to Colombia, Venezuela, Ecuador, Peru, Paraguay, Brazil, Bolivia and Argentina. With the exception of the type species, *Libidibia coriaria*, all other species of the genus have smooth bark with a patchwork pattern of white, grey and green, described as “leopard-skin bark” (*Lewis*, 2005). Flowers are typically yellow (the standard petal usually with reddish orange insect guides on the inner surface), with microscopic tentacle-like papillate trichomes on the standard petal surface (*Lewis*, 2005), while fruits are dark brown to black, tannin-rich, woody and indehiscent. All *Libidibia* species have a distinctive wood anatomy, well defined by short-storied homocellular rays and axial parenchyma, and lacking prismatic crystals in the ray cells and growth rings (*Gasson et al.*, 2009). A number of species, including *Libidibia ferrea*, *Libidibia punctata* and *Libidibia coriaria*, possess dark punctate glands on the abaxial surface of their leaflets, although the quantity of these glands is variable (pers. obs.). The type species, *L. coriaria*, is somewhat atypical for the group as it has rough fissured

bark rather than the leopard-skin pattern of all other species, white (not yellow) flowers that lack the papillate trichomes, and tightly curled indehiscent fruits.

While we did not manage to sequence the *rps16* locus from *Stahlia monosperma* due to nucleotide repeats, preliminary phylogenetic analyses based on plastid *trnD-trnT* sequences (results not shown) suggest that *Stahlia* is related to the *Libidibia* clade, as previously suggested (*Nores et al.*, 2012; *Simpson et al.*, 2003). Although *Stahlia*, a tree endemic to Puerto Rico and the Dominican Republic, appears morphologically unique with its pinnate leaves and a bright red, sub-fleshy, oval to orbicular fruit, its floral morphology, indehiscent fruit, and dark punctate glands on the abaxial leaflet surfaces show strong similarities to *Libidibia*. Based on these morphological and genetic affinities, we consider that *Stahlia* should be transferred to the genus *Libidibia* (Fig. 3).

4.3. *Guilandina*

Our results support *Guilandina* as a monophyletic group (Fig. 2A, BS: 54%, PP: 0.99) that includes the type species *Guilandina bonduc* L. and hence the reinstatement of the genus as proposed by *Lewis* (2005) and others (see below). Few species of *Guilandina* have been included in previous phylogenetic analyses (*Bruneau et al.*, 2008; *Manzanilla and Bruneau*, 2012; *Nores et al.*, 2012), and thus the status of the genus has remained uncertain. In addition, confusion was caused because previous studies (*Bruneau et al.*, 2001, 2008; *Manzanilla and Bruneau*, 2012; *Nores et al.*, 2012) have mistakenly included *Caesalpinia crista* as an exemplar of *Guilandina*. *Guilandina crista* Small was published as a name that included in synonymy *C. crista* L., *G. bonduc* L. and *Guilandina bonducella* L., but we can see in our results that the multiple accessions of *G. bonduc* and *C. crista* we sampled are not closely related, the latter species placed in a clade with *Pterolobium stellatum* and a species from *Caesalpinia* sect. *Nugaria* (Fig. 2A; see Section 4.6.2 below).

Guilandina is a pantropical genus of lianas and scandent shrubs characterised by unisexual flowers (morphologically the flowers of at least some species appear to be hermaphrodite, but lack pollen in the anthers and are thus cryptically pistillate; *Gillis and Proctor*, 1974), few-seeded, oval-shaped dehiscent fruits, and are often armed with rigid trichomes or prickles. The seeds are hard and globose and adapted for long-distance oceanic dispersal by flotation (*Britton and Rose*, 1930; *Lewis*, 2005; *Polhill and Vidal*, 1981). *Guilandina* is one of the most morphologically and chemically (*Bell*, 1981) distinctive segregates of *Caesalpinia* s.l., prompting recognition as a subgenus of *Caesalpinia* (*Gillis and Proctor*, 1974; *Polhill and Vidal*, 1981), or reinstatement to generic rank (e.g., *Verdcourt*, 1979). Despite the clear morphological diagnosability of *Guilandina* as a genus, taxonomic work is needed to resolve species delimitation and associated nomenclatural problems to produce a new species-level taxonomic revision. Species-level phylogenies of *Guilandina* may prove to be challenging and complex, as putative hybrids are thought to occur in the Caribbean region (*G.P. Lewis*, pers. obs.) and all species have the potential to disperse long distances in water, as found for other pantropical plant species with sea-drifted seeds, e.g. *Hibiscus tilliaceae* and allies in the Malvaceae (*Takayama et al.*, 2006); and a number of legume species: *Canavalia rosea* and allies (*Vataranpast et al.*, 2011), *Entada*, and the *Vigna marina-luteola* complex, *Kajita et al.*, 2013), possibly resulting in a reticulate pattern of species evolution.

4.4. *Mezoneuron*

Mezoneuron also has been viewed as distinct from *Caesalpinia* s.l. based on its characteristic dorsally winged, usually thin, oblong, chartaceous and indehiscent fruits, even though in some *Mezoneuron* species the fruit is discoid in shape and coriaceous to sub-woody. The indehiscent, dorsally winged fruit typical of most *Mezoneuron* species provides a potential morphological synapomorphy for this clade. While

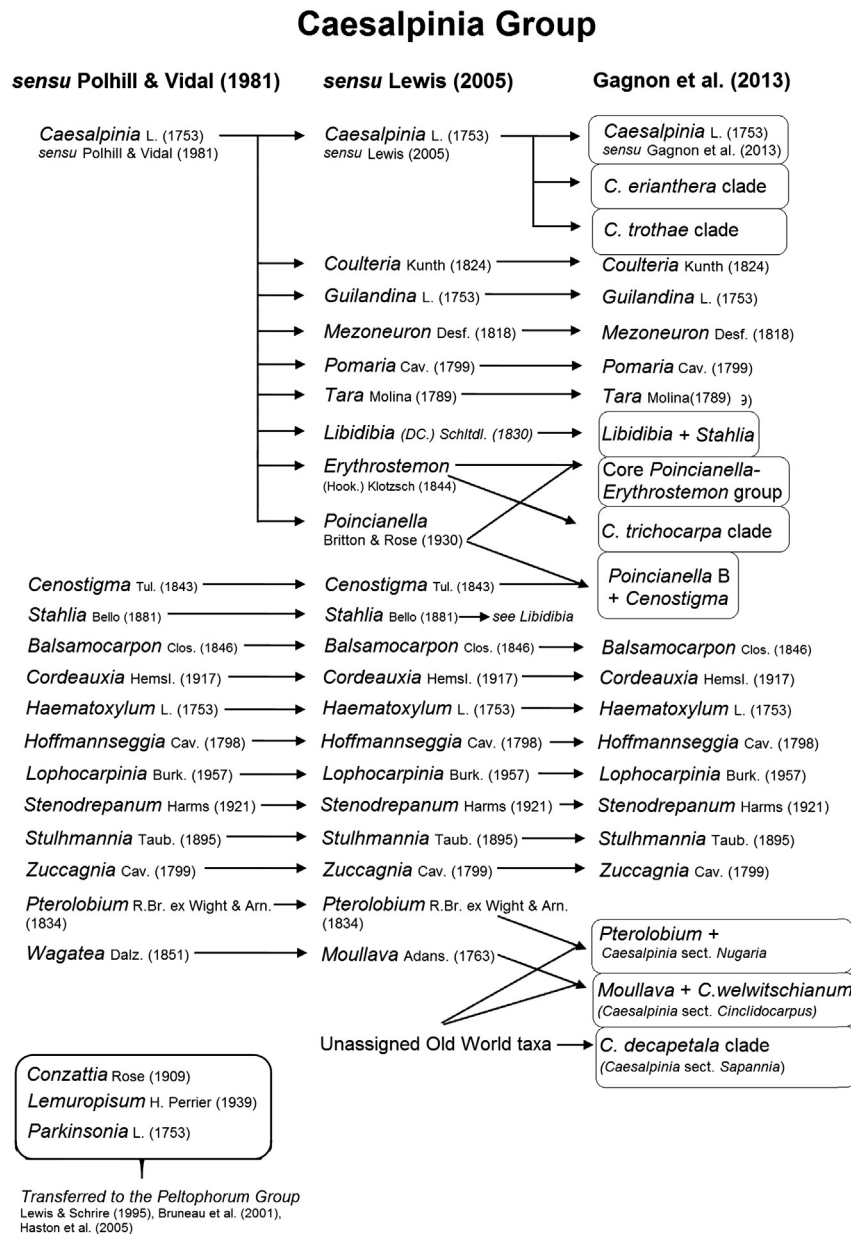


Fig. 3. Comparison of generic classifications of the *Caesalpinia* Group proposed by Polhill and Vidal (1981), Lewis (2005), and this study.

Mezoneuron is usually considered to have wind-dispersed fruits it is also capable of dispersal by water (Lewis, 1998), which might explain its wide distribution from Africa and Madagascar, across the Indian sub-continent into Indonesia and Polynesia. Furthermore, fossils unequivocally assigned to *Mezoneuron* by Herendeen and Dilcher (1991) are known from North America, indicating that there has been a significant shift in the range of this genus. As for *Guilandina*, *Mezoneuron* has been variously recognised as a separate genus (Brenan, 1967; Lock, 1989; Verdcourt, 1979) or as a subgenus or section of *Caesalpinia* (Hattink, 1974; Herendeen and Zarucchi, 1990; Herendeen and Dilcher, 1991; Vidal and Hul Thol, 1976). The monophyly of *Mezoneuron* is supported by our results (Fig. 2A, BS: 72%, PP: 1.0), with a sister relationship to the *Pterolobium* clade (albeit lacking support) that was also found in other studies (Bruneau et al., 2008; Manzanilla and Bruneau, 2012; Nores et al., 2012).

4.5. *Caesalpinia sensu stricto*: two new clades

Caesalpinia s.s. as it was defined by Lewis (2005), is clearly polyphyletic with three distinct clades revealed in our study (Fig. 2A, B). This is perhaps not too surprising given the great morphological diversity and wide geographical distribution of the approximately 25 species placed in *Caesalpinia* s.s. by Lewis (2005). The species of the three clades together occupy much of the Succulent Biome as defined by Schrire et al. (2005). The type species, *C. brasiliensis* L., is placed in a group of Neotropical species, here re-circumscribed as a less speciose *Caesalpinia* s.s. (Fig. 2B). This clade includes the Caribbean species *Caesalpinia barahonensis* and *Caesalpinia bahamensis* (the latter known to be bat-pollinated; Koch et al., 2004), the widespread Guatemalan and Mexican (Sonora) species *Caesalpinia pulcherrima* (widely cultivated as an ornamental throughout the tropics and known to be butterfly-pollinated,

Cruden and Hermann-Parker, 1979), and the northern Andean species *Caesalpinia cassioides* from the dry valleys of Colombia, Ecuador and Peru. All these species are armed (except for some cultivated forms of *C. pulcherrima*), eglandular shrubs, that have explosively dehiscent pods with twisting valves, similar to those found in the *Poincianella-Erythrostemon* group.

A separate clade of species previously attributed to *Caesalpinia* s.s. (sensu Lewis, 2005), here informally designated as the *C. trothae* clade (Figs. 2A & 3), is made up of strictly African species that are found in dry forests and thickets from the Horn of Africa, through the arid 'corridor' that crosses Tanzania, Botswana, Namibia and Mozambique, to South Africa. While this clade has not previously been identified in phylogenetic analyses due to sparse taxon sampling, previous authors have noted the morphological similarity of the species in this assemblage, all spiny, multi-branched shrubs with reddish-pink flowers. For example, Brenan (1963) commented that *C. trothae*, *Caesalpinia glandulosopedicellata* and *Caesalpinia rubra* shared similar features and were probably related. Brummitt et al. (2007) also remarked that *Caesalpinia rostrata*, a South African endemic, not sampled here, showed affinities with *C. rubra* and *C. trothae*, including gland-dotted leaflets, similar bracts and anvil-shaped pods with an acuminate tip, characters which might provide synapomorphies for this clade.

The third robustly supported clade arising from the former *Caesalpinia* s.s. of Lewis (2005), here informally designated as the *C. erianthera* clade (Fig. 2B, BS: 96%, PP: 1.0), includes species distributed across the Caribbean, Central America and South America, to Madagascar, Somalia and the Arabian Peninsula. Both Simpson et al. (2003) and Nores et al. (2012) found a similar clade based on their *trnL-trnF* phylogenies, which included the same species except for *Caesalpinia buchii* and *C. erianthera*. However, with only sparse sampling of *Caesalpinia* s.s. sensu Lewis (2005) in their phylogenies, they could not confidently assert that this was a potentially new generic group. While this clade has not yet been characterised in depth, we note that all members are eglandular, spiny shrubs.

4.6. The *Poincianella-Erythrostemon* group: three different lineages

Together, the genera *Poincianella* and *Erythrostemon* comprise 47 species (Lewis, 1998), although two species, *Caesalpinia aphylla* Phil. and *Caesalpinia pumilio* Griseb., have since been transferred to *Hoffmannseggia* (Lewis and Sotuyo, 2010; Simpson et al., 2004, respectively). The genera *Poincianella* and *Erythrostemon* were revised by Lewis (1998) as a unit because of the difficulties of distinguishing between them morphologically. Our results suggest that *Erythrostemon* and *Poincianella* together form a polyphyletic assemblage as found by Nores et al. (2012) and Simpson et al. (2003), consisting of three distinct lineages (Figs. 2 & 3): a core *Poincianella-Erythrostemon* (P-E) clade (Fig. 2D, BS: 96%, PP: 1.0), the *C. trichocarpa* clade (Fig. 2C, BS: 98%, PP: 1.0) that is sister to *Pomaria*, and a third weakly supported clade composed of the two species of *Cenostigma* together with a subset of *Poincianella* species previously referred to as the *Poincianella B* group (Fig. 2C; Lewis and Schrire, 1995), with a centre of species diversity in South America, but also spanning across Central America and the Caribbean.

4.6.1. The core *Poincianella-Erythrostemon* (P-E) clade

The type species of *Erythrostemon* (*Erythrostemon Gilliesii* Klotzsch) and *Poincianella* (*Poincianella mexicana* (A. Gray) Britton & Rose) are both placed in the large core P-E clade. Within this core P-E clade, *Erythrostemon* is supported as monophyletic, albeit with weak to moderate support, and relationships amongst species are unresolved. Except for *Caesalpinia caudata* from North America and *Caesalpinia calycina* from Brazil, species of *Erythrostemon* are all found in South America, with a centre of diversity in Bolivia and Argentina, and are thus geographically separated from the rest of the core P-E group species,

which are restricted to Mexico and Central America (Lewis, 1998). The distinction between *Erythrostemon* and *Poincianella* in this core P-E clade is further complicated by the unresolved placement of *Caesalpinia placida* from southern Baja California, which is morphologically more similar to species from the *Erythrostemon* clade, but geographically is much closer to other species of the *Poincianella* group.

The P-E clade recovered here forms a group of unarmed shrubs and small to medium size trees (generally 3 to 10 metres in height), with fruits with dehiscent, twisting valves. Within the *Caesalpinia* Group, there is currently no known defining synapomorphy for this clade. For example, a prevalent feature of the P-E clade is the presence of gland-tipped trichomes in inflorescences, but this is also found in *Pomaria*, *Poincianella B*, the *C. trichocarpa* clade and certain species of *Hoffmannseggia*. Furthermore, no obvious morphological synapomorphies are known that distinguish the *Erythrostemon* clade from the rest of this core P-E clade, due to the variable and highly homoplasious nature of morphological characters within each genus (Lewis, 1998). As an example, most species of *Erythrostemon* have black glands sunken into the crenulate depressions of leaflet margins (Lewis, 1998), but certain species (*Caesalpinia exilifolia*, *Caesalpinia coluteifolia* and *Caesalpinia angulata*) have eglandular leaflets. In the core P-E clade, species traditionally assigned to *Poincianella* have either eglandular leaflets or a sub-marginal ring of glands on the lower leaflet surfaces (*C. placida*, has the more typical *Erythrostemon* leaflet gland pattern but as indicated above occupies an unresolved position within the core P-E clade). Pollination syndromes in the P-E group also show a wide range of variation. For example, species traditionally placed in *Erythrostemon* are bee-pollinated, except *E. gilliesii* which is hawk moth-pollinated (Coccuci et al., 1992) and *Caesalpinia coulterioides* which has tubular flowers suggestive of hummingbird pollination. Members of *Poincianella* placed within the core P-E group encompass yellow-flowered species (often the standard petal inner surface blotched or network veined orange-red) thought to be principally pollinated by large solitary bees (e.g., of the genus *Xylocopa*), species with pendulous racemes of small pink flowers pollinated by territorial bees of the genus *Centris* (e.g. *Caesalpinia hintonii*, *Caesalpinia epifanioi*, *Caesalpinia laxa*, *Caesalpinia macvaughii*, *Caesalpinia melanadenia*), and orange, red or red and yellow flowered species, some with the standard petal to some degree laterally compressed, pollinated, at least in part, by hummingbirds (e.g., *Caesalpinia coccinea*, *Caesalpinia exostemma* and *Caesalpinia hughesii*). In most respects the core P-E clade forms a morphologically and ecologically coherent group of shrubs and small treelets of seasonally dry tropical forests with a bicentric amphitropical distribution restricted to the Neotropics. Based on current evidence we see no phylogenetic or morphological basis for separating *Erythrostemon* as a distinct genus from *Poincianella* in the core P-E group, though perhaps a study revisiting the morphology of this group and providing stronger resolution for the molecular phylogenies is needed before we can affirm that the P-E group should be treated as a single genus.

4.6.2. *C. trichocarpa* clade: a small group of Andean species

The second lineage of the polyphyletic *Poincianella-Erythrostemon* groups, sensu Lewis (1998), here informally designated as the *C. trichocarpa* clade (Fig. 2C), occurs as sister to the genus *Pomaria* in our Bayesian analysis. This robustly supported clade comprises four to five species of suffrutescent to medium-sized shrubs restricted to mid-elevation seasonally dry inter-Andean valleys in Ecuador, Peru, Bolivia and Northwest Argentina. Although there are no obvious morphological synapomorphies for this group, species of this smaller clade have dark glands in depressions of the leaflet margin typical of the *Erythrostemon* clade and they have short stipitate glandular trichomes similar to those seen in *Pomaria* and in the P-E clade. However, *Pomaria* has a set of diagnostic synapomorphies including lateral (not terminal) stigmas, anthers nestled within a cucullate lower sepal, and orange glandular dots (drying dark red or black) on leaflets, calyces and fruits, that are not shared with the *C. trichocarpa* clade.

4.6.3. *Poincianella B* (sensu Lewis and Schrire, 1995) and *Cenostigma*

The *Poincianella B* clade (Fig. 2C) was first uncovered by Lewis and Schrire (1995), and also noted in the phylogenies of Simpson et al. (2003) and Nores et al. (2012) as a strongly supported clade composed of two species: *Caesalpinia eriostachys* and *C. pluviosa*. The relationship between species of *Poincianella B* (sensu Lewis and Schrire, 1995) and the two species of *Cenostigma* (Fig. 2C) is very weakly supported in this analysis, but differs from previous studies which placed *Cenostigma* as a genus outside of the *Caesalpinia* Group (Nores et al., 2012; Simpson et al., 2003). By sampling more than one specimen of each of the two species of *Cenostigma*, our study firmly establishes placement of the genus within the *Caesalpinia* Group, as also found by Manzanilla and Bruneau (2012; but in their study *Cenostigma* occurs in the *Mezoneuron* clade). Furthermore, *Cenostigma* shares with *Poincianella B* key morphological and anatomical features, which supports their position together in a clade distinct from both the core P-E and the *C. trichocarpa* clades.

A number of key characters distinguish *Poincianella B* from the rest of *Poincianella* in the core P-E group. A survey of the wood anatomy of 19 species of *Poincianella* s.l. revealed that *Caesalpinia gaumeri*, *Cerriostachys*, *Poincianella pyramidalis*, and *Poincianella pluviosa* (all *Poincianella B* species) differ from the other *Poincianella* species in having regularly storied rays and axial parenchyma (Gasson et al., 2009). Lewis (1998) noted that *C. eriostachys*, *C. gaumeri* and all of the Brazilian species of the clade share a distinct stigma with a sub-terminal bulbous chamber narrowing to a papillate-fringed pore that is distinct within the *Poincianella-Erythrostemon* group sensu Lewis (1998). de Queiroz (2009) in his study of the legumes of the caatinga vegetation of northeastern Brazil also used the presence of alternate to sub-opposite leaflets to distinguish *Poincianella* from other genera in *Caesalpinia* s.l. First reported by Lewis (1998), leaflet arrangement can be extremely variable within species and even on individual plants, with both alternate and opposite leaflets occurring in some species (e.g. in *P. pluviosa*, and in *Caesalpinia marginata*, unusual in the group in having singly pinnate, not bipinnate, leaves). Although not sampled here, morphological evidence suggests that the Caribbean species, *Caesalpinia glandulosa*, *Caesalpinia myabensis*, *Caesalpinia pellucida* and *Caesalpinia pinnata*, probably belong in the *Poincianella B* group (Gasson et al., 2009; Lewis, 1998).

Perhaps the most important distinguishing features of the *Poincianella B* group are its unique glandular structures and indumentum, which are not found in the core *Poincianella-Erythrostemon* clade, but which are present in the genus *Cenostigma*. These include internal secretory cavities, which consist of resin ducts present in the lamina of leaflets and in inflorescences (Lersten and Curtis, 1994; Rudall et al., 1994). Some species of *Poincianella B* (*P. pluviosa* and *C. eriostachys*, Lewis, 1998) also have an indumentum of stellate hairs on leaflets and inflorescence rachis. This character is restricted elsewhere in tribe *Caesalpinieae* to the genus *Cenostigma*, and the more distantly related genus *Dimorphandra* (Lersten and Curtis, 1996), and needs to be carefully re-assessed in other members of *Poincianella B*. *P. pluviosa* and *C. eriostachys* also share with *Cenostigma* the development of a fluted trunk in mature individuals, a feature also seen in species of *Haematoxylum*. Finally, *Poincianella B* species and *Cenostigma* have fruits with conspicuously thickened sutures, a character not observed in the P-E clade. While our results do not resolve the relationships of *Cenostigma*, certain morphological features within the *Poincianella B* + *Cenostigma* clade support the Bayesian and parsimony topologies recovered in our analyses. More exhaustive morphological studies and more informative loci will need to be sampled before we can properly assess the degree to which the *Poincianella B* clade is related to *Cenostigma* and whether the two should be united under one generic name.

4.6.4. *Caesalpinia echinata*

C. echinata is the only species tentatively placed in the P-E group by Lewis (1998) that did not group closely with any of the three segregate

clades identified in this study, i.e. the core P-E group, the *Poincianella B* clade, or the *C. trichocarpa* clade, but is instead unresolved within a large and poorly-supported polytomy (Fig. 2B). The taxonomic treatment of this species has long been problematic within *Caesalpinia* s.l., as it possesses a unique combination of morphological characters that are individually encountered in other genera of *Caesalpinia* s.l. and indeed across the larger *Caesalpinia* Group as a whole. This species is usually a large tree with upwardly curved thorns (arising from woody protuberances) arming the trunks and main branches. It has wood with a rich red-dye (not unlike that of species of *Haematoxylum* and *Caesalpinia sappan*, the latter an Asian species), and its floral morphology is similar to that of the *Poincianella B* group. It also has prickly pods superficially similar to those of *Guilandina*, although its seeds are laterally compressed and not globose as in *Guilandina*. Lewis (1998) placed *C. echinata* within his P-E group based on similarities in floral morphology, and the presence of red subepidermal glands, which were assumed to be homologous to the internal secretory cavities of the *Poincianella B* group. However, the species was not included in Lersten and Curtis' (1994, 1996) surveys of leaflet secretory structures in the tribe *Caesalpinieae*, and the glands of *C. echinata* have not been studied in detail. Wood anatomy also suggests that *C. echinata* may not belong in *Poincianella* in its broadest circumscription (Gasson et al., 2009). In addition, the different accessions of *C. echinata* sampled did not form a monophyletic group, perhaps reflecting well-known intraspecific variation. Population genetics studies using RAPDs (Cardoso et al., 1998), chloroplast microsatellite markers (Lira et al., 2003) and AFLPs (Cardoso et al., 2005) have shown that there is significance among population variation between three morphological variants of *C. echinata* that are distinct in leaflet size, pinnation, and colour of the heartwood, and which occur in allopatric localities along the Brazilian coast (Lewis, 1998; Lima et al., 2002).

4.7. Unassigned Old World taxa: new genera?

Our analysis sheds new light on the affinities of some of the Old World taxa not previously sampled in phylogenetic studies and left unassigned to genera in Lewis's (2005) generic system for the *Caesalpinia* Group. These taxa are placed in three newly recognised clades, the *C. decapetala*, *Caesalpinia* sect. *Nugaria*, and *Caesalpinia* sect. *Cinclidocarpus* clades (Fig. 2A). These clades correspond in part to Vidal and Hul Thol's (1976) infrageneric system for Asian *Caesalpinia* that includes sections *Sappania*, *Cinclidocarpus* and *Nugaria*, originally proposed by de Candolle (1825) and Benthams (1865). We discuss the composition, status and affinities of these clades and how they might be treated taxonomically.

4.7.1. *C. decapetala* clade (section *Sappania* DC.)

Moderate support (Fig. 2A, BS: 74%, PP: 1.0) was found for the monophyletic *C. decapetala* clade, comprising the three Asian species *C. decapetala*, *Caesalpinia parviflora* and *Caesalpinia oppositifolia*. This group is likely also to include *C. sappan* and *Caesalpinia godefroyana*, which although not sampled here, share similar geography and morphology (Hattink, 1974; Vidal and Hul Thol, 1976). Vidal and Hul Thol (1976) also included *C. mimosoides*, *Caesalpinia aestivalis* and *Caesalpinia caesia* in *Caesalpinia* section *Sappania*, but we exclude them from this clade. *C. aestivalis* is now known to be a synonym of *Pterolobium punctatum* and *C. caesia* is better placed in section *Nugaria* based on fruit morphology. *C. mimosoides* remains unresolved in our molecular analyses and in contrast to the rest of the species in the *C. decapetala* clade, *C. mimosoides* lacks idioblasts (Lersten and Curtis, 1994). *C. mimosoides* also has other distinctive features, such as straight rigid, needle-like trichomes and a vesicular, gland-covered fruit (Hattink, 1974), whereas the remaining species of the *C. decapetala* clade have oblong, laterally compressed, dehiscent pods with a sharp beak.

4.7.2. Does *Caesalpinia* sect. *Nugaria* represent a distinct genus, sister to *Pterolobium*?

The second clade of previously unassigned Asian taxa comprises *C. crista*, *Caesalpinia vernalis* and the type species of the genus *Pterolobium*, *P. stellatum* (Fig. 2A, BS: 79%, PP: 1.0). *Pterolobium*, as traditionally circumscribed, is a distinctive genus of 11 species, all of them scrambling shrubs and lianas with winged, samaroid pods (Vidal and Hul Thol, 1974). *Pterolobium* was placed by Pohill and Vidal (1981) in their *Caesalpinia* Group based on floral and vegetative characters. Despite the absence of a wing, the one-seeded and discoid to subelliptic fruits of *C. vernalis* and *C. crista* resemble those of *Pterolobium* (Ruth Clark, Royal Botanic Gardens, Kew, unpublished data). *C. vernalis* and *C. crista* were placed in *Caesalpinia* sect. *Nugaria* DC. by Vidal and Hul Thol (1976), a group of eight species with non-samaroid fruit. It is interesting to note that some of the species of this section have non-samaroid fruits with a small wing (*Caesalpinia sinensis* and *C. caesia*) or a narrow keel on one side of the pod (*Caesalpinia magnifoliolata*). These are possibly an intermediate form between the samaroid pods of *Pterolobium* and the wingless fruits of *Caesalpinia* section *Nugaria*. More complete taxon sampling of both *Pterolobium* and *Caesalpinia* section *Nugaria* is needed to verify the generic status of these two groups.

4.7.3. *Caesalpinia* sect. *Cinclidocarpus* (based on *Cinclidocarpus* Zollinger)

M. spicata and *C. welwitschiana*, two unassigned Asian species that did not group with the other Asian clades (i.e., the *Mezoneuron* + *C. decapetala* + *Pterolobium* + *Caesalpinia* section *Nugaria* clade), form an unsupported sister group in our phylogenetic analyses (Fig. 2A). *M. spicata* (synonym *Wagatea spicata* Dalzell), a liana from the Indian subcontinent, has long been considered a distinct genus in the *Caesalpinia* Group based on its densely flowered spicate inflorescences of flowers that have a showy red calyx with the sepals fused into a small tube at the base. *C. welwitschiana* is a scrambling liana from Central Africa previously referred to *Mezoneuron*, but which Brennan (1963) replaced into *Caesalpinia* because its fruit is similar to that of the Asian species *Caesalpinia tortuosa* and *Caesalpinia digyna*, neither of which were sampled in our study. Vidal and Hul Thol (1976) placed the latter two species in *Caesalpinia* section *Cinclidocarpus*, distinguishing them from section *Sappania* based on their indehiscent fruits. Closer morphological examination of these two species suggests a similar fruit type to that of *M. spicata* and *C. welwitschiana*. Descriptions of these four species all mention that they have straight, indehiscent, oblong to elliptic, somewhat laterally compressed fruits that are constricted between the seeds (subtorulose), ending with a small beak. They all have fruits with thickened sutures, and an exocarp and endocarp that are strongly adnate when dried (Brenan, 1967; Brummitt et al., 2007; Hattink, 1974). Inclusion of *C. digyna* and *C. tortuosa* in the molecular analysis is needed to test the apparently close relationship among these four species.

5. Conclusion

The greatest strength of the analyses presented here is the significantly expanded taxon sampling compared with previous studies. Our analyses have revealed a number of new distinct clades that merit consideration as new genera, and provide the most comprehensive hypothesis of phylogenetic relationships for the group to date. Conversely, reliance on a single plastid locus means that, while we find moderate or strong support for individual clades, our phylogeny lacks resolution and support across most of the backbone of the tree, such that the branching order and relationships among these major clades remain obscure. Our analyses clearly indicate that *Caesalpinia* s.l. is non-monophyletic, and that five of the reinstated genera proposed by Lewis (2005), *Tara*, *Coulteria*, *Libidibia*, *Guilandina*, and *Mezoneuron*, form well-supported clades with good diagnostic morphological characters. However, our results also suggest that some of the other genera segregated and reinstated by Lewis (1998, 2005) are non-monophyletic

and will probably need to be further subdivided. The *Poincianella-Erythrostemon* group recognised by Lewis (1998, 2005), and *Caesalpinia* s.s. (sensu Lewis, 2005), are two such groups which, based on our analyses, are non-monophyletic. While it would be premature to outline a complete generic system for the *Caesalpinia* Group at this stage, we suggest that the *C. trothae*, *C. erianthera*, and *C. trichocarpa* clades merit recognition as new genera. Better phylogenetic resolution and more morphological studies are needed to clearly assess if the core P-E clade should be treated as a single genus, and whether species of the *Poincianella B* group should be transferred to *Cenostigma*. The remaining issues of generic delimitation will require both the inclusion of additional Asian taxa in the analysis, and generation of additional sequence data to increase resolution and support in critical parts of the tree.

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