

Global distribution patterns of the Leguminosae: insights from recent phylogenies

BRIAN D. SCHRIRE, MATT LAVIN AND GWILYM P. LEWIS

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Recent large-scale molecular phylogenies derived from DNA sequences of the chloroplast regions *matK*, *rbcL*, and *trnL* were used to identify the major subgroups of legumes and the inter-relationships among these groups. Monophyletic legume clades were scrutinized for global distribution patterns and four generalised areas of endemism at the biome level were identified. These include 1) a fire intolerant, succulent-rich and grass poor, dry tropical forest, thicket and bushland biome (Succulent), 2) a fire tolerant, succulent poor and grass-rich, seasonally dry tropical forest, woodland and savanna biome (Grass), 3) a tropical wet forest biome (Rainforest), and 4) a temperate biome including both the Northern and Southern Hemispheres (Temperate). The Succulent biome links Central and North America and the Caribbean, with circum-Amazonian dry forest refugia (*e.g.*, the Caatinga of north-east Brazil and inter-Andean dry forests), the dryland regions of north-east to southern tropical Africa and Madagascar, and parts of Arabia extending to India (as exemplified by the distribution of the New World Phaseolinae and its sister Old World *Vigna sens. strict.*). This biome is inhabited by many subclades throughout the legume phylogeny. Different methods of cladistic vicariance analyses all suggest that lineages confined to the Succulent biome gave rise to sublineages occupying all other biomes, and that evolutionary shifts between the Rainforest and Grass biomes are frequent. In contrast, shifts from temperate into tropical biomes are infrequent. Rainforest clades in general may be most recently derived in legumes, a suggestion supported by molecular phylogenetic studies. These results provide no support for a putative Southern Hemisphere origin of the legume family, but rather are in agreement with the fossil record that suggests a rapid diversification of legumes throughout much of the world, perhaps originating in and around the margins of the Tethys seaway, during the Early Tertiary.

Brian D. Schrire, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK. E-mail: B.Schrire@rbgkew.org.uk

Matt Lavin, Plant Science and Plant Pathology, 119 ABS, Montana State University, Bozeman MT 59717, USA. E-mail: mlavin@montana.edu

Gwilym P. Lewis, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK. E-mail: G.Lewis@rbgkew.org.uk

Introduction

This analysis of the distributions of the c. 730 genera in Leguminosae was made possible by a number of recent developments. A survey and

update of circumscriptions of all legume genera has just been completed for *Legumes of the World* (Lewis *et al.* in prep.) and this has provided the most current and comprehensive data bearing on species numbers and distribu-

tions. In addition, the systematics of the Leguminosae has benefited from major contributions to the understanding of the morphology and classification of the family (Polhill & Raven 1981; Polhill 1994), and more than ten years of intensive molecular phylogenetic research, which now covers nearly all areas of the family.

A “supertree” derived from a *matK* phylogeny (Wojciechowski *et al.* 2004) and augmented by *trnL* analyses of Caesalpinioideae (*e.g.* Bruneau *et al.* 2000, 2001; Fougère-Danezan *et al.* 2003; Herendeen *et al.* 2003a; Forest unpubl. data) and Mimosoideae (Luckow *et al.* 2000, 2003), and *trnL* and *rbcL* analyses of Papilionoideae (Doyle *et al.* 2000; Pennington *et al.* 2001; Kajita *et al.* 2001), underpins the relationships discussed in this paper. These analyses have resulted in often radically redefined generic and tribal limits and a largely well-supported pattern of overall relationships. Although circumscriptions will continue to change and be refined as more taxa are sampled, the emerging legume supertree is largely stable and reveals a novel pattern of taxon-area relationships that bears on legume biogeography.

Raven & Polhill (1981) hypothesised that legumes differentiated some time before the end of the Cretaceous in Africa. This hypothesis finds little support from fossil evidence, which suggests that the family diversified at the earliest by the Late Palaeocene to Early Eocene (Herendeen *et al.* 1992; Herendeen 2001; Herendeen pers. comm.). In addition, the numerous recent molecular phylogenetic analyses of the family (*e.g.* Lavin *et al.* 2000) reveal very little in the way of a vicariant relationship between Africa and South America as suggested by Raven and Axelrod (1974). Phylogenetic results together with fossil evidence suggest that dispersal and vicariance, putatively linked to the Tethys seaway (Herendeen *et al.* 1992; Lavin *et al.* 2001b), is more likely to

explain present legume distributions. The aims of this paper, therefore, are the construction of a taxon-biome supertree of Leguminosae that summarises the major terminal taxa (*i.e.*, well-supported legume subclades) and the interrelationships among these recently characterised groups. By assigning each of these major subclades to a large-scale biome, four of which are circumscribed in this present study, cladistic vicariance analyses can be undertaken on the taxon-biome supertree to detect a generalised pattern of area relationships for legumes. As such, we seek to detect the generalities of legume biogeography, including any historical imprint on the modern distribution of the family.

The Legume Supertree

Methods

A chloroplast *matK* phylogeny representing a comprehensive sampling of all major legume groups (Wojciechowski *et al.* 2004) served as the backbone for the supertree (summarised in Fig. 1). In addition, major legume subclades detected in a range of phylogenetic analyses of chloroplast *trnL* and *rbcL* sequences were used in supertree construction because they represented a more exhaustive sampling of various local subclades (Figs. 2-12). The local subclades included further sampling of legume sister groups (Forest unpubl. data), various legume subgroups (Kajita *et al.* 2001), caesalpinoids (Herendeen *et al.* 2003a), mimosoids (Luckow *et al.* 2003), and papilionoid legumes (Crisp *et al.* 2000; Hu *et al.* 2000; Wojciechowski *et al.* 2000; Lavin *et al.* 2001a; Pennington *et al.* 2001). A strict supertree (*sensu* Sanderson *et al.* 1998) was readily constructed manually because of the high compatibility of all the component trees. Essentially, the large-scale *matK* phylogeny (Wojciechowski *et al.* 2004) represented all major clades of legumes, and the other molec-

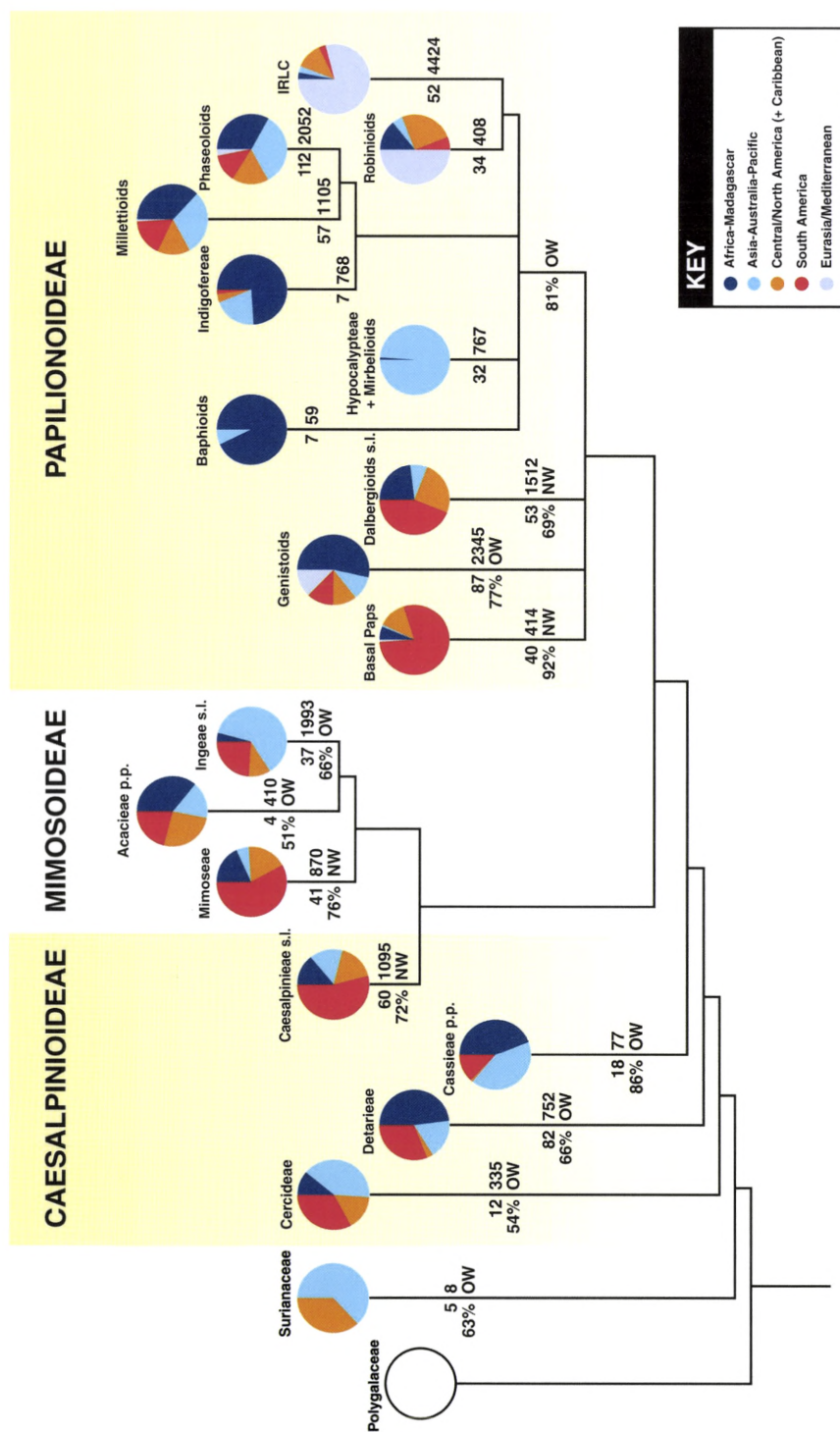


Fig. 1. Simplified phylogeny of Leguminosae based on Doyle *et al.* 2000; Bruneau *et al.* 2000, 2001; Pennington *et al.* 2001; Kajita *et al.* 2001; Luckow *et al.* 2000, 2003; Fougère-Danczan *et al.* 2003; Herendeen *et al.* 2003a; Forest unpubl. data; Wojciechowski 2003; Wojciechowski *et al.* 2004. Pie charts highlight the percentage of species of each group per major geographic region, and the numbers of genera and species in each of the major subclades. Occurrences in each of the major subclades in the Old World (OW) and New World (NW) are reported (whichever is highest). Predominantly neotropical versus palaeotropical and temperate clades are readily visualized in colour combinations, with red and orange denoting the New World, dark and light blue for the Old World, and grey for temperate subclades.

ular phylogenetic studies identified in more detail the constituents of these monophyletic *matK* subclades. Chronograms derived from rate-smoothed bayesian consensus trees of the *matK* phylogeny (Lavin *et al.* 2004) provided comparative clade ages for the family, based on thirteen time constraints derived from fossil evidence.

Results

Relationships for a total of 125 local subclades were resolved in the legume supertree, including the putative outgroup family Surianaceae (Figs. 2-12). A condensed version of this tree (Fig. 1) reflects a broad pattern of relationships, with local subclades compressed into a number of well supported larger clades. Terminal taxa follow larger groupings now well established in the legume literature, including such well-supported subclades of papilionoid legumes now referred to as the genistoids, dalbergioids, baphioids, mirbelioids, millettoids, phaseoloids, robinoids and the inverted-repeat-loss-clade, or IRLC.

The three subfamilies of Leguminosae comprise some 19, 400 species with the monophyletic Mimosoideae (17% of species) and Papilionoideae (72% of species) derived within the paraphyletic Caesalpinioideae (11% of species). Overall, fewer species occur in the basal-most branching subclades of the family (Fig. 1; Table 1) and the most speciose diversifications, dominated by shrubby or herbaceous species, are found in clades nested high in the supertree. For example, a third of all legume species occur in less than ten local subclades, and are traditionally ranked at the genus level: *Astragalus*, the various clades within *Acacia*, *Indigofera*, *Crotalaria*, *Chamaecrista* and *Senna*, and *Mimosa*. In papilionoid legumes, herbaceous or shrubby taxa with drier affinities are sometimes sister to large arborescent clades. For example, *Hypocalyptus* and the mirbelioids are sister to the tropical millettoid-phaseoloid

alliance and *Adesmia* is sister to the dalbergioids *sens. strict.* This provides no support for the traditional view of an arborescent habit always mapping ancestrally to the shrubby or herbaceous habit (Lavin *et al.* 2001a; Schrire *et al.* 2003). The basally branching clades of the family (*e.g.*, Cercideae, Detarieae and Cassieae *pro parte*) have more species in the Old World. The crown clade linking the large Papilionoideae – and Caesalpinieae *sens. lat.* plus Mimosoideae – diversifications, however, has predominantly neotropical diversifications in the basal groups Caesalpinieae *sens. lat.*, Mimoseae and Basal Papilionoideae, although there is a trend towards more palaeotropical taxa in the derived parts of the Mimosoideae and Papilionoideae. A predominance of species in temperate regions occurs in only three speciose papilionoid clades nested high in the tree, *i.e.* in the genistoids, phaseoloids and the IRLC.

Detection and assignment of biomes

Methods

Most of the major terminal taxa used in the legume supertree represented well supported clades that could be described in general ecological terms involving moisture (wet to dry), temperature (tropical to temperate), and disturbance (fire-history to no fire-history) gradients. The generalised combination of these has resulted in four areas of endemism at the biome level for legumes that are described below. These areas reflect major Zonobiomes (Breckle 2002), *e.g.* tropical wet (Zonobiome I), two areas of tropical dry (in Zonobiomes II and III), and temperate (Zonobiomes IV-X).

Assignment of the major subclades of legumes to one or more biomes initially involved ascertaining the global distributions of c. 730 legume genera, many of which have been newly circumscribed to meet the criterion of monophyly (Lewis *et al.* in prep.).

Table 1. Number of species in each major clade of legumes, per major geographical region. This table is the basis for the numbers in Fig. 1.

TAXONOMIC GROUP	Number of genera/ species	Africa- Madagascar	Asia-Australia- Pacific	Central/ North America & Caribbean	South America	Eurasia/ Mediterranean
CAESALPINIOIDEAE TOTALS	172/ 2259	587	457	254	953	8
Cercideae	12/ 335	47	127	37	116	8
Detarieae	82/ 752	358	136	24	234	–
Cassieae p.p. (Dialiinae inc. Duparquetiinae)	18/ 77	33	33	1	10	–
Caesalpinieae (incl. Cassieae s.s.)	60/ 1095	149	161	192	593	–
MIMOSOIDEAE TOTALS	82/ 3273	385	1343	472	1072	1
Mimoseae	41/ 870	155	51	158	505	1
Acacieae s.s.	4/ 410	142	65	110	93	–
Ingeae (incl. Acacieae p.p.)	37/ 1993	88	1227	204	474	–
PAPILIONOIDEAE TOTALS	476/ 13854	3504	2511	1857	1909	4073
Basal Papilionoideae	40/ 414	24	2	54	328	6
Genistoids	82/ 2345	1261	247	262	275	300
Dalbergioids (incl. Amorpheae)	53/ 1512	342	127	380	663	–
Baphioids	7/ 59	55	4	–	–	–
Hypocalypteae & Mirbelioids	32/ 767	3	764	–	–	–
Indigofereae	7/ 768	566	157	30	15	–
Millettioids	57/ 1105	411	336	167	189	2
Phaseoloids	112/ 2052	676	703	355	266	52
Robinioids	34/ 408	57	22	101	24	204
IRLC	52/ 4424	109	149	508	149	3509
LEGUMINOSAE TOTALS	730/ 193864	476 (23%)	4311 (22%)	2583 (13%)	3934 (20%)	4082 (21%)

Within each genus patterns were especially sought among range restricted taxa, e.g. the genus *Caesalpinia sens. strict.* has a worldwide distribution, however narrowly restricted taxa are essentially limited to dry tropical areas in North America (twelve species in the

Caribbean and three species in Mexico to Central America) with two species in South America, and in Africa (four species in north-east Africa and Arabia, five species in southern Africa, one species in Madagascar and one species in central Africa).

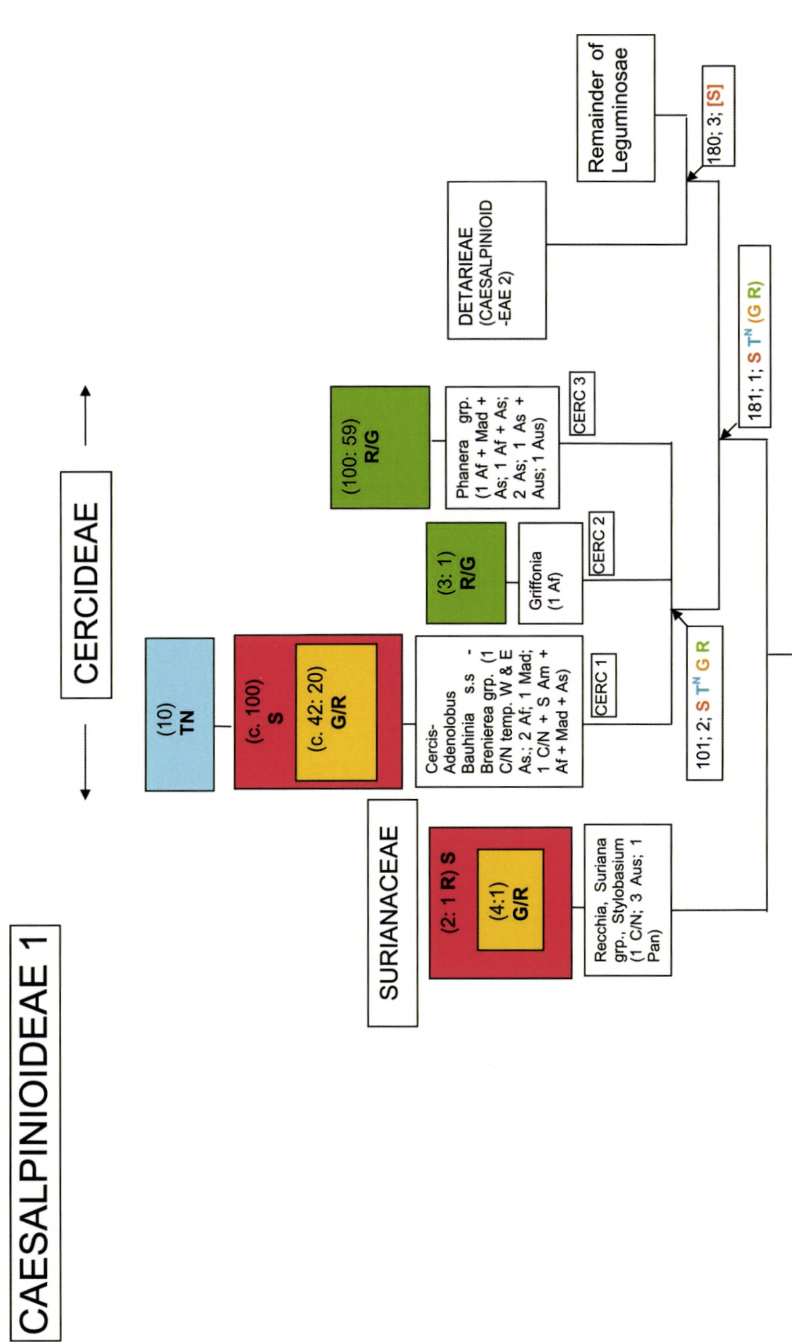


Fig. 2. Taxon-biome supertree of Cercideae (Caesalpinioideae 1) – This and Fig. 3-12 show the major legume subclades, representing a more exhaustive sampling of various local subclades than were used in the *matK* phylogeny. Colour-coded biomes (as in Fig. 13) were superimposed on the supertree: S = Succulent; R = Rainforest; G = Grass; TN = Temperate Northern Hemisphere; TS = Temperate Southern Hemisphere. Af = Africa; Mad = Madagascar; As = Asia; Aus = Australia; Pac = Pacific; C/N = Central and North America & Caribbean; S Am = South America; Eur/Med = Eurasia & Mediterranean; Pan = Panropical. The ratio's above each group = the proportion of e.g., (R) to (G) biome species in the group if R/G, or vice versa if G/R. Clades are named, e.g. DET 1 = Detarieae *sens. strict.* 1, according to their position within the major subclades. The nodes as numbered in the BPA and TASS analyses respectively, followed by the DIVA analysis result, are provided in boxes with arrows pointing at the critical nodes in the taxon-biome supertree to which they refer. The DIVA areas are also colour coded as in Fig. 13, and are listed in decreasing order of occurrence among possible optimisations in the analysis, i.e. the first area is either optimised most frequently or at least no less so than the others. Biomes in square brackets = the only optimisation found; biomes underlined = present in all optimisations, and biomes in ordinary brackets = present in only one of a number of optimisations.

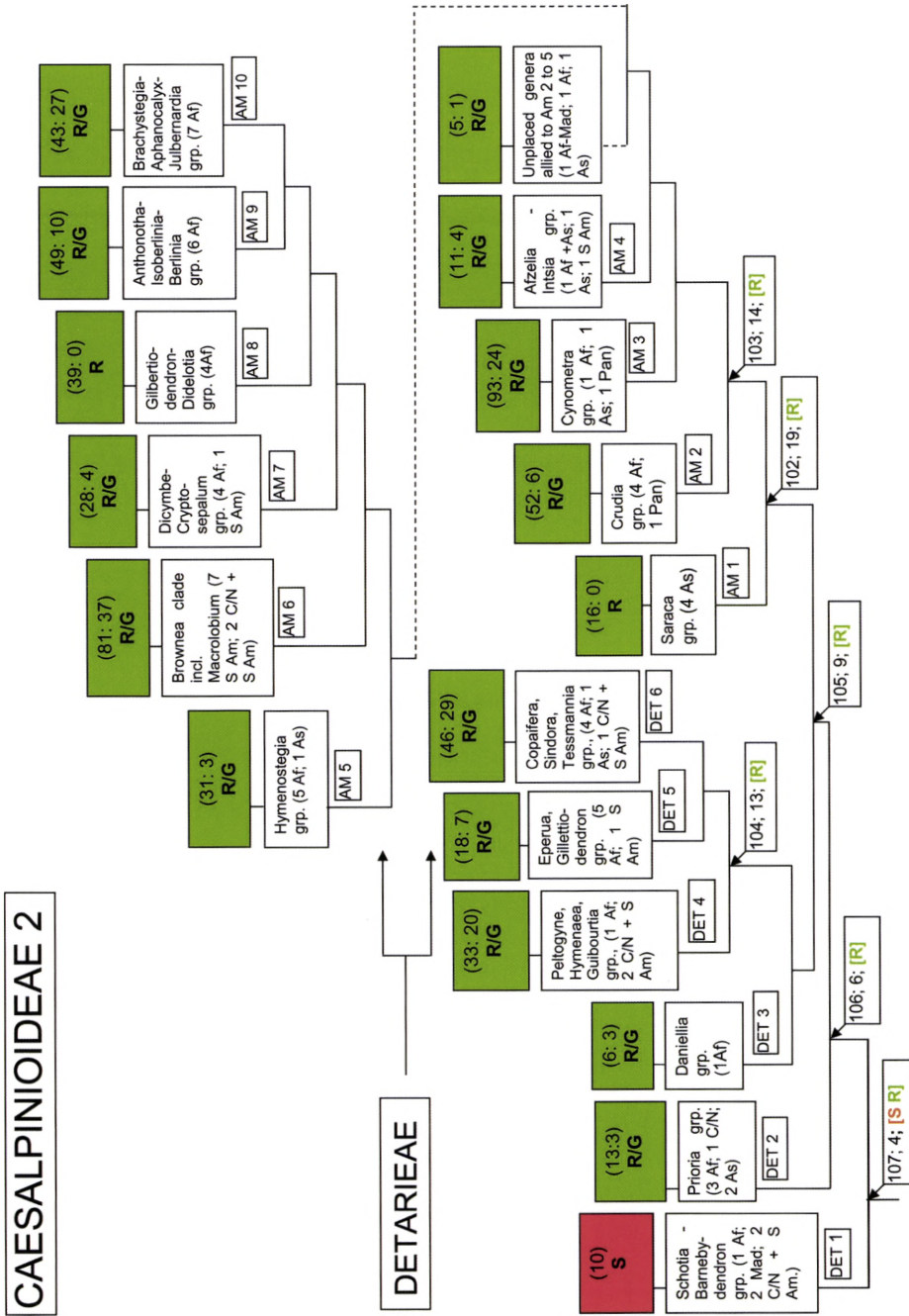


Fig. 3. Taxon-biome supertree of Detarieae (Caesalpinioideae 2) – For detailed explanation, see legend to Fig. 2.

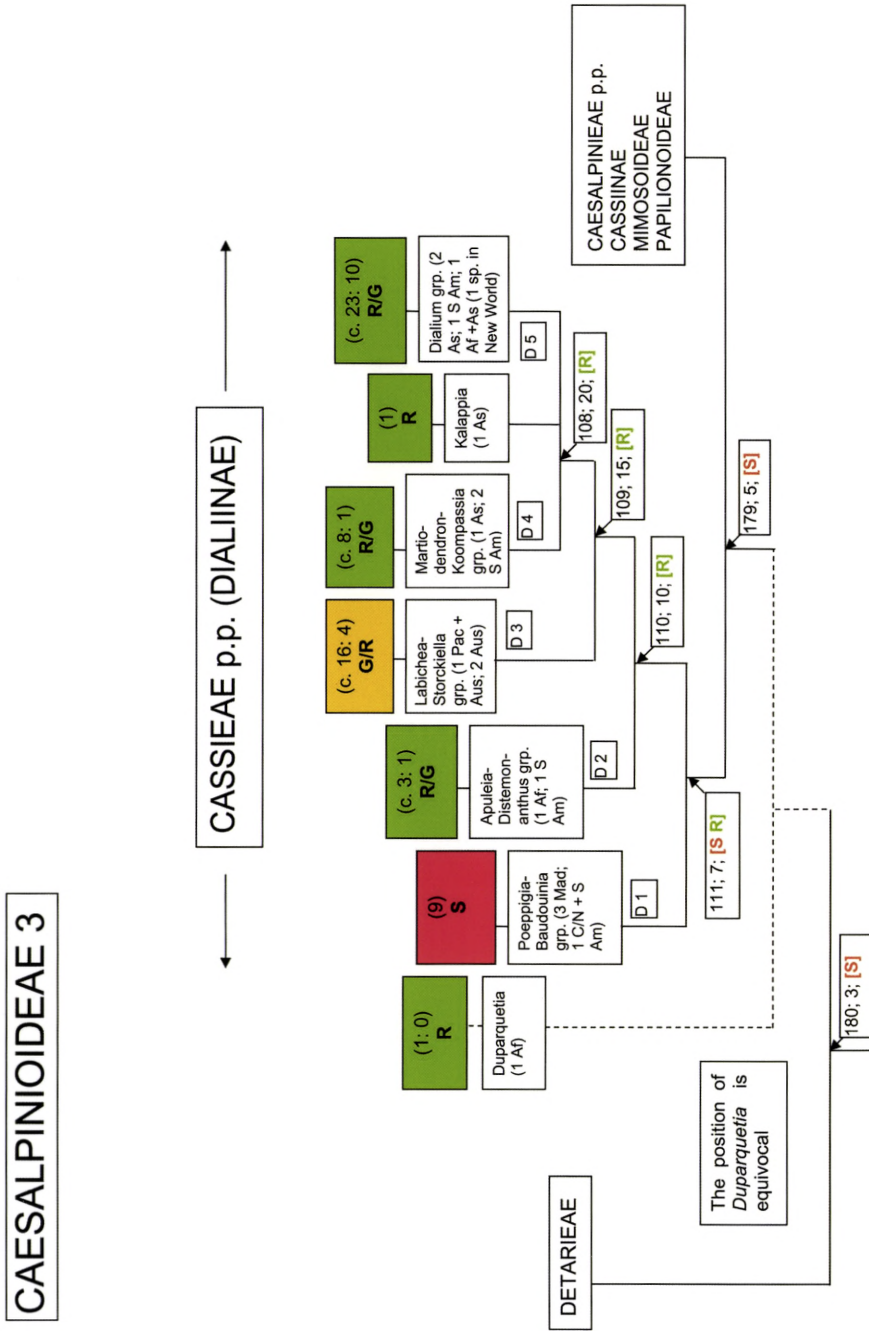


Fig. 4. Taxon-biome supertree of Cassieae p.p. – Dialiinae (Caesalpinioideae 3) – For detailed explanation, see legend to Fig. 2.

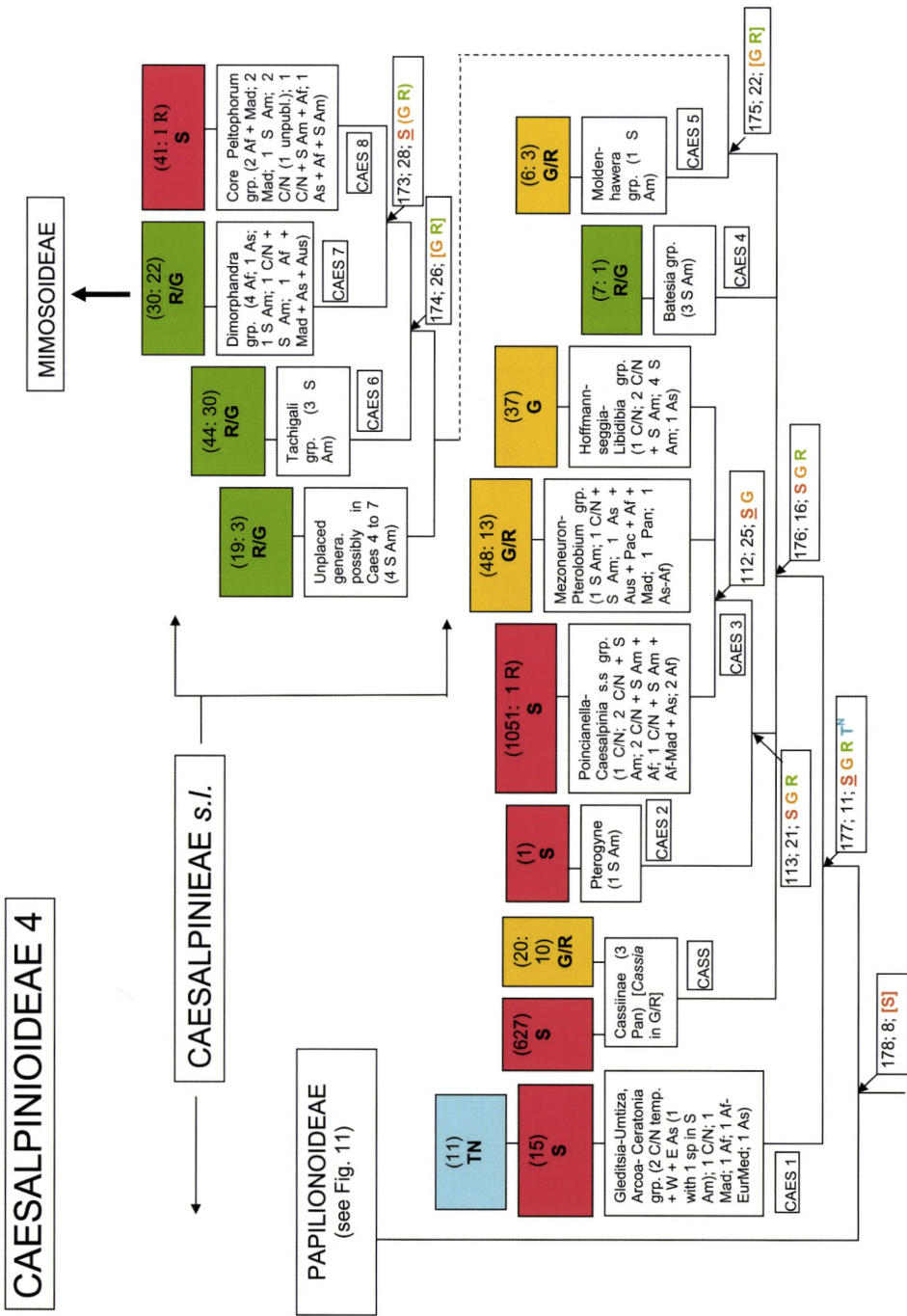


Fig. 5. Taxon-biome supertree of Caesalpinieae s.l. (Caesalpinioideae 4) – For detailed explanation, see legend to Fig. 2.

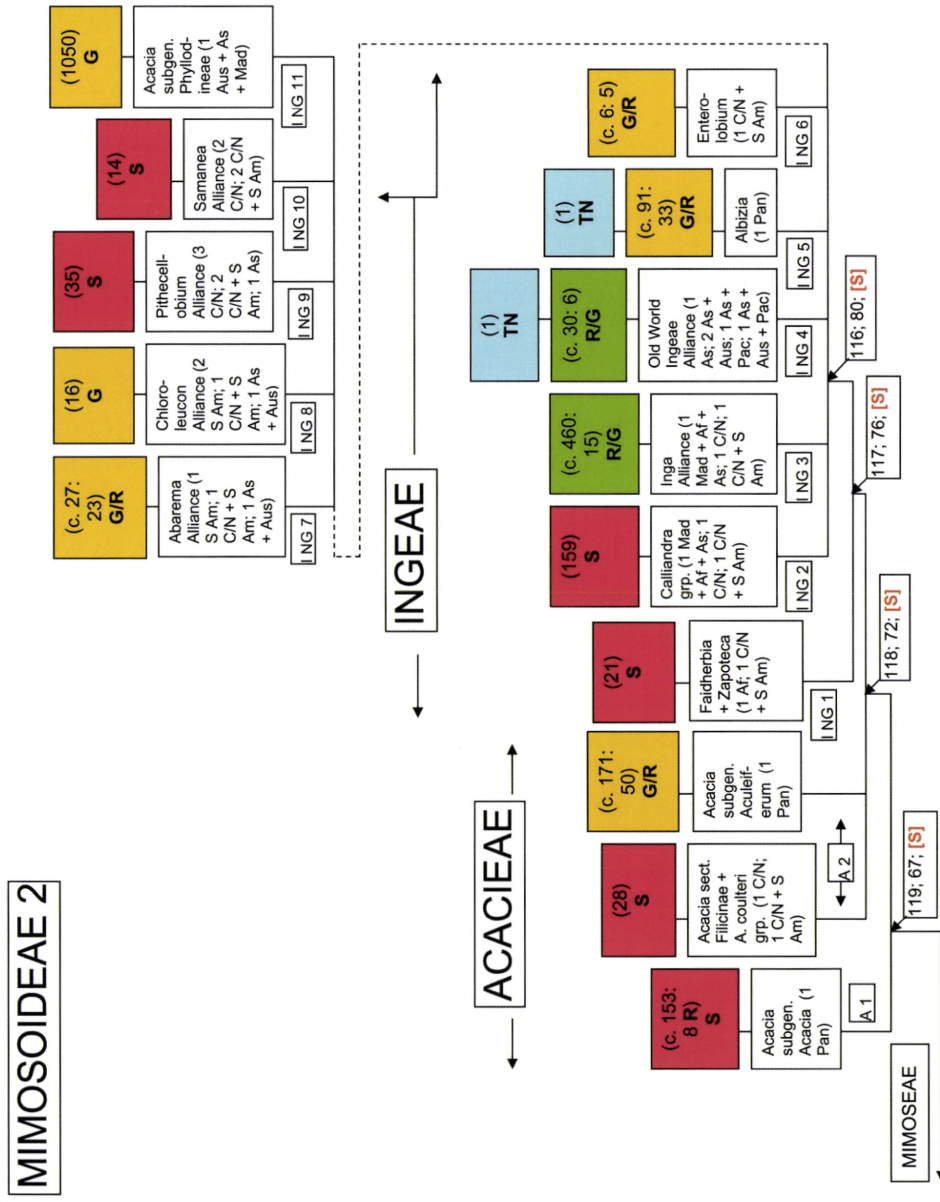


Fig. 7. Taxon-biome supertree of Acaciae-Ingeae (Mimosoideae 2) – For detailed explanation, see legend to Fig. 2.

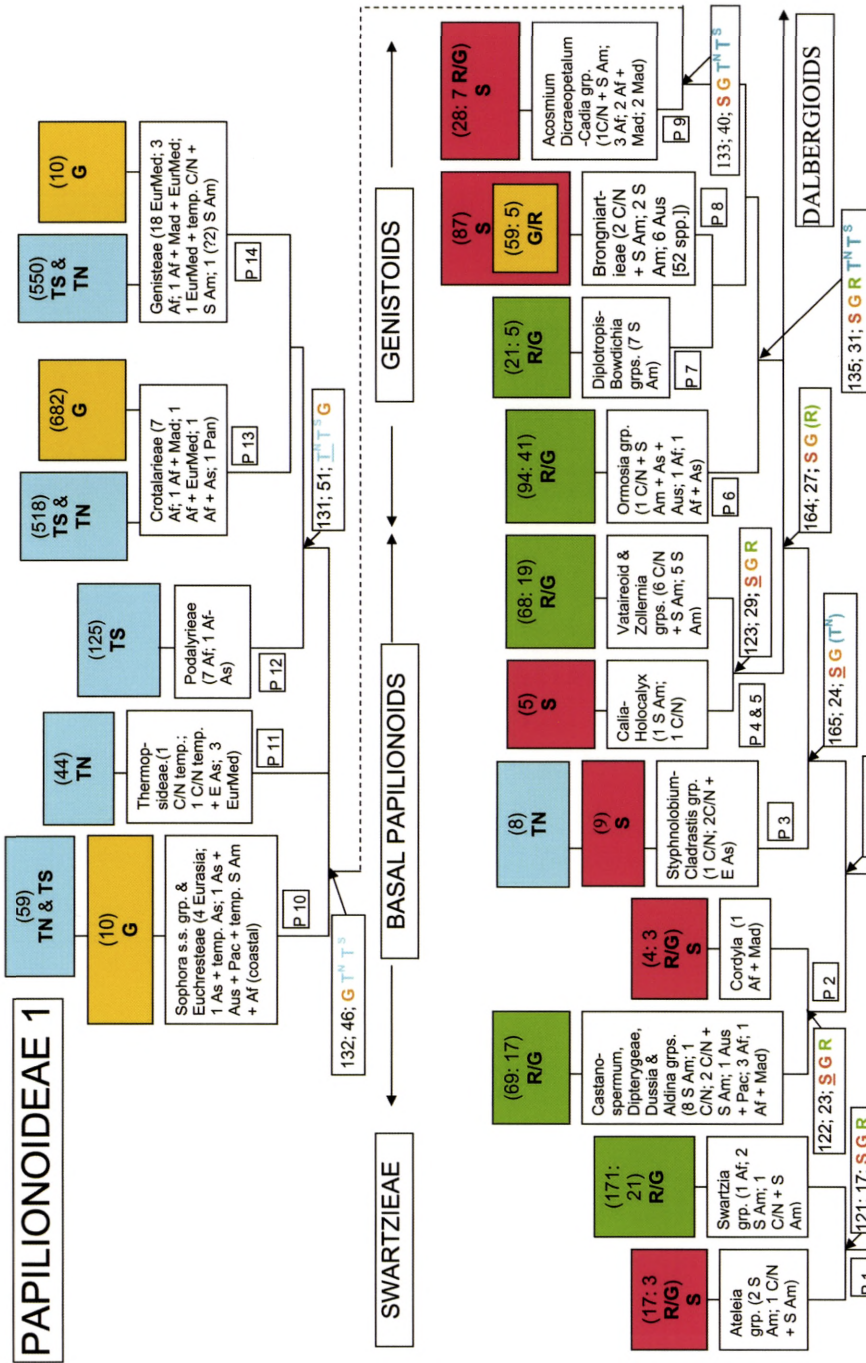


Fig. 8. Taxon-biome supertree of basal papilionoids and genistoids (Papilionoideae 1) – For detailed explanation, see legend to Fig. 2.

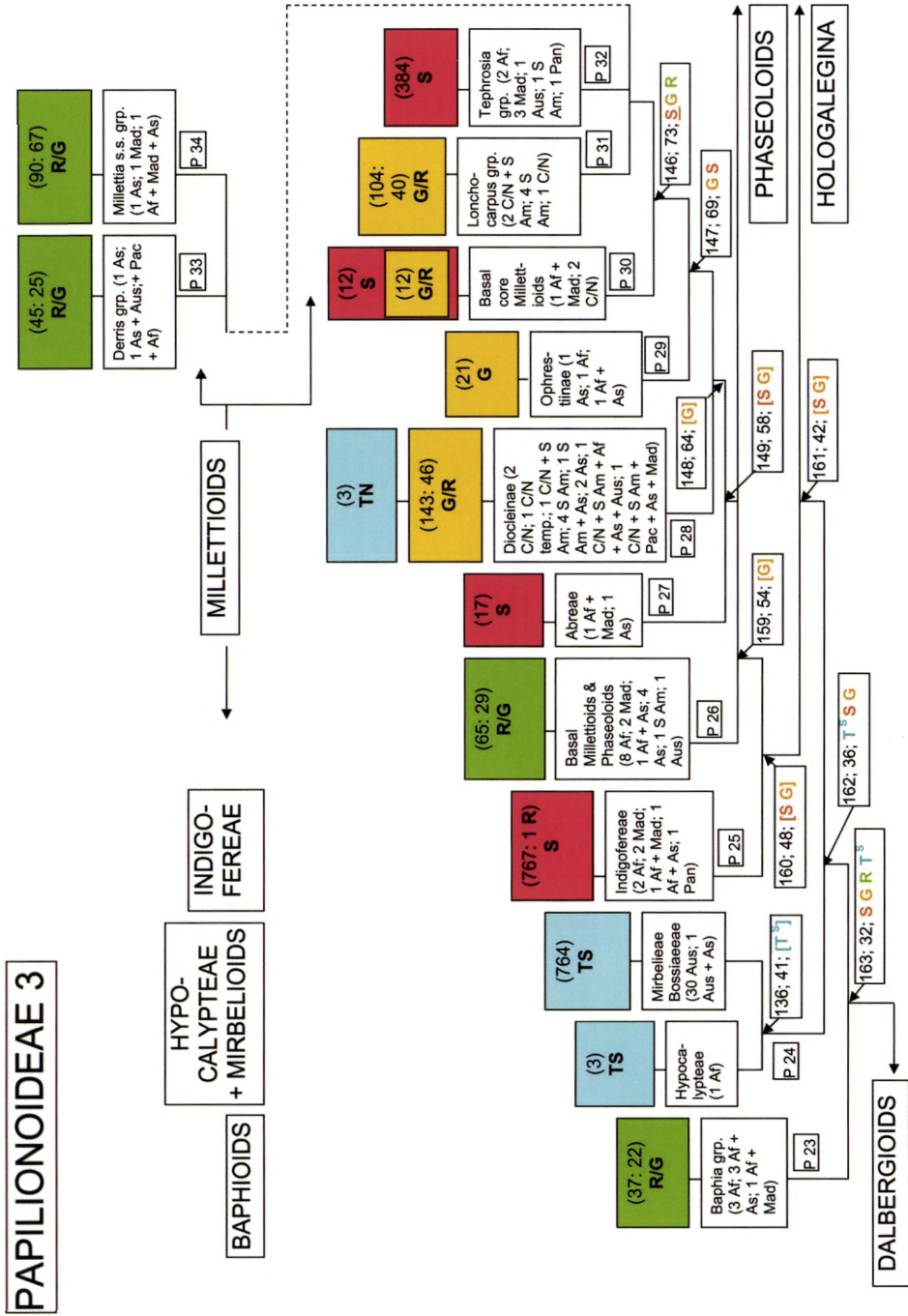


Fig. 10. Taxon-biome supertree of baphioids, mirbelioids and millettoids (Papilionoideae 3) – For detailed explanation, see legend to Fig. 2.

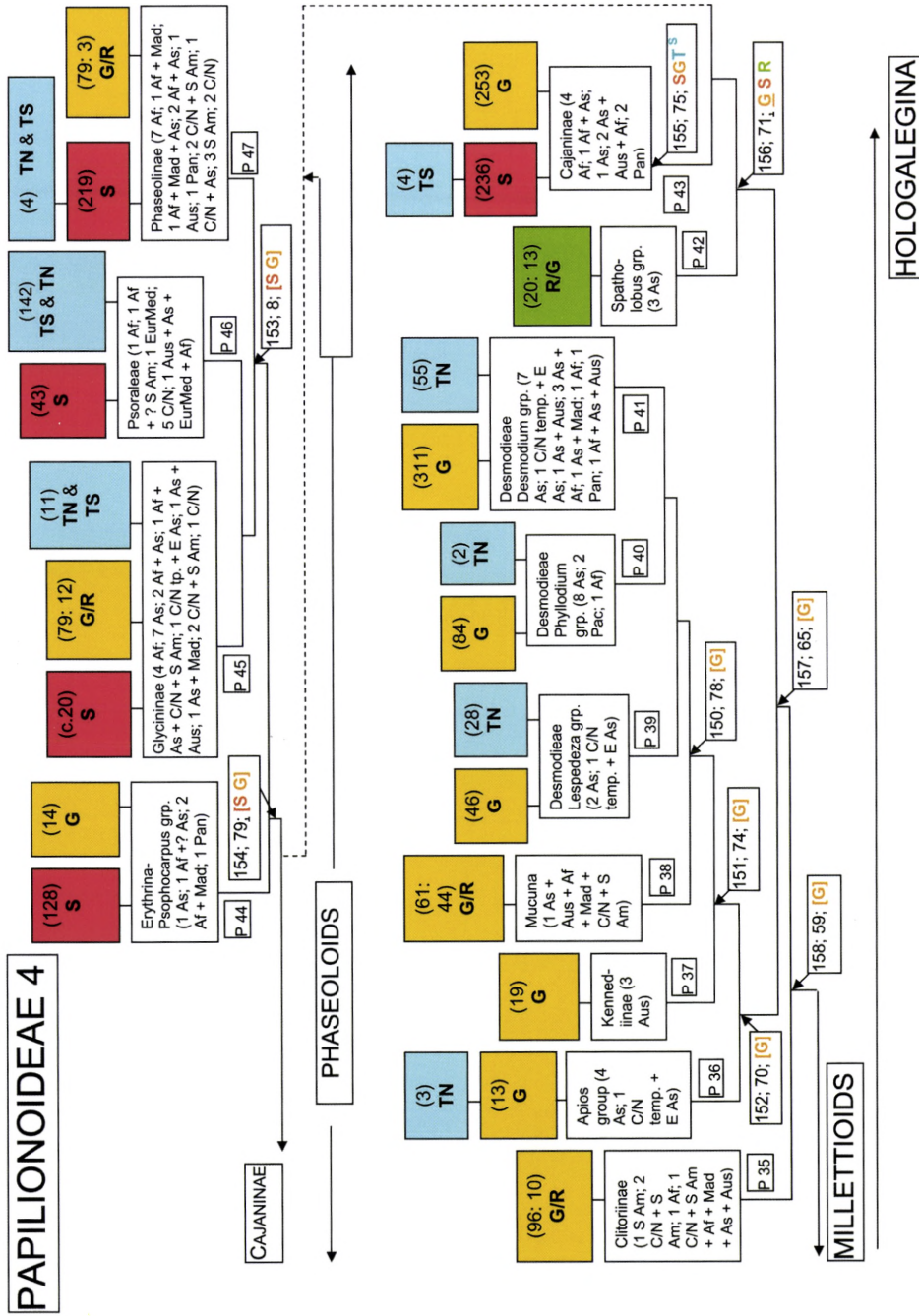


Fig. 11. Taxon-biome supertree of phaseoloids (Papilionoideae 4) – For detailed explanation, see legend to Fig. 2.

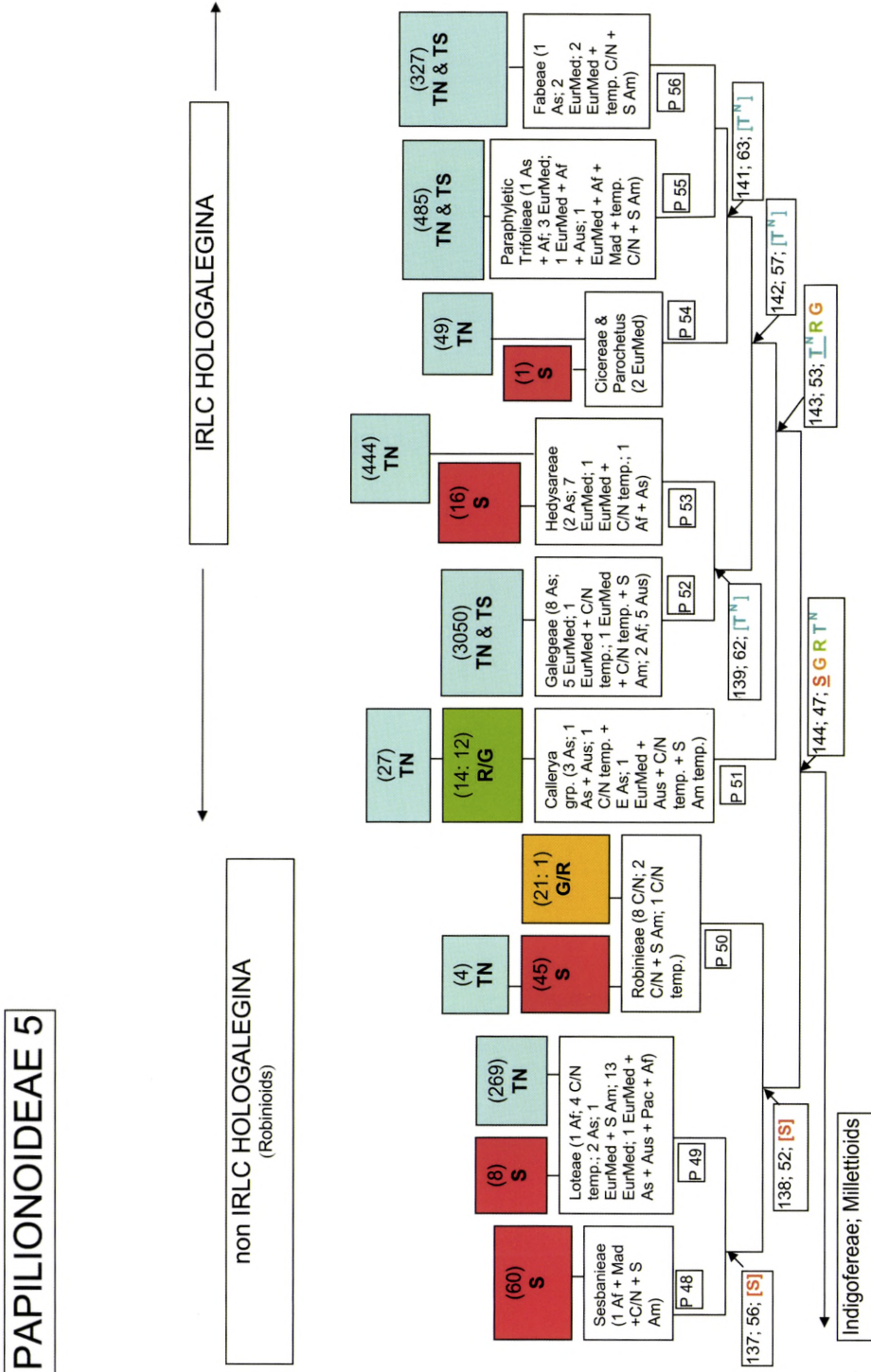


Fig. 12. Taxon-biome supertree of Hologalegina (Papilionoideae 5) – For detailed explanation, see legend to Fig. 2.

Distribution and ecology are highly constrained in legumes, with clades being strongly correlated to distinct geographical areas and habitats. A high probability exists, therefore, that sister species of a clade will occupy a similar vegetation type. *Caesalpinia sens. strict.* was thus attributed to a global distribution pattern suggestive of a semi-arid, succulent-rich, tropical dry forest, bushland and thicket vegetation, poor in understory grasses and lacking tolerance (i.e. being susceptible) to fire disturbance. Such habitats are characteristic of Zonoecotone II/III and Zonobiome III (Breckle 2002). Geographically these occur in the red areas of the map (Fig. 13) and putatively represent the remnants of a persistent dry vegetation type that was linked in the Tertiary, from circum-Amazonian South America through Central America, Mexico and the Caribbean, along the Tethys seaway to Africa, Arabia and India. In Africa this extended from the Horn southwards to southern Africa and Madagascar. Such Succulent (S) biome taxa are often sister to clades containing a combination of Grass (G) biome taxa (i.e. in Zonobiome II, but excluding Zonoecotone II/III; Breckle 2002) and Rainforest (R) biome taxa (Figs. 2-12).

All genera could be assigned to at least one of these four global biomes on the basis of having a predominance of range restricted species occurring there. Many genera of course have secondary (and a few have tertiary) centres, apparently associated with subsequent diversifications into neighbouring biomes (i.e. this hypothesis is at least supported where generic phylogenies are available). Such secondary diversifications have predictable occurrences, e.g. Succulent (S) biome taxa frequently have secondary Grass (but not Rainforest) centres while this is rarely the case in reverse with predominantly Grass (G) biome taxa. The latter associate much more closely with Rainforest taxa such that many genera with a predominance of species in one biome also have substantial cen-

tres in the other. Many legume terminals assigned to Rainforest areas, therefore, had to be designated as also inhabiting the tropical Grass biome (i.e. R/G or G/R in Figs. 2-12). Clades in the Temperate biome are subdivided into northern (TN) and southern (TS) regions, based on their distinctive patterns of diversification across the phylogeny. Although each colour-coded box in the taxon-biome supertree (Figs. 2-12) denotes the predominant biome for that clade, the species numbers given are for the entire clade and not for the designated biome (unless boxes are divided to represent this split where the data for species numbers per biome are known). It is likely, therefore, that some species in single boxes may be centred in secondary (or tertiary) neighbouring biomes.

When doubt existed about the precise affinity of a terminal taxon to the Succulent (S) biome, it was scored as the Grass (G) or Temperate biome. For example, some elements in the Mezoneuron group [Caesalpinieae], Piptadenia group [Mimoseae] and in the Adesmia clade [Papilionoideae], may need to be rescored when species relationships are better understood. This avoided a bias in scoring the Succulent (S) biome for too many legume terminals. Undoubtedly more legume genera will be scored (S) as legume relationships are clarified. Also current assessments of the number of truly Rainforest (R) taxa are likely to be over estimates since:

(1) Amazonian South America is a complex mosaic including drier savannas and Campina forests on white sands (in which many legumes occur);

(2) the Atlantic forests of eastern Brazil comprise large areas of dry Tabuleiro forests;

(3) the Guineo-Congolian and Swahelian wet forest regions of Africa also include areas of drier forest;

(4) much of Indo-China and north-eastern India comprises seasonally dry forests under the influence of a monsoon climate.

Many species are also environmentally flexible in being able to exist in both wet and dry habitats. Wet gallery or riverine forest may be part of a mosaic within seasonally dry forest. Greater numbers of Succulent, and fewer Rain-forest, biome taxa in the analysis should thus reinforce the pattern of global distributions presented here.

Results and Discussion

The analysis of distributions of all genera in Leguminosae identified four generalised areas of endemism at the biome level (Fig. 13). These include:

(1) a **Succulent (S)** biome, comprising a non fire-adapted (or non-resistant and intolerant to fire), succulent-rich and grass poor, dry tropical forest, thicket and bushland biome (Zonocotone II/III and Zonobiome III [Breckle 2002] and highlighted as the red area in Fig. 13). Legume subclades inhabiting this biome are prone to bimodal or erratic rainfall patterns, and have a northern range – but with predictable Southern Hemisphere occurrences – characterised by a predominance of amphi-Atlantic disjunct taxa. Legume genera in Succulent (S) biome clades are listed in Table 2, which identifies c. 26 amphi-Atlantic and only four pantropical disjunctions occurring largely between (and rarely within) genera. No New World – Asian disjunctions are found among (S) biome taxa. Pennington *et al.* (2000, 2004) refer to the Neotropical Succulent biome as seasonally dry tropical forests (SDTF's).

The present-day Succulent (S) biome encompasses regions in:

(a) the Neotropics, i.e. in semi-arid tropical to subtropical Mexico, Central America and the Caribbean (particularly the Greater Antilles; Wolfe 1975; Lavin *et al.* 2001b), linked frequently to circum-Amazonian “Pleistocenic Arc” dry forest elements in South America

including the inter-Andean valleys of Ecuador and Peru, the Piedmont area of north-western Argentina and central Bolivia, the Misiones region of north-eastern Argentina and adjacent Paraguay, and the Caatinga of eastern Brazil (Prado & Gibbs 1993; Pennington *et al.* 2000, 2004). The Neotropical centre of Succulent (S) biome clade distributions is thus mainly North and Central America and the Caribbean with distinctive and predictable South American occurrences. Neotropical centres are linked (with intervening fossil evidence from Tertiary tropical North America and Europe [Herendeen *et al.* 1992]) across to:

(b) the Old World, in the succulent-rich Somalia-Masai regional centre of endemism (White 1983) of the Horn of Africa, with various dry forest and thicket “arid corridor” disjunctions and extensions through to the Nama-Karoo, Succulent Karoo, Desert and Thicket biomes of southern and south-western Africa (Verdcourt 1969; de Winter 1971; Cowling 1983; Rutherford & Westfall 1986; Thulin 1994; Low & Rebelo 1996; Jürgens 1997; Thulin & Lavin 2001; van Wyk & Smith 2001); western Madagascar (Leroy 1978; Schatz 1996; Jansa *et al.* 1999; Lavin *et al.* 2000; Meve & Liede 2002; Du Puy *et al.* 2002; Schrire *et al.* 2003) and Arabia to West Asia and north-west India (Quézel 1978; White & Léonard 1991; Miller & Cope 1996; Kürschner 1998; Conti *et al.* 2002; Bardhan *et al.* 2002). The Nubo-Sindian local centre of endemism (subzone 3 of the Sahara – Sindian Regional Zone, White & Léonard 1991) is a critical part of this distribution as it is a floristic continuation of the Somalia-Masai regional centre of endemism in the Horn of Africa (Fig. 13). The remaining two subzones (Sahara and Arabia) comprise mixed (S) and (T) biome elements and are thus coloured yellow (Fig. 13), but their affinity is to the Succulent (S) biome.

The *Umtiza* clade (Herendeen *et al.* 2003b),

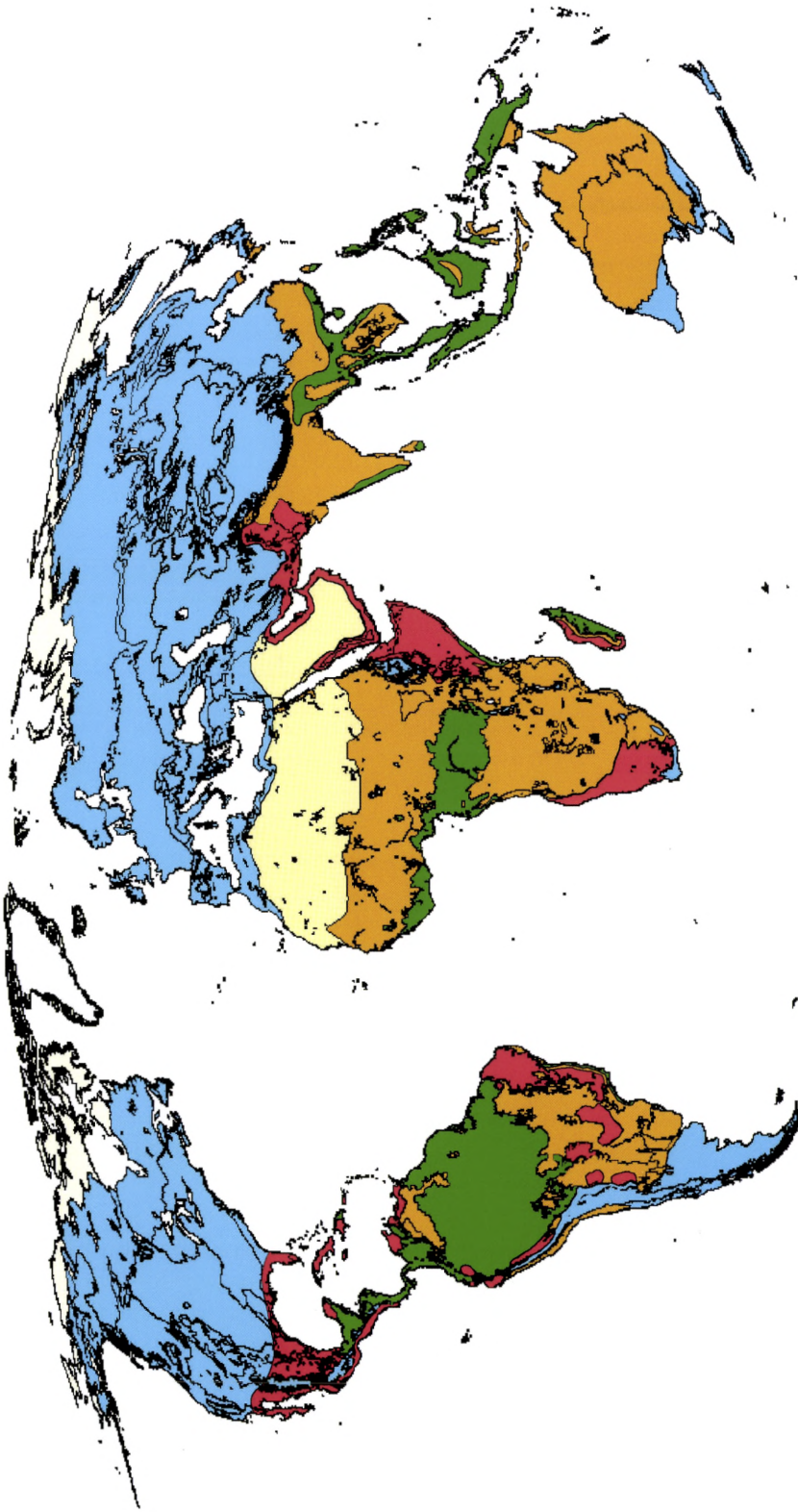


Fig. 13. World map with four generalised legume distribution patterns at the biome level: Red = Succulent (S) biome; Brown = Grass (G) biome; Green = Rainforest (R) biome and Blue = Temperate (T) biome.

sister and basally branching in the large Caesalpinieae *sens. lat.* plus Mimosoideae clade (Fig. 1) is exemplary of a Succulent (S) biome distribution (Fig. 14). Previous tribal affinities of the various elements of the Umtiza clade (Polhill & Raven 1981; Polhill 1994) are: *Gleditsia* – *Gymnocladus* (from eastern Asia and North America), and *Acrocarpus* (south-east Asia) were in two separate groups placed basally in tribe Caesalpinieae; *Arcoa* (Caribbean) & *Tetrapterocarpon* (Madagascar) were in the more derived Dimorphandra group of tribe Caesalpinieae; *Ceratonia* (north-east Africa and Mediterranean) was in its own subtribe in tribe Cassieae and *Umtiza* (South Africa) was in the Cynometra group of tribe Detarieae.

These genera have thus been placed in three separate caesalpinoid tribes with no suggestion previously of the close relationships existing between them. The legume phylogeny has thus not only presented new patterns of relationships between genera that were previously widely separated taxonomically, but has elucidated new associations supported by previously unforeseen morphological synapomorphies. In this case the presence of dioecy was found to occur in all but two genera in the clade and monoecy is considered to be a reversal in *Arcoa* and *Umtiza* (Herendeen *et al.* 2003b). In addition, these novel geographical patterns of association of genera are repeated frequently across the phylogeny, *e.g.* the Umtiza clade pattern is largely repeated in the Cercis, Schotia and Poeppegia clades, each sister to large Rainforest (R) and Grass (G) biome diversifications making up the rest of tribes Cercideae, Detarieae and Cassieae subtribe Dialiinae respectively (Fig. 1). Most of the Umtiza clade genera are narrowly distributed and comprise one to a few species inhabiting Succulent (S) biome vegetation, such as the monotypic *Arcoa* from the Dominican Republic and its sister genus, *Tetrapterocarpon* with two species from Madagascar. The reiterated amphi-Atlantic dis-

junctions within the Umtiza clade are consistent with an original distribution of this lineage along the margins of the Tethys seaway. North – south disjunctions between *Gleditsia* and *Gymnocladus* and the semi-arid southern African genus *Umtiza* similarly characterise *Cercis* and *Adenolobus* (Cercideae), *Prosopis* and *Xerocladia* (Mimoseae) and outside the legumes, *Ephedra* and the remarkable genus *Welwitschia* in the Gnetopsida (Farjon *pers. comm.*). A further north – south disjunction is noted between northern temperate *Gleditsia* and the southern Brazilian and Argentinian species, *Gleditsia amorphoides* Taub. In the recent ITS analysis of Schnabel *et al.* (2003), this species is revealed as being sister to the rest of the extant northern temperate lineages of *Gleditsia*. The affinity of this species is to the (S) biome Misiones and Piedmont nuclei of “Pleistocenic Arc” vegetation (Prado *pers. comm.*).

Disjunctions in the Succulent (S) biome occur in both species-poor basally branching lineages, *e.g.* in the Cercis, Schotia, Poeppegia, Umtiza and Basal Papilionoideae (*i.e.* Cladrastis) clades, or in speciose clades nested high in the tree. Speciose sister clades with \pm equivalently sized amphi-Atlantic diversifications (where each are well supported as well as the two together being well supported), reflect a pattern of reciprocal monophyly (Cunningham & Collins 1998; Lavin *et al.* 2001b). Examples of genera (or sections within them) showing this pattern include *Bauhinia sens. strict.*; *Caesalpinia sens. strict.*; *Chamaecrista* and *Senna*; *Mimosa* and *Acacia* subgenus *Acacia*; the Diphysa-Ormocarpum clade, *Chapmannia* and *Stylosanthes*; *Sesbania*, the *Indigofera* subclades, *Tephrosia*, *Erythrina*, and the *Vigna-Phaseolus* clade (Table 2). Few amphi-Atlantic disjunctions occur in predominantly Rainforest and Grass (R/G) biome clades (*e.g.* the *Hymenaea-Guibourtia-Peltogyne* clade in the Detarieae [see below]).

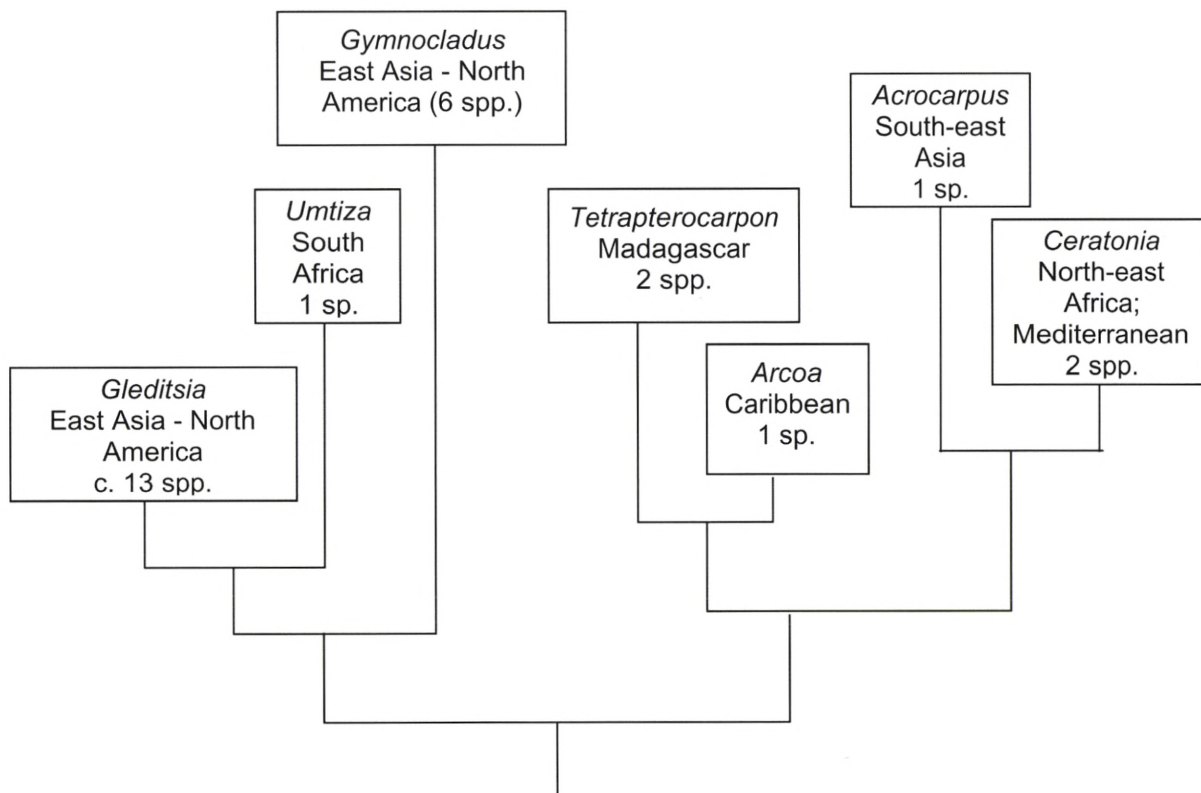


Fig. 14. Umtiza clade after Herendeen *et al.* 2003b.

(2) a **Grass** (G) biome, comprising a fire-adapted (i.e. prone to, and tolerant of or resistant to fire), succulent poor and grass-rich, seasonally dry tropical forest, woodland and savanna biome (Zonobiome II excluding Zonoecotone II/III [Breckle 2002], and highlighted in brown in Fig. 13). Legume genera inhabiting this biome are prone to a unimodal rainfall pattern and they also occupy the Rainforest (R) biome (Zonobiome I), suggesting dispersal or habitat switching is common between these two, which are constantly in flux within a dynamic environment. Distribution centres are confined largely to the seasonally dry tropics of the southern continents and Asia. The Neotropical Grass biome areas are

referred to as savannas by Pennington *et al.* (2000, 2004).

The main area of Grass (G) biome clade distributions in the neotropics is in South America, in seasonally dry forest (but not the "Pleistocene Arc" SDTF's *sensu* Pennington *et al.* 2000, 2004), woodland (cerrado), savanna and grassland environments, and in the Old World similar habitats predominate in the Sudanian and Zambezian regional centres of endemism (Savanna, Grassland and Forest biomes *sensu* Rutherford & Westfall 1986) in Africa, to the seasonally dry forest, monsoon and more open vegetation types in Madagascar and tropical Asia to Australia. Clades are distributed more commonly right across the tropics in (G/R)

Table 2. Analysis of New World – Old World disjunctions in Leguminosae, *i.e.* amphiatlantic, New World – Asia (including Australia and the Pacific) or pantropical, for each of the five areas of endemism. S = Succulent biome; G = Grass biome; R = Rainforest biome; TN = Temperate Northern Hemisphere; TS = Temperate Southern Hemisphere. Intrageneric disjunctions (*i.e.* those trans-oceanic disjunctions occurring within genera) are in bold, while intergeneric disjunctions (*i.e.* those trans-oceanic disjunctions occurring between genera) are not in bold.

Taxon and R/M (if reciprocally monophyletic)	Succulent (S)			Grass (G) & Rainforest (R)			Temperate/ Tethyan (TN & TS)		
	Amphi- Atlantic Disjunction	New World – Asia/ Disjunction	Pantropical Disjunction	Amphi- Atlantic Disjunction	New World – Asia/ Aus./ Pacific Disjunction	Pantropical Disjunction	Amphi- Atlantic Disjunction	New World – Asia/ Aus./ Pacific Disjunction	Montane Pantropical Disjunction
Surianaceae					<i>Racchia</i> & <i>Suriana</i> <i>Sylobastium</i>				
Cercideae	1) <i>Cercis</i> <i>Adenolobus</i>							<i>Cercis</i>	
R/M	2) <i>Bauhinia</i> s.s.								
	3)				New World <i>Schnella</i> – Old World <i>Phanera</i> <i>Barclaya</i>				
Detarieae	1) <i>Barnebyden-</i> <i>dron</i> <i>Schotia</i>								
	2)							<i>Prioria</i> <i>Oxystigma</i> <i>Kingioden-</i> <i>dron</i>	
	3)			<i>Eperua</i> <i>Daniellia</i>					
	4)			<i>Hymenaea</i> <i>Guibourtia</i>					
R/M	5)							<i>Copaifera</i> ; <i>Copaifera</i> <i>Tesmannia</i> <i>Sindora</i>	

6)								Cruidia; <i>Cruidia,</i> <i>Talbotiella</i> <i>Saraca</i>			
7)								Cynometra; <i>Cynometra</i> <i>Plagiosiphon</i> <i>Manilloa</i>			
8)								<i>Brodriguesia</i> <i>Afzelia</i> <i>Intisia</i>			
9)									<i>Dicymbe</i> <i>Polystemon-</i> <i>anthus</i>		
Cassieae p.p. (Dialiinae)	1)	<i>Poepfigia</i> <i>Baudouinia</i>									
	2)								<i>Apuleia</i> <i>Distemo-</i> <i>nanthus</i>		
	3)								<i>Andro-</i> <i>calymma</i> <i>Koompassia</i> <i>Labichea</i>		
	4)										
Caesalpinieae	1)	<i>Umitiza</i> <i>Gleditsia</i>							Dialium; <i>Dicorynia</i> <i>Dialium</i> <i>Zenia</i>		<i>Gleditsia</i> <i>Gymnocla-</i> <i>odus</i>
	2)	<i>Arcoa</i> <i>Ceratomia</i>									
(Cassieae s.s.)	3)										<i>Cassia</i>
											<i>Senna</i> <i>Chamaecri-</i> <i>sta</i>

from those in South America by a preponderance of *Lonchocarpus* species (Sousa & Delgado-Salinas 1993; Wendt 1993). Sousa & Delgado-Salinas (1993) noted that the wet forests in Mesoamerica are floristically different from those in South America and Gentry (1982) emphasised the fundamental difference between the Tertiary floras of South America and North America, thus underscoring the demarcation of the biomes circumscribed here.

(3) a **Rainforest** biome (Zonobiome 1), with distribution centres confined to the humid tropics (wet forests) worldwide

Recent molecular analyses show that most Rainforest (R) and Grass (G) biome clades comprise elements that are widely scattered across the tropics, but without the relatively narrow and predictable areas of distribution of the Succulent (S) clades, except in a general sense of being restricted to one or other continental region of the wet tropics. Such clades show a high degree of interrelatedness between component genera across the southern continents and tropical Asia, despite the long periods that these landmasses have been isolated from each other. The three legume groups containing the highest proportions of (R) biome taxa, however, show that some 91 percent of genera in the Detarieae, 94 percent in Dialiinae and 95 percent in Basal Papilionoideae, are restricted to only one of three continental regions (i.e. Neotropics, Africa – Madagascar or Asia – Pacific – Australia). Genera in the (R) biome areas, therefore, although individually limited in their distributions, belong to clades whose sister genera are distributed across the tropics. This pattern is reflected in the predominance of pantropical or New World – Asian (rather than amphiatlantic) disjunctions occurring within these clades (see discussion under the (G) biome above).

Early diverging elements of legume clades (c. 60 – 55 Ma) apparently became distributed across the Tethyan seaway, which was subject throughout the Tertiary to a seasonally dry tropical climate (Scotese 2001). Such elements are thus considered likely to have seeded southwards into seasonally dry vegetation types emerging in South America, eastern to southern Africa and Madagascar, and Asia. This hypothesis derives from the high degree of intergeneric relatedness found across the tropics, while also accounting for the high levels of generic endemism arising through subsequent diversification into the (R/G) biomes of the individual southern continents and Asia. When fossil evidence is available for taxa in the (R) biome, this too supports a Tethyan (i.e. tropical North American) link existing between them in the Tertiary (despite there being no extant northern taxa), e.g. the amphiatlantic *Swartzia-Bobgunnia* clade in Papilionoideae, and the reciprocally monophyletic amphiatlantic *Hymenaea-Guibourtia* clade in Detarieae (Herendeen 1992; Graham 1992; Axelrod 1992; Lavin & Sousa 1995). An original Tethyan-wide distribution is thus also hypothesised to account for the current distributions of (R) and (G) biome taxa.

The (R/G) clades thus have high percentages of intergeneric – and consequently low proportions of intrageneric – disjunctions, while largely (G/R) clades show much lower percentages of genera restricted to one continental region and this is correlated to higher numbers of intrageneric disjunctions. Examples of pantropical (R/G) intrageneric disjunctions (Table 2) include *Copaifera*, *Cynometra*, *Parkia*, *Dalbergia*, *Pterocarpus* and *Desmodium*, while intergeneric pantropical disjunctions occur between, e.g. *Prioria* (Central America), the *Oxystigma* group (Africa) and *Kingiodendron* (Asia); *Brodriguesia* (South America), *Afzelia* (Africa – Asia) and *Intsia* (Asia); or *Platycamus* (South America) and the Old World millet-

toids. Many examples also occur of neotropical – south-east Asian disjunctions, *e.g.* *Androcalymma* (South America) and the *Koompassia-Labichea* groups (Asia – Australia); *Leucaena* (Neotropics) and *Schleinitzia* (Asia – Pacific); *Cojoba-Zygia* (Neotropics) and the *Archidendron* group (Asia – Australia); within *Ormosia* (Neotropics – Asia & Australia); and the *Tipuana* group (South America) and *Inocarpus* (Asia). Amphi-Atlantic disjunctions occur between, *e.g.* *Eperua* (South America) and *Stemonocoleus-Eurypetalum* (Africa); *Dicymbe* (South America) and the *Polystemonanthus* group (Africa); *Dinizia* (South America) and *Aubrevillea* (Africa), and within *Pentaclethra* (Neotropics – Africa).

(4) a **Temperate** biome, with distribution centres confined to montane tropical, Mediterranean, warm and cold temperate regions of the Northern and Southern Hemispheres. Temperate clades are principally either Northern (TN) or Southern (TS) Hemisphere in distribution. Northern Hemisphere (TN) taxa generally comprise elements derived directly from Succulent (S) or Grass (G) biome clades (Figs. 2-12). Southern Hemisphere (TS) taxa, *e.g.* the *Adesmia*, *Hypocalyptus*, mirbelioid, *Podalyrieae*, *Crotalariaeae*, *Genisteeae* and possibly *Psoraleeae* clades, however, are themselves principally sister (and often basally branching) to the rest of their clade components, although the phylogeny indicates they all have (S) or (G) biome outgroups.

Legume clades with a temperate distribution are listed in Table 2 and c. 16 Asian – New World disjunctions, two pan-temperate (montane tropical) disjunctions in *Amphicarphaea* and *Psoraleeae*, and one amphi-Atlantic disjunction (*Lupinus*) occur in temperate biome clades. Tropical (S) and (G) biome clades have each diversified independently into temperate regions resulting in distinctive (TN) and (TS) centres, particularly in papilionoid legumes

(Figs. 2-12). Predominantly (TS) clades often have substantial secondary diversifications back into the (S) and (G) biomes but this is rarely the case in predominantly (TN) clades. The component analysis in this study resolves the two temperate areas in a basal polytomy (Fig. 15), revealing that temperate-inhabiting clades are often related to each other, and otherwise in an inconsistent pattern of relationships with the other three biomes.

Temperate distribution patterns include a subtropical, mediterranean or temperate North American to northern Mexican distribution sometimes linked to Andean and warm temperate South American distributions (*e.g.*, some *Amorpheae* and *Adesmieae* in the *dalbergioids* and various tribes in the IRLC, *e.g.* *Galegeae* and *Fabeae*). Mediterranean and Macaronesian distributions are commonly linked through montane tropical Africa to warm temperate South Africa (*e.g.*, the genistoid tribes *Crotalariaeae* and *Genisteeae*, the phaseoloid tribe *Psoraleeae*, and *Galegeae* and *Trifolieae* in the IRLC). Southern, central and eastern Europe are commonly linked to montane west to eastern Asia, or cold temperate central and north-eastern Asia (*e.g.* tribes in the IRLC). Temperate Australasian distributions may be isolated (*e.g.* the mirbelioids) or linked to northern patterns (*e.g.* *Psoraleeae*). All (TN) biome clades are derived from (S) or (G) biome clades (Figs. 2-12). The *Sophora* group, including *Thermopsidaeae*, and the IRLC tribes best illustrate this pattern. Most (TS) biome clades, however, are sister or basally branching to other clades (*e.g.* *Adesmia* sister to the rest of the *dalbergioids*, *Podalyrieae* to the derived genistoids, and *Hypocalypteae-mirbelioids* to the bulk of *Papilionoideae*). Temperate (TS) biome clades have thus largely reoccupied tropical or montane tropical areas, whereas this is rare in (TN) biome diversifications, with the exception of some members of the *Sophora* group.

The (T) biome comprises taxa that essentially link present-day montane-tropical areas with (TN) and (TS) areas. A Succulent (S) biome area involving the Saharo – Sindian – west-Asian regions (White & Léonard 1991) is often sister to major (TN) Eurasian and Mediterranean clades, which may have disjunct subclades in the temperate New World. Examples include Loteae of the robinoid legumes and the IRLC (especially the temperate tribes Galegeae, Hedysareae, Cicereae, Trifolieae and Fabeae). A group of derived genistoids including the Podalyrieae, Crotalariae and Genisteeae have their basal elements in warm temperate southern Africa, although the (S) biome Acosmium-Dicraeopetalum clade is putatively an outgroup of this alliance. Members of these genistoid groups appear to either migrate northwards through montane tropical Africa to the Mediterranean and Macaronesian regions (*e.g.*, *Lotononis* and *Argyrolobium*) and subsequently to the New World (*e.g.*, *Lupinus*), or to secondarily invade the tropics (*e.g.* *Crotalaria*). The Brongniartiae have a neotropical distribution disjunct to tropical and warm temperate Australia. Within Psoraleeae, the *Cullen-Bituminaria* and New World Psoraleeae diversifications closely track the distributional pattern observed in the Loteae, although *Cullen* has an extensive derived Australian diversification (Grimes 1997). The putatively basal southern African *Otholobium* and *Psoralea* lineages, however, reiterate the “out of Africa” pattern seen in the derived genistoids. The Surianaceae may be the immediate outgroup of the Leguminosae (Forest unpubl. data), and have a disjunct distribution in Central and North America and Australia (Crayn *et al.* 1995), which is similar to that of the Brongniartiae in the genistoid subclade.

Older diversifications in the (TN) endemic regions (based on the rates analyses of Lavin *et al.* 2004) are associated with basal branching clades in the family and include taxa now

restricted to warm temperate or subtropical North America and eastern Asia, linked (where these exist) to mesophytic forest refugia in between, *e.g.* in montane tropical regions in west Asia (*i.e.* the Caucasus), the Himalayas in southern Asia and China. Examples of taxa with this distribution type are *Cercis* (Cercideae; Davis *et al.* 2002b), *Gleditsia* and *Gymnocladus* (Caesalpinieae), and *Styphnolobium* and *Cladrastis* (Basal Papilionoideae). Such older northern temperate diversifications thus reflect a Tethyan-wide Tertiary tropical dry forest distribution which existed prior to temperate conditions being superimposed on these areas. However, more recent genistoid and IRLC temperate legume diversifications (again based on the rates analyses of Lavin *et al.* 2004), appear to have occurred within co-existing temperate conditions.

Of the four main biomes (*i.e.* temperate considered as one) identified here, the Succulent (S) biome is perhaps most novel and in need of distinction from the similar biome that generally encompasses Southern Hemisphere (and Asian) tropical grass-rich vegetation.

Cladistic vicariance analyses

Methods

The biogeographical analysis involved the standard forms of cladistic vicariance analysis (*e.g.* Morrone & Carpenter 1994), including Component (Page 1993), Three-Area-Statements (Nelson & Ladiges 1991), Brooks Parsimony Analysis (Brooks & McLennan 1991), and Dispersal Vicariance Analysis (Ronquist 1996). All three assumptions for treating widespread taxa (0, 1, and 2; Nelson & Ladiges 1991) were investigated. Assumption 1 is most appropriate, however, given that the areas of endemism used in this analysis are tantamount to globally distributed biomes. In other words, a clade belonging to one biome is expected to be nested within a paraphyletic (and progenitor)

clade that is confined to another biome. Because Component 2.0 has a limitation of 100 terminal taxa, 24 terminals in the legume supertree were pruned before component analysis. Terminals were pruned only if a sister taxon had an identical area assignment. This provided an opportunity to evaluate the effects of deleting various subsets of terminal taxa on the final areagram. Only results that were consistently obtained through cladistic vicariance analysis are reported in this study. Component 2.0 (Page 1990, 1993) performs branch swapping on the taxon-biome supertree (Figs. 2-12), to produce an areagram that minimizes paralogy, dispersal, and extinction. Appendix 1 includes one of the data sets analysed by Component 2.0. Searches included swapping with subtree-pruning-regrafting, treating missing areas as uninformative, and mapping (assumption 0) or not (assumption 1) widespread associates. The taxon-biome supertree for legumes was reconciled against 1000 randomly resolved area cladograms to estimate a confidence interval for the number of "leaves added" and "losses."

Three-area-statements analysis (TASS; Nelson & Ladiges 1991, 1994) implements assumption 2. Terminal and interior nodes, as well as areas, were alphanumerically coded to obtain a TASS input file. The output file from TASS was converted to Nexus format and analysed with the branch-and-bound search algorithm in PAUP* (Swofford 2002). Brooks parsimony analysis (BPA; Brooks & McLennan 1991, pp. 206-225) requires additive binary coding of the taxon-biome supertree. To create the area matrix, the "inclusive O-ring" was used because there is no reason to consider that different species from the same area (i.e., with paralogous relationships) are actually occupying different cryptic areas of endemism. Because BPA invokes assumption 0 (Morrone & Carpenter 1994), both reversible and non-reversible parsimony were used to analyse the

area matrix using the branch-and-bound search option in PAUP. This is because non-reversible parsimony can reduce somewhat the influence of widespread taxa on area relationships (Brooks & McLennan 1991, p. 217)

For the Dispersal-Vicariance Analysis (DIVA; Ronquist 1996), the supertree used in the Component analysis was variously resolved to obtain a fully bifurcating input tree, which is required of this program. Only results not affected by the various arbitrary bifurcations are reported here. The standard biogeographic assumptions (i.e., 0, 1, and 2) are not invoked and thus all biomes occupied by a given terminal are assigned. Because DIVA is biased toward optimising greater numbers of areas along branches residing further from the terminals, basal internodes optimised with only one or two areas can be viewed as robust results.

Results

Component analyses

The taxon-biome cladogram (Figs. 2-12), described in nexus format (Appendix 1), yielded essentially one tree, which was rooted differently depending on the mapping of widespread taxa (compare left and right-hand area cladograms in Fig. 15). Regardless of the assumption (0 or 1) used to treat widespread taxa, the area relationships consistently resolved the Succulent (S) biome as sister to a clade containing both the Grass (G) and Rainforest (R) biomes (Fig. 15). Some notable examples of such (S) biome subclades include: the *Cercis-Adenolobus* group (Fig. 2), the *Schotia-Barneydendron* group (Fig. 3), the *Poeppegia-Baudouinia* group (Fig. 4), the Umtiza clade (Fig. 5), the Zapoteca group (Fig. 7), the *Ateleia*, *Styphnolobium-Cladrastis*, and the *Acosmium-Dicraeopetalum* groups (Fig. 8), tribe *Amorpheae* (Fig. 9) and tribe *Indigofereae* (Fig. 10). The (T) biome (divided into TN and TS) were resolved as sis-

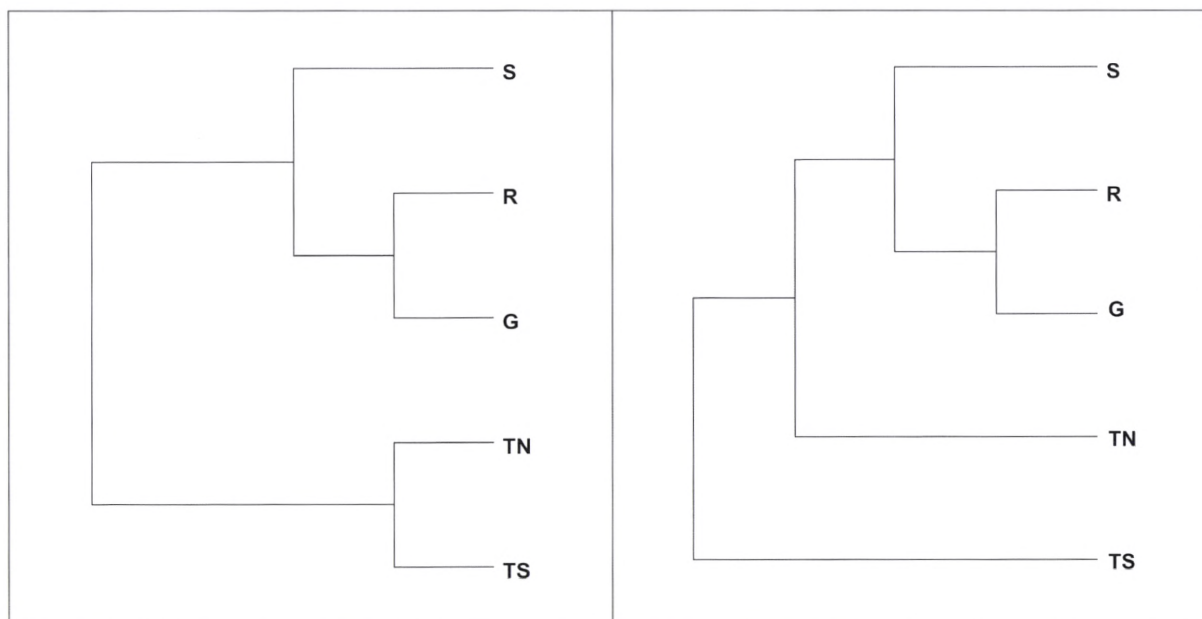


Fig. 15. Area cladograms resulting from the component analysis. Results using either assumption 0 (widespread taxa indicate relationships) or assumption 1 (widespread taxa indicate at least paraphyletic area relationships). Left-hand figure: minimising leaves added. Right hand figure: minimising losses. These patterns are significant at the $p=0.6\%$ level. The basal position of the (TN) and (TS) areas is most likely a function of no pattern derived from the input taxon-biome cladogram suggesting a particular association of temperate taxa with tropical ones (i.e., temperate lineages have been derived variously from either the (S), (G) or (R) biomes). This is illustrated by the consensus of these two area cladograms, which would show (TN,TS (S,(R,G))). Using assumption 2 (widespread taxa are completely uninformative) yields completely unresolved area relationships. So any pattern detection must assume that widespread terminal taxa indicate something about area relationships. The scattered distribution of (S) biome taxa throughout the legume phylogeny indicates that, like all other biomes, it was part of the ancestral area of legumes.

ter to the former three biomes. This is due to the temperate legume clades tending to be related to other temperate clades and all temperate clades collectively lacking any consistent pattern of relationship with the other biomes.

Three Area Statements

The taxon biome cladogram (Figs. 2-12) was entered interactively into TASS, and yielded an input file (Appendix 2) that ultimately output an area matrix (Appendix 3). This was subjected to a branch and bound search algorithm in PAUP (Swofford 2002), which produced two

trees each with a length of 21, a consistency index of 0.67, and a retention index of 0.53. The strict consensus was completely unresolved, which is the likely outcome of invoking assumption 2 when most terminal taxa are widespread (i.e., occupy two or more areas).

Brooks Parsimony Analysis

Additive binary coding of the taxon biome cladogram (Figs. 2-12) resulted in an area matrix involving the five areas of endemism and 181 terminal and internal nodes (Appendix 4). This matrix was subjected to a maximum parsimony branch and bound search

algorithm, which produced one tree with a length of 178, a consistency index of 0.87, and a retention index of 0.79. Irreversible parsimony also resulted in a single tree with length 190, a consistency index of 0.82, and a retention index of 0.81. In either case, an unrooted BPA tree (Fig. 16a), identical to the unrooted tree produced with Component 2.0, resolves an intermediate position of the Succulent (S) biome with respect to the two temperate and two other tropical areas. A total of 30 biome shifts in the taxon-biome cladogram was detected between the (S) and the combined (G/R) biomes. A total of 14 shifts was detected between the (S) biome and the combined (TN) and (TS) areas (i.e., (S) is sister to (TN) or (TS) areas in 14 instances). In contrast, only c. 14 shifts occur between the combined (G/R) biomes and the two temperate areas, (TN) and (TS) (Fig. 16b). Notably, there are very few instances in legumes where a tropical clade is nested within a paraphyletic temperate clade (e.g., *Crotalaria* and allied genera in the genistoids), suggesting that tropical gives rise to temperate but rarely vice versa.

DIVA Analysis

The input file for the DIVA analysis is shown in Appendix 5. The areas optimised for each of the internal nodes are indicated in Figs. 2-12. The (S) biome is consistently optimised in all of the four possible optimisations at the basal node of Leguminosae. The (TN) area is optimised in three of the four optimisations, reflecting the scoring of *Cercis*. The (G) and (R) biomes are each optimised only once at this node. The Succulent (S) biome is unequivocally optimised at the next five basal nodes, all of which subtend the diversification of all the other major clades in the legume family. The dry (S) and (G) biomes are both optimised along the remaining basal nodes in the Papilionoideae. Only three of 18 such nodes include the (R) biome as a possible optimisa-

tion. The (G) biome becomes more prevalent and sometimes the only optimisation in the millettoids and phaseoloids. The DIVA analysis indicates that (R) biome taxa are unequivocally derived right across the family (e.g. in the Detarieae, Dialiinae, Caesalpinieae *sens. lat.* plus Mimosoideae, Basal Papilionoideae, genistoids, baphioids, dalbergioids and sporadically in a few higher papilionoid groups, e.g. millettoids, *Callerya* and *Spatholobus*). The exception is the basally branching tribe Cercideae, where the optimisation is equivocal for all four biomes.

Biogeography of Leguminosae

The Raven & Axelrod (1974) hypothesis of a West Gondwana origin of legumes requires the family diversification (i.e., the legume crown clade) to be at least 100 – 90 Ma in age (Lavin *et al.* 2000; Davis *et al.* 2002a), when Africa and South America were last in near contact, although Raven & Axelrod (*l.c.*) do suggest that dispersal routes existed over islands and ridges between these continents until c. 65 Ma. In addition, Morley (2001) noted that the tropical angiosperm fossil record is biased to Laurasian collection localities, and that if more fossils were available from South America and Africa, the stratigraphic record for many groups would be longer. Legumes are thus considered by Morley (*l.c.*) to be primitively a member of an “equatorial megathermal belt”, i.e. supporting a West Gondwana origin. Morley (2003) considers a South America-Africa trans-Atlantic dispersal route to have been available along the Walvis ridge until the late Cretaceous.

Although legumes show high extant diversity in Africa and South America, fossil data alone indicates that a Mesozoic age for legume diversification is unlikely. The clear message derived from fossil legume studies such as Herendeen *et al.* (1992), Herendeen and Dilcher (1992),

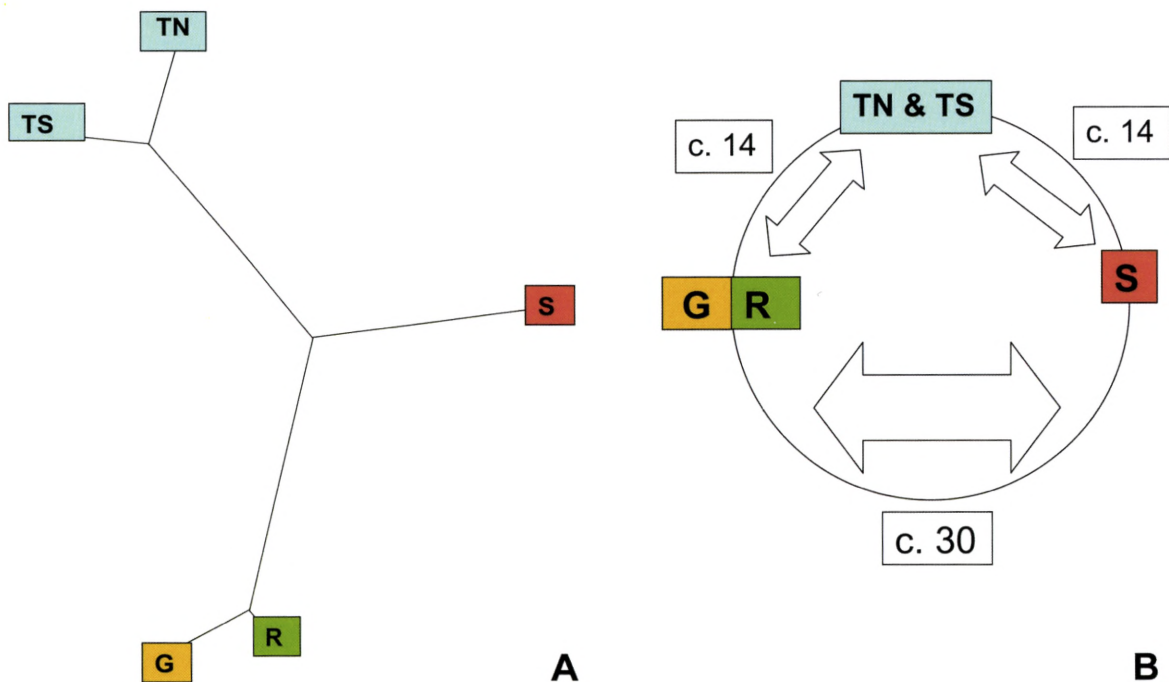


Fig. 16. (16A) Unrooted Brooks Parsimony Analysis tree, identical to that produced with Component 2.0. This resolves an intermediate position of the Succulent (S) biome with respect to the two temperate and two other tropical areas (i.e., Grass (G) and Rainforest (R) biomes). (16B) Diagram showing the degree of connectivity between the biomes. The Succulent (S) biome displays 30 instances of being sister to the Grass (G) and Rainforest (R) biomes, and 14 instances of being sister to the (TN & TS) areas. Grass (G) and Rainforest (R) biomes are only sister to (TN & TS) areas in 14 instances.

Herendeen (2001) and Jacobs (2003) is that all three subfamilies of legumes are well represented in the fossil record in North America, Europe, Africa, and Asia by at least fruits and leaves from recent times back to the Palaeocene-Eocene boundary. Putative legume fossils from earlier than this include only pollen and wood specimens that lack any specific legume synapomorphies, and even then such fossils go back at most to the latest Cretaceous. Given the temporal and spatial continuity of diverse legume macrofossils throughout the Cenozoic and the abrupt absence of deciduous legume leaflets and pods prior to the Late Palaeocene, the origination of legumes must have an age not much older than 60 Ma. Remarkably, the rapid diversification of the

family must have occurred soon after and by the middle Eocene (c. 50 Ma) nearly all of the major lineages of the family have a fossil record in North America, Europe, Africa, and Asia (Axelrod 1992; Lavin 1998; Herendeen *et al.* 1992; Herendeen 2001; Lavin *et al.* 2004).

Most of the amphi-Atlantic disjunctions in the legume family lie within the Succulent (S) biome of the Neotropics and Africa to adjacent Asia. Rather than a West Gondwana origin, this pattern could represent the historical legacy of a once widespread Tethyan distribution. The Arcto-Tertiary Geoflora hypothesis (Chaney 1947) and Boreotropics hypothesis *per se* (as developed by Wolfe 1975 and Tiffney 1985a, b) are excluded from discussion here in favour of a more narrowly defined Tethyan seaway expla-

nation, despite attempts to broaden the original concept (*e.g.*, Lavin & Luckow 1993). A once widespread Tethyan distribution involving seasonally dry tropical vegetation is different from the boreotropics hypothesis, which was erected to explain Tertiary similarities in “paratropical” floras of the mid-latitude Northern Hemisphere.

Good evidence of the long association of legumes with seasonally dry areas comes from fossil sites rich in legumes (*e.g.*, Herendeen *et al.* 1992; Herendeen, 2001), and the presence of a tropical seasonal climate (Scotese 2001) and deciduous forests in and around the margins of the Tethys seaway at the same period that legumes were initially diversifying (*e.g.*, Upchurch & Wolfe 1987). Many of the adaptations that distinguish legumes are to a seasonally dry warm climate. These include compound leaves, which photosynthesise rapidly in favourable periods (and exhibit leaf nyctinasty to promote its efficiency) while avoiding excessive water loss through leaflet shed in unfavourable periods (Rundel 1989). The high nitrogen metabolism of all legumes (Sprent 2001) is likely to confer a competitive edge in colonising seasonally dry environments whereby leaves are produced economically and opportunistically in unpredictable climates (McKey 1994). Deciduous leaves with a short life span influence interactions with herbivores as rapid leaf turnover allows phenological escape from herbivores and pathogens (McKey 1994 and references therein). Diverse and mobile chemical defences in legumes (Janzen 1981), such as alkaloids and other small molecules, can be shifted from senescing leaves to other organs and from seeds to seedlings, compared with the non-mobile defences of tannins and fibres. Seed adaptations (Gunn 1981; van Staden *et al.* 1989), include hard testas, long dormancy, long viability and the ability to store nitrogen in seeds promoting rapid seedling development. Ant associations, *e.g.* extrafloral

nectaries, pearl bodies, beltian bodies (in *Acacia*), hollow stems and thorns, have arisen numerous times conferring considerable competitive advantage in legumes (Janzen 1981; McKey 1989), although in themselves such ant associations and mobile chemical defences would be advantageous in a range of habitat types. The widespread occurrence of wind dispersal by winged fruits and seeds, especially samaras (Augsburger 1989), attest to the long association between legumes and open environments.

The persistence of legume floras in the Succulent (S) biome indicates that remnants of early Tethyan distributions are likely to be most evident within this biome. The fundamental drought tolerance of the (S) biome remained unchanged during late Neogene and Quaternary climatic change (Axelrod 1975; Quézel 1978; Maley 1980; Marrero *et al.* 1998). Lineages occupying (G) and (R) biomes have been less persistent, a result of the predictable water requirement of these biomes being affected by climatic fluctuations (Axelrod 1992; Janis 1993; Maley 1996; Pennington *et al.* 2002, 2004). The greater persistence of lineages in the (S) biome is supported by the results of the DIVA analysis (Figs. 2-12) where this area is optimised along many of the basal branches of the legume phylogeny, either as the sole biome or the most consistently optimised biome. The BPA vicariance analysis also shows that the (S) biome is more highly connected to the other biomes, than any of the other biomes are to each other (Fig. 16). This emphasises the underpinning role of the (S) biome as a source area of taxa for the other biomes. The cladistic vicariance analyses (*i.e.*, Component, TASS, BPA, and DIVA) all suggest that tropical dry areas have been occupied by legumes since their inception, which counters Morley's (2001) assertion of a megathermal wet origin of legumes.

A biogeographic metacommunity alternative

The biomes identified in this study could equally be viewed as the result of dispersal assembly, where taxa with similar ecological preferences ultimately disperse to similar ecological settings worldwide. If closely related species tend to be similar ecologically, as revealed by the study of community phylogenetic structure (*e.g.* Webb 2000; Webb *et al.* 2002), and if dispersal has enormous consequences over large spatial and temporal scales (*e.g.* Hubbell 2001), then biogeographic structure observed in phylogenies of globally distributed legume taxa may be the result not of continental history but rather of the metacommunity processes of immigration, extinction, speciation, and ecological drift.

Legume clades inhabiting the Succulent (S) biome are distinguished from those in the Grass (G) biome by a different set of phylogenetically linked centres of endemism; the former has narrow centres of endemism distributed predominantly in the red areas shown in Fig. 13, whereas centres of the latter occur in the brown areas. The notable pattern detected in this analysis is that legume taxa are much less likely to disperse back to the (S) biome from the (R) and (G) biomes. This may be due in part to the relative abundance of many (R/G) habitats compared to the relative scarcity of (S) habitats, and the greater aridity (*i.e.* drought tolerance) and often bimodal to erratic pattern of rainfall of many extant (S) areas (White 1983; Garcillán *et al.* 2003). The great age of plant taxa occupying the (S) habitats (*e.g.* Pennington *et al.* 2004; Lavin *et al.* 2004), therefore, may not be due just to persistence of vegetation and component lineages that are adapted to unpredictable rainfall, but also to the reduced rate of recent dispersal into this dry biome.

Dispersal and persistence of taxa having a

predilection to the (S) biome is well exemplified by the continental structure in the phylogeny of the Umtiza clade (Herendeen *et al.* 2003b). Disjunct Northern Hemisphere species of once supposed sister genera *Gleditsia* and *Gymnocladus* have been explained by Tertiary intercontinental land bridges (*e.g.* Schnabel *et al.* 2003). Now *Gleditsia* of the Northern Hemisphere is known to be sister to *Umtiza* of a (S) biome local region in South Africa. This ecological pattern is matched by the one disjunct South American species, *Gleditsia amorphoides*, which inhabits (S) biome local regions in the Piedmont and Misiones centres of “Pleistocene Arc” vegetation (Prado pers. comm.). The Umtiza clade provides another example with the endemic Dominican Republic *Arcoa*, which is sister to the Madagascan *Tetrapterocarpum*. Historical migrations among tropical or temperate deciduous forests worldwide is a more parsimonious explanation of the global distribution of the Umtiza clade, than invoking the extinctions of certain lineages in particular regions of continents, some of which were putatively connected by now submerged land bridges, each of which has a different age (Lavin *et al.* 2004).

The Umtiza clade is also typical of clades confined to, or centered in the (S) biome in that it shows two common biogeographic patterns that are otherwise uncommon in the other biomes. One is that trans-Atlantic clades predominate and often show reciprocal monophyly, or a deep phylogenetic split separating Old and New World sister clades. This may manifest itself as continentally confined clades each showing a large degree of phenotypic divergence. The second is a lack of species that are distributed on both sides of the Atlantic within the (S) biome.

The pattern of reciprocal monophyly is also well illustrated by the *Diphysa-Ormocarpum* clade and *Chapmannia* (Lavin *et al.* 2000), and a clade including Old World *Vigna sens. strict.*

and New World Phaseolinae (Lavin *et al.* unpublished data). Even the genus *Wajira*, largely confined to the Somalia-Masai region centered in the Horn of Africa, represents a monophyletic group well separated from its closest sister by over 10 Ma (Thulin *et al.* in press). The deep split separating sister clades, resulting in the pattern referred to as reciprocal monophyly, is a signature of long isolation of each of the sister lineages (Lavin *et al.* 2000). The pattern of reciprocal monophyly is also revealed in clades occupying the mainland and continental islands (*e.g.*, the robinoid genera *Pictetia* and *Poitea* in the Greater Antilles; Lavin *et al.* 2001b), but not in clades occupying the mainland and oceanic islands (*e.g.* Hawaiian Silverswords [Asteraceae]; Baldwin 1997).

Regular dispersal of new taxa into local regions of a global metacommunity means a few immigrants will establish over time, some will become more common through ecological drift, and some residents will go extinct as a result of this process (Hubbell 2001). The lack of detected reciprocal monophyly in most (G) and (R) clades can thus be explained by immigration into local regions of these global metacommunities increasing resident extinction rates through ecological drift, thus reducing species accumulation within trans-oceanic sister clades. In (S) clades, however, the predilection of legumes to persist in this biome has not resulted in an extinction rate that eliminated the pattern of reciprocal monophyly. The build-up of more or less equivalently sized trans-oceanic clades with time, therefore, is likely to be the result of restricted dispersal into local regions of this biome and standing diversity being generated mostly by endemic speciation.

A manifestation of reduced immigration rates into the local regions of the global (S) metacommunity is that lineages of species separated from sister clades for sufficient time come to occupy continentally confined, widely

disjunct (mostly ampho-Atlantic) distributions. The Umtiza-clade pattern is widely repeated in other endemic taxa of the (S) biome. For example, in the *Ormocarpum* clade, *Diphysa* is confined to Mesoamerica, *Pictetia* to the Greater Antilles, *Zygocarpum* to the Horn of Africa region, *Ormocarpopsis* and *Peltiera* to Madagascar, and *Ormocarpum* to eastern and central Africa and Madagascar, although one species is widespread in Asia (Lavin *et al.* 2000). In contrast in (R/G) clades, although intra-generic species diversity is to a greater or lesser extent continentally confined, relations between genera (and often within large genera) are characterised by either pantropical distributions (*e.g.* within *Cynometra*, or between *Prioria* [Central America], *Oxystigma* [Africa] and *Kingiodendron* [Asia], in Detarieae), or by Africa – Asia distributions (*e.g.* many millet-toids and phaseoloids), or New World – Asia distributions (*e.g.* within *Ormosia* [genistoids], or between *Tipuana* [South America] and *Inocarpus* [Asia] in the dalbergioids), or by ampho-Atlantic distributions (*e.g.* between *Hymenaea* and *Guibourtia* [Detarieae] or *Swartzia* and *Bobgunnia* [Swartzieae]). Such ampho-Atlantic distributions are relatively few in number and they show less phylogenetic continental structure (*i.e.* less congruent, narrowly defined and predictable distributions) compared to the (S) biome. Genera within the (R/G) biomes, experiencing higher immigration rates, thus can only be assigned to continental-wide Rainforest (R) or Grass (G) biome areas.

The second common biogeographic pattern of the lack of widely distributed species in the Succulent (S) biome contrasts to intercontinental species distributions in the (TN), (R), and (G) biomes. Examples here include *Astragalus alpinus*, *A. americanus*, and *A. aboriginum* (Barneby 1964), *Oxytropis campestris*, *O. podocarpa*, and *O. viscida* (Barneby 1952), all widespread in the (TN) biome, and *Andira iner-*

mis, *Lonchocarpus sericeus*, and *Machaerium lunatum* which variously inhabit (R/G) biomes in the Neotropics and Africa (*e.g.* Thorne 1972; Pennington 2003). Lists of intercontinentally distributed species would include over 150 (R/G) taxa distributed throughout the tropical wet oceanic islands of the world (Lavin unpublished data). Notably, many of these intercontinentally distributed species have infra-specific taxa confined to one continent (or oceanic island), suggesting that immigration is an ongoing process that over time manifests itself as phenotypically divergent populations. The presence of widespread species in the (R/G) and (TN) biomes which also comprise relatively more recent diversifications than in the (S) biome, again points to the more current role of dispersal assembly (*i.e.* species assembly through immigration) in the former biomes.

The lack of species distributed among distinct regions of the (S) biome can be found also intra-continently in South America (Prado & Gibbs 1993; Murphy & Lugo 1995; Pennington *et al.* 2000, 2003, 2004; Lewis *et al.* 2003; Linares-Palomino *et al.* 2003; Prado 2003; Wood 2003) and Africa (Verdcourt 1969; de Winter 1971; Thulin 1994; Jürgens 1997). Jürgens (1997; his Figs. 2 and 4) illustrates two of the most common Africa-wide disjunctions between the arid north and south of Africa. His Fig. 2 represents an essentially (S) biome Horn of Africa disjunction with the south-west African, Karoo-Namib regional centre of endemism (White 1983) and also identified by Lebrun 1947 and Quézel 1978, as the tropical eremic flora or "Rand flora". Disjunctions here are common at the sister species, section and genus level, but few examples have been identified of intraspecific disjunctions occurring between these regions (Thulin 1994). However, Fig. 4 of Jürgens (1997) describes a more general northern and southern African disjunction that while inclusive of the (S) biome, also has substantial diversifications into the (G)

biome Sudanian (in the north) and Zambebian (in the south) regional centres of endemism (White 1983). Examples of intraspecific disjunctions (ranked at variety and subspecies level) are common between these two areas.

The (S) biome African "arid corridor" or Afro-arid element (*e.g.* Nordenstam 1974), is thus characterised by disjunct taxa being found predominantly above the species level. Widespread taxa have thus probably decreased in species abundance and the resulting refugia have been isolated from one another for at least one to two million years, more than sufficient time for speciation to occur (Cowling & Hilton-Taylor 1997; Hubbell 2001).

The predominance of reciprocal monophyly, the abundance of genera confined to the same single regions within continents, and the lack of intercontinentally distributed species among the legume taxa centered within the Succulent (S) biome regions of the world are likely to be the result of one process: the contraction in size of the Succulent (S) biome during recent geological times. The (S) biome has apparently been restricted in size as a target area for sufficient time to reduce successful immigration into the local regions of this metacommunity. Well delimited species or clades of species are thus largely limited to old lineages. The drought tolerance of the (S) biome is probably the most important factor limiting the immigration, especially from other biome elements which have a high water requirement.

Fossil and molecular evidence suggest that trans-oceanic disjunctions in legume taxa neither arose at the same time nor under the same set of geophysical and climatic conditions. Rather, such disjunctions have multiple geographic origins, dispersion pathways and divergence times. Of 59 trans-oceanic clades of taxa ranked at the species level and above, and dated with a rate-smoothed bayesian likelihood analysis of cpDNA *matK* sequences (Lavin *et al.*

2004), 51 have ages between 1 and 22 Ma. As the dates of this major peak of disjunctions post-date large-scale continental movements and the existence of putative stepping-stone land-bridges, metacommunity processes (*sensu* Hubbell 2001) must explain these disjunctions in legumes, rather than processes invoking singular historical continental events.

The detection of diminished immigration rates within just the Succulent (S) biome allows a natural experiment to be carried out to test the idea that metacommunity processes have resulted in continentally structured phylogenies. Certain parameters can be assumed to be equal among legume communities occupying all of the biomes circumscribed in this study, such as per capita individual birth rates, speciation and extinction rates, and ecological drift. The main difference, reduced immigration rates over evolutionary time scales among the local regions of the global (S) biome, would result in a high beta-diversity (*i.e.*, high levels of local endemism).

The relative species abundance curves for pooled (S) biome samples would thus bear the signature of a steep slope in the rare abundance classes because diversity here would be reduced due to low immigration rates. A shallow slope in the high to middle abundance classes would be expected because of a high beta-diversity (*i.e.*, diversity being generated almost entirely by endemic speciation and thus few if any widespread species potentially being universally abundant). Such a species abundance curve would contrast to those taken from pooled samples from other biomes that would be expected to have a steeper slope in the high abundance class (widespread and abundant species are expected) and a shallower slope in the rare abundance classes (higher immigration rates are expected to augment endemic standing diversity). As such, a diminished fundamental biodiversity parameter and a concomitant greater phylogenetic

structure (cf. Hubbell 2001) would be estimated from species abundance curves taken from the global Succulent biome metacommunity. Comparing local and metacommunity diversity from the different biomes circumscribed in this study will be the future of our research direction on legume biogeography.

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APPENDIX 1. One input file for the Component 2.0 analysis.

S = Succulent biome; G = Grass biome; R = Rainforest biome; TN = Temperate Northern Hemisphere; TS = Temperate Southern Hemisphere.

#NEXUS

BEGIN TAXA;

DIMENSIONS NTAX=5;

TAXLABELS

S R G TN TS;

ENDBLOCK;

BEGIN DISTRIBUTION;

TITLE = 'Leguminosae';

NTAX=100;

[species][area]

RANGE

Suriana S G R,

Cercis S TN,

Griffonia R G,

Phanera R G,

Schotia S,

Prioria R G,

Peltogyne R G,

Copaifera R G,

Crudia R G,

Cynometra R G,

Hymenostegia R,

Poeppigia S,

Apuleia R G,

Labichea G R,

Kalappia R,

Dialium R G,

Gleditsia S TN,

Cassiinae S G R,

Pterogyne S,

Poincianella S,

Mezoneuron G R,

Hoffmannseggia G,

Batesia R G,

Moldenhawera G R,

Tachigali R G,

Peltophorum S,

Dimorphandra R G,

Pentaclethra R G,

Entada G R,

Plathymenia S,

Newtonia R G,

Prosopis S,

Neptunia G,

Leucaena S G R,

Dichrostachys S,

Piptadenia R G,

Mimosa S,

Acacia S,

Filicinae S,

Aculeiferum G R,

Faidherbia S,

Calliandra S,

Inga R G,

Abarema G R,

Samanea S R,

Pithecellobium S,

Phyllodineae G,

Ateleia S,

Swartzia R G,

Castanospermum R G,

Cordyla S,

Cladrastis S TN,

Calia S,

Vataireoid R G,

Amorpheae S TN,

Adesmia G TS,

Discolobium S,

Pterocarpus G R,

Chapmannia S,

Dalbergia G R,
 Aeschynomene G S,
 Diphyssa S,
 Baphioid R G,
 Hypocalyptus TS,
 Mirbelieae TS,
 Indigofera S,
 BasalMillet R G,
 Abrus S,
 Dioclea G R TN,
 Ophrestia G,
 BasalCoreMillet S,
 Tephrosia S,
 Derris R G,
 Clitoria G R,
 Apios G TN,
 Kennedia G,
 Mucuna G R,
 Desmodium G TN,
 Spatholobus R G,
 Cajanus S TS,
 Erythrina S G,
 Phaseolus S G R TN,
 Glycine S G R TN TS,
 Sesbania S,
 Lotus S TN,
 Robinia S G R TN,
 Callerya R G TN,
 Galega TN TS,
 Hedysarum S TN,
 Cicer TN,
 Trifolium TN TS,
 Fabae TN TS,
 Ormosia R G,

Diplotropis R G,
 Brongniartia S G R,
 Acosmium S,
 Sophora G TN TS,
 Thermopsidae TN,
 Podalyrieae TS,
 Genisteae G TN TS;

[taxon cladogram for Fabaceae]

TREE

Fabaceae=(Suriana,((Cercis,Griffonia,Phanera),((Schotia,
 (Prioria,((Peltogyne,Copaifera),(Crudia,(Cynometra,Hym
 enostegia))))),((Poeppigia,(Apuleia,(Labichea,(Kalap
 pia,Dialium))))),((Gleditsia,(Cassiinae,(Pterogyne,(Poin
 cianella,Mezoneuron,Hoffmannseggia)),Batesia,(Molden
 hawera,(Tachigali,(Peltophorum,(Dimorphandra,(Penta
 clethra,(Entada,(Plathymenia,Newtonia,(Prosopis,(Neptu
 nia,(Leucaena,Dichrostachys)),Piptadenia,(Mimosa,(Aca
 cia,(Filicinae,Aculeiferum,(Faidherbia,(Calliandra,Inga,A
 barema,Samanae,Pithecellobium,Phyllodine
 ae))))))))))))),((Ateleia,Swartzia),((Castanosper
 mum,Cordyla),(Cladrastis,((Calia,Vataireoid),(Ormosia,((
 Diplotropis,Brongniartia),(Acosmium,(Sophora,Ther
 mopsidae,(Podalyrieae,Genisteae))))),((Amorpheae,(Ad
 esmia,((Discolobium,(Pterocarpus,Chapmannia)),(Dal
 bergia,Aeschynomene,Diphyssa))),((Baphioid,((Hypoca
 lyptus,Mirbelieae),((Indigofera,(BasalMillet,(Abrus,(Dio
 clea,(Ophrestia,(BasalCoreMillet,(Tephrosia,Der
 ris))))),((Clitoria,((Apios,(Kennedia,(Mucuna,Desmod
 ium))),((Spatholobus,(Cajanus,(Erythrina,(Phaseolus,Glyc
 ine)))))))))((Sesbania,Lotus),Robinia),(Callerya,((Gale
 ga,Hedysarum),(Cicer,(Trifolium,Fabae)))))))))))));
 ENDBLOCK;

APPENDIX 2. Input file for TASS 1.6 analysis.

S = Succulent biome; G = Grass biome; R = Rainforest biome; TN = Temperate Northern Hemisphere; TS = Temperate Southern Hemisphere.

100	2	25	99 100	57	G R	G R
81	3	0	1	58 59	G R	S
2	4	26	2 3	60 61	S	G R
2	2	53 54	0	0	G R	S
3	2	55	4 5	62 63	S	TN; G R
2	2	63	6	64	G R	G
2	2	71	7 8	65	G	S
2	2	27	9	66	S; G R	S
2	2	56	10	67	S	G R
2	2	0	11 12	0	S	G R
2	2	0	13 14	68	S	TN; G
2	2	28	15	69	S	G
2	2	0	16	70 71	G R	G R
2	2	64 65	17 18	0	S	TN; G
2	2	66	0	72	S	G R
2	2	72 73	19	0	G	TS; S
2	2	0	20	73	S	S; G
2	2	29	21 22	74	S; R	S;TN;G R
4	2	57	0	75	G R	TS;S;TN;G R
2	3	60 61 62	23 24	76	G R	
2	2	67 68	0	77	S	
2	2	0	0	78	G R	
2	2	83	25	79	G R	
2	2	30 31	26	80	S	
2	2	58 59	0	0	S; TN	
2	2	69 70	27	0	S	
2	2	74	0	81	G R	
3	6	77	28	0	S; TN	
2	2	84	29 30 31 32	0	TS; G	
4	1	32 33	33	S; G R	S	
2	0	75 76	0	S; TN	G R	
2	2 3 4	0	34	G R	S	
2	0	85	35	G R	G R	
2	5	91	36	S	S	
2	0	34	37	G R	S; G	
2	6	37	38	G R	G R	
2	12	78 79	39 40	G R	G R	
2	0	80	41 42	G R	S; G R	
2	0	86	43	G R	S	
2	13	0	44 45	R	TS;TN; G	
2	17	35 36	0	S	TN	
2	0	38	46	G R	TS	
2	7 8	81 82	0	G R	TS;TN;G	
2	9	87	47 48	R	G R	
2	14	92	49	G R	TS	
2	18 19	96	50	S; TN	TS	
2	48 49	39 40	0	S; G R	S;TN;G R	
3	0	88	51	G R	S	
3	10 11	93	52 53	S	S; TN	
2	15 16	97	54	S	TN; G R	
2	20	41	55	G	TS; TN	
3	24	89 90	0	G R	S; TN	
2	50 51	94 95	0	G R	TN	
2	52	98	56	G R	TS; TN	
2	21 22 23	42 43 44 45 46 47		S	TS; TN	

