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FLORAL EVOLUTION IN THE DETARIEAE (LEGUMINOSAE): PHYLOGENETIC EVIDENCE FOR LABILE FLORAL DEVELOPMENT IN AN EARLY-DIVERGING LEGUME LINEAGE

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Premise of research. We examine floral evolution and phylogenetic relationships in the monophyletic Detarieae and related lineages of Caesalpinioideae. Tribe Detarieae (82 genera) includes nearly half of the genera in subfamily Caesalpinioideae and represents some of the most diverse legumes with respect to floral morphology.

Methodology. A total of 67 floral ontogenetic and morphological characters were combined with DNA sequences from the plastid *trnL-F* and *matK* regions of 34 Detarieae species and representatives of Cassieae, Cercideae, Caesalpinieae, Papilionoideae, and Mimosoideae, for which we have near-complete ontogenetic series. The morphological and ontogenetic characters were optimized onto the resulting most parsimonious phylogenetic trees and Bayesian topology to study character evolution.

Pivotal results. Our study supports previously proposed relationships within the tribe Detarieae and among caesalpinioid lineages and indicates that certain features (bracteole and hypanthium characters, sepal initiation, anther position in bud, overlap in timing of initiation of organ whorls) are phylogenetically informative for particular clades whereas others (reductions in petal and stamen number, sepal and petal initiation patterns) have evolved multiple times in parallel in the Detarieae and other Caesalpinioideae. These analyses suggest that modifications that occur early in ontogeny can be good phylogenetic characters for distinguishing both major taxonomic groups and more closely related taxa and that morphological differences that differentiate species within genera can be caused by changes that occur at all stages of ontogeny. Phylogenetic distribution of character states and ontogenetic evidence suggest that in the Caesalpinioideae, loss or suppression of organs within a whorl, both of which are very common, usually does not affect development in subsequent whorls.

Conclusions. Our analyses reveal several switches from zygomorphy to actinomorphy (and vice versa), but in Caesalpinioideae (contrary to Papilionoideae), zygomorphy is likely not clearly associated with higher diversification rates. This study suggests that floral initiation patterns are much more variable in Caesalpinioideae than in the other two subfamilies. Although particular patterns may be canalized in certain lineages of the subfamily (Cercideae, Caesalpinieae), in other clades (Detarieae, Dialiinae) floral development is more labile, explaining the high diversity in floral morphology encountered overall in the paraphyletic Caesalpinioideae.

Keywords: floral development, floral evolution, Leguminosae, Detarieae (Caesalpinioideae), phylogenetic analyses.

Introduction

Among the four tribes currently recognized in the paraphyletic subfamily Caesalpinioideae (Lewis et al. 2005), the monophyletic Detarieae (82 genera, ~750 species) includes nearly half of the genera in the subfamily and is one of the morphologically most diverse lineages in the economically important family Leguminosae. The tribe includes large tree species that predominate in wet forest habitats of the African, American, and Asian tropics, but they also form ecologically dominant elements in other habitat types (e.g., *Brachystegia* forests of East Africa; Léonard 1957; White 1983). Many members of the clade are of economic importance for their gums and resins (*Hymenaea*), oils (*Copaifera*), food (*Tamarindus*), timbers, and ornamentals (Langenheim 2003). Dated to ~54 Ma, the De-

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tarieae clade represents, with tribe Cercideae and the genus *Duparquetia*, one of the first branching lineages of the Leguminosae (Bruneau et al. 2008). By itself, it encompasses the breadth of floral diversity encountered in present-day legumes, the specialized papilionoid flower notwithstanding.

A remarkable diversity in floral morphology is observed in the Detarieae, with striking differences in floral symmetry; sepal, petal, and stamen numbers; and fusion and suppression of floral organs (Tucker 2003*b*). The typical pentamerous legume ground plan with alternate whorls of five sepals, five petals, two whorls of five stamens each, and a single carpel has been modified in numerous ways in this tribe. Species range from having radially symmetrical (actinomorphic) flowers with all 21 floral parts, as in *Cynometra*, to actinomorphic flowers with a reduced number of petals (e.g., *Librevillea*). Other species have bilaterally symmetrical (zygomorphic) flowers due to reductions in numbers of petals (e.g., *Amherstia*) or stamens (e.g., *Tamarindus*) or due to the enlargement of the adaxial petal (e.g., *Tetraberlinia*), and several species completely lack petals (e.g., *Brachystegia*).

The work of S. C. Tucker on the Caesalpinioideae over the past 3 decades (Tucker 1984*b*, 1987, 1989, 1992, 1996, 1997, 1998, 2000*a*, 2000*b*, 2000*c*, 2000*d*, 2001*a*, 2001*b*, 2002*a*, 2002*b*, 2002*c*, 2003*a*) has provided an unprecedented quantity of fundamental floral developmental data that can be used to inform us on patterns and processes of floral evolution in one of the most morphologically diverse angiosperm families. Fundamental ontogenetic data are required (Cronk 2001; Buzgo et al. 2004; Kellogg 2004; Endress 2011), but these data are best understood in a phylogenetic framework to identify homologous structures (Specht and Bartlett 2009) and to highlight characters that rarely change in phylogeny versus those that have evolved multiple times in parallel. Evolutionarily stable features serve as good diagnostic characteristics for clades and are of taxonomic interest. They also allow the identification of developmental constraints and of morphological potential (Rudall and Bateman 2003; Specht and Bartlett 2009). In contrast, characters that have evolved multiple times independently in various lineages could be indicative of labile structures derived in parallel from evolutionary precursors (Scotland 2010, 2011; Marazzi et al. 2012) and possibly subject to natural selection (Endress and Matthews 2012; but see Edwards 2009). Although these can serve as local synapomorphies in phylogenetic analyses, they also become interesting candidates for adaptive characters related to shifts in pollination systems or for adaptation to changing environments.

Based on her long-term floral ontogenetic studies, Tucker (2003*b*) reported that the principal differences in flowers among the legume subfamilies were in symmetry, sepal and petal aestivation, fusion, loss or increase of floral organs, and heterogeneity of organs within a whorl. She showed that floral asymmetry is expressed late in ontogeny (Tucker 1999) and that loss of floral organs in the caesalpinioid legumes can be the consequence of suppression during development, after initiation of all 21 floral organs, or of absence of the organ at initiation but that the two processes can lead to differences in mature flower morphology (Tucker 1988). Tucker (1984*a*, 1997) also postulated that modifications that occur late in ontogeny differentiate taxa at low taxonomic levels (e.g., species), whereas differences that occur early in ontogeny delineate higher-level taxonomic groups ("hierarchical theory"). Although detailed floral developmental studies are available for several legumes (summarized in Tucker 2003*b*; see also Ramirez-Domenech and Tucker 1988, 1989; Klitgaard 1999; Krüger et al. 1999; McMahon and Hufford 2002, 2005; Prenner 2004*a*, 2004*c*, 2004*d*, 2011, 2013*a*; Marazzi et al. 2007; Marazzi and Endress 2008; Prenner and Klitgaard 2008; Moco and Mariath 2009; Teixeira et al. 2009; Sampaio et al. 2013), floral evolution has been examined in a phylogenetic context in Papilionoideae (Pennington et al. 2000; Mansano et al. 2004; Cardoso et al. 2012, 2013; Klitgaard et al. 2013) and for Fabales (Bello et al. 2009, 2012) but only rarely for caesalpinioid legumes (Tucker and Douglas 1994). Such an analysis is particularly important in light of the paraphyletic multilineage phylogenetic structure of caesalpinioid legumes (Bruneau et al. 2001, 2008; Wojciechowski et al. 2004). This diverse paraphyletic group, from which are derived the other two subfamilies, forms the genetic base for the wide variation in floral diversity encountered in the Leguminosae.

Here we examine both floral evolution and phylogenetic relationships, focusing on the morphologically diverse tribe Detarieae but also including representatives of other caesalpinioid lineages. In conjunction with molecular data, ontogenetic and morphological data are used as a source of phylogenetic characters for better resolving clades, based on the premise that combining multiple sources of characters should better resolve relationships within the tribe (Endress 2002, 2011; Wiens 2004; Ronse de Craene and Wanntorp 2011). In light of these analyses, we determine which morphological characters best diagnose clades within the tribe and which ontogenetic characters are good indicators of phylogenetic relationships and at which taxonomic level. The phylogenetic analyses also allow us to identify the more labile floral characters that have evolved multiple times in the Detarieae and other caesalpinioid legumes and thus are candidates for adaptive characters associated with extrinsic factors, such as pollination biology. We also use the phylogenetic framework to propose general trends in floral evolution in the Detarieae and more broadly in caesalpinioid legumes (evolution of zygomorphy; loss, suppression, or fusion of floral organs; heteromorphy). Finally, we conclude by comparing the pattern observed in legumes with that seen in other Fabales in order to better understand floral evolution and developmental patterns in ancestral legumes and in eudicots as a whole.

Material and Methods

Taxon Sampling

A total of 34 species from 28 of 82 genera, representative of each of the major clades of tribe Detarieae sensu Mackinder (2005) and of the mature morphological variation observed in the tribe, were sampled. Our sampling also included seven Cassieae, one Caesalpinieae, and two Cercideae species as outgroup taxa to root our phylogenetic trees and to illustrate floral diversity in caesalpinioid legumes (app. A). One Mimosoideae and two Papilionoideae were included as placeholder taxa, nominally representative of these two subfamilies. All species were studied in detail and scored for floral ontogenetic and morphological characters (app. A), and for each species, we also analyzed plastid DNA sequences. The sampling for the ontogenetic analyses determined the sampling for the molecular data. For all but five of the species sampled for ontogenetic characters, we were able to obtain DNA sequences. For these five taxa we obtained DNA sequences from a closely related species with similar/equal floral morphologies: *Anthonotha crassifolia* (Baill.) J. Léonard was combined with molecular data from *Anthonotha macrophylla* P. Beauv., *Cynometra webberi* Bak. f. with data from a *Cynometra* species from Tanzania, *Isoberlinia scheffleri* (Harms) Greenway with data from *Isoberlinia angolensis* (Benth.) Hoye & Brenan, *Tetraberlinia tubmanniana* J. Léon. with data from *Tetraberlinia polyphylla* (Harms) J. Léonard ex Voorh., and *Lecointea hatschbachii* Barneby was concatenated with *Lecointea peruviana* Standl. Given that the focus of this study is at the generic level, this procedure was considered justified albeit not ideal. No *trnL-F* sequences were available for *Labichea punctata* Benth.

Ontogenetic and Morphological Methods

Initial analyses for the taxa scored were undertaken by Tucker (1984*b*, 1989, 1993, 1996, 1998, 2000*a*, 2000*b*, 2000*c*, 2001*a*, 2001*b*, 2002*a*, 2002*b*, 2002*c*, 2003*a*), Kantz (1996), Mansano et al. (2002), Herendeen (2000), Herendeen et al. (2003*a*, 2003*c*), Prenner and Klitgaard (2008), and Fougère-Danezan et al. (2009). Most floral ontogenetic characters were scored from the micrographs in these studies. Numerous unpublished micrographs produced by S. C. Tucker were also examined, and for nine species, additional scanning electron micrographs were generated to score certain characters. Flower buds were dissected in 70% ethanol, dehydrated through an alcohol series to absolute ethanol, and critical-point dried using a Balzers CPD 030 (BAL-TEC AG, Liechtenstein) at the Natural History Museum, London (NHM), or an Autosamdri-815B (Tousimis Research, Rockville, MD) at the Royal Botanic Gardens, Kew (RBGK). Dried material was further dissected and mounted onto specimen stubs using nail polish, coated with platinum using a Cressington 208HR sputter-coater (Cressington Scientific Instruments, Watford, UK), or an Emitech K550 (Emitech, Ashford, UK) and examined at the NHM using a Hitachi S-2500 SEM and with a Hitachi cold-field emission SEM S-4700-II (Hitachi High Technologies, Tokyo) at RBGK or examined uncoated using a LEO 1455VP (Zeiss, Oberkochen, Germany). For all species studied, macromorphological characters were scored from herbarium specimens (BM, BR, K, L, MT, P, US, WAG; app. A). Flowers were softened in boiling water with a few drops of dishwashing detergent added, dissected, and studied under LM.

A total of 67 binary or multistate unordered characters encompassing 30 floral ontogenetic and 37 floral macromorphological characters were scored (app. B). The matrix was developed considering that in the 40 binary characters, presence or absence changes can mean origin, loss, or gain of an entire character (15 characters) or switches or reversals to another state (25 characters); that for 22 multistate characters, changes in character states represent switches or reversals to another state; and that for five multistate characters with a mix of presence states plus absence of the character, changes can mean origin of a character state, switch or reversal to another state, or loss or gain of the character.

Molecular Methods and Sequence Alignment

Sequences from the plastid *trnL* (UAA) intron, the intergenic spacer between the *trnL-5′* exon and *trnF* (GAA) exon, the *matK* gene, and the flanking 3′-*trnK* intron were obtained from previously published studies (Bruneau et al. 2001, 2008; Pennington et al. 2001; Gervais and Bruneau 2002; Herendeen et al. 2003*c*; Fougère-Danezan et al. 2003; Luckow et al. 2003; Miller et al. 2003; Mansano et al. 2004), and 34 are new sequences generated for this study (either from silica gel–dried leaves or from herbarium specimens). Methods for DNA extraction, polymerase chain reaction amplification, and sequencing are described in Bruneau et al. (2001, 2008). Sequences were aligned, and where alignments were straightforward, gaps were treated as separate presence/absence characters as noted in these same two studies. Because no major incongruence was found in initial analyses of the separate plastid DNA data sets, sequences were concatenated to form a single molecular data set. All sequences are deposited in GenBank, and the molecular data matrix is available from A. Bruneau.

Phylogenetic Analyses and Character Optimization

Phylogenetic analyses were performed on the morphological (i.e., ontogenetic plus macromorphological) data alone, on the molecular data alone, and on the concatenated morphological and molecular data. These three matrices were analyzed using parsimony, and the concatenated matrix also was analyzed using Bayesian inference.

Parsimony analyses were implemented using PAUP* (ver. 4.0b10; Swofford 2000), using a heuristic search strategy. An initial series of trees was generated by retaining a maximum of five most parsimonious trees per replicate from 1000 random-addition replicates with the tree-bisection-reconnection (TBR) branch-swapping option. This initial set of most parsimonious trees then was used as the source of starting trees for a heuristic analysis, with TBR branch swapping and retention of a maximum of 20,000 trees. Strict consensus trees were constructed for each analysis. Support values were generated by the bootstrap procedure using a heuristic search with TBR branch swapping, retaining a maximum of two trees for each of one subreplicates, for a total of 5000 bootstrap replicates.

The Bayesian analyses were implemented in Mr. Bayes (ver. 3.2.2; Ronquist et al. 2012). A nucleotide substitution model was selected using the Akaike Information Criterion as implemented in Modeltest (ver. 3.7; Posada and Crandall 1998); this was done separately for the *matK*, *trnL*, and *trnL-F* data sets. The Bayesian estimation consisted of two independent runs, each for 10,000,000 generations, sampling trees and parameters every one-thousandth generation. Each run consisted of four simultaneous Markov chains with eight swaps per generation. We used the GTR+I+Γ nucleotide substitution model with the base frequency, substitution rates, and among-site variation variables estimated from the data. Parameters were estimated independently ("unlinked") among partitions for the proportion of invariable sites, shape parameter of the gamma distribution, nucleotide frequencies, and substitution rates. Indels were coded as for the parsimony analyses. The indel and the morphology partitions were treated as standard data and

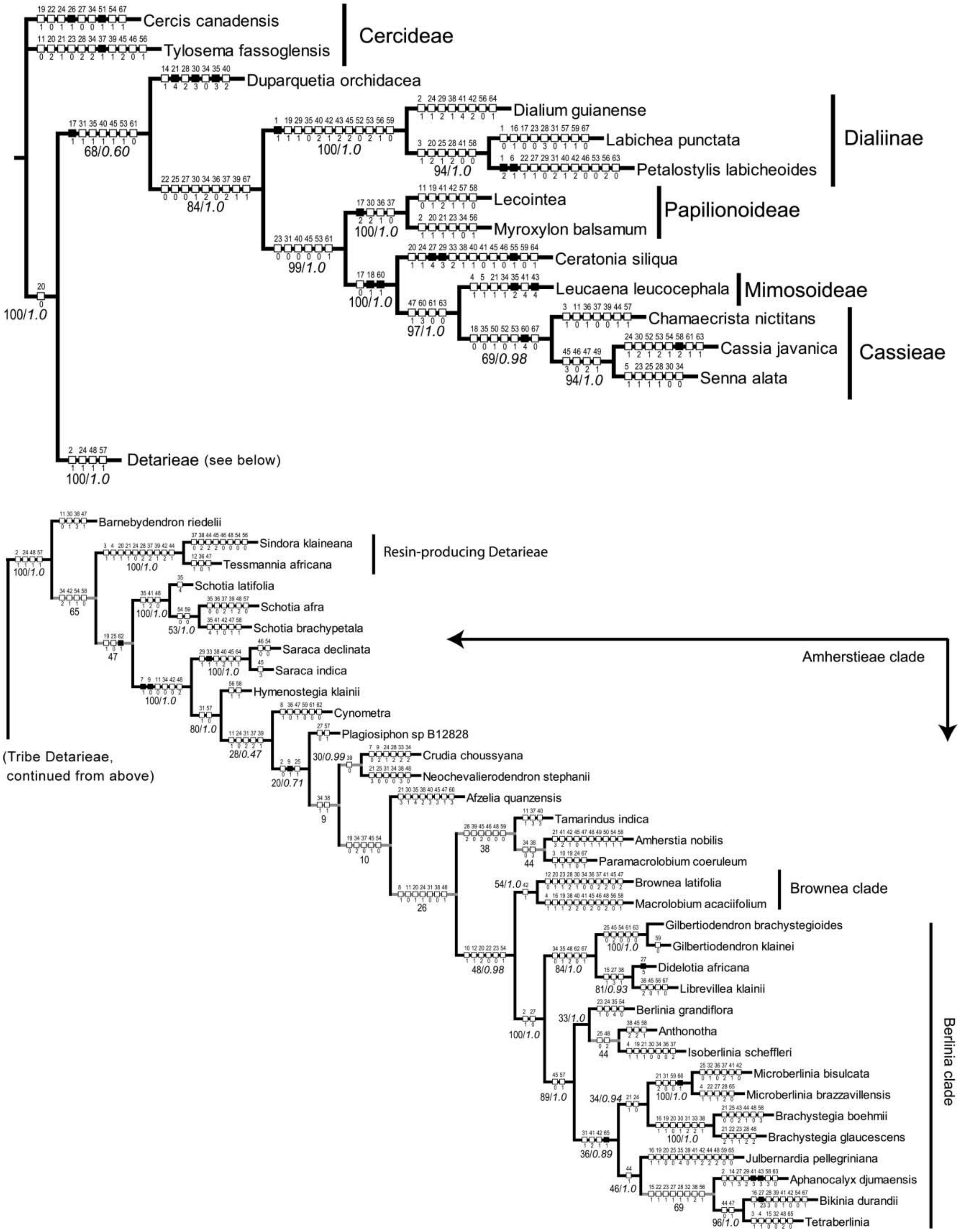
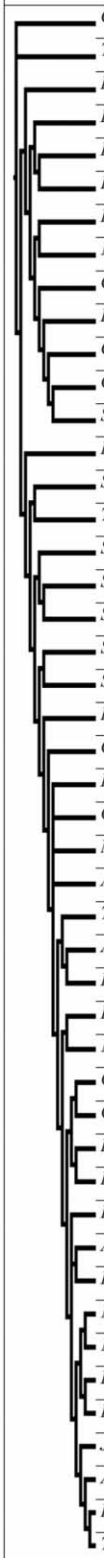


Fig. 1 One of 10 most parsimonious trees obtained from the phylogenetic analysis of floral ontogenetic, morphological, and sequence data (consistency index 0.54, retention index 0.78, length 2231). Ontogenetic and morphological characters are optimized onto this tree using the parsimony criterion as implemented in WinClada (Nixon 1999). White hash marks indicate homoplasious character states; black hash marks indicate unique occurrences but in which reversals can occur. Bootstrap support for each clade is indicated below the branches, followed by posterior probabilities from the Bayesian majority-rule consensus indicated in italics. Unsupported clades in the strict consensus or in the Bayesian consensus trees are indicated by gray lines.



	bract-eoles	calyx	corolla	stamen whorls	gynoecium	ovules	initiation patterns
Cercis canadensis	Bt	K5^{c}↓	C3:2$^{\text{larger}}$↓	A5+5↓	$\underline{G}$1↓ free	V∞	H:U:U:U
Tylosema fassoglensis	Bt	K(2):3↓	C1$^{\text{smaller}}$:4↓	A2^{c}:2:1^{c}+5^{c}↓	$\underline{G}$1↓ free	V2	H:U:U:U
Duparquetia orchidacea	Bt	K4^{c}:1^{0}↓	C3:2$^{\text{smaller}}$↓	A4:1^{0}+5^{0}↓	$\underline{G}$1↓ free	V2–5	B:B:S:na
Dialium guianense	Bt	K5^{c}↓	C1^{r}:4^{0}	A2+0↓	$\underline{G}$1↓ free	V1	B:na:S:na
Labichea punctata	Bt	K5↓	C1^{0}:4*	A1^{0}1:1^{0}1:1^{0}+5^{0}↓	$\underline{G}$1↓ free	V2-3	H:na:na:na
Petalostylis labicheoides	Bt	K(2):3↓	C5*	A2^{r}:3+5^{r}↓	$\underline{G}$1↓ free	V∞	B:S:H:na
Lecointea hatschbachii	Bt	K5*	C1:4↓	A5+5↓	$\underline{G}$1↓ free	V∞	U:U:B:U
Myroxylon balsamum	Bt	K5*	C1$^{\text{larger}}$:4↓	A5+5↓	$\underline{G}$1↓ free	V2	U:U:U:U
Ceratonia siliqua (mostly unisexual)	Bt	K5^{c}*	C5^{0}	A5+5^{0}↓	$\underline{G}$1↓ free	V∞	H:na:H:na
Leucaena leucocephala		K5*	C5*	A5+5↓	$\underline{G}$1↓ free	V∞	H:S:S:S
Cassia javanica	Bt	K5^{c}*	C5↓	A2^{r}:3+1^{r}:4↓	$\underline{G}$1↓ free	V∞	H:U:U:U
Chamaecrista nictitans	Bt	K5*	C2$^{\text{larger}}$:3↓	A5+5↓	$\underline{G}$1↓ free	V∞	H:S:U:U
Senna alata		K5↓	C5*	A2^{s}:3 + 1^{s}:4↓	$\underline{G}$1↓ free	V∞	H:H:U:U
Barnebydendron riedelii	Bt	K(2):3^{c}↓	C3:2^{r}↓	A5+5↓	$\underline{G}$1↓ free	V∞	H:S:U:U
Sindora klaineana	Bt	K(2):3↓	C1:4^{r}↓	A(2):3^{r}+5^{r}↓	$\underline{G}$1↓ free	V1-2	H:U:U:U
Tessmannia africana	Bt	K(2):3↓	C5↓	A(5+4):1↓	$\underline{G}$1↓ adnate	V6-7	?:U:?:?
Schotia afra	Bt	K(2):3^{c}*	C5↓	A(5+5)↓	$\underline{G}$1↓ adnate	V∞	H:?:B:U
Schotia brachypetala	Bt	K(2):3^{c}*	C3:1$^{\text{smaller}}$1↓	A(5+5)↓	$\underline{G}$1↓ adnate	V∞	H:U:U:U
Schotia latifolia	Bt	K(2):3^{c}↓	C3:2^{r}↓	A(5+5)↓	$\underline{G}$1↓ adnate	V4	H:U:B:U
Saraca declinata	Bt	K(2):3*	C1^{r}:4^{s}*	A1^{0}:4 + 5^{0}↓	$\underline{G}$1↓ adnate	V1-8	H:U:U:na
Saraca indica	Bt	K(2):3*	C1^{0}:4^{s}*	A2^{0}:3 + 5^{0}↓	$\underline{G}$1↓ adnate	V∞	H:S:U:na
Hymenostegia klanei	Bt	K(2):3^{c}↓	C3:2$^{\text{smaller}}$↓	A5+5↓	$\underline{G}$1↓ adnate	V2	H:U:U:U
Cynometra webberi	Bt^{c}	K(2):3↓	C5*	A5+5↓	$\underline{G}$1↓ free	V∞	H:S:U:U
Plagiosiphon sp Breteler 12828	Bt	K5↓	C1$^{\text{smaller}}$:4↓	A3:2^{r}+5^{r}	$\underline{G}$1↓ adnate	V2-6	H:S:U:?
Crudia choussyana	Bt	K(2):3^{c}↓	C5^{0}	A5+5↓	$\underline{G}$1↓ adnate	V4	H:U:U:U
Neochevalierodendron stephanii	Bt	K(2):3↓	C3:2^{r}↓	A(5+5)↓	$\underline{G}$1↓ adnate	V∞	H:U:U:U
Afzelia quanzensis	Bt	K(2):3↓	C1:4^{r}↓	A2^{r}:3 +1^{0}:4↓	$\underline{G}$1↓ adnate	V∞	H:S:U:U
Tamarindus indica	Bt	K(2):3^{c}↓	C5↓	A2^{r}:(3)+1^{0}:4^{r}↓	$\underline{G}$1↓ adnate	V∞	H:U:U:U
Amherstia nobilis	(Bt)^{c}	K(2):3↓	C3:2^{r}↓	A(5+4):1^{r}↓ or A(5+4):1^{0}↓	$\underline{G}$1↓ adnate	V∞	H:U:B:U
Paramacrolobium caeruleum	(Bt)	K(2):3↓	C1$^{\text{large}}$:2:2^{r}↓	A(2^{s}:3+5^{s})↓	$\underline{G}$1↓ adnate	V∞	H:U:U:?
Brownea latifolia	(Bt) or (Bt)^{c}	K(2):3^{c}↓	C5*	A(5+4):1^{r}↓	$\underline{G}$1↓ adnate	V∞	H:S:B:U
Macrolobium acaciifolium	(Bt)	K5^{c}↓	C1:4^{r}↓	A2^{0}:3 +5^{0}↓	$\underline{G}$1↓ adnate	V1	?:U:H:?
Gilbertiodendron brachystegioides	(Bt)	K5^{c}*	C1$^{\text{larger}}$:4↓	A2^{r}:3 +5^{r}↓	$\underline{G}$1↓ free	V∞	H:U:U:U
Gilbertiodendron klainei	(Bt)	K5*	C1$^{\text{larger}}$:4↓	A2^{r}:3 +5^{r}↓	$\underline{G}$1↓ ?	V∞	H:U:U:U
Didelotia africana	(Bt)^{c}	K5^{r}↓	C5^{r}↓	A5 (pattern unknown)	$\underline{G}$1↓ free	V∞	?:?:?:?
Librevillea klainei	(Bt)	K5^{r}↓ or K1:4^{r}↓	C5^{r}↓ or C1:4^{r}↓	A5+5↓	$\underline{G}$1↓ free	V2	?:?:?:?
Berlinia grandiflora	(Bt)	K5↓	C1:4^{r}↓	A(5+4):1↓	$\underline{G}$1↓ adnate	V∞	H:?:U:U
Anthonotha crassifolia	(Bt)	K5^{c}*	C1:4^{r}↓	A2^{r}:3 +5^{r}↓	$\underline{G}$1↓ adnate	V?	H:U:U:U
Isoberlinia angolensis	(Bt)	K5^{c}*	C5↓	A5+5↓	$\underline{G}$1↓ adnate	V4-8	H:H:U:U
Microberlinia bisulcata	(Bt)	K5*	C5*	A(5+4):1↓	$\underline{G}$1↓ adnate	V∞	H:U:U:U
Microberlinia brazzavillensis	(Bt)	K(2):3↓	C1$^{\text{larger}}$:4↓	A(5+4):1↓	$\underline{G}$1↓ adnate	V∞	H:U:B:U
Brachystegia boehmii	(Bt)	K5*	C5^{r}	A(5+5)↓	$\underline{G}$1↓ free	V∞	H:?:B:B
Brachystegia glaucescens	(Bt)	K(2):3↓	C5^{r}	A5+5↓	$\underline{G}$1↓ free	V4-10	H:S:B:U
Julbernardia pellegriniana	(Bt)	K5^{c}*	C1:4$^{\text{smaller}}$↓	A5+5↓	$\underline{G}$1↓ adnate	V∞	H:U:U:U
Aphanocalyx djumaensis	(Bt)	K4^{0}:1↓	C1:4^{0}↓	A(5+4):1↓	$\underline{G}$1↓ adnate	V?	na:na:E:E
Bikinia durandii	(Bt)	K(2):2^{r}:1^{c}↓	C1:4^{r}↓	A(5+4):1↓	$\underline{G}$1↓ adnate	V2-3	?:?:U:?
Tetraberlinia tubmanniana	(Bt)	K(2):3^{c}↓	C1:4^{r}↓	A5+5↓	$\underline{G}$1↓ adnate	V2-3	H:?:B:U

modeled using the mk model of Lewis (2001) as implemented by Ronquist et al. (2012). All sample points prior to reaching stationarity of the chains were discarded (equivalent to discarding the first 1000 trees). All analyses used the default priors. Convergence was assessed by comparing majority-rule consensus trees from the two analyses and by using Tracer (ver. 1.3; Rambaut and Drummond 2007) to compare density plots of the estimated parameters and of the likelihoods from the two analyses. The posterior probabilities for individual clades were compared for congruence and summarized on a majority-rule consensus.

Morphological and ontogenetic characters were optimized onto the topologies obtained from the combined morphological and molecular analysis. Studying morphological evolution by optimization of morphological characters onto a combined analysis using those same characters has been criticized as being circular (de Queiroz 1996; but see Luckow and Bruneau 1997 for an alternative perspective), but, more importantly, it is clear that parsimony optimization will minimize homoplasy and thus might represent an underestimation of the number of times a character has evolved, particularly when discussing a character with a single origin. Regardless, we chose the combined analysis as it currently represents the best-resolved hypothesis of species relationships. All characters were optimized onto each of the most parsimonious trees, as well as onto the fully resolved Bayesian consensus topology, to account for phylogenetic uncertainty. The program WinClada (Nixon 1999) was used to optimize characters following the parsimony criterion, and all equally parsimonious optimizations were explored when discussing character evolution.

Results

Phylogenetic Analyses

Both the parsimony and Bayesian analyses of the ontogenetic and morphological data yielded completely unresolved consensus trees (results not shown) in which tribe Detarieae is not supported as monophyletic. The combined *trnL* intron, *trnL-F* spacer, and *matK*/*trnK* data yielded a well-resolved parsimony strict consensus tree (from 202 most parsimonious trees; consistency index without apomorphies [CI′] of 0.65; retention index [RI] of 0.85) and Bayesian majority-rule consensus in which tribe Detarieae is strongly supported as monophyletic (100% bootstrap, 1.0 posterior probability [PP]; results not shown). However, in both analyses there is low resolution among taxa in this clade, with only 21 nodes resolved. Only 18% (575 from a total of 3122 characters) of characters are parsimony informative.

The combined ontogenetic and molecular parsimony analyses yielded 10 trees (CI′ 0.66, RI 0.78). The strict consensus tree is well resolved at the level of tribes and major groups, but within Detarieae only 11 of the 32 nodes are supported with bootstrap values higher than 85% (fig. 1). A similar pattern of relationships is obtained from the Bayesian analysis of the combined data (PP indicated on fig. 1). In both these analyses, as in all previously published phylogenetic studies of the group (Bruneau et al. 2000, 2008), the tribe Detarieae is strongly supported as monophyletic, with *Barnebydendron*, *Schotia*, *Tessmannia*, and *Sindora* comprising the first-diverging lineages within this clade. The latter two represent the resin-producing Detarieae, but their relationship with the South African *Schotia* is not well resolved, and in the Bayesian analysis, *Schotia* occurs as sister to *Barnebydendron* (PP 0.63). Other clades recognized in recent analyses (Bruneau et al. 2000, 2008) are also supported as monophyletic (e.g., Brownea clade, Amherstieae clade, Berlinia clade), but as in other phylogenetic analyses, there is low resolution at the base of the Amherstieae clade (i.e., relationships between *Afzelia*, *Plagiosiphon*, *Neochevalierodendron*, and *Crudia* are not resolved).

Morphological and Ontogenetic Character Evolution

The 67 morphological and ontogenetic characters were optimized onto each of the 10 most parsimonious trees and onto the Bayesian consensus topology obtained from the analysis of the combined morphological and molecular data but are illustrated on one arbitrarily chosen most parsimonious tree (fig. 1). The mean CI (0.26; median CI 0.20) and mean RI (0.39; median RI 0.33) for the morphological and ontogenetic characters (regardless of topology studied) indicate that, in general, these characters and character states are highly homoplasious (CI, RI, and length of characters indicated in app. B). Certain characters and character states seem to be less labile and provide more phylogenetic information at the taxonomic level sampled here. For example, of all the ontogenetic and morphological characters scored, only eight have an RI above or equivalent to 0.80, and, of these, five are bracteole characters (characters 7–10, 12; app. B). Most other floral characters switch states or are lost or gained numerous times during the evolution of this group. Of the 62 nonautapomorphic characters, 40 have an RI lower than 0.5 (low phylogenetic information), and 49 have a CI lower than 0.5 (multiple changes), and this pertains to early ontogenetic characteristics (21 of 30 characters with RI <0.5, 24 with CI <0.5) as well as the mature flower morphology (19 of 32 characters with RI <0.5, 25 with CI <0.5). Below we briefly describe the morphology and de-

Fig. 2 Floral formulae of Caesalpinioideae and related outgroup taxa studied. Initiation patterns for each whorl, in an acropetalous direction starting with the outer whorl: H, helical; U, unidirectional; B, bidirectional; S, simultaneous. Within whorls, the adaxial condition is noted first; r indicates that the organs are initiated but become rudimentary during development; 0 indicates that organs are not initiated; c denotes a petaloid organ; s denotes a staminode; adnate or free refers to whether the gynoecium is adnate or not to the hypanthium (when present); parentheses indicate organ fusion; a question mark indicates zygomorphic; an asterisk indicates radially symmetrical. The caesalpinioid 9 + 1 stamen arrangement is denoted by A(5+4):1 to indicate the fusion of the five outer (antesepalous) whorl stamens with the four inner (antepetalous) whorl stamens, even though the free stamen is the median adaxial stamen of the antepetalous whorl. Adapted from Prenner et al. (2010). A = androecium, two whorls indicated by plus sign; Bt = bracteoles; C = corolla; G1 = gynoecium with single carpel, superior ovary; K = calyx; V = number of ovules.

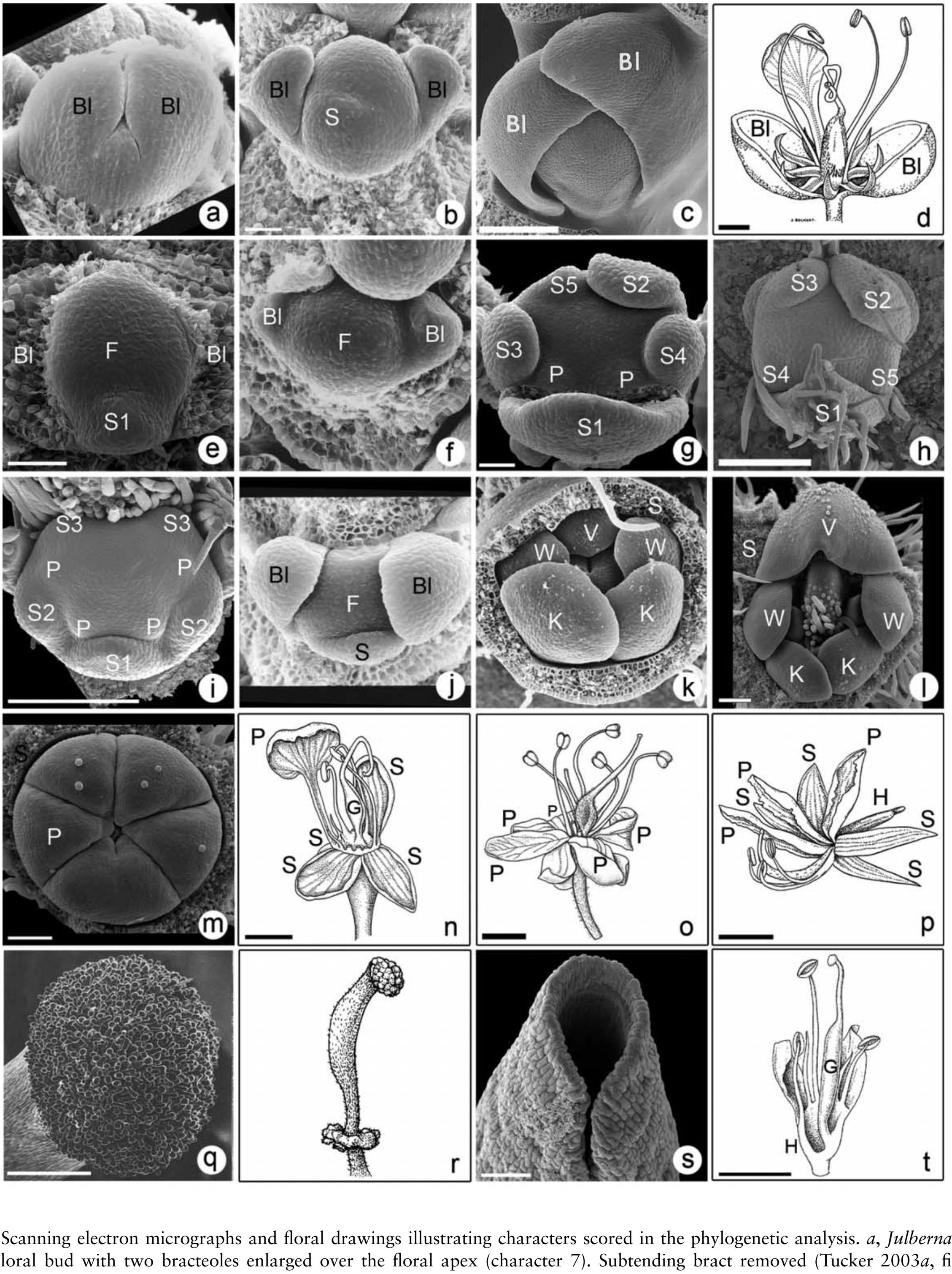


Fig. 3 Scanning electron micrographs and floral drawings illustrating characters scored in the phylogenetic analysis. *a*, *Julbernardia pellegriniana*. Floral bud with two bracteoles enlarged over the floral apex (character 7). Subtending bract removed (Tucker 2003*a*, fig. 5*D*). *b*, *Schotia brachypetala*. Floral bud with two small bracteoles that do not cover the floral apex (character 7) and initiation of first sepal (Tucker 2001*a*, fig. 9). *c*, *Saraca declinata*. Massive imbricate bracteoles enveloping the floral apex (character 9; Tucker 2000*b*, fig. 3*b*). *d*, *Gilbertiodendron brachystegioides*. Flower with valvate bracteoles (character 9), a showy vexillary petal, four linear petals and five linear sepals, three functional stamens, two staminodia, and gynoecium (Tucker 2002*b*, fig. 89*a*). *e*, *Machaerium arboreum* (Papilionoideae). Floral apex elongated in the sagittal plane (omega shaped) with bracteole scars (character 12) and first sepal in abaxial position. *f*, *Schotia brachypetala*. Floral apex that is circular in shape (character 12) preceded by two bracteoles (Tucker 2001*a*, fig. 8). *g*, *Senna marilandica*. Flower bud with all five sepals

velopment of the inflorescence structure and each of the main floral organs studied (see fig. 2 for floral formulas).

Inflorescence structure. In the basally branching part of the Detarieae (*Barnebydendron* and *Schotia*), the resin-producing Detarieae, the first-diverging lineages of the Amherstieae clade, and most members of the Berlinia clade, the inflorescence is compound (character 2). The other Detarieae (Brownea clade, *Tamarindus*, *Amherstia*, *Paramacrolobium*, *Afzelia*, *Crudia*, *Neochevalierodendron*, *Aphanocalyx*) have a simple inflorescence, as do most of the other Leguminosae studied here, except the Dialiinae. Most taxa with compound inflorescences have a racemose arrangement, but it is generally cymose in the Dialiinae (character 1). The flower subtending bracts tend to have a helical arrangement in the legumes studied, but in *Paramacrolobium* and *Tetraberlinia* and in a few outgroup taxa (*Labichea*, *Petalostylis*, *Chamaecrista*), the bracts are distichous (character 3).

Bracteoles. In the taxa studied, two bracteoles typically are present and opposite (character 6). These can be large and persistent throughout development or small and inconspicuous, sometimes becoming caducous (character 11). Young bracteoles are massive and nearly surround the floral apex (character 7; figs. 3*a*, 4) in all Amherstieae clade taxa except *Crudia*. In *Schotia*, *Barnebydendron*, the resin-producing Detarieae, and the outgroup taxa, bracteoles are small and do not surround the floral apex (figs. 3*b*, 4). Within the Amherstieae clade, the large bracteoles enclose the bud until bud maturity (character 8) in *Amherstia*, *Tamarindus*, and *Paramacrolobium* and in taxa of the Berlinia and Brownea clades. In other taxa with massive bracteoles in young bud, the bracteoles stop growing earlier and become relatively smaller as the flower bud matures (e.g., *Saraca*, *Hymenostegia*, *Plagiosiphon*, *Crudia*, *Neochevaliodendron*, *Afzelia*). Bracteoles are valvate in most Amherstieae clade genera except *Saraca*, *Hymenostegia*, and *Cynometra*, where they are imbricate (character 9; figs. 3*c*, 3*d*, 4). Bracteoles are distant in *Crudia*, the resin-producing Detarieae, *Schotia*, *Barnebydendron*, and the outgroup taxa. In taxa with massive valvate bracteoles that enclose the mature bud, bracteoles can be fused (character 10), as in the Berlinia and Brownea clades and *Paramacrolobium*. Elsewhere, the bracteoles are free. The postbracteole primordium can be circular or omega shaped in the Detarieae (character 12; figs. 3*e*, 3*f*, 4). It is omega shaped in the Berlinia clade, in *Macrolobium*, and in *Tessmannia*, whereas it is circular in all other taxa studied.

Sepals. In legumes, as in most eudicots, five sepals are generally initiated (character 14), but in *Duparquetia*, four are initiated, and in *Aphanocalyx*, which has only a single sepal at maturity, only one sepal is initiated. In a number of other taxa, sepals may be suppressed or have an aborted development (resorbed) early in development (character 15; *Didelotia*, *Librevillea*, *Bikinia*). In most of the Detarieae, except in the Brownea clade and most of the Berlinia clade, the two adaxial sepals (character 22) fuse to form a tetramerous calyx (fig. 4). In all other legumes studied, except *Tylosema* and *Petalostylis*, sepals do not fuse, at least not entirely.

In legumes, the sepal and petal whorls alternate. In Caesalpinioideae and Papilionoideae, a sepal is found in the abaxial median position (but a petal occurs in the adaxial median position), whereas in Mimosoideae, a sepal occurs in the adaxial median position (with a petal in the in abaxial median position). Although this is usually consistent in the Mimosoideae and Papilionoideae and also rarely varies in other eudicots (mostly adaxial; Bello et al. 2007), the pattern is more variable in the Caesalpinioideae, where, for example, in *Ceratonia*, the median sepal is adaxial (character 18). In addition, the position of the first sepal primordium is extremely variable in the Detarieae, occurring either in the strict median or off the saggital plane (character 19; fig. 3*j*). In most Caesalpinioideae, sepals are initiated in a helical pattern, with the first initiating in the abaxial position (fig. 3*g*), except in *Duparquetia* and some of the Dialiinae taxa, where sepals are initiated bidirectionally (fig. 3*h*; character 17). In the Papilionoideae, sepals are often initiated in a unidirectional pattern (fig. 3*I*), with the first initiating in the median abaxial position. In most Mimosoideae, sepals are initiated in a helical pattern, with the first sepal to initiate in a median adaxial position. Sepal aestivation both in early development (character 20) and at maturity (character 21) is extremely variable in the Detarieae, being imbricate, valvate, or open, with the majority having imbricate sepal aestivation.

Petals. In most legumes, petal initiation begins only once the sepal whorl has completed its initiation (acropetal initiation, character 16), but in a few members of Detarieae the two whorls overlap (*Macrolobium*, *Brachystegia*, *Julbernardia*, *Bikinia*). In legumes, five petals are generally initiated (character

initiated in a helical pattern, starting on the abaxial side (character 17). *h*, *Dialium orientale*. Floral bud with all five sepal primordia present, initiated in a bidirectional pattern, with the lateral pair (S4, S5) initiated last (character 17). *i*, *Swainsona formosa* (Papilionoideae). Floral bud with all five sepals initiated in a unidirectional pattern, the last two forming on the adaxial side (character 17). *j*, *Cynometra webberi*. First sepal initiated in abaxial and nonmedian position (character 19; Tucker 2001*a*, fig. 86). *k*, *Cercis canadensis*. Ascending cochleate petal aestivation (character 35; Tucker 2003*b*, fig. 2*f*). *l*, *Machaerium arboreum* (Papilionoideae). Floral bud with descending cochleate aestivation of petals (character 35). Sepals removed. *m*, *Inga feuillei* (Mimosoideae). Valvate corolla, showing edge-to-edge temporary fusion of petals that will split apart at anthesis (character 35). *n*, *Afzelia quanzensis*. Flower at anthesis showing median petal larger than all four remaining petals (character 37). In this species there is one large petal and four rudimentary petals (Tucker 2002*b*, fig. 57*a*). *o*, *Cynometra webberi*. Flower at anthesis (not all 10 stamens are shown) with all petals equal (character 37; Tucker 2001*a*, fig. 4*a*). *p*, *Tamarindus indica*. Flower at anthesis showing median petal equal to the two laterals (but different from the two abaxials, which are reduced; character 37; Tucker 2000*c*, fig. 3*a*). *q*, *Brownea X crawfordii*. Capitate stigma (character 60; Owens and Lewis 1996, fig. 1*a*). *r*, *Ceratonia siliqua*. Peltate stigma of pistillate flower (character 60; Herendeen et al. 2003*b*, fig. 2*i*). *s*, *Senna alexandrina*. Stigma tapering to a small pore (character 60). *t*, *Schotia latifolia*. Longitudinal section showing gynoecium stipe adnate to adaxial side of hypanthium and stamens attached to summit of hypanthium (character 62; Tucker 2001*a*, fig. 3*b*). *e*, *g*–*i*, *l*, *m*, *s*: originals. Bl, bracteole; F, floral apex; G, gynoecium; H, hypanthium; K, keel petal; S, sepal; P, petal; V, vexillium; W, wing petal. Scale bars = 50 μm (*a*, *e*–*g*, *j*, *s*), 100 μm (*b*, *h*, *k*–*m*), 200 μm (*i*, *q*), 500 μm (*c*), 2 mm (*d*, *o*), 5 mm (*p*, *t*), 10 mm (*n*, *r*).

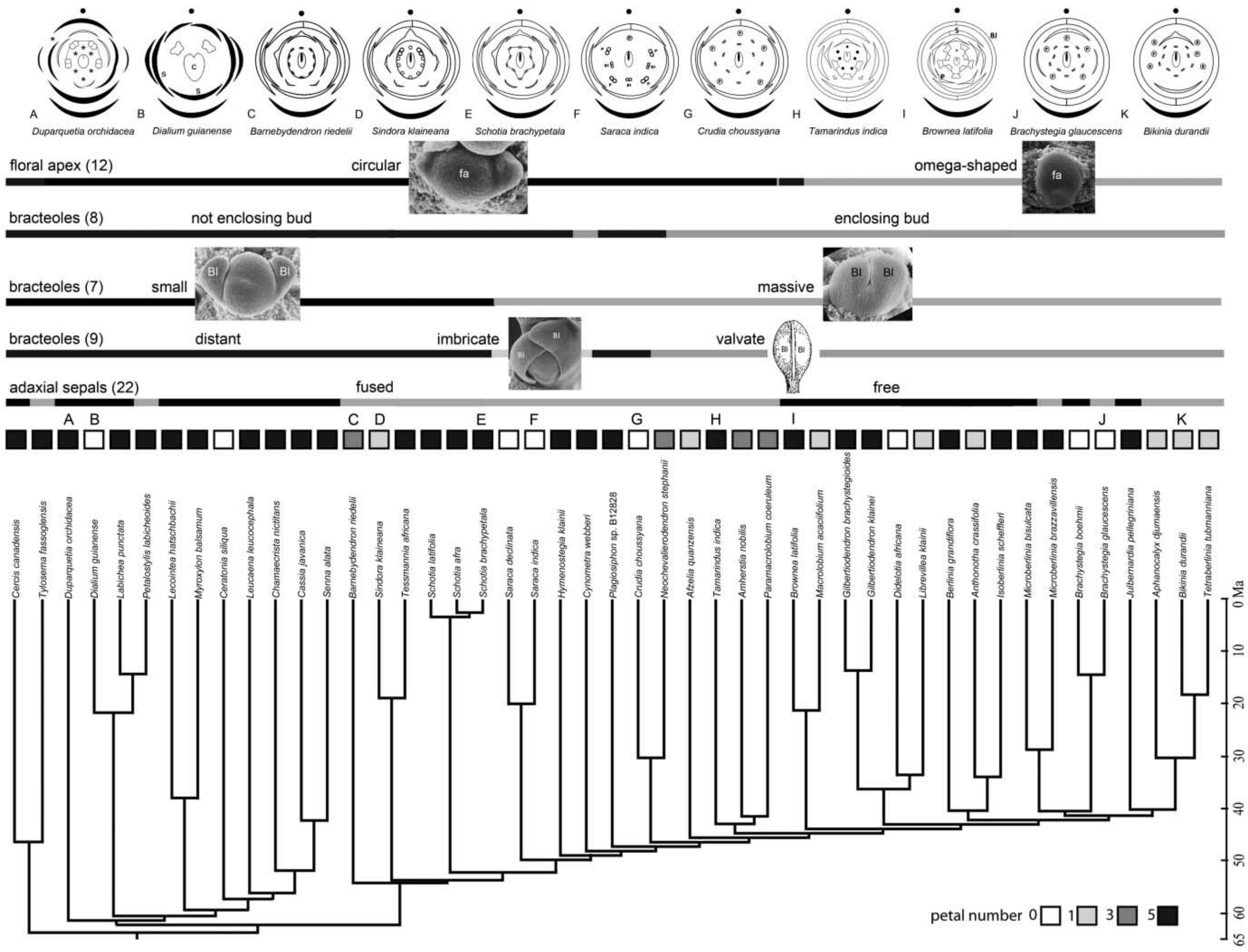


Fig. 4 Chronogram indicating approximate divergence times, phylogenetic distribution of particular floral characters, and floral diagrams to illustrate diversity of floral evolution in Detarieae and other Caesalpinioideae. Divergence times from Bruneau et al. (2008); floral diagrams from Fougère-Danezan (2005).

29), but in certain taxa studied, only four petals initiate (e.g., *Labichea*, *Saraca*) or a single petal initiates (e.g., *Aphanocalyx*, *Dialium*). As with sepal initiation, the pattern of petal initiation (character 30) varies among Caesalpinioideae but generally is fixed and unidirectional (or sometimes simultaneous) in Papilionoideae and simultaneous in Mimosoideae. However, in contrast to the sepals, the position of the first-formed petal is extremely variable in the Detarieae and Dialiinae, either being on the adaxial or abaxial side or with several petals initiating simultaneously (character 31). In other legumes studied, the first petal(s) to initiate is (are) on the abaxial side. In several members of Detarieae, the petals are resorbed or absent (character 38; e.g., *Brachystegia*, *Crudia*; several resin-producing Detarieae not scored here), leading to a reduction in the number of petals at maturity (to one or three petals). Complete petal suppression also occurs in *Ceratonia* and *Dialium*, and in *Saraca* the primordia in petal positions differentiate into stamens (see Tucker 2000*b*; character 33).

Petal aestivation (character 35; fig. 3*k*–3*m*) is extremely variable in caesalpinioid legumes but is generally constant in Papilionoideae (imbricate descending) and in Mimosoideae (valvate). The imbricate descending pattern also is seen in the two *Gilbertiodendron* species where the standard is larger than the four other smaller petals and occurs outermost (even in bud). Petal size at anthesis (character 36) is extremely variable, even among close relatives (e.g., between the two *Microberlinia* species studied). Most of the Amherstieae clade genera (except *Hymenostegia*, *Cynometra*, *Neochevalierodendron*, *Tamarindus*, *Brownea*, *Isoberlina*, *Microberlinia bisulcata*) have a median petal larger than the lateral ones, whereas most basally branching members of Detarieae have a median petal the same size as the laterals (character 37; fig. 3*n*, 3*o*, 3*p*). In the Brownea and Berlinia clades, the lateral petals also are similar in size to the two abaxial ("keel") petals, while the lateral petals differ from the keel petals in most other Detarieae. In yet other Detarieae, all the petals are equal in size.

Stamens. Stamens generally initiate after all the petal primordia have been initiated, but there is an overlap with petal initiation in *M. bisulcata*, *Aphanocalyx*, and *Bikinia* of the Berlinia clade (character 32). In addition, the two stamen whorls overlap in most of the Berlinia clade and the basally branching Detarieae, a condition that does not occur in most other legumes (character 57). In general, the Detarieae are diplostemonous, but a few taxa have more than five stamens per whorl, and others have fewer than five stamens per whorl (character 45). In *Saraca indica*, three stamens are initiated, and because four of the petals develop into stamens, there is a total of seven stamens at maturity. In the other *Saraca* species studied, in *Macrolobium*, *Dialium*, and *Labichea*, fewer than five stamens are initiated (character 40), and there are fewer than five stamens at maturity (character 45). In contrast, in *Sindora* (with staminodes present), *Gilbertiodendron*, *Paramacrolobium*, *Anthonotha*, *Tylosema*, *Cassia*, and *Senna*, 10 stamens initiate, but there are fewer than five fertile stamens at maturity. In *Tamarindus*, fewer than 10 stamens (but more than five) develop, and only three are present at maturity. In all other Detarieae studied and most of the outgroup taxa, there is the same number of stamens at maturity as the number initiated.

The development of the stamen whorls is also quite variable (characters 41–44). The initiation of antesepalous stamens is extremely variable in the legumes, and although there is a tendency for the first stamen to be abaxial, it may be lateral and in some taxa it is adaxial. The antepetalous stamens generally have a unidirectional order of initiation starting on the abaxial side, but this is also quite variable.

Staminodes are variably present but are consistently present in *Tamarindus*, *Amherstia*, and *Paramacrolobium* (character 46). Whether the stamens are free, grouped in a sheath (monadelphous, with one side open), or form a 9+1 (diadelphous) arrangement (character 48) is also variable within the Detarieae, although the latter condition occurs only in some taxa of the Berlinia clade. Differences in anther morphology and size (characters 49–50) within or between whorls occur mostly in the heteromorphic *Cassia*, *Senna*, and *Chamaecrista*, although *Amherstia* also has dimorphic anthers. In many of the derived Detarieae, anthers are declinate (inverted) in bud, whereas anthers are erect in bud in the basally branching Detarieae lineages and in most other legumes (character 54).

Gynoecium. Carpel development is precocious (initiated with the petals) in almost all Detarieae taxa (character 58). In *Aphanocalyx* (a single petal initiated, only one present at maturity) and in *Brachystegia boehmii* (five petals initiated, none present at maturity), the carpel initiates with the sepals, possibly because the development of petals is suppressed early on. However, in the other species of *Brachystegia* studied (also with five petals initiated and none at maturity), the carpel is concurrent with the petals. In other Caesalpinioideae, the carpel initiates once all other organ primordia have initiated (except in *Labichea*, *Petalostylis*, and *Lecointea*). The carpel margin at inception is sealed in most legumes studied, but open carpels occur sporadically throughout the Caesalpinioideae (character 59). Although most legumes studied have several ovules per ovary, only two are found in *Aphanocalyx*, *Bikinia*, and *Tetraberlinia* and only one is seen in *Macrolobium*, *Sindora klaineana*, and *Dialium* (character 56).

In most Detarieae, except in *Gilbertiodendron* and *Cynometra*, a hypanthium is present (character 61). A hypanthium also occurs in the Cercideae, *Lecointea*, *Ceratonia*, and *Cassia* but is absent in all other taxa surveyed. The ovary is attached to the side of the hypanthium in most Detarieae except *Didelotia*, *Librevillea*, *Barnebydendron*, *Sindora*, and *Tessmannia* (character 63; fig. 3*t*). The ovary is usually stipitate, but it is sessile in *Gilbertiodendron* and *Aphanocalyx* and in various other non-Detarieae studied, where the sessile ovary is attached centrally. A nectariferous disk is present in *Saraca*, *Ceratonia*, and *Dialium* (character 64). A ring meristem (character 65) is present only in some Berlinia clade genera.

Discussion

Phylogenetically Informative Floral Characters

The remarkable range and complex pattern of floral and vegetative modifications found in Detarieae have proved a considerable challenge to the establishment of a widely accepted and clearly circumscribed infratribal classification. Detarieae was long recognized as two distinct tribes (Léonard 1957; Cowan and Polhill 1981*a*, 1981*b*; Breteler 1995) divided primarily on bracteole aestivation, whether valvate or imbricate. Cowan and Polhill (1981*a*, 1981*b*), following the system of Léonard (1957; see also Léonard 1996), subdivided the tribe Amherstieae into four generic groups and tribe Detarieae into six groups. This system was modified slightly to accommodate newly described genera by Polhill (1994), who recognized a single Detarieae s.l., as does Mackinder (2005). These informal generic groupings were based on a combination of characteristics including whether flowers are distichously or spirally arranged, whether bracteoles are free or connate, the number and aestivation pattern of sepals, the number of petals and stamens, whether stamens are free or form a sheath, the number of leaflets, and the presence or absence of punctate glands. Although recent phylogenetic analyses suggest that none of the informal generic groups is monophyletic (Bruneau et al. 2001), several well-supported clades have been described within Detarieae (Wieringa 1999; Wieringa and Gervais 2003; Redden and Herendeen 2006; Fougère-Danezan et al. 2007, 2009; Redden et al. 2010; Mackinder and Pennington 2011). In addition, relationships among caesalpinioid lineages are now better understood (Bruneau et al. 2008; LPWG 2013). These studies, along with the analyses presented here, provide the necessary phylogenetic framework for critically evaluating character evolution in tribe Detarieae and in related caesalpinioid lineages.

Bracteoles, which are generally present and opposite in the Leguminosae, are one of the most distinctive characteristics of the Detarieae. These distinctive bracteoles are generally persistent at anthesis, whereas the presence or absence of bracteoles is much more variable in other legumes, where bracteoles can be present, absent, or caducous or have an arrested development (i.e., "suppressed" sensu Prenner 2004*d*). Massive bracteoles that nearly surround the floral apex in early stages of development (character 7; figs. 3*a*, 4) are a characteristic unique to members of the Detarieae, but these occur only in the Amherstieae clade. In mature bud stage (characters 8–10), these bracteoles completely surround the bud in a subset of the Amherstieae clade that closely corresponds to the Macrolobieae of Breteler (1995; condition also found in *Cynometra*). In other taxa with massive bracteoles in young bud, the bracteoles become relatively smaller as the flower matures and the sepals take over the protective function later in development.

Breteler (1995) redefined the tribes Amherstieae and Detarieae (Cynometreae) as circumscribed by Léonard (1957), basing the new classification on the form, function, and position of the bracteoles. Breteler (1995) described tribe Macrolobieae, with valvate bracteoles that envelope and protect the bud and resemble a calyx, to accommodate all Amherstieae sensu Cowan and Polhill (1981*a*), except *Amherstia*, *Humboldtia*, and *Tamarindus*. He also modified Detarieae (in the narrow sense) to include genera with bracteoles present or not but that when present do not protect the flower prior to anthesis. Although recent phylogenetic analyses (Bruneau et al. 2001, 2008; Redden and Herendeen 2006) do not support Breteler's (1995) tribal division, in part because the genus *Macrolobium* does not group with other Macrolobieae, the presence of valvate bracteoles is a character that diagnoses most but not all of the Amherstieae clade (fig. 4), corresponding to a clade that includes all of Macrolobieae sensu Breteler, plus a few other genera (here *Brownea*, *Afzelia*, and *Neochevalierodendron*). In addition, bracteoles are fused in all Macrolobieae sensu Breteler (1995; plus *Brownea*), except *Tamarindus* and *Amherstia*, whereas they are free in other legumes. Thus, the presence of massive bracteoles that protect the floral apex during development or at maturity and that can be valvate or fused appears to be an independent phylogenetic character that defines mostly inclusive clades within the Detarieae (fig. 4) but that do not correspond entirely to previously described tribes or taxonomic groups within the Detarieae s.l.

Based on her studies of bracteole development, Tucker (2000*a*, 2000*c*, 2001*a*, 2001*b*, 2002*a*) also identified two main groups of Detarieae: (*a*) species with a circular floral apex (fig. 3*f*), associated with bracteoles that remain small during development, and (*b*) species with a crescent- or omega-shaped floral apex with large bracteoles that envelope the bud. The omega-shaped floral apex (fig. 3*e*) is distinctive of the Berlinia clade plus *Macrolobium* (and *Tessmannia* in the resin-producing Detarieae; character 12). Most of these are the taxa with massive, fused, and valvate bracteoles that enclose the bud in early development (fig. 4). These are described by Tucker (2002*a*) as a suite of characters in which the presence of the massive bracteoles just after floral initiation encloses the floral bud and forces the floral apex to become laterally elongated and tapered abaxially and adaxially (omega shaped). However, our phylogenetic analyses suggest that taxa with massive bracteoles in early development do not necessarily have an omega-shaped floral apex, but the converse seems causal, that is, that taxa with an omega-shaped floral apex develop massive bracteoles (except possibly in *Tessmannia*; fig. 4). Thus, it appears that massive bracteoles in early development are a precursor to the massive, valvate, and fused bracteoles that protect the bud at maturity. Interestingly, fused bracteoles are correlated with the presence of distant sepals, except in *Brachystegia* and *Julbernardia*, which have imbricate sepals, and in *Brownea*, which has valvate sepals, suggesting that, indeed, bracteoles and sepals may alternatively assume the protective function in the developing floral bud (see also Ronse de Craene 2008). This protective function of the bracteoles was also noted by Endress (1994) and Prenner (2004*d*), who suggested that, as the first two floral organs, bracteoles may mediate the onset of the sepal whorl (see also Prenner 2004*b*).

Our analyses also suggest that even though highly homoplasious, a suite of other floral features tends to characterize the Detarieae. For example, declinate (inverted) anthers in bud is a character state that defines most of the Detarieae. Even if not seen in all Detarieae, other legumes rarely have declinate anthers in bud (character 54). Likewise, even though a hypanthium is present in some other legumes (Cercideae, Papilionoideae, some Cassieae, and Caesalpinieae), it is rarely absent in Detarieae. In addition, in most Detarieae with a hypanthium (except *Barnebydendron* and some resin-producing Detarieae; see Fougère-Danezan et al. 2009), the gynoecium is adnate to the side of the hypanthium (character 62) rather than being centrally attached—a feature uncommon within the Leguminosae and historically considered a diagnostic feature of the group. Cardoso et al. (2013) also report this unusual character state as derived within two genera in the early-branching papilionoid lineages, *Vataireopsis* and *Amburana*, and G. Prenner (unpublished data) notes its presence in the genus *Angylocalyx*. A compound inflorescence (character 2), either cymose or racemose, also is present in the first-diverging lineages of Detarieae. This distinguishes these species from most other legumes, even though compound inflorescences have been reported from other legumes not studied here (Tucker 1987; Klitgaard 1999; Prenner 2013*b*). Finally, although not studied here, other important diagnostic features for tribe Detarieae include the presence of intrapetiolar stipules and leaf phloem transfer cells; striate, highly modified pollen; and storage cotyledons with thickened walls that accumulate amyloids (Cowan and Polhill 1981*b*; Watson 1981; Breteler 1995; Banks and Klitgaard 2000; Herendeen et al. 2003*a*).

When examined in a phylogenetic framework, most developmental and mature flower characters appear highly homoplasious, clearly illustrating the complex pattern of floral evolution that was noted by Cowan and Polhill (1981*a*) for Detarieae and by Polhill et al. (1981) more generally for Caesalpinioideae. Nonetheless, in addition to the bracteole characters mentioned above, a few other floral developmental characters appear phylogenetically stable as indicated by the RI, CI, and length of each character (app. B). For example, in most Detarieae, carpel initiation occurs at the same time as petal initiation (character 58), whereas it initiates later with the outer stamen whorl in most other legumes. Timing of initiation between the two stamen whorls is also fairly stable and diagnoses certain clades within Detarieae (character 57). A few sepal development characters appear relatively stable in the caesalpinioid lineages studied: the order of sepal initiation (character 17), whether the adaxial sepal is median or off the saggital plane (character 19), and the aestivation pattern (character 20). In addition, fusion of the adaxial sepals to form a four-merous calyx is highly characteristic of the Detarieae (character 22), although there is a reversal to the five free sepals in the Berlinia and Brownea clades (with massive bracteoles) and fused adaxial sepals occur elsewhere in the legumes (table 1). Tucker (2000*a*, 2000*d*, 2002*a*) also described the presence of a ring meristem, a raised meristematic circular ridge that initiates petal and stamen primordia, which is restricted to

Table 1

Species Studied That Deviate from the Legume Ground Plan through Loss, Suppression, or Fusion of Floral Organs within Whorls

Loss	Suppression	Fusion
Sepal whorl (fewer than five sepals):		
Aphanocalyx djumaensis (1)	*Librevillea klainei* (0 or 1)	*Tylosema fassoglensis* (4)
Duparquetia orchidacea (4)	*Didelotia africana* (1)	*Petalostylis labicheoides* (4)
	Bikinia durandii (1 or 2)	All Detarieae (4) studied except *Anthonotha*, *Berlinia grandiflora*, *Brachystegia boehmii*, *Brownea latifolia*, *Gilbertiodendron brachystegioides*, *Gilbertiodendron klainii*, *Isoberlinia angolensis*, *Julbernardia pelligriniana*, *Macrolobium acaciifolium*, *Microberlinia bisulcata*
Petal whorl (fewer than five petals):		
Saraca declinata (0)	*Crudia choussyana* (0)	
Saraca indica (0)	*Afzelia quanzensis* (1)	
Aphanocalyx djumaensis (1)	*Anthonotha* (1)	
Labichea punctata (4)	*Bikinia durandii* (1)	
Dialium guianense (0) (one petal initiated and then suppressed)	*Brachystegia boehmii* (1)	
	Brachystegia glaucescens (1)	
	Librevillea klainei (1)	
	Macrolobium acaciifolium (1)	
	Sindora klaineana (1)	
	Tetraberlinia (1)	
	Amherstia nobilis (3)	
	Barnebydendron riedelii (3)	
	Neochevalierodendron stephanii (3)	
	Paramacrolobium coeruleum (3)	
Stamen whorls (fewer than five stamens per whorl):		
Dialium guianense (2 + 0)	*Tylosema fassoglensis* (2 + 0)	
Labichea punctata (2 + 0)	*Sindora klaineana* (2 + 0) and (3 + 5) staminodes	
Duparquetia orchidacea (4 + 0)	*Anthonotha* (3 + 0)	
Ceratonia siliqua (5 + 0)	*Gilbertiodendron brachystegioides* (3 + 0)	
Saraca indica (7 + 0) from four petal primordia and three abaxial antesepalous stamen primordia; (3 + 0) at initiation	*Gilbertiodendron klainii* (3 + 0)	
Afzelia quanzensis (3 + 4) from (5 + 4)	*Macrolobium acaciifolium* (3 + 0)	
Tamarindus indica (3 + 0) from (5 + 4)	*Paramacrolobium coeruleum* (3 + 0)	
Saraca declinata (4 + 0) from four petal primordia; no stamens develop into stamens; (3 + 0) at initiation	*Plagiosiphon* sp. (3 + 0)	
Petalostylis labicheoides (3 + 0) at maturity from (5 + 0) at initiation (two antesepalous stamens become staminodes)	*Cassia javanica* (3 + 4) plus (2 + 1) staminodes	
	Senna alata (3 + 4) plus (2 + 1) staminodes	
	Didelotia africana (five total, missing ontogenetic data)	

Note. The number of organs per whorl at maturity is given in parentheses. For the stamen whorls, the number of stamens in the antesepalous whorl is given first, followed by the number in the antepetalous whorl.

certain taxa in the Berlinia clade (character 65; fig. 1). The presence of a ring meristem has sometimes been suggested to be correlated with a divergence from the normal pattern and number of petal and stamen initiation (Tucker 2003*c*). However, in our analyses all five taxa with a ring meristem have the typical 10 stamens, and although only one has five petals at maturity, three lose petals because of suppression during development and one because of absence of petal primordia at initiation (table 1). In addition, numerous other caesalpinioid taxa deviate from the typical petal initiation patterns, yet they do not have a ring meristem.

Trends in Floral Evolution in the Caesalpinioid Legumes

As noted by Tucker (1997), phylogenetic analyses provide indirect evidence for floral evolution, which can be compared and combined with direct evidence of possible changes through observations and comparisons of floral development in related lineages of early-diverging legumes. The family is a good model for studying and discussing floral character evolution in angiosperms in general, because legumes are highly diverse morphologically but all have flowers that derive from the five-merous ancestral ground plan typical of many eudicots, and for many legumes floral developmental data are available.

Hierarchical theory. Tucker (1997) noted that because early-occurring changes would disrupt subsequent processes in a developmental cascade, nonterminal changes are likely to be selected against in evolution. Seen as a modification of the biogenetic law (reviewed in Barabé 1990), wherein general characteristics are the first to appear in ontogeny, Tucker's hierarchical theory further suggested that processes that occur early in development would tend to be stable at higher taxonomic levels, in particular at the subfamily level in legumes. As a consequence, Tucker (1997) postulated that within a subfamily, floral symmetry, pattern and timing of organ initiation among whorls (overlapping or not), whether development within whorls is simultaneous or successive, number of whorls, number of organs per whorl, and position of parts within each whorl should be stable. Although these trends appear to generally be consistent in the Papilionoideae and Mimosoideae, as noted above and in Tucker (1997), much more variation is seen within the Caesalpinioideae, in floral symmetry and number of organs per whorl, for example. However, taking into consideration the paraphyletic nature of this latter subfamily and reconsidering floral patterns instead within each distinct lineage, more support is obtained for the idea of stability in these early ontogenetic processes, at least for some lineages, e.g., Cercideae (Tucker 1984*a*, 2002*c*), Cassiineae (Tucker 1996), and Caesalpinieae (Kantz and Tucker 1994; Kantz 1996), although the latter two are also paraphyletic. In other lineages, such as the Detarieae and Dialiinae (here represented by only three species), floral symmetry and number of organs per whorl remain extremely variable (Zimmerman et al. 2013).

At the tribal level, Tucker (1984*a*, 1997) suggested that taxa would be differentiated based on changes that occur early or at midstage development. Examples of midstage processes include corolla aestivation patterns, elongation of organs, fusion among organs, and petal and stamen heteromorphy. Although within the Detarieae, fusion of the two adaxial sepals is a character that is fairly stable or phylogenetically consistent within the tribe and that differentiates it from other caesalpinioid lineages, differences in corolla aestivation patterns, in organ elongation, and in petal and stamen morphologies frequently occur. Thus, in general, the Detarieae, with their highly labile floral developmental patterns in early and midstage development processes, appear to contradict the idea that relatively early ontogenetic processes will be stable at higher taxonomic levels.

Tucker (1984*a*, 1997) also noted that changes that occur late in development are more generally labile and tend to differentiate closely related species. Although our species sampling is too low to fully examine this hypothesis, in *Saraca*, *Brachystegia*, *Microberlinia*, and *Gilbertiodendron*, we have data for two species each, and in *Schotia*, we have studied three species. In these genera, the species are differentiated based on early-stage (e.g., relative timing of petal initiation, number of petals at initiation, stamen order of initiation, position of first stamen initiated within a whorl), midstage (e.g., fusion of adaxial sepals, sepal aestivation, relative size of sepals, differentiation of petals, relative length of stamen whorls, fusion of carpel margins), and late-stage (e.g., anther position in bud) developmental processes. This suggests that, at least in the Detarieae, species differentiation within genera can be caused by changes that occur at all stages of ontogeny. However, since the focus of this study was at the generic level, few characters were scored that generally are used for species-level distinctions, and it may well be that most species distinctions are the result of characters that are expressed late in ontogeny. Certainly this appears to hold for several Papilionoideae (Tucker 1994, 2003*b*; Pennington et al. 2000; Cardoso et al. 2012, 2013; Klitgaard et al. 2013).

Evolution of organ initiation patterns in legumes. Order of organ initiation within a whorl, along with heterochrony, is one of the principal developmental processes that governs floral zygomorphy in legumes (Tucker 1991; Prenner and Klitgaard 2008; also Rudall 2010). Within whorls, organs can initiate simultaneously or in an acropetal manner (Tucker 1997). In the Mimosoideae, organs generally initiate simultaneously, except in the sepal whorl, where initiation is commonly helical (Ramirez-Domenech and Tucker 1988, 1989) or, rarely, reversed unidirectional, starting on the adaxial side (Prenner 2004*c*; Gómez-Acevedo et al. 2007). In Mimosoideae with polyandrous androecia (mainly of Ingeae and Acacieae), individual stamens are frequently formed on a common ring meristem in an acropetal direction and in a more or less irregular pattern (Prenner 2011). In the other two subfamilies, initiation is mostly acropetal, but the patterns are variable. Initiation can be helical (fig. 3*g*), bidirectional (fig. 3*h*), or unidirectional (fig. 3*i*), and which organ within the whorl initiates first may also be variable, at least among lineages. Unidirectionality is a common pattern of organ initiation in the Papilionoideae, where it often is seen in all organ whorls (Tucker 2003*b*, 2003*c*). Unidirectional development also is expressed in earlier-formed organ whorls in the Papilionoideae than, for example, in the Caesalpinioideae, where it tends to be expressed only in the stamen whorls. Unidirectionality is considered an advanced (or highly specialized) expression of zygomorphy because it occurs early in ontogeny (Tucker 1984*b*), in contrast to differential growth of petals and other floral organs, which occurs later in development.

Although unidirectional organ formation is found frequently in Papilionoideae, Klitgaard (1999) and Prenner (2004*d*) noted greater variability in sepal formation, including whorled, bidirectional, and sequential patterns, all of which may be derived from the general helical pattern typical of caesalpinioid legumes. Indeed, all of the Caesalpinioideae studied have a helical pattern of sepal initiation, except members of the Dialiinae clade and *Duparquetia*, which have a bidirectional initiation pattern (Tucker 1998; Prenner and Klitgaard 2008; Zimmerman et al. 2013). In contrast, petal initiation is much more variable in the Caesalpinioideae, with species expressing simultaneous, helical, bidirectional, or unidirectional patterns of initiation, with the development of the first petal either on the abaxial or adaxial sides or at several petal primordia sites simultaneously. No obvious phylogenetic pattern can be discerned regarding the pattern of petal initiation in caesalpinioid legumes, even within clades, in contrast to the relative stability encountered in Mimosoideae (simultaneous) and Papilionoideae (unidirectional). In the Caesalpinioideae, the two stamen whorls tend to express a bidirectional or unidirectional pattern of development, but the pattern can differ between whorls within a species, at least in the Detarieae, and close relatives do not necessarily share the same pattern. The two Cercideae studied have unidirectional stamen initiation in both whorls, as do members of the Cassiineae, but as with the Detarieae, the pattern in the Dialiinae also appears to be extremely variable. However, denser taxon sampling is required to more clearly establish a trend in this clade (Zimmerman et al. 2013). Thus, the stabilized pattern of organ initiation, which characterizes the Mimosoideae and Papilionoideae (but for exceptions see Klitgaard 1999; Prenner 2004*c*, 2004*d*), appears to be derived from an extremely variable genetic base with a highly labile organ initiation pattern.

Loss or suppression of organs. The absence of petals at maturity appears to be highly homoplasious in the Detarieae, as well as in the Dialiinae (Tucker 1998), although it helps to delimit certain clades in the resin-producing Detarieae (Fougère-Danezan et al. 2009). In the Detarieae, the corolla can consist of five well-developed petals, three large plus two rudimentary or absent petals, or one large and four rudimentary or absent petals or there can be complete absence of petals (table 1). As noted by Tucker (1989), it is always the adaxial petal that remains: the losses or suppressions happening first on the abaxial side of the flower. In the taxa sampled, we consider 15 changes in corolla morphology in the Detarieae alone (fig. 4). In the resin-producing Detarieae, represented here by only two species, Fougère-Danezan et al. (2009) noted that the complete loss of petals occurs six times in parallel in the group. Similarly, stamens are also frequently lost during development, leading to flowers with fewer than 10 stamens at maturity (table 1). Functional stamen number (diplostemonous, haplostemonous, less than or more than haplostemonous; character 45; fig. 1) changes 27 times in the small subset of legumes studied.

Absence of petals or stamens at maturity can result either from noninitiation or from suppression during development. The latter is considered a more common process, and although this appears to be the case for the petal whorl, in the stamen whorl, noninitiation is as frequent as suppression during development (table 1). Rudall and Bateman (2004) suggest that loss is a very different process from heterochronic reduction (differential reduction of organs within a whorl) or heterotopic relocation, and Tucker (2000*d*) noted that organ loss through noninitiation can profoundly affect subsequent organogeny. Prenner (2004*d*), for example, suggested that loss of bracteoles in the Papilionoideae could influence the development of the sepal whorl. However, in *Duparquetia*, the absence of one sepal does not affect the development of subsequent whorls (Prenner and Klitgaard 2008), and the authors postulated that stability in the subsequent whorls is the result of the distinct plastochrones observed in sepal development in *Duparquetia*.

In other legumes where development within whorls appears successive (albeit with widely diverse patterns) and where there often is overlap between the development of whorls (e.g., in many Detarieae), it is not clear whether organogeny of subsequent whorls is affected by loss of organs in a preceding whorl. For example, in the five legumes surveyed that have lost petals because of noninitiation of primordia (table 1), four (two *Saraca* species, *Labichea punctata*, and *Dialium guianense*) have fewer than 10 stamens, whereas in *Aphanocalyx* with a single petal primordium, stamen development follows the usual pattern of two alternating whorls of five stamens. In the other 14 taxa with fewer than five petals, absence is due to suppression during development, and of these, five have fewer than 10 stamens at maturity. Thus, stability among whorls does not appear to be related to whether absence is due to noninitiation of primordia or to later suppression during development. Of course, development may be altered in individual species, and this may be due to loss of organs in preceding whorls, such as in *Saraca*, which has no petals at maturity but has a highly unusual development in the stamen whorls, with petal primordia converted to stamens and some stamens developing into staminodes (Tucker 2000*b*; for an example in *Gleditsia* see also Tucker 1991).

Floral zygomorphy. Floral zygomorphy, considered a key feature correlated with higher net diversification rates in various lineages (Endress 1999, 2001; Sargent 2004; Busch and Zachgo 2009; Klitgaard et al. 2013), is of particular interest in the caesalpinioid legumes, where our phylogenies predict multiple switches from actinomorphy (polysymmetry) to zygomorphy (monosymmetry) and vice versa. Floral zygomorphy is expressed in several different forms in this group: through loss or suppression of sepals, petals, or stamens during development (fig. 2; table 1), as noted above, or by differentiation of organs within whorls (heterochrony). In several members of Detarieae, the flowers are radially symmetrical at initiation and remain radially symmetrical at anthesis (e.g., *Microberlinia bisulcata*). In other Detarieae, flowers are radially symmetrical at initiation, but due to either heterochrony in whorls (usually petals or stamens) or suppression of organs, the flowers are zygomorphic at maturity.

Clearly, zygomorphy is not a homologous character state in the Leguminosae. For example, *Tetraberlinia tubmanniana* is radially symmetrical at initiation but is zygomorphic at maturity because of suppression of petals during development to yield one large and four reduced petals. In the two *Gilbertiodendron* species studied, flowers are also radially symmetrical at initiation, and five petals are present at anthesis, but only three stamens are present at maturity because of suppression during development. In yet other taxa with radially symmetrical flowers at initiation, the flowers become zygomorphic because of differential development of organs within one or several of the whorls. In papilionoids with radially symmetrical flowers at anthesis, for example, it is the absence of the typical differential development among organs of the same whorl (from a unidirectional initiation pattern) that results in actinomorphy (Tucker 1999; Pennington et al. 2000; Citerne et al. 2006). More rarely, species that are zygomorphic at initiation may become radially symmetrical at maturity (e.g., *Dialium*, *Schotia*, *Saraca*, *Hymenostegia*, *Neochevalierodendron*) because of changes in the calyx whorl, such as fusion of the two adaxial sepals. In the basally branching lineages of the Amherstieae clade, calyx symmetry mostly changes from zygomorphic at initiation to actinomorphic at maturity, whereas in the Berlinia clade, initially radially symmetrical calyces either remain actinomorphic at maturity or become zygomorphic.

Zygomorphy may also result from changes in color or organ orientation (Specht and Bartlett 2009), but Rudall and Bateman (2004) consider these more subtle heteromorphic differences within whorls less likely to be associated with phylogenetic relationships. Heteromorphy in the Caesalpinioideae is particularly important in the petal whorl, although it also occurs in the stamen whorl. In general, petals tend to be expressed similarly within a flower, although the pattern can be fixed on either the abaxial side or the adaxial side. Regardless, little differentiation in micromorphology of the petals is observed in caesalpinioid legumes contrary to that seen in papilionoids, where there is a dorsiventral patterning of the flower associated with cell form (Ojeda et al. 2009).

Although the taxon sampling is far from complete in the phylogeny presented, taking into account both the uncertainty in phylogenetic reconstruction and different character optimizations, overall our phylogenetic analysis suggests that an actinomorphic calyx, both at initiation and at anthesis, is the derived state in legumes (characters 23, 25; fig. 1; see also Pennington et al. 2000). In contrast, because of the diversity of petal initiation patterns observed in Caesalpinioideae, it is difficult to assess whether radial symmetry or zygomorphy is plesiomorphic in early development. At anthesis, a zygomorphic corolla can be considered the plesiomorphic condition, but this occurs due to several nonhomologous processes (as evaluated by characters 36–39; fig. 1). Thus, as noted by Bello et al. (2007) for the Fabales more generally, floral symmetry varies from whorl to whorl, being actinomorphic in all whorls, zygomorphic in some whorls, or strongly zygomorphic in the entire flower. In Quillajaceae and Surianaceae, actinomorphy is the plesiomorphic condition (Bello et al. 2007), and it likely also is in the Polygalaceae, where flowers tend to be strongly zygomorphic in all whorls but only in the derived tribe Polygaleae (Bello et al. 2012).

Unlike in other groups, where floral zygomorphy has been interpreted as a key innovation and appears to be associated with increased net diversification rates (Endress 1999; Pennington et al. 2000; Sargent 2004; Cardoso et al. 2012, 2013; Klitgaard et al. 2013; but see Kay et al. 2006), zygomorphy in the caesalpinioid legumes is highly labile, is expressed in many different ways at different stages of development, and does not appear to be associated with clades that have higher net diversification rates relative to clades with radially symmetrical flowers. Although this remains to be formally tested, switches from zygomorphy to actinomorphy at anthesis occur eight times in our analyses, with three reversals to zygomorphy (CI 0.09, RI 0.28; character 68; fig. 1). Genera of the Detarieae tend to be quite small (only nine of 82 genera have more than 20 species) with a high proportion of monospecific genera (35%; Mackinder 2005). Of the nine largest genera in the tribe, only three genera from distinct clades have zygomorphic flowers at maturity: *Macrolobium* (80 species), *Anthonotha* (30 species), and *Gilbertiodendron* (26 species). The largest genus, *Cynometra*, with 90 species, has actinomorphic flowers. Similarly, in members of the Dialiinae where zygomorphy is primarily the result of organ loss in flowers, most genera have very few species. However, the pattern is more complex in other caesalpinioid genera studied. For example, in *Chamaecrista*, with ~330 species, all species have highly asymmetric (enantiomorphic) flowers, and in *Senna*, with ~300 species, approximately half the species have asymmetric flowers and half have actinomorphic or symmetric flowers. In the genus *Senna*, Marazzi and Endress (2008) consider extrafloral nectaries a key innovation.

In contrast to most of these relatively species-poor zygomorphic caesalpinioid clades, the species-rich Papilionoideae, with its tendency toward a uniform floral developmental pattern (generally unidirectional organ development in all whorls; fig. 3) and strongly zygomorphic flowers, is suggestive of a group in which floral zygomorphy might be considered a key innovation (Westerkamp 1997; Pennington et al. 2000). Alternatively, the apparent absence of correlation between net diversification rates and floral zygomorphy in the caesalpinioid legumes might be an indication that in the Papilionoideae, higher net diversification rates are a consequence of other characteristics or of a combination of these (e.g., nitrogen fixation). In papilionoids, reversals from zygomorphy to actinomorphy occur only in the basally branching subclades of the Papilionoideae, and changes happen at the generic level (Pennington et al. 2000; Cardoso et al. 2012, 2013; Klitgaard et al. 2013). Pennington et al. (2000) also note that despite apparent multiple origins of actinomorphic flowers in these lineages, actinomorphic flowers do not occur in more derived tribes of Papilionoideae. They suggest that in groups where papilionoid flowers have become more specialized (e.g., in the extensive fusion of petals and stamens), it is more difficult to revert to a nonpapilionoid form during development. This does not seem to be the case for caesalpinioid clades, which are all of similar ages (Bruneau et al. 2008) and appear to have a highly variable genetic base to floral development that could allow reversals to occur relatively easily.

Floral Evolution in Fabales and Early-Diverging Legume Lineages

Recent floral development studies of Quillajaceae, Surianaceae, and Polygalaceae, the other three families in Fabales along with Leguminosae (Doyle et al. 2000; Bello et al. 2009), by Bello et al. (2007, 2010, 2012) revealed several shared floral traits that might prove to be plesiomorphic for the Fabales clade. Among these are the presence of dichasial cymes, actinomorphic flowers with a median adaxial sepal and abaxial petal, contort petal aestivation, free petals that are similar in shape, and free stamens with dorsifixed and longitudinally dehiscent anthers. A comparison with the first-diverging legume lineages allows us to postulate a general ground plan for ancestral legumes from which would be derived the diverse floral morphologies encountered in the family.

Cymose inflorescences occur in a few lineages in the legumes, but particularly in the Dialiinae clade, including *Poeppigia* (Zimmerman et al. 2013), and in the Caesalpinieae (Herendeen et al. 2003*a*). In general, however, the first-diverging legumes have racemose inflorescences, and our phylogenetic analyses suggest that this is the plesiomorphic state for the Leguminosae and that cymose inflorescences have evolved independently in a few lineages. As in the other three Fabales families, most caesalpinioid legumes have free petals and stamens, the latter connate in Polygalaceae. Fusion of sepals and stamens occurs in some caesalpinioid legumes (table 1; Tucker 2003*b*), but these are clearly derived states relative to the general pattern found in most of the Fabales clade (Bello et al. 2012). Many caesalpinioid legumes also have petals that are similar in shape, but in some Cercideae (Tucker 1989, 2002*c*), in Detarieae, in the Caesalpinieae grade (Kantz 1996), and in *Duparquetia* (Prenner and Klitgaard 2008), there is variation in shape and size within the petal whorl. Because of the variable phylogenetic distribution of this character among the first-diverging legume lineages, it is difficult to clearly identify an actinomorphic corolla as the plesiomorphic state within the family, but Bello et al. (2012) note that petal differentiation appears to be derived independently in the species-rich tribe Polygaleae (Polygalaceae) and in many legumes. As in the other Fabales, most caesalpinioid legumes also have dorsifixed and longitudinally dehiscent anthers, a condition that may be plesiomorphic in Fabales. However, contrary to that seen in Quillajaceae, Surianaceae, and Polygalaceae, legumes have a single carpel. Thus, the general pattern at maturity is one of racemose inflorescences with five-merous flowers composed of five free sepals and petals, two whorls of five stamens with dorsifixed and longitudinally dehiscent anthers, and a single carpel.

In terms of floral ontogeny, *Quillaja* and *Suriana* have a calyx that is initiated helically (Bello et al. 2007), and this also occurs in Polygalaceae (Prenner 2004*b*) and in most Caesalpinioideae, except *Duparquetia* and some Dialiinae, where sepals have a bidirectional pattern of initiation (fig. 1). This suggests that a helical pattern of sepal initiation is likely the plesiomorphic state for the Fabales. The position of the median sepal (and petal) is also a characteristic that is relatively fixed in legume lineages. Most caesalpinioid legumes have a median sepal that is on the abaxial side, whereas in Polygalaceae, Quillajaceae, and Surianaceae, the median sepal is on the adaxial side (Bello et al. 2007, 2012). This clearly indicates that a median sepal on the abaxial side is a synapomorphy for the Leguminosae and that the condition found in the Mimosoideae and sporadically in some caesalpinioid lineages (e.g., *Ceratonia*), where the median sepal is on the adaxial side, is derived within the family.

In Quillajaceae and Surianaceae, petals are initiated in a helical pattern (Bello et al. 2007); they may also be helical in Polygalaceae (Prenner 2004*b*), but the pattern is more complex with rapid initiation of petals starting on the abaxial side (Bello et al. 2010). In the Caesalpinioideae, although helical, simultaneous, bidirectional, and unidirectional patterns of petal initiation were observed (fig. 1), the unidirectional pattern appears to be the plesiomorphic condition and may be a synapomorphy for the family (see also Tucker 2002*c*).

Stamen initiation in *Quillaja* is unidirectional and asymmetric, and in Suriancaeae it is simultaneous in each whorl (Bello et al. 2007). In Polgalacaeae the initiation is almost simultaneous but likely occurs in a helical manner in both whorls of four stamens (Prenner 2004*b*). In the caesalpinioid legumes, stamen development mostly occurs in two whorls, with the unidirectional pattern being the most common and plesiomorphic pattern for both whorls. Given the complexity of stamen development in Fabales, it is not clear whether the unidirectional pattern of stamen initiation would be a synapomorphy for the Leguminosae or the plesiomorphic state in the Fabales as a whole. Reduction in number of stamens from the ancestral two whorls of five has occurred sporadically in several genera of Detarieae, as well as in several other Caesalpinioideae (fig. 1; table 1). In the legumes, stamen initiation occurs after all petals have initiated. This successive pattern of initiation is similar to that found in Surianaceae, Quillajaceae, and Polygalaceae, and this is likely the plesiomorphic state for the family Leguminosae.

General Conclusion

Within the legumes, variation in patterns of floral development is at its maximum in the Caesalpinioideae, reflecting the paraphyletic nature of this subfamily. In the other two subfamilies, floral evolution appears more clearly channeled, as it is within each of the Caesalpinioideae clades. Nevertheless, certain clades of Caesalpinioideae, in particular, the Detarieae and Dialiinae, express more diverse patterns of floral development, with floral variation due to fusion and suppression of organs, heterochrony, and homeosis. Notably, this broad floral developmental ground plan typical of these two clades does not appear to be associated with increased speciation and diversification relative to other clades with more canalized developmental patterns. Floral patterns that are fixed in different clades as a result of different functional constraints appear to be the case in monocots (Rudall and Bateman 2004), but as noted by Jaramillo et al. (2004) for other taxa, developmental processes can be quite labile, and similar ontogenetic pathways can give rise to homoplasious structures. Evolution of floral form corresponding to shifts in organogenesis, organ identity, and floral patterning may be the result of changes in expression or regulation of essential developmental genes (Specht and Bartlett 2009). Thus, certain ontogenetic characters seem to be good phylogenetic characters for diagnosing clades at different taxonomic levels in the legumes, but other developmental differences can be highly homoplasious, whether they occur early or late in ontogeny.

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Appendix A

Sampling of Species for Floral Ontogenetic, Morphological, and Molecular Analysis of Detarieae and Related Genera

Taxa denoted with an asterisk are those where two different species were combined in the final combined morphological and molecular matrix. For the ontogenetic and mature flower data, literature sources and specimen data for SEM and floral dissections (in italics) are noted. For the molecular data, the GenBank accession number, followed by specimen voucher information (in italics), is noted, starting with *trnL* intron sequences, then *trnL-F* spacer sequences and *matK* sequences. The original study where the data were generated is indicated by a superscript: a = Bruneau et al. (2001); b = Bruneau et al. (2008); c = Fougère-Danezan et al. (2003); d = Herendeen et al. (2003*b*); e = Luckow et al. (2003); f = Pennington et al. (2001); g = Gervais and Bruneau (2002); h = Miller et al. (2003); i = Martin F. Wojciechowski, Arizona State University, unpublished sequence.

Detarieae. ***Afzelia quanzensis* Welw.**: Tucker (2002*b*), Herendeen et al. (2003*a*), *Swynnerton 57 & 144* (*BM*), *Azancot de Menezes 1256* (*BM*); AF365130 *Goyder 3727* (*K*)[a]; KF794164 *Goyder 3727* (*K*); EU361848 *Goyder 3727* (*K*)[b]. ***Amherstia nobilis* Wall.**: Tucker (2000*c*), Herendeen et al. (2003*a*), Fougère-Danezan et al. (2009), *Nielson Jones s.n.* (*BM*), *Kerr s.n.* (*BM*); AF365210 *Baker 490* (*KEP*)[a]; AF549295 *Baker 490* (*KEP*)[c]; EU361849 *Baker 490* (*KEP*)[b]. ***Anthonotha crassifolia**** (as *Macrolobium crassifolium* (Baillon) Léon. in Tucker 2002*b*): Tucker (2002*b*), *Deighton 4682 & 5425* (*K*); (no molecular data). ***Anthonotha macrophylla* P. Beauv.***: (no morphological data); AF365234 *Wieringa 2996* (*WAG*)[a]; KF794165 *Wieringa 2996* (*WAG*); EU361853 *Wieringa 2996* (*WAG*)[b]. ***Aphanocalyx djumaensis* (D. Wild.) J. Léon.**: Tucker (2000*a*), Herendeen et al. (2003*a*), *Bosch 630* (*K*), *Eward 4562* (*K*); AF365249 *Breteler 13056* (*WAG*)[a]; KF794166 *Breteler 13056* (*WAG*); EU361856 *Breteler 13056* (*WAG*)[b]. ***Barnebydendron riedelii* (Tul.) J. H. Kirkbr.** (as *Phyllocarpus septentrionalis* Donn Smith in Tucker 2002*b*): Tucker (2002*b*), Herendeen et al. (2003*a*), Fougère-Danezan et al. (2009), *Lewis 1224* (*K*); AF365209 *Kew 1953–35501, Brammall* (*K*)[a]; AY958491 *Kew 1953–35501, Brammall* (*K*)[c]; EU361868 *Kew 1953–35501, Brammall* (*K*)[b]. ***Berlinia grandiflora* (Vahl.) Hutch. & Dalz.**: Tucker (2002*b*), *Robertson 106* (*BM*), *Le Testu 7331* (*BM*), *Kitson 1909* (*BM*); EU361748 *Jongkind 2516A* (*WAG*)[b]; KF794167 *Jongkind 2516A* (*WAG*); EU361882 *Jongkind 2516A* (*WAG*)[b]. ***Bikinia durandii* (F. Hallé & Normand) Wieringa** (as *Monopetalanthus durandii* F. Hallé & Normand in Tucker 2000*a*): Tucker (2000*a*), Wieringa (1999); AY116896 *Wieringa 3021* (*WAG*)[g]; KF794168 *Wieringa 3021* (*WAG*); EU361883 *Wieringa 3021* (*WAG*)[b]. ***Brachystegia boehmii* Taub.**: Tucker (2000*a*), *Jackson 32* (*BM*), *Swynnerton 257* (*BM*), *Schlieben 5575* (*BM*); EU361749 *Gerreau 3054* (*NY*)[b]; KF794169 *Gerreau 3054* (*NY*); EU361886 *Gerreau 3054* (*NY*)[b]. ***Brachystegia glaucescens* Burtt, Davy & Hutch.**: Tucker (2000*a*), *Corby 1377* (*BM*), *Hornby 3326* (*K*); KF794160 *Mackinder 33* (*K*); KF794170 *Mackinder 33* (*K*); KF794161 *Mackinder 33* (*K*). ***Brownea latifolia* Jacq.** (syn. *B. coccinea* Jacq. ssp. *capitella*): Tucker (2000*c*), Herendeen et al. (2003*a*), *Howard 18785* (*BM*), *Velasquez 322* (*BM*), *Riley 60* (*BM*); EU361753 *Steyermark 88845* (*NY*)[b]; KF794171 *Steyermark 88845* (*NY*); KF794162 *Steyermark 8845* (*NY*). ***Crudia choussyana* Standl.**: Tucker (2001*b*), *Hughes 1249* (*K*); EU361788 *Hughes 1249* (*FHO*)[b]; KF794174 *Hughes 1249* (*FHO*); EU361921 *Hughes 1249* (*FHO*)[b]. ***Cynometra webberi* Bak. F.***: Tucker (2001*a*), *Taylor 1888* (*BM*), *Graham 2168* (*BM*); (no molecular data). ***Cynometra* sp.***: (no morphological data); EU361791 *Herendeen 16-XII-97–1* (*US*)[b]; KF794176 *Herendeen 16-XII-97–1* (*US*); EU361924 *Herendeen 16-XII-97–1* (*US*)[b]. ***Didelotia africana* Baill.**: Tucker (2000*a*), *Talbot 1461* (*K*), *Letouzey 10159* (*K*); AF365260 *Breteler 14374* (*WAG*)[a]; KF794179 *Breteler 14374* (*WAG*); EU361933 *Breteler 12529* (*WAG*)[b]. ***Gilbertiodendron brachystegioides* (Harms) J. Léon.**: Tucker (2002*b*), Herendeen et al. (2003*a*), *de Wilde 1306* (*K*), *Mildbraed 7777* (*K*); AF365238 *Breteler 12862* (*WAG*)[a]; KF794182 *Breteler 12862* (*WAG*); EU361954 *Breteler 12862* (*WAG*)[b]. ***Gilbertiodendron klainii* (Pierre ex Pellegr.) J. Léon.**: Tucker (2002*b*), *BKT* (*P*); EU361811 *Breteler 12283* (*WAG*)[b]; KF794183 *Breteler 12283* (*WAG*); EU361955 *Breteler 12283* (*WAG*)[b]. *Hymenostegia klainei* Pierre ex Pellegr.: Tucker (2002*a*), Herendeen et al. (2003*a*), *Klaine 69 & 264* (*K*), *Morel 150* (*K*); AF365141 *Wieringa 2575* (*WAG*)[a]; KF794184 *Wieringa 2575* (*WAG*); EU361976 *Wieringa 2575* (*WAG*)[b]. ***Isoberlinia angolensis* (Benth.) Hoye & Brenan***: Tucker (2002*a*), *Raimundo 1059* (*BM*), *Gossweiler 9507* (*BM*), *Hoyle 815* (*BM*), *LeWalle 528* (*BM*), *Stol 1954* (*BM*), *Buchanan 396* (*BM*); (no molecular data). ***Isoberlinia scheffleri* (Harms) Greenway***: (no morphological data); AF365221 *Herendeen 16-XII-97–2* (*US*)[a]; KF794185 *Herendeen 16-XII-97–2* (*US*); EU361983 *Herendeen 16-XII-97–2* (*US*)[b]. ***Julbernardia pelligriniana* Troupin**: Tucker (2003*a*), Herendeen et al. (2003*a*), *Le Testu 7482 & 9354* (*BM*); AF365266 *Leal 40* (*WAG*)[a]; KF794186 *Leal 40* (*WAG*); EU361986 *Leal 40* (*WAG*)[b]. ***Librevillea klainei* (Pierre ex Harms) Hoyle**: Tucker (2000*a*), *Klaine 7 & 3260* (*K*); AF365262 *van Bergen 423* (*WAG*)[a]; KF794187 *van Bergen 423* (*WAG*); EU361993 *Wieringa 2554* (*WAG*)[b]. ***Macrolobium acaciifolium* (Benth.) Benth.**: Tucker (2002*b*), *Lewis 1676* (*K*); EU361820 *Korning 47735* (*AAU*)[b]; KF794188 *Korning 47735* (*AAU*); KF794163 *Korning 47735* (*AAU*). ***Microberlinia bisulcata* A. Chev.**: Tucker (2002*a*), *Brenan 9319* (*K*), *Binuyo 35488* (*K*); AF365223 *Rickson sn* (*OSC*)[a]; KF794189 *Rickson sn* (*OSC*); EU362002 *Rickson s.n.* (*OSC*)[b]. ***Microberlinia brazzavillensis* A. Chev.**: Tucker (2002*a*), Herendeen et al. (2003*a*), *Service Forestier 2* (*K*), *Sita 696* (*K*); AF365222 *Wieringa 2516* (*WAG*)[a]; KF794190 *Wieringa 2516* (*WAG*); EU362003 *Wieringa 2516* (*WAG*)[b]. ***Neochevalierodendron stephanii* (A. Chev.) J. Léon.**: Tucker (2002*b*), Herendeen et al. (2003*a*), *Le Testu 5754, 7080 & 7328* (*BM*); AF365151 *Breteler 13262* (*WAG*)[a]; KF794192 *Breteler 13262* (*WAG*); EU362006 *Breteler 13262* (*WAG*)[b]. ***Paramacrolobium coeruleum* (Taub.) J. Léon.**: Tucker (2002*b*), Herendeen et al. (2003*a*), *Donald 2365* (*K*), *Samdi 483* (*K*), *Small 27* (*K*): AF365242 *Breteler 13350* (*WAG*)[a]; KF794193 *Breteler 13350* (*WAG*); EU362017 *Herendeen 11-XII-97–1* (*US*)[b]. ***Plagiosiphon*** **sp.** (as *Cynometra* sp. in Tucker 2001*a* based on *Breteler 12828* (*WAG*)): Tucker (2001*a*); EU361789 *Breteler 12828* (*WAG*)[b]; KF794175 *Breteler 12828* (*WAG*); EU361926 *Breteler 12828* (*WAG*)[b]. ***Saraca declinata*** **Miq.**: Tucker (2000*b*), Herendeen et al. (2003*a*), *Kerr 10072 & 15843* (*BM*), *Winkler 3199* (*BM*), *Lakschakara 582* (*BM*); EU361831 *Manos 1417* (*DUKE*)[b]; KF794196 *Manos 1417* (*DUKE*); EU362033 *Manos 1417* (*DUKE*)[b]. ***Saraca indica*** **L.**: Tucker (2000*b*), *Kerr 3515, 18217 & s.n.* (*BM*); EU361832 *Rickson s.n.* (*OSC*)[b]; KF794197 *Rickson s.n.* (*OSC*); EU362034, *Rickson s.n.* (*OSC*)[b]. ***Schotia afra*** **Thunb.**: Tucker (2001*a*), Herendeen et al. (2003*a*), Fougère-Danezan et al. (2009), *Gilliand A130* (*BM*); AF365122 *Hodgkiss 1* (*BOL*)[a]; AY958527 *Hodgkiss 1* (*BOL*)[c]; EU362037 *Hodgkiss 1* (*BOL*)[b]. ***Schotia brachypetala*** **Sond.**: Tucker (2001*a*), Herendeen et al. (2003*a*, 2003*b*), Fougère-Danezan et al. (2009), *Codd 4442* (*BM*), *Chase 1602* (*BM*), *Rudalis 686* (*BM*), *Macowan 70* (*BM*); AF365123 *Kew 1971–1851, Chase 3096* (*K*)[a]; AY232752 *Kew 1971–1851, Chase 3096* (*K*)[d]; EU362038 *Kew 1971–1851, Chase 3096* (*K*)[b]. ***Schotia latifolia*** **Jacq.**: Tucker (2001*a*), Herendeen et al. (2003*a*), Fougère-Danezan et al. (2009), *Macowan 77* (*BM*), *Mahon s.n.* (*BM*); AF365124 *Kew 1948–52201, Bruneau s.n. 26/06/1995*[a]; AY958528 *Kew 1948–52201, Bruneau s.n. 26/06/1995*[c]; EU362039 *Kew 1948–52201, Bruneau s.n. 26/06/1995*[b]. ***Sindora klaineana*** **Pierre ex Pellegr.**: Tucker (2003*a*), Fougère-Danezan et al. (2009), *Klaine 22* (*K*); AY187228 *Breteler 14415* (*WAG*)[c]; AF549284 *Breteler 14415* (*WAG*)[c]; EU362045 *Breteler 14415* (*WAG*)[b]. ***Tamarindus indica*** **L.**: Tucker (2000*c*), Herendeen et al. (2003*a*), *Burtt 773* (*BM*), *Chase 4723* (*BM*), *Robson 982* (*BM*), *Sousa 12355* (*BM*), *D'Aray 230B* (*BM*); AF365206 *JBM 2138–76, Archambault s.n. 8/06/1999*[a]; KF794199 *JBM 2138–76, Archambault s.n. 8/06/1999*; EU362056 *JBM 2138–76, Archambault s.n. 8/06/1999*[b]; ***Tessmannia africana*** **Harms**: Tucker (2002*a*), Herendeen et al. (2003*a*), Fougère-Danezan et al. (2009), *Le Testu 7476, 9391 & 9591* (*BM*), *Louis 14607* (*BM*), *Tisserent 2082* (*BM*); AF365191 *Breteler 12275* (*WAG*)[a]; AY958532 *Breteler 12275* (*WAG*)[c]; EU362057 *Breteler 12275* (*WAG*)[b]. ***Tetraberlinia tubmanniana*** **J. Léon.***: Tucker (2002*b*), *Bus 1829* (*K*), *de Wilde 3836* (*K*); (no molecular data). ***Tetraberlinia polyphylla*** **(Harms) J. Léon. ex Voorh.***: (no morphological data); AF365230 *Wieringa 3151* (*WAG*)[a]; KF794200 *Wieringa 3151* (*WAG*); EU362061 *Wieringa 3151* (*WAG*)[b].

Cassieae. ***Cassia javanica*** **L.**: Tucker (1996), *Owens K54084* (*K*), *Sarawak Forest Dept. S3750* (*K*); EU361782 *Fougère 6* (*MT*)[b]; KF794173 *Fougère 6* (*MT*); EU361910 *Fougère 6* (*MT*)[b]. ***Chamaecrista nictitans*** **(L.) Moench**: Tucker (1996), Herendeen et al. (2003*b*), *Sousa 12019 & 12197* (*BM*), *Chorley 57* (*BM*); AF365093 *Klitgaard 654* (*K*)[a]; AY232767 *Klitgaard 654* (*K*)[d]; EU361914 *Klitgaard 654* (*K*)[b]. ***Dialium guianense*** **(Aubl.) Sandw.**: Tucker (1998), Fougère-Danezan et al. (2009), *Espinoza 130* (*BM*), *Ducke 10570* (*BM*), *Villa 530* (*BM*); AF365079 *Klitgaard 686* (*K*)[a]; KF794178 *Klitgaard 686* (*K*); EU361930 *Klitgaard 686* (*K*)[b]. ***Duparquetia orchidacea*** **Baill.**: Herendeen et al. (2003*a*), Prenner and Klitgaard (2008), *Coombe 177* (*K*), *Polhill 5217* (*K*), *Breteler 12253* (*WAG*); EU361800 *Bruneau 1098* (*K*)[b]; KF794180 *Bruneau 1098* (*K*); EU361937 *Bruneau 1098* (*K*)[b]; ***Labichea punctata*** **Benth.**: Tucker (1998), *Pritzel 593* (*K*), *Birchwolfe s.n.* (*K*), *Morrison 321 & 20156* (*K*); AF365076 *Nordetam 703* (*US*)[a]; no *trnL-F* sequence available; EU361989 *Nordentam 703* (*US*)[b]. ***Petalostylis labicheoides*** **R. Brown**: Tucker (1998), Herendeen et al. (2003*b*), *Lambert 595* (*K*), *Ashby 3880* (*BM*); AF365077 *Coveny 12062* (*MO*)[a]; KF794195 *Coveny 12062* (*MO*); EU362024 *Coveny 12062* (*MO*)[b]. ***Senna alata*** **(L.) Roxb.**: Tucker (1996), Herendeen et al. (2003*b*), *Burnham 43* (*BM*), *Atwood 2031* (*BM*); AF365091 *Bruneau 1076* (*K*)[a]; AY232769 *Bruneau 1076* (*K*)[d]; EU362042 *Bruneau 1076* (*K*)[b].

Caesalpinieae. ***Ceratonia siliqua*** **L.**: Tucker (1992), Kantz (1996), Herendeen et al. (2003*b*), *Franquinho 40 & 41* (*BM*); AF365075 *Wieringa 3341* (*WAG*)[a]; AY232764 *Wieringa 3341* (*WAG*)[d]; EU361911 *Wieringa 3341* (*WAG*)[b].

Cercideae. ***Cercis canadensis*** **L.**: Tucker (2002*c*), Herendeen et al. (2003*b*), Fougère-Danezan et al. (2009), *Raven 26927* (*BM*), *Spongberg & Boufford 1780* (*BM*), *Seward* (*BM*); AF365054 *JBM 1397–91, Gervais s.n. 07/7/1997*[a]; AY232755 *JBM 1397–91, Gervais s.n. 07/7/1997*[d]; EU361912 *JBM 1397–91, Gervais s.n. 07/7/1997*[b]. ***Tylosema fassoglensis*** **(Kotschy ex Schweinf.) Torre & Hillc.**: Tucker (1984*b*), *Jackson 1063* (*BM*), *Migoed 1925–6* (*BM*), *Chase 5149* (*BM*), *Nolde 170* (*BM*); EU361743 *Herendeen 21-XII-97–6* (*US*)[b]; KF794201 *Herendeen 21-XII-97–6* (*US*); EU361874 *Herendeen 21-XII-97–6* (*US*)[b].

Mimosoideae. ***Leucaena leucocephala*** **(Lam.) de Wit**: Tucker (1989), *Adams 8300* (*BM*), *White[f]oord 7305* (*BM*), *Brunt 2083* (*BM*); AF278493 *Luckow 3270* (*BH*)[e]; AF278493 *Luckow 3270* (*BH*)[e]; AF523094 *Miller 531* (*CANB*)[h].

Papilionoideae. ***Lecointea hatschbachii*** **Barneby***: Mansano et al. (2002), *Hatschbach 51288* (*K*); (no molecular data); ***Lecointea peruviana*** **Standl.***: (no morphological data); AF365039 *Klitgaard 679* (*K*)[a]; AY232779 *Klitgaard 679* (*K*)[d]; EU361990 *Klitgaard 679* (*K*)[b]. ***Myroxylon balsamum*** **(L.) Harms**: Tucker (1993), *Klitgaard 204* (*K*); AF309850 *Pennington 647* (*E*)[f]; KF794191 *179350* (*ASU*); FJ151488 *Martinez 4051* (*ASU*)[i].

Appendix B

Floral Morphological and Ontogenetic Characters and Character States Scored for Detarieae and Related Genera

Consistency index (CI), retention index (RI), and length (L) values are those obtained from the parsimony optimization onto each of the 10 most parsimonious trees (variation between trees is noted), and if different, values for optimization onto the Bayesian majority-rule consensus are noted (in brackets).

1. *Inflorescence structure: indeterminate—raceme, spike, head, panicle (0); determinate—cymose (1); flowers solitary (2).* A diversity of inflorescence types is present in the Leguminosae, with several intermediate states observed. It is sometimes difficult to distinguish among the numerous types of racemose inflorescences. However, most legumes can be clearly classified as having either an indeterminate racemose type of inflorescence or a determinate cymose inflorescence (Weberling 1992). The majority of Leguminosae are racemose (Weberling 1989), with acropetal, successive order of flower initiation and development (Tucker

2003*b*). In the Mimosoideae, flower development is synchronous. Cymose inflorescences are more common in the Caesalpinioideae than in the other two subfamilies. CI 0.66, RI 0, L 3.

2. *Inflorescence structure: simple* (*0*); *compound* (*1*). Inflorescences can be simple or branched (compound with first- or second-order branches). However, this character can vary within an individual. We thus are scoring the ability to produce compound inflorescences. Taxa with solitary flowers are scored as inapplicable. CI 0.16, RI 0.72, L 6.

3. *Arrangement of bracts and subtended flowers: helical* (*0*); *distichous* (*1*). Most Leguminosae have a helical arrangement of bracts, but in a few taxa the bracts are arranged distichously. CI 0.20, RI 0.33, L 5.

4. *Pedicel: present* (*0*); *absent* (*1*). The presence or absence of a pedicel is difficult to assess in some Leguminosae. In this study a pedicel has been defined as an elongate, narrow structure that occurs below the hypanthium or receptacle. A pedicel can be jointed or not. If jointed, then the remaining portion after flower dehiscence is considered a prolongation of the inflorescence axis and not a pedicel per se. None of the Detarieae taxa included here has a jointed pedicel, but they occur in other Caesalpinioideae (e.g., *Caesalpinia*). CI 0.16, RI 0.16, L 6.

5. *Bracteoles: present* (*0*); *absent* (*1*). Two bracteoles preceding each flower are usually present in the Leguminosae. These can occur in different positions along the pedicel or at the base of the flower. They may be large, showy, and persistent (as in some Detarieae), or they may be small, inconspicuous, and sometimes caducous. In taxa with cymose inflorescences, the younger flowers form in the axils of two bracteoles that are located at the base of the terminal flower. For this reason, it appears that the central flower lacks bracteoles once the lateral flowers have formed (Tucker 2003*b*; Prenner et al. 2009). CI 0.50, RI 0, L 2.

6. *Bracteoles: opposite* (*0*); *alternate* (*1*). Bracteoles can be opposite or alternate, but in the taxa scored here the bracteoles are always opposite. Uninformative character; alternate bracteoles are present only in *Petalostylis labicheoides*. L 1.

7. *Young bracteoles: small and not surrounding floral apex* (*0*); *massive and nearly surrounding floral apex* (*1*). At early stage of flower development, before sepal initiation, most Leguminosae have small bracteoles with narrow bases that cover at most ~20% of the circumference of the floral apex (Tucker 2000*a*). In contrast, in some Detarieae the bracteoles are large, encircle ~90% of the circumference of the floral apex, and are in contact adaxially (Tucker 2002*a*). Figure 3*a*, 3*b*. CI 0.50, RI 0.93, L 2.

8. *Bracteoles in mature bud: not directly enclosing the bud* (*0*); *enclosing the bud* (*1*). In flower buds that contain fully differentiated floral organs, before anthesis, either bracteoles enclose the bud or the bracteoles are small and do not enclose the flower. CI 0.50, RI 0.95, L 2 [CI 0.33, RI 0.90, L 3].

9. *Bracteoles in mature bud: imbricate* (*0*); *valvate* (*1*); *distant* (*2*). This character was recorded at the same stage of development as character 8. Taxa with small bracteoles that do not overlap were scored as distant. Figure 3*c*, 3*d*. CI 0.50, RI 0.90, L 4.

10. *Bracteoles in mature bud: free* (*0*); *fused* (*1*). In most taxa with valvate bracteoles, the bracteoles are fused, at least at the base. In *Brownea* the bracteoles are fused for up to two-thirds of the length. CI 0.50, RI 0.94, L 2 [CI 1.0, RI 1.0, L 1].

11. *Bracteoles in flowers at anthesis: persistent in flower* (*0*); *absent, which includes suppressed or resorbed after initiation and caducous* (*1*). In several taxa bracteoles are caducous and absent at anthesis. Taxa that lack bracteoles at initiation (see character 5) were scored as inapplicable for character 11. CI 0.12, RI 0.58, L 8 [CI 0.14, RI 0.64, L 7].

12. *Shape of floral primordium: circular* (*0*); *omega shaped* (*1*). Following bracteole initiation but before sepal initiation, the floral apex can be circular and dome shaped. Alternatively, Tucker (2000*a*, 2001*a*) has noted that several Detarieae have a postbracteole floral meristem that is elongate in the radial plane and narrow in the tangential plane. Figure 3*e*, 3*f*. CI 0.33, RI 0.85, L 3.

13. *Sexual expression: bisexual* (*0*); *unisexual* (*1*). Here we distinguish between taxa that consistently produce perfect (hermaphroditic) flowers and those that can produce unisexual flowers (pistillate and staminate). This character has been circumscribed only to distinguish perfect flowers from all other possible states. It does not take into account the distribution of the unisexual flowers within inflorescences or between individuals (monoecious, dioecious, andromonoecious, polygamodioceous, etc.), which can be variable within species and occur through different developmental pathways. In all Caesalpinioideae with unisexual flowers examined, floral buds are bisexual at first, but later in development either the stamens or the carpel is suppressed (Tucker 2003*b*). This character is uninformative in this data set, but *Anthonotha crassifolia* has both bisexual and unisexual flowers, as do *Ceratonia siliqua* and *Leucaena leucocephala*.

14. *Number of sepals initiated: five* (*0*); *fewer than five* (*1*); *more than five* (*2*). In legumes usually five sepals are initiated. Even in taxa that display four sepals or fewer in the mature flower, five sepals generally initiate. However, in *Aphanocalyx djuamensis* (Detarieae) only one sepal is initiated, and in *Duparquetia*, only four are initiated. CI 0.50, RI 0, L 2.

15. *Sepal suppression or resorption during differentiation: all sepals initiate and develop* (*0*); *one, two, three, four, or five sepals are suppressed after initiation* (*1*). In certain taxa, although five sepals initiate, not all sepals differentiate as distinct organs to reach flower maturity. Rudiments may or may not be present. In taxa with sepal suppression, the number of fully differentiated sepals may vary at maturity. For this reason the suppression of one to four sepals was included as a single state. In the taxa examined with sepal suppression, usually four or five of the sepals are suppressed after initiation. CI 0.33, RI 0.33, L 3.

16. *Timing of sepal initiation: all successively* (*0*); *one or more delayed relative to the next whorl* (*1*). In most taxa, organ whorls initiate in an acropetal fashion, without overlap among whorls. In a few taxa, one or more of the sepals initiate later, with the petals or one of the two stamen whorls. CI 0.20, RI 0.20, L 5.

17. *Sepal order of initiation: helical* (*0*); *bidirectional* (*1*); *unidirectional* (*2*). This character captures the major differences in patterns of sepal initiation that are found in the Leguminosae. In the Caesalpinioideae, all three patterns of sepal initiation are

possible, while Mimosoideae have mainly helical or simultaneous (not observed here) order of sepal initiation, and the unidirectional pattern is prevalent in subfamily Papilionoideae. Figure 3*g*–3*i*. CI 0.50, RI 0.60, L 4.

18. *Median* (*sagittal*) *sepal position: abaxial* (*0*)*; adaxial* (*1*). In legumes, the median sepal can initiate in the abaxial or adaxial position. This character differentiates members of the Mimosoideae that have an adaxial median sepal from the Papilionoideae and most Caesalpinioideae, which have the median sepal on the abaxial side. CI 0.50, RI 0, L 2.

19. *Position of abaxial* (*or adaxial*) *sepal at initiation: median* (*0*)*; nonmedian* (*1*). The median sepal (generally abaxial in Caesalpinioideae and Papilioinoideae and adaxial in Mimosoideae) frequently is in the median plane, but it can initiate in a nonmedian position. Figure 3*j*. CI 0.09–0.10, RI 0.50–0.55, L 10–11 [CI 0.08, RI 0.45, L 12].

20. *Sepals at initiation: imbricate* (*0*)*; valvate* (*1*)*; distant* (*2*). Sepal imbrication patterns were scored at two stages: at the end of early-stage development when all organs are present and sepals are well developed (character 20) and in mature buds just prior to anthesis (character 21). At the end of early stage, sepals may be imbricate (overlapping) or valvate (touching), or they may not touch at all (distant or open). CI 0.14, RI 0.55, L 14 [CI 0.12, RI 0.48, L 16].

21. *Sepals at maturity: imbricate* (*0*)*; valvate* (*1*)*; distant* (*2*)*; imbricate with two sepals overlapping* (*3*)*; cuculate* (*4*). In mature buds, the sepal imbrication pattern may be more complex. Sepals can be imbricate but with both edges of the lateral sepals inside the abaxial and adaxial sepals. In a few legumes, one sepal is much larger and completely covers the bud (cuculate; e.g., *Duparquetia*). CI 0.18, RI 0.14, L 22.

22. *Two adaxial sepals at maturity: free* (*0*)*; fused to appear as one* (*1*). In several Detarieae, the adaxial sepals fuse during early development to form a tetramerous calyx. In these taxa, the fusion is permanent and thought to occur through intercalary growth of the receptacle, rather than through edge-to-edge fusion of the two sepals, which may be permanent or temporary (Tucker 2003*b*). CI 0.14, RI 0.68, L 7 [CI 0.12, RI 0.63, L 8].

23. *Calyx symmetry at end of early-stage development: radial* (*0*)*; zygomorphic* (*1*). Calyx symmetry was evaluated at the end of early-stage development when all organs are present (character 23) and also at maturity (at anthesis, character 25). In some taxa, one state of calyx symmetry was observed at initiation, and a different state was seen at maturity. CI 0.10, RI 0.40, L 10 [CI 0.09, RI 0.33, L 11].

24. *Sepals: sepaloid, green* (*0*)*; petaloid* (*1*). The calyx and corolla may be differentiated in both color and texture, or the sepals can be similar to the petals by being colored or membranaceous. CI 0.08–0.09, RI 0.38–0.44, L 11–12 [CI 0.07, RI 0.33, L 13].

25. *Calyx symmetry at maturity: radial* (*0*)*; zygomorphic* (*1*). Radial symmetry occurs early in several Caesalpinioideae and persists to maturity. However, in others, the flowers become asymmetrical through differential organ development. The reverse may also occur, where an initially asymmetrical calyx is actinomorphic at maturity. CI 0.09–0.10, RI 0.52–0.57, L 10–11 [CI 0.07, RI 0.42, L 13].

26. *Calyx base: symmetrical* (*0*)*; gibbous* (*1*). In taxa with a calyx tube, the base may be asymmetrical (gibbous). In this data set, only *Cercis canadensis* has a gibbous calyx base (autapomorphic). L 1.

27. *Number of sepals at maturity: five* (*0*)*; four* (*1*)*; two* (*2*)*; one* (*3*)*; variable* (*4*)*; none* (*5*). At maturity, modifications to the typical pentamerous calyx can occur due to fusion of two sepals or due to suppression or resorption of sepals. In certain taxa, the number of sepals at maturity varies within a single inflorescence (state 4). Most Detarieae have either five or four sepals at maturity. CI 0.26, RI 0.44, L 19 [CI 0.25, RI 0.40, L 20].

28. *Width of sepal lobes: sepal lobes uniform* (*0*)*; abaxial sepal*(*s*) *broader* (*1*)*; adaxial sepal*(*s*) *broader* (*2*)*; adaxial and abaxial sepals broader* (*3*). This character is used to evaluate patterns of calyx symmetry at maturity due to sepal size and not to evaluate whether the median sepal is abaxial or adaxial. CI 0.13, RI 0.31, L 23 [CI 0.11, RI 0.17, L 27].

29. *Petal number initiated: five* (*0*)*; four* (*1*)*; one* (*2*)*; none* (*3*). Most taxa initiate five petals, but in a few species of Detarieae and Cassieae fewer than five petals are initiated. In *Aphanocalyx* one petal is initiated, and in *Saraca* four petals are initiated. In the Dialiinae, *Dialium* also initiates only a single petal, whereas four are initiated in *Labichea* and none are initiated in *Ceratonia* (Caesalpinieae). CI 0.33, RI 0, L 9.

30. *Petal order of initiation: helical* (*0*)*; simultaneous* (*1*)*; unidirectional* (*2*)*; bidirectional* (*3*). As with sepal initiation, the pattern of petal initiation varies among Caesalpinioideae but is generally fixed and unidirectional in Papilionoideae and simultaneous in Mimosoideae. CI 0.27, RI 0.11, L 11.

31. *Position of first petal*(*s*) *initiated: abaxial* (*0*)*; adaxial* (*1*)*; several simultaneous* (*2*). In Caesalpinioideae, the first petal to initiate may occur on the abaxial or adaxial side, although in a few taxa several petals may initiate at once. In most Papilionoideae the first petal to initiate is abaxial. No taxa were seen where the first petals were lateral. CI 0.15, RI 0.26, L 13 [CI 0.13, RI 0.13, L 15].

32. *Timing of petal initiation: all successively* (*0*)*; one or more delayed relative to the next whorl* (*1*). As with sepals, in some taxa one or more petals may initiate with one of the two stamen whorls rather than successively with all of the other petals. CI 0.33, RI 0, L 3.

33. *Petal primordia: differentiate as petals with or without rudiments* (*0*)*; differentiate as stamens* (*1*)*; all resorbed or absent* (*2*). Petals may differentiate into stamens or staminodia or be resorbed and absent at maturity. CI 0.28, RI 0.37, L 7.

34. *Petal aestivation at end of early-stage initiation: imbricate* (*0*)*; valvate* (*1*)*; distant* (*2*). Petal aestivation was evaluated at the end of early-stage development when all organs are present (character 34) and in mature buds before anthesis (character 35). At early-stage development, the petals may be distant or touching (imbricate or valvate). CI 0.08–0.09, RI 0.15–0.23, L 22–24 [CI 0.09, RI 0.23, L 22].

35. *Position of median petal in late bud: imbricate ascending, standard innermost* (*0*)*; imbricate descending, standard outermost* (*1*)*; valvate* (*2*)*; imbricate* (*3*)*; distant* (*4*). This character describes petal imbrication patterns across the Leguminosae. Because the imbrication pattern of all petals is complex and may sometimes vary among flowers, here we examined only the position of the median sagittal (the "standard" or "vexillum") petal. The position of the median petal is a character that classically distinguishes the Caesalpinioideae (standard petal innermost) from the Papilioinoideae (standard outermost). However, the distinction is not always clear, and in some taxa, the petals may be imbricate (standard petal with one edge in and the other edge out relative to the lateral petals) or valvate (touching but not overlapping), or the standard petal may be distant (not touching the lateral petals). Figure 3*k*–3*m*. CI 0.14, RI 0.08, L 27.

36. *Petal size at anthesis: five equal or subequal* (*0*)*; five different sizes* (*1*). This character was used to capture corolla symmetry at anthesis, in a general manner. It does not differentiate between differences in petal size that are due to organogenesis and those that are due to petal suppression. The patterns of asymmetry within the corolla are described in characters 37–39. CI 0.11, RI 0.20, L 9.

37. *Differentiation of the median petal blade: median petal larger than the remaining petals* (*0*)*; median petal smaller than the remaining petals* (*1*)*; all petals equal* (*2*)*; median petal equal to the laterals* (*3*). This character was used to capture symmetry of the median (abaxial or adaxial) petal relative to the other petals. Figure 3*n*–3*p*. CI 0.13, RI 0.51, L 23 [CI 0.12, RI 0.46, L 25].

38. *Petal suppression: none suppressed* (*0*)*; all suppressed, absent, or rudimentary* (*1*)*; one large and two rudimentary or absent* (*2*)*; three large and two rudimentary or absent* (*3*). The five petals may differ in size because of differences in organ development (noted in character 36) or because of suppression or resorption (this character). In the latter case, all petals may be suppressed or only some of the petals may be suppressed. Usually only the two adaxial petals are suppressed (state 3) or the two adaxial and the two lateral petals are suppressed (state 2). CI 0.11–0.12, RI 0.30–0.33, L 25–26 [CI 0.10, RI 0.24, L 28].

39. *Differentiation of the lateral petals: uniform and different from the "keel" petals* (*0*)*; uniform and similar to the "keel" petals* (*1*). The two petals opposite the median petal (either adaxial or abaxial) generally are uniform and equal in size. However, they may differ from or be similar in size to the lateral petals. This character is independent from character 37, which establishes whether the median petal differs from the other petals. CI 0.10, RI 0.25, L 10 [CI 0.09, RI 0.16, L 11].

40. *Stamen number initiated: diplostemonous* (*0*)*; haplostemonous* (*1*)*; less than haplostemonous* (*2*)*; more than haplostemonous* (*3*). In most Leguminosae, two whorls of five stamens each are initiated (diplostemonous). In a few taxa, only one stamen whorl of five stamens initiates (haplostemonous). Because stamen number tends to be either the same or double the petal and sepal number, we use diplostemonous and haplostemonous rather than the absolute number of stamens, which can depend on petal and sepal number. In addition, when fewer than five (or fewer than 10) stamens initiate, this number tends to be variable among flowers. For example, taxa that initiate fewer than five stamens may have flowers with three or four stamens, and flowers that initiate fewer than two complete stamen whorls may have flowers with six, seven, eight, or nine stamens. CI 0.18, RI 0.23, L 16 [CI 0.23, RI 0.41, L 13].

41. *Antesepalous stamen order of initiation: helical* (*0*)*; unidirectional* (*1*)*; bidirectional* (*2*)*; erratic* (*3*)*; simultaneous* (*4*). The first stamen whorl to initiate is the antesepalous or outer stamen whorl, where stamens initiate opposite the sepals. Although in Caesalpinioideae stamens of both whorls usually initiate in a unidirectional manner, all other patterns of initiation are observed. In addition, in some taxa the stamens initiate apparently randomly and the order varies among flowers (erratic, state 3). CI 0.21, RI 0.06, L 19.

42. *Position of first antesepalous stamen*(*s*) *initiated: abaxial* (*0*)*; lateral* (*1*)*; adaxial* (*2*). The first stamens to initiate mostly occur in the abaxial position, but lateral and adaxial positions of the first antesepalous stamen also were observed. CI 0.14, RI 0.29, L 14.

43. *Antepetalous stamen order of initiation: unidirectional* (*0*)*; bidirectional* (*1*)*; erratic* (*2*)*; simultaneous* (*3*). The second stamen whorl to initiate is the antepetalous or inner stamen whorl, where the stamens initiate opposite the petals. As with the antesepalous stamen whorl, most taxa have a unidirectional pattern of initiation; however, the two stamen whorls can initiate in manners independent of one another. CI 0.42, RI 0, L 7.

44. *Position of first antepetalous stamen*(*s*) *initiated: abaxial* (*0*)*; lateral* (*1*)*; adaxial* (*2*). As with the antesepalous stamen whorl, in most taxa the first antepetalous stamen to initiate is abaxial, but other patterns are observed. CI 0.28, RI 0, L 7.

45. *Functional stamen number: diplostemonous* (*0*)*; haplostemonous* (*1*)*; less than haplostemonous* (*2*)*; more than haplostemonous* (*3*). The same scoring scheme was applied to account for stamen number at maturity as for stamen number at initiation (character 40). This character applies only to number of functional stamens and not to number of staminodes, which when present tend to vary in number among flowers of an individual. CI 0.10–0.11, RI 0.28–0.31, L 27–28 [CI 0.11, RI 0.34, L 26].

46. *Staminodes: present* (*0*)*; absent* (*1*). Staminodes may vary in morphology from structures that resemble petals to structures that resemble stamens but have nonfunctional pollen. It is not always possible to determine whether the pollen is functional from herbarium specimens, and very little information is available about breeding systems of Caesalpinioideae in the literature. Thus, staminodes here refer primarily to structures that morphologically are different from stamens; some flowers with staminodes that resemble stamens but have nonfunctional pollen may have been overlooked. CI 0.12, RI 0.30, L 8 [CI 0.10, RI 0.10, L 10].

47. *Filament length* (*of functional stamens*)*: equal* (*0*)*; two whorls of different lengths* (*1*)*; several lengths unrelated to stamen whorls* (*2*). Stamens may have filaments that are equal in length, that differ between the two stamen whorls, or that vary in

length irrespective of stamen whorl (but consistent among flowers). This character applies only to functional stamens, because staminodes often have filaments that vary in length among flowers. CI 0.18, RI 0.35, L 11.

48. *Filament connation: sheath* (*0*)*; some free, some connate* (*1*)*; all free* (*2*). In the group of taxa studied, filaments may be connate to form a sheath with one side open, or some stamens may be connate in groups of three or more, or all the filaments may be free. Most Caesalpinioideae have free stamens. Stamen fusion into a tube is prevalent in members of the Papilioinoideae, and it occurs in tribe Ingeae of the Mimosoideae but was not observed in the taxa studied here. CI 0.11, RI 0.23–0.28, L 17–18 [CI 0.10, RI 0.14, L 20].

49. *Number of anther morphs per flower: one* (*0*)*; two* (*1*). A maximum of two different anther morphs was observed in the taxa studied. This character applies only to functional stamens, not to staminodes, which may have many different and variable anther morphs. CI 0.50, RI 0.50, L 2.

50. *Fertile anther size* (*functional stamens*)*: uniform* (*0*)*; dimorphic or heteromorphic* (*1*). As for the previous character, anther size was evaluated only for functional stamens. CI 0.50, RI 0.66, L 2.

51. *Stamen fenestrations: absent* (*0*)*; present, pseudofenestrations* (*1*). In the taxa studied, true fenestrations, resulting from edge-to-edge fusion of the free stamen to the sides of the filament tube in a diadelphous androecium, are not present. However, pseudofenestrations are present in *Cercis* (autapomorphic). These are the result of the bending at the base of filaments that otherwise are free but tightly appressed. L 1.

52. *Anther attachment to filament: basifixed* (*0*)*; dorsifixed* (*1*). The filament may be attached at the base of the anther or on the dorsal side to form a versatile anther. This character is scored at maturity because anthers tend to be all basifixed in bud. In the taxa studied here, all of the stamens have either one condition or the other (anther attachment can vary among whorls in *Cassia grandis*; see Herendeen et al. 2003*b*), but in some legumes both basifixed and dorsifixed anthers occur in a flower. CI 0.33, RI 0.50, L 3.

53. *Anther dehiscence: longitudinal* (*0*)*; porate, terminal* (*1*)*; interrupted longitudinal or terminal slits* (*2*). In most taxa, anther dehiscence occurs through longitudinal slits along the length of the anthers. In some members of tribe Cassieae (e.g., *Duparquetia*, *Cassia*), the anthers dehisce by terminal pores, and in still others, dehiscence occurs through short terminal slits. CI 0.28, RI 0.16, L 7.

54. *Anther position in bud: erect* (*0*)*; inverted or declinate in bud* (*1*). Stamens in bud, just before anthesis, may be erect, or the filament may be bent just below the anther so that they are inverted (declinate). CI 0.08, RI 0.50, L 12 [CI 0.09, RI 0.54, L 11].

55. *Style adaxial groove: absent* (*0*)*; present* (*1*). Certain Caesalpinioideae have a pronounced groove on the adaxial surface of the style (here autapomorphic for *Ceratonia*). L 1.

56. *Ovule number: mostly one* (*0*)*; mostly two* (*1*)*; three or more* (*2*). In general the number of ovules tends to be fixed, with some taxa consistently producing only one ovule, others consistently producing two, and others producing a large number. However, variation can occur among flowers for those that produce one or two ovules, and for this reason, we chose to describe these as producing “mostly one” or “mostly two” ovules. CI 0.16, RI 0.16, L 12 [CI 0.15, RI 0.08, L 13].

57. *Timing of initiation between stamen whorls: no overlap* (*0*)*; overlap between the two whorls* (*1*). In the Leguminosae, with exception of the carpel that is frequently formed precociously (see character 58), taxa mostly initiate all organs of a single whorl before the initiation of the next acropetalous whorl. However, delay in initiation may occur, with some organs causing overlap in initiation among whorls. CI 0.12, RI 0.63, L 8.

58. *Timing of carpel initiation: with petals* (*0*)*; with outer stamen whorl* (*1*)*; with inner stamen whorl* (*2*)*; with sepals* (*3*). Carpel initiation was defined as the state where an obvious mound is present. In the Leguminosae, carpel initiation is precocious and generally occurs with the petals but may occur earlier with the sepals or slightly later with one of the two stamen whorls. CI 0.20, RI 0.36, L 15 [CI 0.18, RI 0.31, L 16].

59. *Carpel margins at ovule inception: open, unsealed* (*0*)*; sealed* (*1*). In apocarpous gynoecia across the angiosperms, the carpels are commonly open in early ontogenetic stages, but the margins become appressed and then fuse to enclose the locule prior to ovule initiation. In some legumes, however, ovule inception begins before the carpel margins fuse (Tucker and Kantz 2001). CI 0.11, RI 0.33, L 9 [CI 0.09, RI 0.16, L 11].

60. *Stigma type: terete, truncate, capitate* (*0*)*; peltate* (*1*)*; concave, tubular* (*2*)*; concave, funnel shaped* (*3*)*; tapering to small pore* (*4*). Stigma type is extremely variable in the Caesalpinioideae. Although certain states are difficult to differentiate one from another, the five recognized here are fixed within taxa and can be differentiated. Figure 3*q*–3*s*. CI 0.57, RI 0.80, L 7.

61. *Hypanthium: not present* (*0*)*; present* (*1*). A hypanthium is often present in the Leguminosae but may be difficult to recognize when the fused portion of the sepals, petals, and stamens is short. CI 0.16, RI 0.44, L 6.

62. *Gynoecium: free, centrally attached* (*0*)*; becomes adnate to side of hypanthium* (*1*). In some members of the Detarieae, the gynoecium is adnate to the side of the hypanthium rather than being attached centrally at the base of the hypanthium. Figure 3*t*. CI 0.33, RI 0.89, L 3 [CI 0.25, RI 0.84, L 4].

63. *Ovary position: sessile* (*0*)*; stipitate* (*1*). The ovary may be stipitate on a short or long stipe. CI 0.20, RI 0.33, L 5.

64. *Nectariferous disk: not present* (*0*)*; present* (*1*). In several Caesalpinioideae a nectariferous disk occurs at the base of the stamens, either as a continuous ring or as a series of individual fleshy nectaries loosely arranged in a disk. CI 0.33, RI 0.33, L 3.

65. *Ring meristem: not present* (*0*)*; present* (*1*). During development, a raised meristematic circular ridge that initiates petal and stamen primordial, called a ring meristem, has been noted in some Leguminosae (Tucker 1990, 2000*a*, 2002*a*; Prenner

2011) and in other families (e.g., Cistaceae: Nandi 1998; Dilleniaceae: Tucker and Bernhardt 2000; Phytolaccaceae: Zheng et al. 2004). In members of the Swartzieae, the ring meristem occurs after petal initiation and is associated with a large increase in the number of stamens per flower (Tucker 2003*c*). In the Detarieae, the ring meristem is similar in form to that seen in the Swartzieae, but only 10 stamens are initiated; the petals are initiated on the ring meristem in some of these taxa. CI 0.25, RI 0.25, L 4.

66. *Stemonozone: not present (0); present (1)*. A stemonozone is defined as a zone of fusion of the sepals and stamens, above the point of attachment of the petals to the hypanthium, when present. CI 1.00, RI 1.00, L 1.

67. *Sepal tube: not present (0); present (1)*. The sepals may be free to the base or to the base of the hypanthium, or they may be connate, at least at their base, to form a sepal tube. This fusion occurs above the level where petals (and stamens) are attached when a hypanthium is present. CI 0.12, RI 0.36, L 8.

68. *Symmetry of flower at anthesis: radial (0); zygomorphic (1)*. This "character" was scored to assess flower symmetry in a general sense. It makes abstraction of asymmetry due solely to the sepal or petal whorls but instead considers the symmetry of all organs relative to the others. Although optimized on the phylogenetic tree to examine the evolution of floral symmetry, this feature was not included in the analysis. CI 0.09, RI 0.28, L 11.

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