

## Morphological evolution in the variable resin-producing Detarieae (Fabaceae): do morphological characters retain a phylogenetic signal?

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- **Background and Aims** Previous molecular phylogenetic studies disagree with the informal generic-level taxonomic groups based on morphology. In this study morphological characters in the caesalpinioid clade Detarieae are evaluated within a phylogenetic framework as a means of better understanding phylogenetic relationships and morphological evolution.
- **Methods** Morphological characters were observed and scored for representative species of Detarieae focusing on the resin-producing genera. Phylogenetic analyses were carried out with morphological characters alone and then combined with DNA sequences.
- **Key Results** Despite a high level of homoplasy, morphological data support several clades corresponding to those recovered in molecular phylogenetic analyses. The more strongly supported clades are each defined by at least one morphological synapomorphy. Several characters (e.g. apetalous) previously used to define informal generic groups evolved several times independently, leading to the differences observed with the molecular phylogenetic analyses. Although floral evolution is complex in Detarieae some patterns are recovered.
- **Conclusions** New informal taxonomic groupings are proposed based on the present findings. Floral evolution in the diverse Detarieae clade is characterized by a repeated tendency toward zygomorphy through the reduction of lateral petals and toward complete loss of petals.

**Key words:** Caesalpinioideae, Detarieae, floral evolution, Leguminosae, morphology, phylogeny, resins, taxonomy.

### INTRODUCTION

Various resin-producing Caesalpinioideae belong to the large tropical tribe Detarieae as defined by Mackinder (2005) and Bruneau *et al.* (2000, 2001), which comprises the previously recognized tribes Amherstieae Benth. emend. Léonard and Detarieae DC. Of the 84 genera in Detarieae, 14 (147–149 species) produce terpenes that frequently make up resins (shown in bold in Tables 1 and 2). These terpenes are principally bicyclic diterpenes (in some genera the diterpenes are both bi- and tricyclic) and sesquiterpenes. The resin-producing genera were previously placed in different generic groups (the *Brownea*, *Crudia*, *Detarium*, *Hymenaea* and *Hymenostegia* groups) of tribe Detarieae *sensu* Cowan and Polhill (1981*b*). However, several molecular phylogenetic studies (Bruneau *et al.*, 2000, 2001, 2008; Fougère-Danezan *et al.*, 2003, 2007) have suggested that the terpene-producing genera occurred in only two clades: the *Prioria* clade, with five of the six genera producing terpenes, and the Detarieae *sensu stricto* (*s.s.*) clade, with nine of the 16 genera producing terpenes. The latter study (Fougère-Danezan *et al.*, 2007) resolved the resin-producing Detarieae as monophyletic, albeit with moderate clade support. Few other members of Fabaceae produce terpenes. Langenheim (1981, 2003) noted that diterpenes produced by species of Detarieae are similar to each other, but differ from those produced in other

groups. It thus appears that diterpenes and particularly bicyclic diterpenes are the most characteristic terpenes of the resin-producing Detarieae.

The resin-producing Detarieae are diverse morphologically. Members of this group are mostly unarmed trees or in rare instances shrubs with compound or rarely unifoliolate leaves. Their flowers are diverse in size and structure (Cowan and Polhill, 1981*b*; Mackinder, 2005). These may be small and apetalous or large and showy, with floral variations occurring in all whorls. The two adaxial sepals are often fused. All five petals can be present (e.g. *Schotia*), all can be absent (e.g. *Prioria*), or some can be absent or reduced and some present (e.g. *Eperua*). Stamens can be free (e.g. *Prioria*) or connate (e.g. *Eperua*) and although most species have ten fertile stamens, some have more (*Colophospermum mopane*) or fewer (e.g. *Stemonocoleus*). Some species with fewer than ten fertile stamens have staminodes with sterile anthers (e.g. *Sindora*) or without anthers (*Augouardia letestui*). The ovary consists of a single carpel (as in most Fabaceae) that is stipitate (e.g. *Schotia*) or not (e.g. *Kingiodendron*), and when present the stipe can be central (e.g. *Prioria*) or fused to the adaxial side of the hypanthium (e.g. *Schotia*).

Because of the great morphological diversity in Detarieae in general and in the resin-producing Detarieae in particular, the taxonomy of this tribe is problematic (cf. Cowan and

Polhill, 1981a, b versus Breteler, 1995) and warrants further study. Moreover, recent molecular studies (Bruneau *et al.*, 2000, 2001, 2008; Fougère-Danezan *et al.*, 2003, 2007) do not support the traditional classification (tribe delimitation and generic groupings; Cowan and Polhill, 1981a, b) based on morphology. Following the results of molecular analyses, the most recent classification of Fabaceae (Lewis *et al.*, 2005) treats Detarieae (Mackinder, 2005) as a single tribe, but no taxonomic groupings are proposed within the tribe. This reflects our current understanding of the group because few attempts have been made to use morphology in a phylogenetic context, in order to better define taxonomic groups. The arguments put forward by Luckow and Bruneau (1997) in favour of the inclusion of ecological characters could also be applied to the inclusion of morphological characters in phylogenetic analyses (see also Jenner, 2004; Wiens, 2004).

The aims of this study are to evaluate the utility of morphological characters, to determine morphological synapomorphies for clades (allowing us to propose new generic groupings) and to understand better the complex floral evolution in this group. To address these issues, we analysed morphological data both alone and in combination with molecular data within a phylogenetic framework focusing on the resin-producing Detarieae.

## MATERIALS AND METHODS

### Sampling

At least one species from each genus belonging to the Detarieae *s.s.* and *Prioria* clades (resin-producing Detarieae) were included in the study. Herbarium specimens from 90 species (40 genera) were selected including three outgroups and nine place-holders for the Amherstieae clade (Appendix 1).

### Methods

Herbarium specimens were observed using a binocular microscope and, when possible, 1–3 flowers were dissected after rehydration (using warm water or water with 10% glycerin). From these observations, 75 morphological characters describing vegetative morphology, inflorescence structure and floral morphology were coded and scored (Appendix 2). The methods for preparing twig wood samples to document vested pits (our only anatomical character) are described in Herendeen (2000). Using information from the literature, 13 characters describing pollen grains (Banks and Klitgaard, 2000; Banks, 2003; Banks *et al.*, 2003), wood anatomy (Gasson *et al.*, 2003), seedlings (Léonard, 1957, 1994; Watson and Dallwitz, 1993), fruits (Gunn, 1991) and seeds (Léonard, 1957; Kooiman, 1960; Gunn, 1991) were added. Because the species selected in those different studies and the present study were not always the same, when no variation was observed in a genus all the species of that genus were considered as having the same character state. When variation was observed, the species for which that character was not observed was scored as missing for this character.

### Analyses

The morphological matrix (see Supplementary Data, available online) was analysed with PAUP\* 4.0b10 (Swofford, 2002). All characters were considered as unordered. The morphological data were also combined with the molecular data of Fougère-Danezan *et al.* (2007) in a concatenated matrix. For all analyses, we used the heuristic search algorithm with tree bisection reconnection (TBR), MULTREES and steepest descent in effect. An initial set of trees was obtained via random stepwise addition (1000 replicates) with 10–50 trees retained per replicate. Those trees were then used as starting trees for a full heuristic search using TBR to search for additional optimal trees, retaining a maximum of 10 000 trees. All the values of consistency indices are calculated without the autapomorphies. Bremer support values (Bremer, 1988, 1994) were generated using autodecay 5.0 (Eriksson, 2001). Values <3 were considered as low (clade poorly supported), values from 3 to 5 as moderate, and values >6 were considered to indicate strong clade support.

The partition homogeneity test or incongruence length difference test (ILD test; Farris *et al.*, 1995) as implemented in PAUP\* was used to test for incongruence among the different data sets. A threshold  $\alpha = 0.01$  was used as recommended by Cunningham (1997).

The evolution of corolla symmetry (i.e. characters 52, 53 and 54 taken together) was reconstructed on one of the most-parsimonious trees using the parsimony criterion in Mesquite 2.6 (Maddison and Maddison, 2009). Because internal transcribed spacer (ITS) sequences for several taxa were missing, the results of the morphology and plastid data (MC), with more complete taxon sampling, rather than the results of the combined analysis of all three data sets (MCN) were used to examine floral evolution. We chose one of the most-parsimonious trees from MC analysis where *Brandzeia* is sister to *Daniellia* because it is the relationship obtained with MCN analysis.

## RESULTS

Analysis of the morphological data yielded 1101 trees (length = 653; CI = 0.19; RI = 0.70; Table 1). Bremer support values were usually low (data not shown). Results of the ILD test indicated a slightly significant incongruence between the morphological data and the plastid DNA data ( $P = 0.01$ ) and between the morphological data and the plastid plus ITS data set ( $P = 0.01$ ). These results are not highly significant and the use of ILD as an indicator of data set combinability has been questioned (see Yoder *et al.*, 2001). The main difference between the morphological and plastid data sets relates to the position of *Brandzeia*. Removing this genus improved the result of the ILD test and increased the resolution at the base of the tree without other modification in the relationships. It was thus decided to combine the morphology and molecular data for analysis. The analysis of morphology and plastid data yielded 4560 trees (MC; length = 1687; CI = 0.38; RI = 0.73; Table 1; Fig. 1). A combined analysis of all three data sets yielded four most-parsimonious trees (MCN; length = 3622; CI = 0.37; RI = 0.62; Table 1).

TABLE 1. Summary of the phylogenetic analyses of morphological characters, combined analyses of morphological and plastid characters (MC) and combined analyses of morphological, plastid and nuclear data (MCN)

Clade	Morphology: $n = 1101$ ; L = 653; CI = 0.19; RI = 0.69	Plastid: $n = 20\ 000^*$ ; L = 1098; CI = 0.53; RI = 0.81	Nuclear (ITS): $n = 2$ ; L = 2285; CI = 0.35; RI = 0.58	Combined (MC): $n = 4560$ ; L = 1687; CI = 0.38; RI = 0.73	Combined (MCN): $n = 4$ ; L = 3622; CI = 0.37; RI = 0.62
<b>Resin-producing Detarieae</b>	–	J65	J54	–	–
<i>Prioria</i> s.l. clade:	B2 (plus <i>Brandzeia</i> and <i>Neopaloxylon</i> )	J96	–	B6	–
<b><i>Colophospermum</i></b>	B9	J100	J100	B46	B88
<i>Hardwickia</i>					
<i>Prioria</i> s.s. clade:	B2	J < 50	J < 50	B3	B10
<b><i>Gossweilerodendron</i></b>					
<b><i>Kingiodendron</i></b>					
<b><i>Oxystigma</i></b>					
<b><i>Prioria</i></b>					
Detarieae s.s. clade	–	J98 (without <i>Daniellia</i> ) J60 (with <i>Daniellia</i> )	–	B5 (without <i>Daniellia</i> ) – (with <i>Daniellia</i> )	B4 (without <i>Daniellia</i> ) – (with <i>Daniellia</i> )
<i>Hymenaea</i> clade:	B1	J99	J98	B8	B17
<b><i>Guibourtia</i></b>					
<b><i>Hymenaea</i></b>					
<b><i>Peltogyne</i></b>					
<i>Eperua</i> s.l. clade:	–	J96	–	B3	B3
<i>Augouardia</i>	–	J99	J93	B6	B14
<i>Stemonocoleus</i>					
<i>Eperua</i> s.s. clade:	B1 (plus <i>Daniellia</i> )	J99	–	B6	B9
<b><i>Eperua</i></b>					
<i>Eurypetalum</i>					
Detarium clade:	B1	J97	J85	B3	B8
<i>Baikiaea</i>					
<b><i>Tessmannia</i></b>					
<i>Sindoropsis</i>					
<b><i>Detarium</i></b>					
<b><i>Copaifera</i></b>					
<i>Pseudosindora</i>					
<b><i>Sindora</i></b>					

Molecular results are from Fougère-Danezan *et al.* (2007). Values preceded by ‘J’ indicate jackknife support, and values preceded by ‘B’ indicate decay indices.  $n$  is the number of trees recovered for each analysis and the asterisk indicates that the maximum number of trees was reached. Genera that have been recorded as producing terpenes are in bold. For other taxa it is not known whether they have been tested and lack resins or whether they never have been tested for the presence of resins.

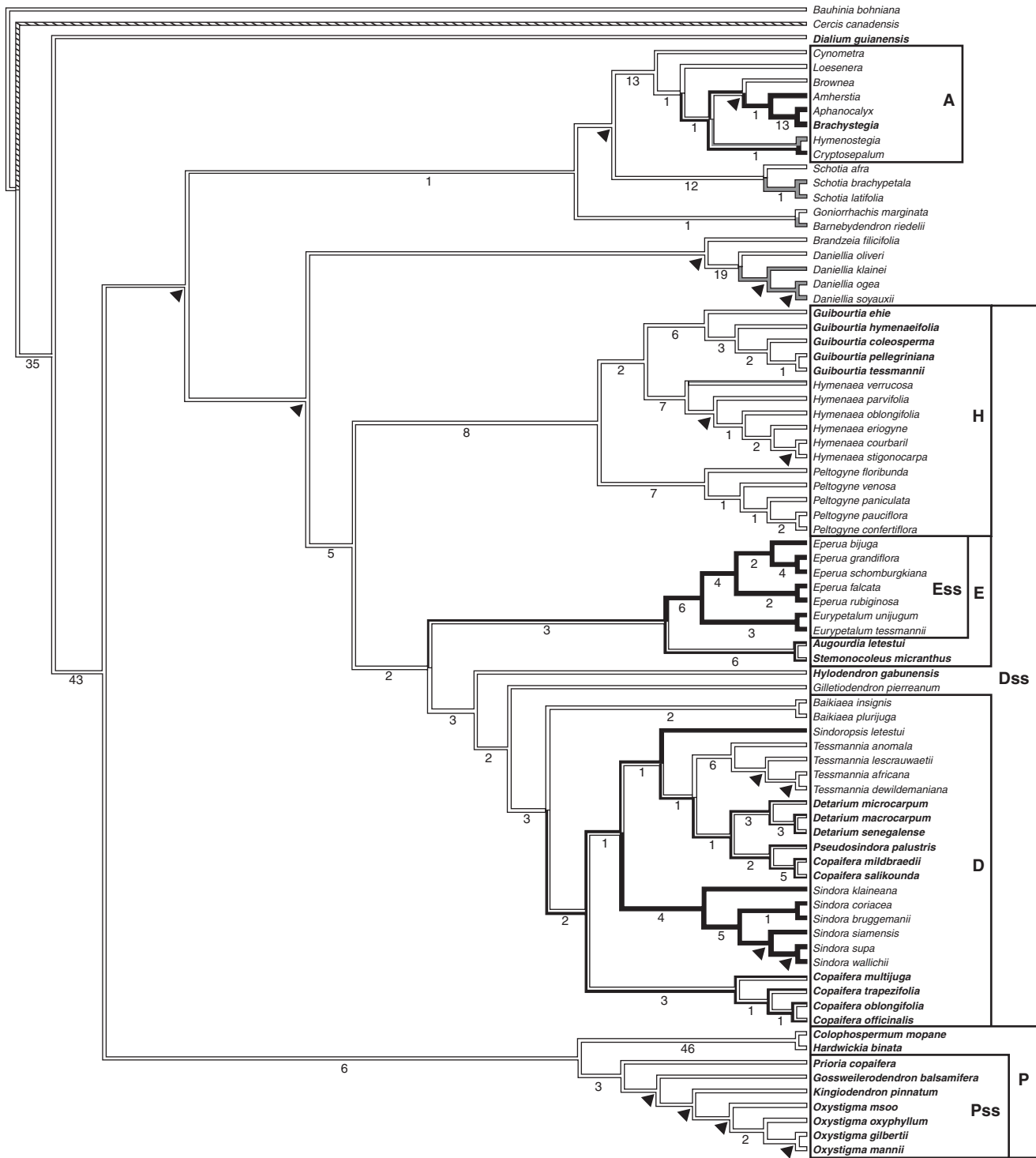


FIG. 1. One of the 4560 most-parsimonious trees obtained in the combined analysis of morphological and plastid data ( $L = 1687$ ,  $CI = 0.38$ ,  $RI = 0.73$ ). Letters in the frames indicate the names of clades (A, Amherstieae clade; D, *Detarium* clade; Dss, Detarieae s.s. clade; E, *Eperua* s.l. clade; Ess, *Eperua* s.s. clade; H, *Hymenaea* clade; P, *Prioria* s.l. clade; and Pss, *Prioria* s.s. clade). Numbers under the branches indicate decay indices. Arrows indicate clades that are not supported in the strict consensus tree. The branches are shaded according to the reconstruction by Mesquite of the ancestral state for corolla pattern: white for five developed petals, hatched for 'Cercis' pattern (applicable only to *Cercis*), grey for three developed petals and black for one developed petal (species in bold are the apetalous species coded as non-applicable for this character).

The results of these analyses are summarized and compared with our molecular study (Fougère-Danezan *et al.*, 2007) in Table 1. Several groups were resolved as monophyletic in

both the morphological analysis and the combined data analyses (MC and MCN). Although the resin-producing Detarieae clade was recovered in the molecular analyses

(Fougère-Danezan *et al.*, 2007), neither the morphological nor the combined analyses resolved this group as monophyletic. The *Prioria sensu lato (s.l.)* clade was strongly supported in the MC combined analysis, and, although also supported in the morphological analysis, it included the genera *Brandzeia* and *Neoapaloxylon*. This clade was strongly supported in previous analyses of plastid DNA but was not recovered in the ITS analyses because the genera *Colophospermum* and *Hardwickia* were placed elsewhere (Fougère-Danezan *et al.*, 2007). The *Prioria s.s.* clade was resolved as monophyletic in all analyses but was poorly supported, except in the combined analyses where it was moderately to strongly supported. The Detarieae *s.s.* clade was resolved as monophyletic in the plastid DNA analyses (Fougère-Danezan *et al.*, 2007) and here in the combined analyses, but not in the morphological analysis. The inclusion of the genus *Daniellia* in this clade was not well supported. The *Hymenaea* clade was always resolved as monophyletic and usually strongly supported (except in the morphological analysis where all support values were low). The *Eperua s.l.* clade was resolved as monophyletic in the combined analyses only (with moderate support), whereas the *Eperua s.s.* clade was resolved as monophyletic in both the morphological and combined analyses, but with strong support only in the latter. The *Detarium* clade was always resolved as monophyletic. It was strongly supported in the previous molecular analyses, and moderately to well supported in the combined analyses presented here. The positions of two genera, *Gilletiodendron* and *Hylodendron*, were ambiguous. As in our previous molecular analyses, in both the morphological and combined analyses *Gilletiodendron* was resolved as sister to the *Detarium* clade with poor support, whereas *Hylodendron* was sister to this entire clade (MC combined analysis), sister to *Gilletiodendron* (MCN combined analysis) or sister to *Stemonocoleus* (morphology alone).

## DISCUSSION

The Detarieae clade has been recognized as monophyletic with strong support for some time (Bruneau *et al.*, 2001), but morphological synapomorphies have yet to be clearly identified (although some characters, such as intrapetiolar stipules, are present in most Detarieae). Our analyses point to several morphological characters that are useful at different phylogenetic levels for defining clades within the resin-producing Detarieae. Characters from the corolla (e.g. characters 52–54) can be useful synapomorphies for closely related genera but are problematic to use at the level of the resin-producing Detarieae as a whole because of convergent evolution (especially apetaly). Apetaly has been used as a primary character to define the *Crudia* group (Cowan and Polhill, 1981b), but members of this generic group are scattered in our analyses, suggesting that loss of petals has arisen several times (six times) in the resin-producing Detarieae (Fig. 1). Some vegetative characters, such as secondary venation (characters 23 and 24), are also synapomorphies for closely related genera or for certain clades (e.g. the *Hymenaea* and *Detarium* clades). Some of the characters previously used for developing classifications have proved to be good synapomorphies in our analyses, such as inflorescence and sepal characters (e.g. characters 32 and 48 for the *Detarium* clade).

In addition, it was found that ovary characters are particularly useful synapomorphies for the *Prioria s.l.* and *s.s.* clades (characters 74 and 75), for closely related genera (character 70; *Eperua s.l.* in part), and even for genera (character 75; *Guibourtia*). Characters from fruits and seeds (characters 77, 87–89) are also useful to support clades (*Prioria s.l.* and *Eperua s.s.*) and at the generic and intrageneric levels. Pollen and wood anatomy characters (characters 78–80, 82) support clades and resolve relationships among closely related genera, as do seedling characters (characters 83–85), which Léonard (1957, 1994) studied in detail and used as a basis for his substantial taxonomic revisions.

### Morphological synapomorphies in Detarieae

The resin-producing Detarieae are not resolved as monophyletic in all analyses and, other than their ability to produce bicyclic diterpenes (Fougère-Danezan *et al.*, 2007), no clear synapomorphies are known for this group (see sub-tribe Detariinae; Table 2). However, within the resin-producing Detarieae, most of the clades recognized in our molecular analyses can also be diagnosed by morphological synapomorphies. These characters are used as a basis for proposing new informal taxonomic groups for the resin-producing Detarieae (Table 2).

The *Prioria s.l.* clade is defined by having only one ovule per ovary. This state also occurs in *Cynometra mannii* and *Guibourtia arnoldiana*, but these species belong to genera usually having two ovules per ovary. A proximal wing is frequently present (*Brandzeia*, *Gossweilerodendron*, *Hardwickia*, *Neoapaloxylon* and some species of *Kingiodendron* and *Oxystigma*) even if not present in all the species of the clade (*Prioria* never has a wing). A similar wing is also observed in the monotypic genus *Hylodendron* (*Detarium* clade). In the *Prioria s.l.* clade, flowers are generally apetalous, except in the monotypic genus *Brandzeia*, which has five petals. Within the clade, some characters are shared with members of the *Prioria s.s.* clade and the two monotypic genera *Colophospermum* and *Hardwickia*, whereas other characters are shared with members of the *Prioria s.s.* clade and the genera *Brandzeia* and *Neoapaloxylon*. *Colophospermum* and *Hardwickia* share with the *Prioria s.s.* clade the absence of amyloids in seeds, present in all other Detarieae examined (Kooiman, 1960). In addition, *Colophospermum* and members of the *Prioria s.s.* clade do not have ‘Zwischenkörper’ (a state unknown for *Hardwickia*), which have been observed in all other Detarieae and in *Cercis* (Banks, 2003). ‘Zwischenkörper’ (character 78; see Appendix 2) are pectic structures associated with the pores of pollen (Banks, 2003). *Brandzeia* and *Neoapaloxylon* share an attenuate stigma with all members of the *Prioria s.s.* clade, except *Kingiodendron* which has a crateriform stigma. *Brandzeia* and *Neoapaloxylon* are quite distinct from members of the *Prioria s.s.* clade by having more numerous smaller leaflets and larger flowers, which in *Brandzeia* have petals. The presence or absence of amyloids and ‘Zwischenkörper’ is unknown in those two genera.

The species of the *Prioria s.s.* clade are roughly similar, with multifoliate leaves possessing a small number of leaflets and small apetalous flowers in dense racemes. In all these species,

TABLE 2. *New groupings and their diagnostic characters*

Tribe Detarieae s.l.	Style bent on the abaxial side of the flower Amyloids in seeds Stipule insertion intrapetiolar Bicyclic diterpenes Molecular characters only Only one ovule per ovary No amyloids in seeds No 'Zwischenkörper' Cotyledons remaining in seed Hypogeal germination Axial canals diffuse Stigma non-papillose, usually attenuate Bifoliolate leaves Strongly asymmetrical leaflets Actinodromous primary venation Peltate stigma Pantoporate pollen Rachis extension Haploid number of chromosomes $n = 17$ Pollen with reticulate ornamentation Bifoliolate leaves Strongly asymmetrical leaflets Primary nerve close to the distal margin of the leaflet Stipule insertion lateral Molecular characters only Only one big developed petal and four vestigial Fertile stamens less than ten Distichous flower arrangement in inflorescence 'Sub-valvate sepals' Axial canals tangentially organized
<b>I. Sub-tribe Detariinae</b>	
<b>1. Daniellia group:</b> <i>Brandzeia</i> , <i>Daniellia</i> , <i>Neoapaloxylon</i>	
<b>2. Prioria group</b>	
a. <i>Prioria</i> sub-group: <i>Gossweilerodendron</i> , <i>Kingiodendron</i> , <i>Oxystigma</i> , <i>Prioria</i>	
b. <i>Hardwickia</i> sub-group: <i>Colophospermum</i> , <i>Hardwickia</i>	
<b>3. Hymenaea group:</b> <i>Guibourtia</i> , <i>Hymenaea</i> , <i>Peltogyne</i> ,	
<b>4. Eperua group</b>	
a. <i>Eperua</i> sub-group: <i>Eperua</i> , <i>Eurypetalum</i>	
b. <i>Stemonocoleus</i> sub-group: <i>Augouardia</i> , <i>Stemonocoleus</i>	
<b>5. Detarium group:</b> <i>Baikiaea</i> , <i>Copaifera</i> , <i>Detarium</i> , <i>Gilletiodendron</i> , <i>Hylodendron</i> , <i>Pseudosindora</i> , <i>Sindora</i> , <i>Sindoropsis</i> , <i>Tessmannia</i>	

*Barnebydendron*, *Goniorrhachis* and *Schotia* are not included because their positions are not well resolved. Genera that have been recorded as producing terpenes are in bold. For other taxa it is not known whether they have been tested and lack resins or whether they never have been tested for the presence of resins.

the cotyledons remain in the seed during germination, which is hypogeal rather than epigeal, typical of other Detarieae and the outgroup taxa (Gasson *et al.*, 2003). In addition, axial canals in the wood are diffuse, except in *Prioria* where they are tangentially organized (Gasson *et al.*, 2003).

Breteler (1999) recently revised the genus *Prioria* to include all species of the *Prioria* s.s. clade. Among the members of this clade, *Kingiodendron* is easily distinguished by its crateriform stigma and unisexual flowers (Table 3). The genus *Gossweilerodendron* has only four sepals (it is difficult to know whether this is due to fusion of the two adaxial sepals or whether only four sepals are initiated), whereas all other genera in this clade have five sepals. The genus *Prioria* has flat cotyledons, whereas they are ruminant or canaliculate in *Kingiodendron* and *Oxystigma*, and plano-convex in *Gossweilerodendron*. The polymorphic genus *Oxystigma* lacks any distinct unifying character (Table 3). An exhaustive species-level sampling of the *Prioria* s.s. clade and further examination of the morphological data are necessary, but, given the morphological diversity encountered in this clade, our results to date do not contradict the proposal that these four genera be united under the single genus *Prioria*. For the moment, we simply consider these four genera as being at least in the same sub-group (*Prioria* sub-group; see Table 2).

The two genera of the *Hardwickia* clade, *Colophospermum* and *Hardwickia*, share bifoliolate leaves (also occurring in the

*Hymenaea* clade, *Aphanocalyx cynometroides* and *Eurypetalum unijugum*), asymmetrical leaflets with an actinodromous primary venation (also in *Aphanocalyx*, *Bauhinia* and *Cercis*), a peltate stigma and pantoporate pollen (Table 3). They also lack axial canals, unlike other members of the *Prioria* clade (Banks and Gasson, 2000). Other characters shared by these two monospecific genera, but not included in our matrix for practical reasons, include a rachis extension beyond the insertion point of the leaflets (Herendeen, 2000), a haploid chromosome number of 17 (Goldblatt, 1981; Breteler *et al.*, 1997; vs.  $n = 12$  or 11 in other studied Detarieae), pollen grains with a reticulate ornamentation (Banks and Klitgaard, 2000), seeds with ruminant cotyledons and wood with a similar anatomy (Breteler *et al.*, 1997; Banks and Gasson, 2000). Breteler *et al.* (1997) suggested their unification because of these shared characters, but Léonard (1999) insisted on keeping them separate, arguing that they are clearly distinct regarding characters of generic importance. Indeed, *Colophospermum* has been interpreted as having four sepals, whereas *Hardwickia* has five, resulting in a difference in calyx structure (alternate for *Colophospermum* and imbricate for *Hardwickia*). However, an ontogenetic study of *Colophospermum* by Krüger *et al.* (1999) showed that the two lateral lobes of the perianth are probably bracteoles, not sepals (Fig. 2). Similarly, the structure of the flower of *Hardwickia* suggests that the two lateral lobes of the perianth are also

TABLE 3. Morphological and anatomical characters that distinguish genera in each of the main clades of the resin-producing Detarieae

<i>Colophospermum</i> and <i>Hardwickia</i>								
Character	<i>Colophospermum mopane</i>				<i>Hardwickia binata</i>			
Sepal number	Four				Five			
Stamen number	20–25				10			
Disk	Present				Absent			
Anther surface	Smooth				Verrucose			
Fruit shape	Asymmetrical, reniform				Symmetrical			
Radicle position	Lateral				Terminal			
Wing on seed	Present				Absent			
Resin vesicle on seed	Present				Absent			
Aspect of the seed after soaking	Mucilaginous				Non-mucilaginous			

<i>Prioria</i> s.s. clade				
Character	<i>Gosswelierodendron</i>	<i>Kingiodendron</i>	<i>Oxystigma</i>	<i>Prioria</i>
Sepal number	Four	Five	Five	Five
Stigma shape	Attenuate	Crateriform	Attenuate	Attenuate
Hermaphroditic or unisexual flowers	Flowers all bisexual	At least some flowers unisexual	Flowers all bisexual	Flowers all bisexual
Cotyledons	Plano-convex	Ruminate	Ruminate or canaliculate	Flat

<i>Hymeanaea</i> clade			
Character	<i>Guibourtia</i>	<i>Hymeanaea</i>	<i>Peltogyne</i>
Petal number	None	Five	Five
Sepal margins	Thin, imbricate	Thin, not imbricate	Thin, not imbricate
Ovule number	Two rarely one ( <i>G. arnoldiana</i> )	Numerous	Numerous
Axial canals	Present, traumatic	Absent	Absent
Endocarp	Thin	Fleshy	Thin
Ovary stipe	Central	Adnate to the adaxial side of the hypanthium	Central
Crateriform glands	Present	Present	Absent

<i>Eperua</i> s.s. clade		
Character	<i>Eperua</i>	<i>Eurypetalum</i>
Stamen sheath	Long	Short
Flower size	Large	Small
Ovule number	Numerous, rarely two ( <i>E. grandiflora</i> )	Two
Secondary venation	Intramarginal vein	Brochidodromous
Mucronate leaflets	Present	Absent
Twisted petiolules	Absent	Present

<i>Detarium</i> clade								
Character	<i>Baikiaea</i>	<i>Copaifera</i>	<i>Detarium</i>	<i>Pseudosindora</i>	<i>Sindoropsis</i>	<i>Sindora</i>	<i>Tessmannia</i>	
Petal number	Five	None	None	None	One	Three or five	Five	
Vestigial petals	None	NA	NA	NA	None	Two or four	None	
Stamen fusion	Nine fused	All free	All free	All free	Nine fused	Nine fused	Nine fused	
Staminodes	None	None	None	None	None	Eight	None	
Anther shape	Rectangular	Rectangular	Square	Rectangular	Rectangular	Rectangular	Rectangular	
Mucronate leaflets	Absent	Present	Absent	Absent	Absent	Absent	Absent	
Ovary stipe	Central	Central	Absent	Adnate to the adaxial side of the hypanthium	Absent	Central	Central	
Stipule fusion	Present	Absent	Absent	Absent	Absent	Absent	Absent	
Marginal vein	Present	Present	Present	Present	Present	Present	Absent	

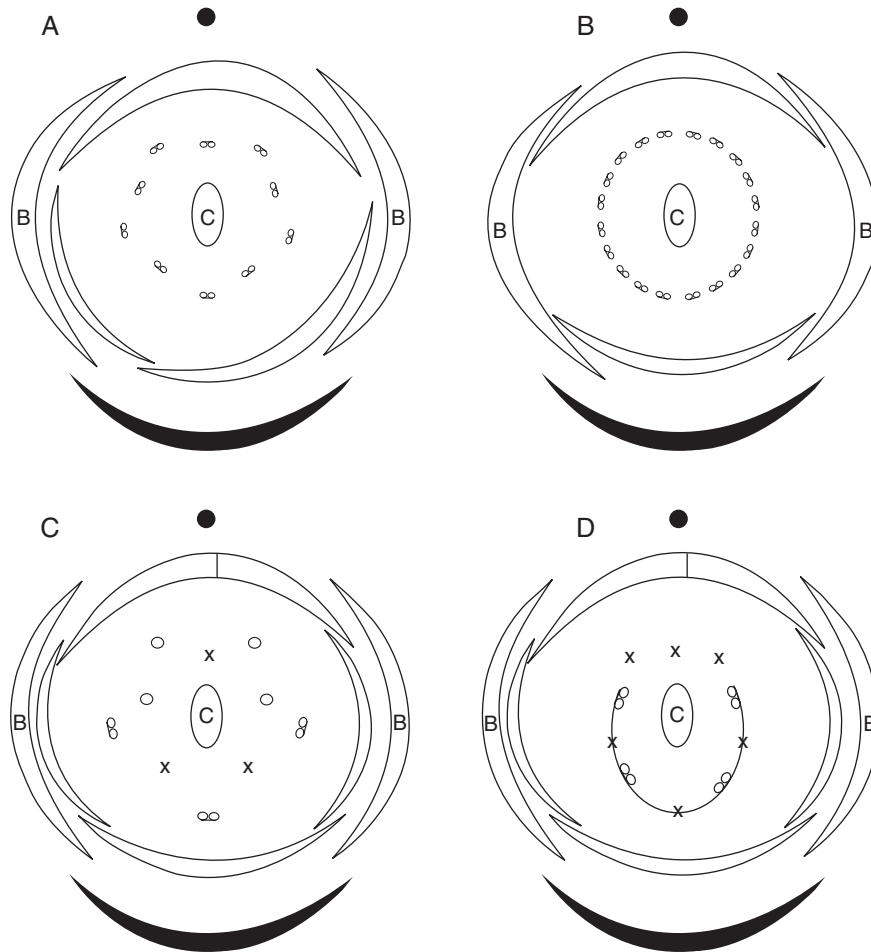


FIG. 2 Floral diagrams for four apetalous species (A) *Hardwickia binata*, (B) *Colophospermum mopane*, (C) *Augouardia letestui* and (D) *Stemonocoleus micranthus*. The ellipse marked with a 'C' is the single carpel. Parts marked with a 'B' are bracteoles. Empty circles indicate staminodes, and crosses indicate putative positions for missing stamens.

likely to be bracteoles (Fig. 2). The differences in flower structure thus appear to be the result of a similar event: the bracteoles becoming larger and closer to the calyx and the loss of the sepals contiguous to the bracteoles. These two genera also differ in stamen number, presence or absence of a staminal disk, anther surface texture, shape and dehiscence of the fruit, and seed morphology (see Léonard, 1999, and Table 3). Therefore, although the unification of the two genera is possible, there remains a question of rank. They are, however, close relatives and are considered to be in the same sub-group (*Hardwickia* sub-group; see Table 2).

As detailed above, members of this clade share several characters with the *Prioria* s.s. clade. The plastid data emphasize a close relationship with the *Prioria* s.s. clade, but the ITS data are more ambiguous. This conflict has been interpreted as an indication of a possible hybrid origin of *Colophospermum* and *Hardwickia* (Fougère-Danezan *et al.*, 2007). Moreover, the long branch observed in the molecular analyses and the large number of morphological apomorphies characteristic of this lineage suggest an accelerated rate of evolution. The relatively high chromosome number ( $n = 17$ ) suggests a triploid origin for this lineage, which may be associated with a hybridization event involving the *Prioria* s.s. clade lineage. As

observed in other groups (Levin, 1983; Wendel, 2000), the apparently accelerated evolution could be the result of a polyploidization event (possibly an allopolyploidization event).

The genus *Brandzeia* (and its close relative *Neoapaloxylon*, sampled in the morphological data set only and thus absent in Fig. 1) is resolved in the morphological data analysis as a close relative of the *Prioria* s.s. clade, despite several non-exclusive characters being shared with the genus *Daniellia*. Although molecular data suggest a close relationship between *Brandzeia* and *Daniellia*, several characters shared by *Brandzeia* and members of the *Prioria* s.s. clade are linked with wind dispersal (one ovule per ovary, fruit indehiscent with a proximal wing) and could thus be the result of convergence. Moreover, several characters among those scored from the literature are missing for *Brandzeia* and *Neoapaloxylon*. We thus consider *Brandzeia* and *Neoapaloxylon* as being in the *Daniellia* group rather than in the *Prioria* group (Table 2).

The boundaries of the Detarieae s.s. clade are not well established, and its only synapomorphy is the protruding apertures of the pollen. This clade is difficult to define morphologically because of its high degree of variability.

Within Detarieae s.s., members of the *Hymenaea* clade have more or less regular flowers with five petals (*Hymenaea* and



*Peltogyne*) or without any petals (*Guibourtia*; see Table 3 for more characters). This clade is better defined by vegetative characters, such as bifoliolate leaves (shared with *Colophospermum*, *Hardwickia*, *Aphanocalyx cynometroides* and *Eurypetalum unijugum*). The leaflets are asymmetrical (often curved) with pinnate secondary venation and the primary vein close to the distal margin. The insertion of the stipules is lateral (also occurring in *Hardwickia*) rather than intrapetiolar, as seen in other Detarieae. The genera *Hymenaea* and *Peltogyne* were included in the same generic group by Cowan and Polhill (1981b), but *Guibourtia* was included in the apetalous *Crudia* group even though morphologically this genus is otherwise similar to members of the *Hymenaea* clade. The three genera of the strongly supported *Hymenaea* clade are thus considered to belong to the same group (*Hymenaea* group; Table 2).

There is no morphological synapomorphy for the *Eperua s.l.* clade because the two monotypic genera *Augouardia* and *Stemonocoleus* are unique and do not seem to share characters with any other genus. These two genera have apetalous flowers with a reduction in the number of fertile stamens, but the patterns are different (Fig. 2). The genus *Augouardia* has three fertile stamens facing the abaxial sepals and four staminodes on the adaxial side, and all the androecium parts are free. The genus *Stemonocoleus* has four fertile stamens fused in a sheath on the abaxial side, but in alternate positions relative to the sepals. Among the resin-producing Detarieae, a reduction in number of fertile stamens also occurs in the genus *Sindora* and in some species of *Eperua*. However, in the genus *Sindora*, the two fertile stamens are on the adaxial side (the others are reduced to staminodes), and in the genus *Eperua*, five sterile stamens alternate with five fertile stamens. The lower number of fertile stamens observed in *Augouardia* and *Stemonocoleus*, with fertile stamens on the abaxial side only, therefore appears to be homologous in the two genera, despite differences in fusion and number of stamens. Those two genera are also included in the *Eperua* group, but in a different sub-group (*Stemonocoleus* sub-group; Table 2).

The genera *Eperua* and *Eurypetalum* (*Eperua s.s.* clade) are undoubtedly closely related. The two genera have a similar flower structure, with nine of the ten stamens abaxially fused in a sheath, one large petal (larger than the calyx lobes) and four vestigial ones. *Sindora klaineana* has almost the same flower structure, but the only developed petal is smaller (comparable with calyx lobes). Despite their similarity in floral morphology, *Eperua* and *Eurypetalum* have been considered to belong to different generic groups (Cowan and Polhill, 1981b). *Eperua* was placed in the *Brownea* group, although it lacks the main character defining this group (connate bracteoles) and shares other characters with other groups within Detarieae. Recent phylogenetic analyses have shown that the genus does not belong to the *Brownea* clade, which includes eight of the ten genera of the *Brownea* group (Bruneau et al., 2000, 2001, 2008; Herendeen et al., 2003). Moreover, *Eperua* lacks the main character defining the clade (woody lip on the placental suture on each valve of the fruit; Redden and Herendeen, 2006). *Eurypetalum* was placed in the *Hymenostegia* group, although it lacks one of the main characters of the group (well developed bracteoles; Cowan and

Polhill, 1981b). The only character supporting its inclusion is the presence of twisting fruit valves, a character shared by *Eperua* and *Eurypetalum*. Their similarity may have been unnoticed because *Eurypetalum* is exclusively African, whereas *Eperua* is exclusively American. In addition, the two genera differ by a number of other characters such as the length of the stamen sheath, size of the flowers, number of ovules per ovary, secondary venation, presence of a mucro on the leaflets and presence of twisted petioles (Table 3). These two genera are treated here as members of the same sub-group (*Eperua* sub-group; Table 2).

Among our well supported clades, the *Detarium* clade is the most variable morphologically, even though it contains only members of the *Detarium* group as defined by Cowan and Polhill (1981b) and excludes one genus (*Goniorrhachis*), which had been included in the group. Some members of this clade have simple flowers that are more or less regular and apetalous (*Copaifera*, *Detarium* and *Pseudosindora*), whereas others have more or less regular flowers with five petals and nine of the ten stamens fused in a sheath (*Baikiaea* and *Tessmannia*; Table 3). However, in a few genera, the flowers are irregular with only one petal developed and with two (Asian *Sindora*) to four (African *S. klaineana*) vestigial petals or without vestigial petals (*Sindoropsis letestui*), and with nine stamens of the ten fused in a sheath, but with either ten fertile stamens (*Sindoropsis letestui*) or two fertile stamens and eight staminodes (*Sindora*). Nevertheless, members of this clade share several characters. The flowers are distichous in the inflorescence (also occurring in *Gilletiodendron* and *Hylodendron* and in the distantly related *Goniorrhachis*), except in *Pseudosindora* (sometimes included in *Copaifera*), which is reported to have spirally inserted flowers (Symington, 1944); however, the specimen observed in the present study was not well enough preserved for this character to be scored. The sepals are imbricate and the overlapped margins have a different texture (character 48; also occurring in *Guibourtia* and the closely related genera *Gilletiodendron* and *Hylodendron*). Those two characters were used by Cowan and Polhill (1981b) to define the *Detarium* group, although the latter was described as ‘sub-valvate sepals’. The wood shows, in most of the species of this clade, some tangentially organized axial canals (also occurring in *Brandzeia*, *Cryptosepalum*, *Daniellia*, *Eperua* and *Prioria*). In contrast, the genus *Baikiaea* has diffuse axial canals (as do the closely related genera *Gilletiodendron* and *Hylodendron*). Exinous bridges over the centre of the pollen aperture occur in four of the seven genera (*Copaifera*, *Pseudosindora*, *Sindora* and *Sindoropsis*) and in the closely related genus *Hylodendron*. Within the *Detarium* clade, intergeneric relationships remain poorly resolved, but each genus is well defined by morphology (Table 3) and combined data, except *Copaifera* which is not resolved as monophyletic in the combined analyses. We thus consider the members of *Detarium* clade as belonging to the same group (*Detarium* group) without defining any sub-groups (Table 2).

#### Floral evolution

Although few ontogenetic studies have been carried out on resin-producing Detarieae, several apetalous species of the

Amherstieae clade were studied by Tucker (2000a, b; 2001b), and one apetalous species, *Colophospermum*, of the resin-producing Detarieae was studied by Krüger *et al.* (1999). Within the Amherstieae clade, in *Crudia* some petal primordia are initiated but do not develop (Tucker, 2001b), in *Brachystegia* all five petals are initiated but none develop (Tucker, 2000a), and in *Saraca* it seems that five petals are initiated but four petal primordia develop later into stamens and one does not develop (Tucker, 2000b). In contrast, in *Colophospermum*, the petals are not initiated (Krüger *et al.*, 1999). It remains to be determined whether all apetalous resin-producing Detarieae have this same developmental pattern, with absence of petals being the result of non-initiation of petal primordia.

Among the species having flowers with petals, several have fewer than five developed petals. These generally follow two patterns: either three petals are developed on the adaxial side and the abaxial ones are reduced (smaller or vestigial), or the median adaxial petal is developed and the four others are vestigial or absent (initiated or not). In the resin-producing Detarieae, the first pattern (3 + 2) occurs more often in early diverging lineages (Fig. 1) such as *Barnebydendron*, *Daniellia* and *Schotia*, and even in some individuals of *Hymenaea verrucosa* (not observed, but see Lee and Langenheim, 1975), whereas the second pattern (1 + 4) predominates in later diverging lineages (*Eperua*, *Eurypetalum*, *Sindora* and *Sindoropsis*). It is thus hypothesized that repeated shifts occur from actinomorphy to zygomorphy through the reduction of lateral petals (the abaxial ones being more labile) in the resin-producing Detarieae. Reversal to an actinomorphic corolla is possible, and complete petal loss is frequent (six losses in resin-producing Detarieae; Fig. 1). This complex pattern of floral evolution may be associated with adaptation to a wide array of pollinators (Lewis *et al.*, 2000), but pollinators are known only for few species of this tribe.

Floral ontogeny depends not only on the interactions of the well-known A, B, C, D and E class genes encoding MADS box transcription factors (Theißen, 2001; Theißen and Saedler, 2001), but also on the interactions between those genes and other genes in a complex genetic network (e.g. see Irish, 2008 for petal organogenesis in *Arabidopsis*). Moreover, several genes have been identified as being involved in this complex network of interactions to establish zygomorphy in *Antirrhinum* (Luo *et al.*, 1996, 1999; Almeida *et al.*, 1997; Galego and Almeida, 2002; Cubas, 2004), and orthologues of one of those genes have been discovered in papilionoid legumes (Citerne *et al.*, 2006).

According to Irish (2008), some genes appear to play a role in the formation of petal primordia and their later development (e.g. RBE), whereas others appear to act on petal growth (e.g. JAG and ANT), although it is not clear when the latter genes start acting. If the same genetic processes apply to legumes, this would strengthen the hypothesis that apetalous flowers with initiated petals (e.g. *Brachystegia*, *Crudia*) are not homologous to apetalous flowers without initiated petals (e.g. *Colophospermum*) as suggested by Tucker (2001b, 2003). Unfortunately, it is impossible to test whether the taxa with petal primordia give rise to the taxa lacking petal primordia because only four apetalous genera in Detarieae have been studied from an ontogenetic point of view. Tucker (2000d)

invoked the ‘suppression’ of regulatory genes to explain changes of floral patterns, but recent improvements in our understanding of the genetic basis of floral development suggest otherwise. Small changes in *cis*-regulatory elements and *trans*-regulatory regions may lead to dramatic effects on the expression (in time and place) of a developmental gene, which will in turn affect the expression of other genes in the developmental regulatory network (Lynch and Wagner, 2008). Several causes can thus lead to the same result (i.e. lack of expression of a developmental gene at a specific time and place) and, as such, structural homology in floral characters could be the result of genetic non-homology. This could explain why similar developmental patterns occur repeatedly during the evolution of the resin-producing Detarieae.

## CONCLUSIONS

Morphology appears to be more in agreement with molecular data than was previously thought on the basis of traditional classifications (Cowan and Polhill, 1981b). Despite a high level of homoplasy, several characters are useful for reconstructing phylogenetic relationships. Among the most promising characters, those from the ovary, fruit and seed should be further investigated.

Although some of the relationships within Detarieae remain poorly resolved, the classification of the tribe should be modified to take into account the groupings suggested by our analyses (Table 2). While the more strongly supported groups are probably correct (sub-tribe Amherstiinae, *Hymenaea* group, *Detarium* group), some others may need further modifications.

## SUPPLEMENTARY DATA

Supplementary data are available online at <http://aob.oxfordjournals.org> and include the complete morphological matrix used for this study.

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## APPENDIX 1

List of specimens used to score morphological characters.

- Amherstia nobilis* Wall., *M.C. Carlson* 513 (F), *s.c.* 596 (L), *Calcutta Botanical Garden s.n.* (L), *M. Fougère-Danezan & M. N. B. Jumaai* 24 (MT), *M. Fougère-Danezan & M.N.B. Jumaai* 29 (MT)
- Aphanocalyx cynometroides* Oliv., *J. Louis* 13815 (K), *J. Louis* 3814 (K), *Le Testu* 8418 (P), *F.J. Breteler* 12868 (WAG)
- Augouardia letestui* Pellegr., *G. McPherson* 15493 (MO), *G. McPherson* 16282 (MO), *G. Le Testu* 2228 (BM), *A.J.M. Leeuwenberg & J.G.M. Persoon* 13651 (P)
- Baikiaea insignis* Benth., *J. Louis* 3464 (US, K), *P.L. Comanor* 1172 (F), *A. Hladik* 1872a (P), *N. Hallé* 2859 (P)
- Baikiaea plurijuga* Harms, *B. de Winter* 3648 (P), *N.B. Zimba et al.* 928 (P)
- Barnebydendron riedelii* (Tul.) J.H. Kirkbr., *B. Krukoff* 5651 (F, MO)
- Bauhinia bohniana* L. Chen, *G. Forrest s.n.* (US), *J.F. Rock* 9045 (US)
- Bikinia letestui* (Pellegr.) Wieringa, *X.M. van der Burgt* 600 (WAG)
- Brachystegia bussei* Harms, *Y.S. Abeid et al.* 1434 (MO), *B.D. Burt* 5004 (US), *C.G. Trapnell* 1807 (P), *H.J. Schlieben* 5898 (P), *P.S. Herendeen & F. Mbago* 20-XII-97-2 (US), *P.S. Herendeen & F. Mbago* 20-XII-97-3 (US), *F.J. Breteler* 11859 (WAG)
- Brownea grandiceps* Jacq., *M. Valverde* 358 (US), *T. Plowman* 13718 (F), *B.J. Pienaar* 218 (WAG)
- Cercis canadensis* L., *T. Burckhardt s.n.* (US), *A.E. Porsild* 23473 (MT)
- Colophospermum mopane* (J. Kirk ex Benth.) J. Léonard, *F. White* 10081 (MO), *H.M. Biegel* 791 (K), *H.D.V. Prendergast HDVP* 618 (K), *J.M. de Aguiar Macedo* 4859 (K), *N.K.B. Robson* 956 (K), *B. de Winter* 3066 (P), *A. de Menezes* 3661 (P), *O. Azancot de Menezes* 1403 (P), *R. Dechamps et al.* 1193 (BR)
- Copaifera coriacea* Mart., *R.M. Harley* 19147 (P), *G. Gardner* 2090 (P)
- Copaifera guianensis* Desf., *R.A.A. Oldeman* B.2594 (P), *B. Maguire* 24015 (P), *J.-J. de Granville et al.* 8166 (BR)
- Copifera langsdorffii* Desf., *W.R. Anderson* 10037 (P), *H.S. Irwin et al.* 18767 (P), *R.M. Harley et al.* 16854 (P), *H.S. Irwin & T.R. Soderstrom* 6898 (WAG)
- Copaifera mildbraedii* Harms, *R. Letouzey* 10725 (P), *R. Letouzey* 12154 (P), *D. Kenfack* 999 (WAG), *F.J. Breteler et al.* 13149 (WAG)
- Copaifera multijuga* Hayne, *A. Ducke* 16910 (P), *G.T. Prance et al.* 14208 (P), *G.T. Prance et al.* 20723 (WAG)
- Copaifera oblongifolia* Mart., *H.S. Irwin et al.* 9500 (P), *H.S. Irwin et al.* 17508 (P), *H.S. Irwin & T.R. Soderstrom* 6050 (BR)
- Copaifera officinalis* L., *J. de Bruijn* 1152 (P, WAG), *J. Léonard* 36 (BR)
- Copaifera salikounda* Heckel, *K.R. Mayer* 204 (US), *L. Ake Assi* 15797 (MO), *J. de Koning* 6970 (WAG), *F.J. Breteler* 13383 (WAG)
- Copaifera trapezifolia* Hayne, *M. Hunger s.n.* (P), *A. Glaziou s.n.* (P), *P.R. Reitz* 5-711 (BR)
- Cryptosepalum tetraphyllum* (Hook. f.) Benth., *F.J. Morton and Gledhill* SL1036 (K), *K. Morton & D. Gledhill* 1036 (WAG)
- Cynometra mannii* Oliv., *W.C. Thompson s.n.* (K), *G. McPherson* 16856 (WAG)
- Daniellia klainei* Pierre ex A. Chev., *A.P. Thomson* 12 (K), *J.M. Reitsma* 1414 (NY), *Hombert* 572 (BR), *F.J. Breteler* 7735 (WAG)
- Daniellia ogea* (Harms) Rolfe ex Holland, *P. Adames* 561 (K), *C.L.M. van Eijnatten* 1341 (WAG), *J. Léonard s.n.* (BR), *A.G. Voorhoeve* 735 (BR)
- Daniellia oliveri* (Rolfe) Hutch. & Dalziel, *W.J.J.O. de Wilde* 625 (K), *W.R. Elliott* 14 (K), *J. Ellenberger* 1053 (P), *W.J.J.O. de Wilde et al.* 4963 (P)
- Daniellia soyauxii* (Harms) Rolfe, *J.J. Wieringa & R.M.A.P. Haegens* 2614 (WAG)
- Detarium macrocarpum* Harms, *A.J.M. Leeuwenberg* 9030 (MO), *G.A. Zenker* 452 (US), *C. Tisserant* 286 (P), *F.J. Breteler* 12528 (WAG)
- Detarium microcarpum* Guill. & Perr., *C.C.H. Jongkind & C.M.J. Nieuwenhuis* 2985 (WAG), *J. Raynal & A. Raynal* 5324 (P)
- Detarium senegalense* J.F. Gmel., *G.P. Cooper* 401 (F), *J.F. Gmel* 57-8-1 (K), *W.E. Broadway* 6917 (F), *s.c.* 1904 (P), *C.R.A. Bambey* 606 (P)
- Dialium guianense* (Aubl.) Sandwith, *B.V. Rabelo et al.* 3118 (US), *D. Neill* 6986 (F), *N. Zamora* 1451 (F), *R. Romero Castaneda* 4789 (US), *T.B. Croat* 20619 (F), *W. Palacios* 1364 (US)
- Eperua bijuga* Mart. ex Benth., *A. Ducke* 16927 (P), *R.L. Froes & G.A. Black* 27281 (P)
- Eperua falcata* Aubl., *S.S. Tillett & C.L. Tillett* 45791 (K), *H. Jimenez-Saa* 14358 (P), *S.A. Mori et al.* 21517 (P), *M.F. Prevost* 1723 (BR)
- Eperua grandiflora* (Aubl.) Benth., *W. Hahn* 3744 (WAG)

Continued

## APPENDIX 1 Continued

- Eperua rubiginosa* Miq., *C. Farney* 1929 (K), *D.B. Fanshawe* 4840 (K), *M. Hoff* 6767 (P), *H.S. Irwin et al.* 57579 (P), *M.J. Jansen-Jacobs et al.* 1437 (P)  
*Eperua schomburgkiana* Benth., *G.T. Prance et al.* 4977 (P), *R.H. Schomburgk* 517 (P)  
*Eurypetalum tessmannii* Harms, *G. McPherson* 16216 (US), *A.M. Louis & F.J. Breteler* 696 (BR), *A.R. Walker s.n.* (P)  
*Eurypetalum unijugum* Harms, *R. Letouzey* 9787 (P), *G. Zenker* 581 (P)  
*Gilletiodendron pierreanum* J. Léonard, *J.J.F.E. de Wilde* 693 (MO), *J.J. Wieringa & R.M.A.P. Haegens* 2289 (WAG), *G. McPherson* 16758 (BR)  
*Goniorrhachis marginata* Taub., *G. & M. Hatschbach et al.* 61982 (MO, BR), *G.P. Lewis et al.* 1976 (K), *G.P. Lewis et al.* 1909 (K), *G.P. Lewis & S.M.M. de Andrade* 1994 (BR)  
*Gossweilerodendron balsamiferum* (Vermoesen) Harms, *G.P. Lewis* 2430 (K), *R. Forressaint* 214 (K), *F.J. Breteler* 10601 (WAG), *J.D. Kennedy* 554 (P), *C. Maudoux* 988 (BR)  
*Guibourtia arnoldiana* (De Wild. & T. Durand) J. Léonard, *J. Wagemans* 1346 (BR)  
*Guibourtia coleosperma* (Benth.) J. Léonard, *N.B. Zimba et al.* 830 (WAG), *O. Azancot de Menezes* 889 (P)  
*Guibourtia demusei* (Harms) J. Léonard, *A. Corbisier* 1479 (US), *J. Leonard* 428 (K), *J. Louis* 9889 (K), *L. White* 1095 (WAG), *R. Letouzey* 10593 (P)  
*Guibourtia ehie* (A. Chev.) J. Léonard, *C. Vigne* 4916 (K), *G. McPherson* 15444 (WAG)  
*Guibourtia hymenaeifolia* (Moric.) J. Léonard, *L. Bernardi* 18946 (P)  
*Guibourtia pellegriniana* J. Léonard, *T. Levry* 33591 (K), *F. Dowsett-Lemaire* 1578 (BR), *G. McPherson* 17057 (BR)  
*Guibourtia tessmannii* (Harms) J. Léonard, *G.M.P.C. Le Testu* 9555 (P), *L. White* 1536 (WAG)  
*Hardwickia binata* Roxb., *M. Anderson* 28 (P), *V. Jacquemont* 237 (P)  
*Hyloidendron gabunense* Taub., *J. Olorunfemi FHI* 43934 (K), *J. Olorunfemi FHI* 30693 (K), *J.J.F.E. de Wilde* 8214 (MO), *Gauchotte* 1791 (P), *A.M. Louis & F.J. Breteler* 464 (P)  
*Hymenaea courbaril* L., *A.C. Smith* 3109 (US), *J. Saunders* 603B (F), *M.J. Jansen-Jacobs* 1365 (US), *G. E. Schatz* 764 (MO), *M.F. Prévost* 3737 (P), *D. Plouvier* 21 (BR), *W. Milliken & R. Miller* 822 (BR), *F.J. Breteler* 4268 (WAG)  
*Hymenaea eriogyne* Benth., *R.M. Harley* 19016 (P)  
*Hymenaea oblongifolia* Huber, *J. Schunke* V. 2129 (US), *R. E. Schultes & I. Cabrera* 14817 (K), *B.A. Krukoff* 6323 (BR)  
*Hymenaea parvifolia* Huber, *G.T. Prance & T.D. Pennington* 1914 (P), *B.A. Krukoff* 6250 (BR), *W. Milliken & R. Miller* 771 (BR)  
*Hymenaea stigonocarpa* Mart. ex Hayne var. *pubescens* Benth., *R.M. Harley* 19831 (P), *T.M. Pedersen* 11122 (L)  
*Hymenaea stigonocarpa* Mart. ex Hayne var. *stigonocarpa*, *R.M. Harley* 18644 (P)  
*Hymenaea verrucosa* Gaertn., *G.E. Schatz et al.* 2345 (US), *J.L. Zarucchi et al.* 7419 (US), *P.S. Herendeen & F. Mbago* 11-XII-97-3 (US), *R.B. & A.J. Faden* 77-771 (US), *J.L. Zarucchi et al.* 7419J (BR), *A. Gomes e Sousa* 3370 (BR)  
*Hymenostegia floribunda* (Benth.) Harms, *G. McPherson* 15843 (MO, WAG), *J.M. & B. Reitsma* 1410 (MO)  
*Kingiodendron alternifolium* (Elmer) Merr. & Rolfe, *E.F. Solevin* 27392 (P), *M.D. Sulit* 6432 (BR)  
*Kingiodendron pinnatum* (Roxb. ex DC.) Harms, *D.H. Nicolson et al.* HFP 2871 (US), *A. Kostermans* 28130 (L, P), *Calcuta Botanical Garden s.n.* (L)  
*Kingiodendron platycarpum* B.L. Burt, *A.C. Smith* 7549 (L), *A.C. Smith* 8185 (P)  
*Loesenera kalantha* Harms, *A.G. Voorhoeve* 961 (MO), *G.P. Cooper* 461 (F), *A. de Gire* 303 (WAG)  
*Neopaloxylon madagascariense* (Drake) Rauschert, *D.K. Harder* et al. 1681 (P), *F. Chauvet* 98 (P)  
*Oxystigma buchholzii* Harms, *S.R.F.K. Bena* 1609 (P), *R. Letouzey* 11916 (P), *J. Léonard* 229 (P)  
*Oxystigma gilbertii* J. Léonard, *J. Dubois* 195 (BR), *J. Dubois* 96 (BR), *J.J.F.E. de Wilde* 8375 (WAG)  
*Oxystigma mannii* (Baill.) Harms, *C. Doumenge* 307 (MO), *R. Letouzey* 14933 (P), *D.W. Thomas* 2355 (P), *D.W. Thomas* 2353 (P)  
*Oxystigma msou* Harms, *L.L. Bancroft s.n.* (K), *P.S. Herendeen & F. Mbago* 18-XII-97-1 (US), *R.B. & A.J. Faden* 74/1265 (K), *Kisena & Shabani* 538 (WAG), *Ruffo & Kmari* 2253 (WAG)  
*Oxystigma oxiphyllum* (Harms) J. Léonard, *J.L.P. Louis* 977 (P), *C. Davio* 50 (BR), *C. Wilks* 2563 (BR), *F.J. Breteler et al.* 11264 (WAG)  
*Peltogyne confertiflora* (Mart. ex Hayne) Benth., *E.P. Heringer* 16633 (US), *E.P. Heringer & F. Eiten* 14102 (US), *E.P. Heringer* 13147 (K), *H.S. Irwin et al.* 31466 (US), *H.S. Irwin et al.* 212119 (WAG)  
*Peltogyne floribunda* (Kunth) Pittier, *M.J. Jansen-Jacobs et al.* 2711 (P), *M.J. Jansen-Jacobs et al.* 2652 (P)  
*Peltogyne paniculata* Benth. subsp. *pubescens* (Benth.) M.F. Silva, *M.J. Jansen-Jacobs et al.* 2646 (P), *J.J. Wurdack & L.S. Adderley* 43505 (P), *R.A.A. Oldeman* 1095 (P)  
*Peltogyne pauciflora* Benth., *R.M. Harley et al.* 16400 (P), *R.M. Harley et al.* 16146 (P)  
*Peltogyne venosa* (Vahl) Benth. subsp. *densiflora* (Spruce ex Benth.) M.F. Silva, *J. Thiel* 687 (P), *G.T. Prance et al.* 15205 (P)  
*Prioria copaifera* Griseb., *R. Foster* 927 (F), *T. B. Croat* 6860 (F), *P. Warner* 498 (P)  
*Pseudosindora palustris* Sym., *J. Léonard s.n.* (BR), *Ashton & Kaling* 5690 (WAG), *Tahir* 12268 (L)  
*Schotia afra* (L.) Thunb., *H.S. Gentry & A.S. Barclay* 18896 (US), *C.G.G.J. van Steenis* 23890 (L), *J.F. Drège s.n.* (P)  
*Schotia brachypetala* Sond., *B.M. Browning et al.* 42 (MO), *H.J. Schlieben* 7245 (F), *J.L. Sidney* 3458 (US), *T. Muller* 677 (K), *G. Dehn* 40239 (P), *Willd* 4122 (BR), *D. Zunguze et al.* 610 (BR)  
*Schotia latifolia* Jacq., *L.E. Codd* 9778 (K), *R.D.A. Bayliss* 8397 (US, BR), *R.D.A. Bayliss* 6952 (US), *P. McOwan* 77 (P), *Codd* 38 (BR)  
*Sindora bruggemanni* de Wit, *Teysmann* 3697 (A), *J.J.F.E. de Wilde* 3967 (WAG), *H.C.D. de Wit* IB77 (L)  
*Sindora coriacea* (Baker) Prain, *S. Phusomsaeng* 223 (L), *Ang Khoon Cheng* 27819 (L)  
*Sindora klaineana* Pierre ex Pellegrin, *G. McPherson* 16828 (BR), *F.J. Breteler et al.* 11403 (WAG), *P. Sita* 3643 (P)  
*Sindora siamensis* Teysm. ex Miq., *D.D. Soejarto et al.* 6006 (L), *J.F. Maxwell* 76-185 (L), *J.F. Maxwell* 92-375 (L)  
*Sindora supra* Merr., *M. Curran* 10653 (P), *M. Ramos* 13230 (P), *M.D. Sulit* 5669 (L)  
*Sindora wallichii* Benth., *Ambriansyah & Z. Arifin* 609 (L), *Ambriansyah & Z. Arifin* 427 (L)  
*Sindoropsis letestui* (Pellegr.) J. Léonard, *G. Le Testu* 2237 (BM, BR), *G. McPherson* 13720 (F), *G. McPherson* 16302 (MO, US, BR), *F.J. Breteler* 12143 (WAG)  
*Siemonocoleus micranthus* Harms, *D.J. Harris et al.* 1067 (MO), *G. Le Testu* 7968 (BM), *R.A.A. Oldeman* 695 (K, P), *R.A.A. Oldeman* 383 (K, P, BR), *F.J. Breteler* (BR)  
*Tessmannia africana* Harms, *G. McPherson* 16311 (MO), *J. Louis* 9230 (US), *F.J. Breteler et al.* 13322 (WAG), *H. Butler* 1364 (BR), *J.J.F.E. de Wilde* 7716 (P), *R. Letouzey* 13569 (P)  
*Tessmannia anomala* Harms, *T. B. Hart* 1160 (MO), *C. Wilks* 2702 (BR), *J. Louis* 9790 (P)  
*Tessmannia dewildemania* Harms, *J. Léonard* 4686 (P), *J.M. Reitsma* 2930 (WAG), *F.J. Breteler et al.* 14618 (WAG)  
*Tessmannia lescrauwaetii* Harms, *Flamigni* 9521 (K), *G. Le Testu* 8562 (BR)

## APPENDIX 2

Morphological characters used. All multistate characters are treated as unordered. Some states may not appear in the matrix (Supplementary Data, available online) but have been kept to ease comparison with other studies on Caesalpinioideae.

- 1 Vestured pits: absent (0), present (1).
- 2 Compound leaf structure: multifoliolate (0), bifoliolate (1), unifoliolate (2).  
Characters 3 and 4 have been considered as independent because some imparipinnate leaves have leaflets with an opposite insertion, whereas others have leaflets with an alternate insertion.
- 3 Pinnation type: imparipinnate (0), paripinnate (1), distal leaflet sub-terminal (2). Leaves with a sub-terminal leaflet exhibit an extension of the rachis beyond the distal-most leaflet, which is inserted on one side of the rachis.
- 4 Leaflet insertion: opposite or sub-opposite (0), alternate (1), variable among leaves on a branch (2). Minor variation in placement of leaflets especially near base and apex of leaf is disregarded; the character is judged in the central portion of the leaf.  
Characters 5 and 6 describe leaflet symmetry.
- 5 Primary vein: straight (0), curved (1).
- 6 Primary vein position: central (0), near distal margin (1), near proximal margin (2).
- 7 Rachis (and/or petiole) grooved adaxially: absent (0), present (1). This character can be difficult to interpret in taxa in which the rachis is prone to collapse on drying. The groove is usually less pronounced or interrupted at leaflet attachment points.
- 8 Rachis (and/or petiole) winged between leaflets pairs: absent (0), present (1).
- 9 Leaflet shape: ovate or obovate, lamina larger on one section of the leaflet only (0), oblong, lamina larger on one part of the leaflet centred on the middle of this one (1).
- 10 Leaflet base: acute (0), obtuse to truncate (1), cordate (2), oblique (3).
- 11 Leaflet base: equal (0), unequal, one of the two margins of the lamina attach lower than the other on the petiolule (1).
- 12 Leaflet apex emarginate or retuse: absent (0), present (1).
- 13 Leaflet apex mucronate: absent (0), present (1).  
Glands are surrounded by a raised rim and show a pore or a concavity in their centre.
- 14 Apical gland: absent (0), present (1). These glands are located on the primary vein on the apex or immediately below. Several species have a bulge in this position but lack a pore; these are considered to lack this character. Other species have this gland but not on every leaflet and have been considered as having it.
- 15 Marginal gland: absent (0), present (1). These glands are located on the leaflet margin on the basal part of the leaflets.
- 16 Crater-like glands on abaxial lamina: absent (0), present (1). These structures are different from the gland dots (which do not show any raised rim) and have sometimes been referred to as 'domatia' in the literature. Crater-like glands are often located on secondary veins or veins of less importance. Their location is consistent within a species.
- 17 Leaflets petiolulate: petiolulate (0), sessile to sub-sessile (petiolule <1 mm long) (1).
- 18 Twisted petiolules: absent (0), present (1). The twisted impression is given by a ridge coming from the distal margin of the lamina to the base of the petiolule on the proximal side.
- 19 Stipule form: scale-like (0), foliose (1). Stipules are considered as foliose when they have a leaf-like lamina and several conspicuous veins that are often branching.
- 20 Stipule base: straight (0), auriculate (1), cordate (2).
- 21 Stipule insertion: lateral (0), intrapetiolar (1). Intrapetiolar stipules are inserted obliquely such that the proximal edge is between the petiole base and the axillary bud.
- 22 Stipule pairs connate basally (intrapetiolar fusion): absent (0), present (1).
- 23 Secondary venation: brochidodromous (0), semi-craspedodromous (1), intramarginal vein (2), cladodromous to craspedodromous (3). For a description of the different states see the *Manual of leaf architecture* (Leaf Architecture Working Group, 1999).
- 24 Leaflet marginal vein: absent (0), present (1).
- 25 Primary venation: pinnate, a single well-defined primary vein present (0), actinodromous, several veins of equal thickness radiate from the base of the lamina (1).
- 26 Basal acrodromous vein: absent (0), present (1). An acrodromous vein is a secondary vein on the proximal side having an ascendant trajectory from the primary vein and then showing a sudden inflexion toward the margin of the leaflet.
- 27 Primary vein continuous to the apex: present (0), absent, ramifies and is lost before reaching the apex (1).
- 28 Trichomes on rachis and/or petiole: absent (0), straight (1), uncinata (2).
- 29 Trichomes on peduncles and/or pedicels: absent (0), straight (1), uncinata (2).
- 30 Inflorescence structure: indeterminate (raceme, spike, panicle, head) (0), determinate (cymose) (1), flowers solitary (2).
- 31 Inflorescence structure: simple (0), compound (1).
- 32 Flower arrangement in inflorescence: spiral (0), distichous (1).
- 33 Pedicel: present (0), absent (1).
- 34 Pedicel jointed: absent (0), present (1). The pedicel shows a pronounced weak point at a consistent position and the unfertilized flowers fall down leaving a piece of the pedicel always of the same size on the peduncle.
- 35 Bracteoles: caducous (0), persistent up to anthesis (1).
- 36 Bracteoles enclosing late flower bud: absent (0), present (1). Bracteoles are as big as the bud and enclose the bud up to anthesis.
- 37 Bracteoles aestivation: distant (0), valvate (1), imbricate (2), adaxial surfaces touching (3).
- 38 Bracteoles position on pedicel (observed on late buds or flowers right after anthesis): low to middle (0), high, attached at the base of the calyx or the hypanthium (1).
- 39 Bracteoles fusion: free (0), connate at least at base (1).
- 40 Flower rotated in development, pedicel twisted: absent (0), present (1).
- 41 Sexuality: perfect (flowers all bisexual) (0), staminate flowers present (1). Among the species observed here, the species of the genus *Kingiodendron* are the only ones not having perfect sexuality (flowers all bisexual). Breteler (1999) also recorded *Eurypetalum tessmannii* as having this state but we have not been able to see any differences between the flowers observed for this species. Breteler (1999) recorded the species of the genus *Kingiodendron* as having both staminate and bisexual flowers (on the same individual), but Verdcourt (1979) considered *Kingiodendron pinnatum* as having functionally unisexual flowers (male or female). Our observations seem to confirm Verdcourt's statement, but more specimens should be observed.

Continued

## APPENDIX 2 Continued

- 42 Hypanthium: absent (0), present (1).
- 43 Hypanthium shape: cup shaped (0), tubular (1).  
Studies on floral ontogeny (Tucker, 2000a, b, c, 2001a, b, 2002a, b, 2003) demonstrate that in *Sindora*, *Schotia* and a couple of species of the Amherstieae clade five sepals are initiated but that the two adaxial sepals fuse late in ontogeny, resulting in four apparent sepals. It is highly probable that all the Detarieae *s.l.* with four sepals undergo this kind of phenomenon. Indeed, several species of the Amherstieae clade have a bilobed or bifurcate adaxial sepal which could be the result of an incomplete fusion. Moreover, the sepal supposed to be the result of the fusion is always in the median adaxial position, which corresponds to the position of the two lateral adaxial sepals in other Fabaceae. When the floral ontogeny is unknown, species having a bigger median adaxial sepal have been considered as having undergone a fusion of the two adaxial sepals. For three genera (*Hardwickia*, *Colophospermum* and *Gossweilerodendron*) of the resin-producing Detarieae, this character has been considered as unknown because *Hardwickia* and *Colophospermum* have fewer than four sepals, making any hypothesis of homology difficult, and *Gossweilerodendron* has four sepals of equal size.
- 44 Sepal number at initiation: five (0), four (1), three (2), two (3), one (4).
- 45 Fusion of the two adaxial sepals: absent (0), present (1).
- 46 Fusion of others sepals: free to base of flower or hypanthium (0), connate at least in basal portion excluding hypanthium (1).
- 47 Calyx aestivation: quincuncial (0), valvate (1), distant (2).
- 48 Sepal thickness: uniform (0), narrow thin margin, bent or foiled (the covered sepal shows a foil followed by a thin margin with a different texture, the margin of the covering sepal is imbricate in this foil) (1), wide thin margin never foiled (2).
- 49 Calyx base gibbous on one side (asymmetrical): absent (0), present (1).
- 50 Outer surface of sepal lobe bearing simple hairs: absent (0), present (1).
- 51 Inner surface of sepal lobe bearing simple hairs or bristles: absent (0), present (1).
- 52 Petal number at anthesis, including vestigial petals: five (0), four (1), three (2), two (3), one (4), zero (5).
- 53 Size of the median petal blade compared with lateral ones: uniform (0), median bigger than the others (1), median smaller than the others (2).
- 54 Size of the lateral petals: uniform, all vestigial or all developed (0), the abaxial ones smaller than adaxial ones (1), the abaxial ones larger than the adaxial ones (2).
- 55 Petal aestivation in late bud: imbricate ascending, standard innermost (0), imbricate descending, standard outermost (1), valvate (2).
- 56 Petal clawed: absent (0), median petal clawed (1), four lateral petals clawed (2), all petals clawed (3).
- 57 Androecium type, total number of parts including staminodes: diplostemonous (0), haplostemonous (1), less than haplostemonous (2), more than diplostemonous (3).
- 58 Staminodes: absent (0), present (1).
- 59 Filament connation: all connate in a tube (0), all connate in a sheath (open on one side) (1), nine connate and one free on the adaxial side (2), all free (3).
- 60 Filament relative length as compared with the perianth at anthesis: shorter or equal to the perianth (0), longer than the perianth (1).
- 61 Simple hairs on filament: absent (0), present (1).
- 62 Anther attachment: basifixed (0), dorsifixed (1).
- 63 Fertile anther size: uniform (0), dimorphic or heteromorphic (1).
- 64 Simple hairs on anther: absent (0), present (1).
- 65 Anther base markedly sagittate: absent (0), present (1).
- 66 Anther dehiscence orientation: introrse (0), latrorse (1), extrorse (2).
- 67 Prolongation of anther connective: absent (0), distal prolongation (1), proximal prolongation (2).
- 68 Anther shape: square (0), rectangular (1).
- 69 Simple hairs on gynoeceum: absent (0), present (1).
- 70 Stipitate ovary: stipe absent (0), stipe present and central (1), stipe present and adnate to the adaxial side of the hypanthium or receptacle (2).
- 71 Style at anthesis: slender, as long or longer than ovary (0), short and stout, clearly shorter than ovary at anthesis (1), absent (2), short but not stout (3).
- 72 Style: curved, bent or coiled abaxially (0), curved, bent or coiled adaxially (1).
- 73 Style adaxial groove: absent (0), present (1).
- 74 Stigma shape: truncate, stigma non-papillose (0), peltate (1), crateriform (2), tubular (3), funnel shaped (4), capitate, more or less bulging but always papillose (5), attenuate (6).
- 75 Ovule number: consistently one (0), consistently two (1), numerous (always more than two) (2).
- 76 Fruit wing: absent (0), placental vascularized wing (1), non-vascularized placental wing (2), vascularized wing on both sutures (3), distal wing (4), proximal wing (5).
- 77 Amyloids in seed (Kooiman, 1960): absent (0), present (1).
- 78 ‘Zwischenkörper’ on pollen: absent (0), present (1). ‘Zwischenkörper’ are pectic structures associated with the pores of pollen and are detected by a positive reaction to Alcian blue (Banks, 2003).
- 79 Exinous projection over the centre of the pollen aperture (Banks and Klitgaard, 2000; Banks, 2003; Banks *et al.*, 2003): absent (0), present (1).
- 80 Protruding aperture on pollen (Banks and Klitgaard, 2000; Banks, 2003; Banks *et al.*, 2003): absent (0), present (1).
- 81 Pollen (Banks and Klitgaard, 2000; Banks, 2003; Banks *et al.*, 2003): triporate or tricolpate (0), pantoporate (1).
- 82 Axial canals in the wood (Gasson *et al.*, 2003): absent (0), diffuse (1), tangentially organized (2), traumatic (3).
- 83 Germination (Léonard, 1957, 1994; Watson and Dallwitz, 1993): epigeal (0), hypogeal (1).
- 84 Appendices on the collar of seedling (Léonard, 1957, 1994): absent (0), present (1).
- 85 Cotyledons on seedling (Léonard, 1957, 1994): spread at ground level (0), spread above ground (1), remain in the seed at ground level (2).
- 86 Two first leaves (Léonard, 1957, 1994): alternate (0), opposite (1).
- 87 Fruit (Gunn, 1991): indehiscent (0), dehiscent on both sutures (1), dehiscent on both sutures with valves coiled (2), dehiscent at apex only (3), dehiscent on ventral suture only (4).
- 88 Endocarp (Gunn, 1991): thin (0), thick, fleshy (1).
- 89 Aril (Léonard, 1957, Gunn, 1991): absent (0), present (1).