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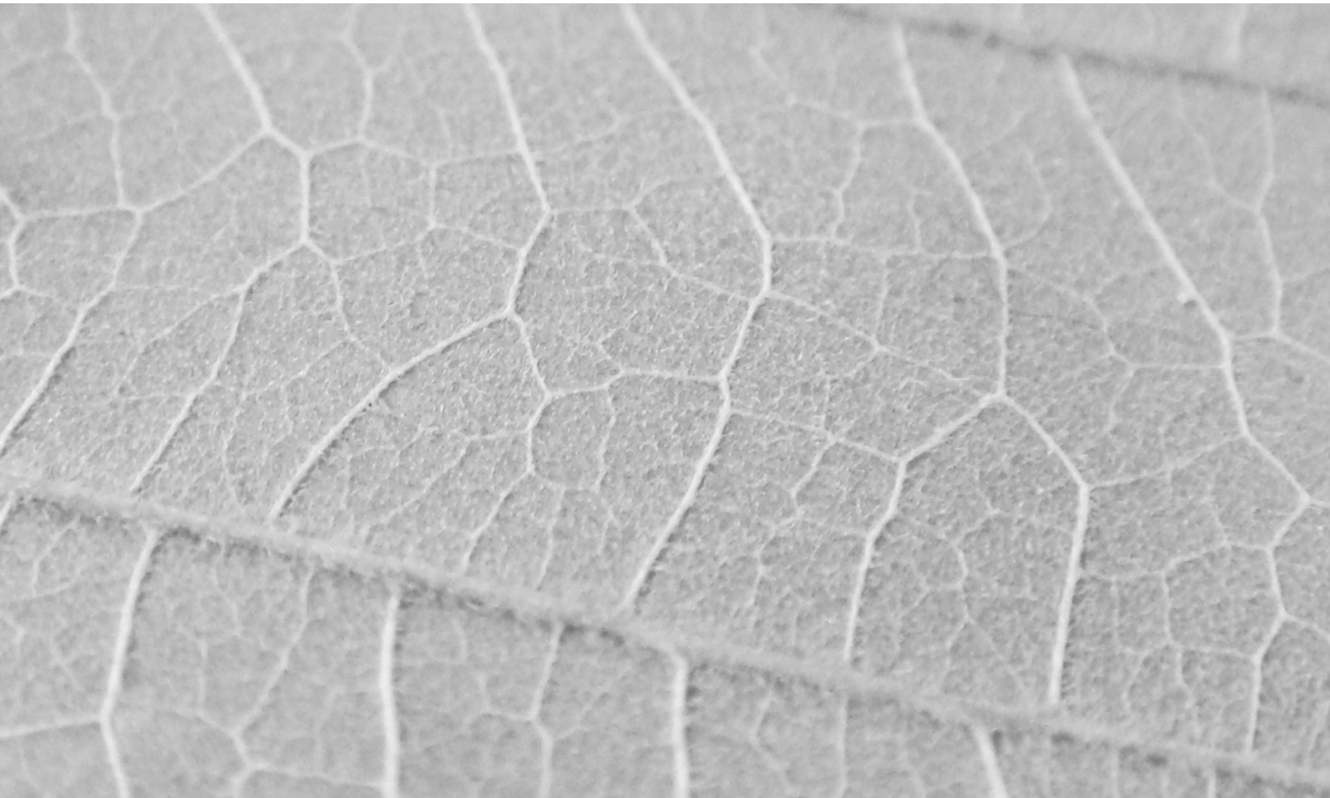
Title: Systematics and biogeography of Aganope, Brachypterum and Derris (Fabaceae) in Asia
Issue Date: 2013-11-28

Chapter 4

Molecular and mophological phylogenetic reconstruction reveals a new generic delimitation of Asian *Derris* (Fabaceae): reinstatement of *Brachypterum* and synonymisation of *Paraderris* with *Derris*



Molecular and mophological phylogenetic reconstruction reveals a new generic delimitation of Asian *Derris* (Fabaceae): reinstatement of *Brachypterum* and synonymisation of *Paraderris* with *Derris*

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Resubmitted after revision to Taxon

Abstract

The genus *Derris* is a problematic taxon within the tribe Millettieae because of the various generic circumscriptions proposed by different authors. Previous molecular phylogenetic studies proved *Derris* s.l. to be polyphyletic and thus unacceptable as a taxon. Moreover, the most recent circumcription of *Derris* s.s. was also not monophyletic. In this study, 29 qualitative morphological characters are analyzed together with the molecular data of our earlier studies. The combined datasets confirm the monophyly of *Brachypterum* and show it to be distinct at the generic level with as synapomorphies: presence of stipellae, more than five flowers per brachyblast, tubular and (or) lobed floral disk, seven to 12 ovules and one-winged pods with obvious seed chambers when dry. In this study, *Paraderris* appeared to be a well supported monophyletic group nested within *Derris* s.s., supported by many synapomorphies such as the long and slender brachyblasts with relatively large flowers borne apically, presence of basal callosities and hairy anthers. *Derris* s.s. only has two synapomorphies, the liana habit and 2-winged pods. Other morphological characters used for previous generic circumscriptions appeared to be based on combinations of plesiomorphies. However, in order to maintain the monophyly of *Derris* s.s., *Paraderris* has to be synonymised with *Derris* s.s., which broadens the generic circumscription for *Derris* s.s. No infrageneric classification of *Derris* s.s. will be provided, because of low support for clades and lack of obvious apomorphies for several clades. Taxonomic treatment and nomenclatural changes are presented where necessary.

Keywords *Aganope*; Asiatic *Derris*; *Brachypterum*; character reconstruction; molecular and morphological phylogeny; *Paraderris*

Introduction

Systematics of legumes are of major importance for not only understanding the evolutionary history, i.e., the origin and diversification of this ecologically and economically important family, but also to provide a predictive classification system that reflects evolution (Systematic Agenda, 2000). Ten years after the Third International Legumes Conference in 1992, phylogenetic studies of legumes using molecular data have advanced from a few tentative inferences based on few, small datasets into an era of much larger analyses based on multiple sequences that provide greater resolution and confidence (Wojciechowski, 2003). Nowadays, DNA sequence data are the main information source more commonly used for the reconstruction of evolutionary histories of legumes and other Angiosperms than morphological information as they can potentially provide a greater number of informative characters (Hillis, 1987; Wortey and Scotland, 2006), which generally increase the phylogenetic accuracy (Hillis, 1987, 1998). Moreover, molecular data reflect gene-level changes, and thus were believed to reflect true phylogenies better than morphological data only (Singh, 2006). This does not mean that morphological data are meaningless, but sometimes in legume systematics, for example the tribe Millettieae, relationships among genera have been notoriously difficult to unravel based on traditional morphological evidence (Hu, 2000; Schrire, 2005). The unsuccessfulness of an attempt to reconstruct the phylogeny of Millettieae based on morphological data was also mentioned by Geesink (1984), whose study of this tribe is still the most comprehensive until now. Moreover, homology of morphological characters is often difficult to interpret accurately without time-consuming ontogenetic and anatomical studies.

Derris Lour. is a good example of a problematic genus within the tribe Millettieae. Due to several generic circumscriptions proposed by various authors, the genus is equivocally recognised by its liana habit, imparipinnate leaves with opposite leaflets, pseudoracemoid/pseudopaniculate inflorescences with whitish or pinkish flowers, indehiscent, usually flat and winged pods, and by accumulation of chemical compounds used as insecticide or fish poison. Many "*Basal Millettoid and Phaseoloid*" genera (currently informally recognized, Gasson et al., 2004; Schrire, 2005), i.e., the palaeotropical *Aganope* Miq. (including *Ostryoderris* Dunn and *Xeroderris* Roberty), *Leptoderris* Dunn and *Ostryocarpus* Hook.f., as well as the neotropical genus, *Deguelia* Aublet, were once considered to be closely related to or were even synonymised with *Derris*, here referred to as *Derris* sensu lato (Bentham, 1860; Thothathri, 1961, 1982). However, many recent molecular studies (Lavin et al., 1998; Hu et al., 2000, 2002; Kajita et al., 2001; Da Silva et al., 2012; Sirichamorn et al., 2012b) have shown that they are distantly related. These results confirm the idea of Geesink (1984), who proposed to raise many infrageneric taxa in *Derris* s.l. to generic level, e.g., *Brachypterum*

(Wight & Arn.) Benth., *Deguelia*, *Ostryocarpus* and *Paraderris* (Miq.) Geesink. One remaining question is the relationship between the Asian *Derris*-like genera i.e. *Brachypterum*, *Derris* s.s. and *Paraderris*, because only insufficient samples of these taxa were included in molecular phylogenetic reconstructions. Sirichamorn et al. (2012b) made more comprehensive phylogenetic analyses based on DNA sequences for which many more species were sampled. The cladogram showed, surprisingly, that *Brachypterum* is monophyletic, clearly separated from *Derris* and should be reinstated as a genus. On the other hand, *Paraderris* (with the exclusion of *Derris (P.) laotica* Gagnep.) appeared to be a weakly supported monophyletic group within *Derris* and should thus be synonymised with *Derris*. These results are in contrast with the generic concept proposed by Adema (2000) and followed by Sirichamorn et al. (2012a), who recognised *Derris* and *Paraderris* as distinct genera and *Brachypterum* as a part of *Derris*. This contradiction may indicate that the morphological characters used in previous traditional classifications are perhaps homoplastic. Although DNA sequence data have resolved phylogenetic relationships, the inclusion of morphological data in phylogenetic analysis is still necessary, or at least desirable (De Queiroz et al., 1995) to be used as a "reality check" for molecular results, to study character evolution (Bremer, 1988), or simply to make taxa recognisable. In this study the phylogenetic analyses based on a combination of both morphological and molecular data will be used (1) to check the phylogenetic relationships of Asian *Derris* as proposed by Sirichamorn et al. (2012b), (2) to discuss trends in character evolution with respect to the key characters used for generic delimitation, (3) to compare the total evidence phylogeny with traditional classification and (4) to create a new classification where necessary.

Materials and Methods

Taxon sampling—The dataset comprised 73 samples of 67 species and is similar to the one used in Sirichamorn et al. (2012b). The taxa do not only represent the *Derris*-like species, but also species of various other genera to complete the phylogeny of tribe Millettieae, because some of the *Derris*-like genera are phylogenetically far apart. The specimen vouchers with GenBank accession numbers, the morphological data matrix and the list of morphological characters are shown in Appendices 4-1 to 4-3, respectively.

Molecular and morphological data— Four molecular markers were sequenced, chloroplast *trnL-F* IGS, *psbA-trnH* IGS and *trnK-matK* ORF and nuclear ITS/5.8S. See Sirichamorn et al. (2012b) for details about DNA extraction, sequencing, and alignment.

In total 29 morphological characters representing six vegetative (characters 1–4, 25 and 27), 22 reproductive traits (characters 5–24, 28, 29) and the colour of dry specimens (character 26) were coded for the phylogenetic analyses. The morphological data matrix was mainly based on the examination of herbarium specimens (K, L, P, WAG), while field and cultivated specimen observations provided a secondary source. Revisions of genera in the Millettieae and Dalbergieae (Bentham, 1860; Buijsen, 1988; Geesink, 1984; Ridder-Numan and Kornet, 1994; Dixon, 1997; Schrire, 2000) and also data from Floras (Miquel, 1855; Baker, 1878; Ridley, 1922; Rudd, 1991; Phan and Vidal, 2001; Wei et al., 2008) were used to code additional groups of Leguminosae. When possible, morphological characters were assessed or validated from several herbarium specimens of each species.

Alignment and phylogenetic analyses— Binary or multistate coding was used for the morphological characters. The presence of multiple states per taxon were treated as polymorphisms when they occurred within one species. All characters were coded as unordered and of equal weight, thus using Fitch parsimomy (Fitch, 1971). DNA sequence alignments were made with Bioedit v. 7.0.9 (Hall, 1999) using CLUSTAL W Multiple alignment (default settings; Thompson et al., 1994) with subsequent manual adjustment. Gaps were coded as present/absent (1/0) characters, following the simple coding model of Simmons and Ochoterena (2000) and ambiguously aligned nucleotides were excluded. *Dalbergia lanceolaria* L.f. was specified as outgroup (Sirichamorn et al., 2012b). The analysis based on only morphological characters was performed with PAUP* v.4.0b10 (Swofford, 2003), using heuristic search, with 10 random addition sequences and TBR branch swapping. Bootstrap support was calculated from 1000 bootstrap replicates, holding 10 trees per replicate, with the same settings as the heuristic search. Unfortunately, the MP analysis yielded more than 50,000 most parsimonious trees and the strict consensus tree (not presented) showed little resolution (see Discussion). The analyses of the combined morphological and molecular dataset were subsequently performed using parsimony (also with PAUP* v.4.0b10) and Bayesian Inference (MrBayes v.3.1.2; Ronquist and Huelsenbeck, 2003). All settings were as in Sirichamorn et al. (2012b). The results of the combined, total evidence data were compared with the purely molecular based phylogeny by Sirichamorn et al. (2012b).

Mesquite v.2.7.5 (Maddison & Maddison, 2011) was used to map morphological characters on the majority rule consensus tree of al post-burn-in trees from the Bayesian analysis of the combined molecular datasets (Fig. 4-1B).

Throughout this manuscript all generic and species names will be used as proposed in the nomenclatural part in which an improved classification is presented.

Results

Phylogenetic reconstruction based on combined morphological and molecular datasets— The combined matrix yielded two most parsimonious cladograms of 5192 steps, with a CI of 0.56 and RI of 0.76 (Table 4-1). The strict consensus tree (not shown) of the combined morphological and molecular data set shows a topology and branch support similar to those found in the molecular analysis by Sirichamorn et al. (2012b), although bootstrap support for the *Paraderris* subclade, "DP", was much higher (compare Fig. 4-1A and 4-1B). The majority rule consensus Bayesian tree of the combined dataset is shown in Fig. 4-1A. This tree is slightly more resolved than the one obtained from the Bayesian analysis of the molecular data (Fig. 4-1B) in Sirichamorn et al. (2012b) as recognizable in the *Brachypterum* clade (indicated by "B" in Fig. 4-1). The parsimony and Bayesian cladograms of the combined data support the recognition of *Aganope*, *Brachypterum*, *Deguelia*, *Leptoderris*, *Lonchocarpus* and *Philenoptera* as distinct genera clearly apart from Derris and Paraderris (indicated by "D" and "DP" respectively in Fig. 4-1), and the latter two together form a monophyletic clade.

Character mapping analyses— The character state changes of the morphological characters are summarised in Fig. 4-2. Some characters that are considered phylogenetically and taxonomically important synapomorphies are presented in Fig. 4-3 (A–E).

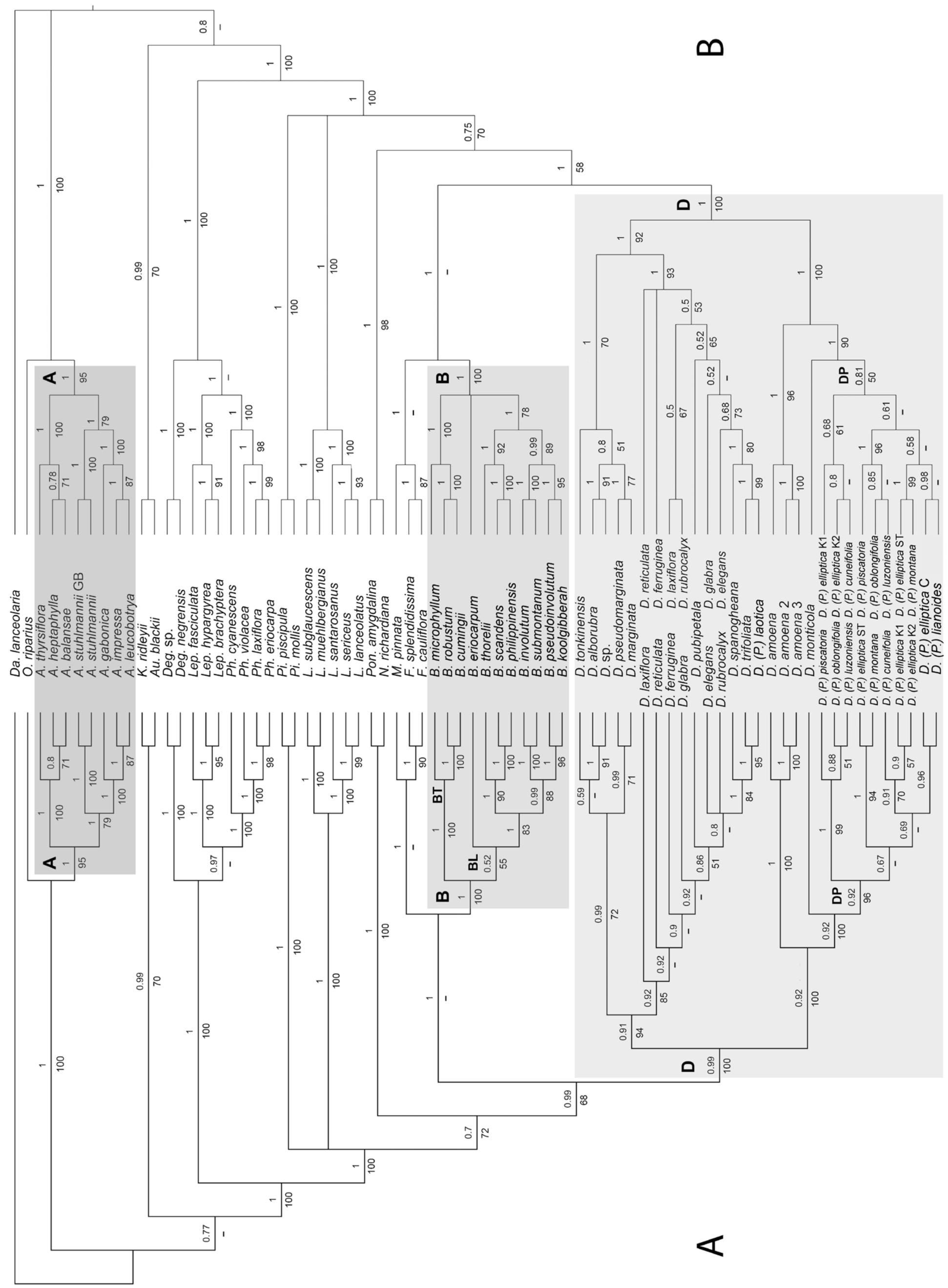
The *Aganope* clade (A in Fig. 4-2) is supported by the following apomorphies: large flowers, standard petals longer than 10 mm [character (char.) 11, state 1, reversal in *A. thyrsiflora* (Benth.) Polhill] and 2-winged pods [char. 21, state 2; Fig. 4-3C, 1-winged parallel in *A. heptaphylla* (L.) Polhill]. The character supporting the Asian *Aganope* subclade (AA in Fig. 4-2) is anthers and connective tissue with hairs (char. 16, state 1). The character supporting the African *Aganope* major subclade (AF in Fig. 4-2) is treelet (shrub)-like habit [character 1, state 1; though multistate for *A. gabonica* (Baill.) Polhill and *A. leucobotrya* (Dunn) Polhill]. The African *Aganope-Ostryoderris* subclade (AO in Fig. 4-2) is supported by the presence of stipellae (char. 3, state 0, Fig. 4-3A) and flower bracts larger than flower buds (char. 9, state 0). The monotypic African *Aganope-Xeroderris* (AX in Fig. 4-2) is supported by tree habit (char. 1, state 0) and the presence of basal callosities on the standard petals (char. 12, state 1).

Characters that support the *Brachypterum* clade (B in Fig. 4-2) are the presence of stipellae [char. 3, state 0, Fig. 4-3A, with three times of a parallel reversal], more than 5 flowers per brachyblast (char. 8, state 2, Fig. 4-3B), tubular or 10-lobed floral disks (char. 17, state 2, Fig. 4-3D, with a reversal in *B. philippinensis*), 7-12 ovules (char. 19, state 3, Fig. 4-3C), 1-winged pods (char. 21, state 1, Fig. 4-3C), and the presence of a seed chamber (char. 22, state 1, Fig. 4-3E).

The *Derris* major clade (D in Fig. 4-2) is supported by a liana habit (char. 1 state 2, Fig. 4-3A) and pods having two wings along both sutures [char. 21, state 2, Fig. 4-3C, with one wing parallel in *Derris trifoliata* Lour., *D. elegans* Graham ex Benth., *D.* (*Paraderris*) *elliptica* (Wall.) Benth., *D.* (*P.*) *montana* Benth., and *Derris* sp.]. The *Paraderris* [excluding *D.* (*P.*) *laotica*] subclade (subclade DP in Fig. 4-2) is supported by elongated brachyblasts (char. 6 state 2) bearing flowers apically (char. 7, state 2), calyx inside with hairs (char. 10, state 1), standard petal longer than 10 mm (char. 11, state 1) and with basal callosities (char. 12, state 1) and hairy anthers (char. 16, state 1).

Discussion

The use of morphological characters in phylogy reconstruction of Asiatic *Derris* and other genera of the tribe Millettieae—Former phylogenetic analyses based on morphological characters only, either showed low resolution (Geesink, 1984), or when more resolution was present, then only few taxa were analysed (Adema, 2000). The latter cladogram deteriorated already when *Deguelia* was added (Adema, 2000). Our analysis of only morphological characters also resulted in a cladogram (not shown) with low resolution. The consistency index (CI) was low (see Table 4-1), which indicated the presence of many homoplastic characters. We used as many morphological characters as possible that were presumed to be phylogeneticly informative or important for taxonomy (Wiens, 2004). However, they were not very helpful in the phylogenetic reconstruction. This is not surprising, because character coding, character conceptualisation and homology assessment are known problems when reconstructing phylogenies using only morphology (Scotland et al., 2003) and often involve subjectivism. In *Derris* and *Brachypterum* the inflorescence type (char. 5) shows intermediate forms that are difficult to code, as they can be panicles with rather apical, short lateral branches or pseudoracemes with basally long brachyblasts [as in B*rachypterum koolgibberah* (F.M. Bailey) Sirich., Adema & Welzen, *Derris alborubra* Hemsl., *D. laxiflora* Benth.


A
B
Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocarpa
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. laxiflora
D. reticulata
D. ferruginea
D. glabra
D. rubrocalyx
D. pubipetala
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) cuneifolia
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) elliptica C
D. (P.) lianoides
A
B
BT
BL
D
DP

and *D. rubrocalyx* Verdc.] or with brachyblasts apically absent (*D. tonkinensis* Gagnep.). These indistinguishable intermediates received the same coding, but are quite likely the result of different, parallel reductions. Moreover, the intermediate inflorescences also affected the interpretation of other characters related to inflorescences such as brachyblast shape (char. 6), flower position on brachyblasts (char. 7), and number of flowers per brachyblast (char. 8). Other problems are characters that require field observations (e.g., reddish pigmentation of young leaves, char. 4), then many unknowns remain, or characters that are more or less continuous and difficult to objectively divide into character states (e.g., leaf texture, char. 25, and position of the seed hilum, char. 23).

Above the species level, morphological ranges become overlapping due to parallel evolution, which results in morphologically complex groups (genera) that are distinguishable only by unique combinations of characters at the most, but sometimes only arbitrarily so (Geesink, 1984).

Contrary to Scotland et al. (2003), Wiens (2004) pointed out the positive role morphological data can play in phylogenetic analyses as they can increase resolution, bootstrap support and phylogenetic accuracy. According to Scotland et al. (2003), the best approach to integrate molecular and morphological data is to map morphological characters onto the molecular phylogeny. In contrast, Wiens (2004) suggested to perform separate analyses to identify areas of strong incongruence between the datasets and then to perform combined analyses, followed by an evaluation of regions in the cladogram “that are strongly contested by different data sets to be clearly resolved until the source of error is identified”. Recent studies have shown that morphology may either be convergent and misleading, thus creating “noise” that blurs phylogenetic signal (Gaubert et al., 2005), or it may provide important support for new clades (Wahlberg et al., 2005; Sierra et al., 2010). Our study indicated that combined molecular and morphological analyses resulted in better resolved cladograms (Fig. 4-1A) than the analysis of only molecular datasets (Fig. 4-1B), e.g., the relationships between tree and liana species of *Brachypterum* are slightly less resolved in the

Fig. 4-1. A: The majority rule consensus Bayesian tree from Bayesian Analysis of all combined molecular and morphological datasets. B: The majority rule consensus Bayesian tree from Bayesian Analysis of the complete molecular dataset from the previous study (Sirichamorn & al., 2012b). Numbers below branches are bootstrap support (BS) values and numbers above branches are Bayesian posterior probabilities (PP). Abbreviation of genera: A. = *Aganope*, Au. = *Austrosteenisia*, B. = *Brachypterum*, D. = *Derris*, Da. = *Dalbergia*, Deg. = *Deguelia*, F. = *Fordia*, K. = *Kunstleria*, L. = *Lonchocarpus*, Lep. = *Leptoderris*, M. = *Millettia*, N. = *Neodunnia*, O. = *Ostryocarpus*, P. = *Paraderris*, Ph. = *Philenoptera*, Pi. = *Piscidia*, and Pon. = *Pongamiopsis*. The abbreviation: “A” = *Aganope clade*; “B” = *Brachypterum* clade; “BT” = *Brachypterum* subclade containing tree-like species; BL” = *Brachypterum* subclade containing liana species; “D” = *Derris* major clade (containing also *Paraderris* subclade) and “DP”= the subclade containing *Paraderris* species [except *D.* (*P.*) *laotica*].

Table 4-1 Tree information and statistics from MP analyses of morphological, molecular and combined data.

Phylogeny based on	**Morphology**	**Molecular**	**Combined analyses**
Number of accessions	72	73	73
Number of parsimony-informative characters (%)	27 (93)	1232 (25)	1259(25)
Number of variable characters (%)	1 (3.5)	919 (18)	914(18)
Number of MP trees	>50000	2	2
MP tree length	126	5024	5192
Consistency Index (CI), all characters	0.34	0.57	0.56
Consistency Index (CI), only informative characters	0.34	0.46	0.45
Retention Index (RI)	0.80	0.76	0.76

molecular phylogeny (Fig. 4-1B) than in the total evidence cladogram (Fig. 4-1A); the latter shows a clear separation of the two subclades containing tree (BT) and liana species (BL), respectively. Moreover, bootstrap support for most nodes increased slightly, and significantly so for the *Paraderris* "DP" subclade (low in the molecular tree: Fig. 1B, BS 50%; strong in the total evidence tree: Fig. 4-1A, BS 92%). However, the support of some nodes decreased, probably due to conflict between morphological and molecular datasets at these nodes. A similar result was reported by Wortley and Scotland (2006), who showed a noteworthy increase in resolution, but no statistically significant effect on clade support when morphology and molecular data were combined in an analysis.

Character evolution in Asiatic *Derris*— *Vegetative characters*: Hutchinson (1973) considered the "tree-like" habit as more primitive than the liana habit. Within the Millettieae the liana habit (character 1, sate 2) seemed to have originated early (Fig. 4-3A), though it is difficult to decide which type is more plesiomorphic as many taxa with a tree-like habit were not sampled here. In our results (Fig. 4-3A), it is most parsimonious to reconstruct the liana habit as a synapomorphy for the *Derris* major clade (+ *Paraderris*), derived from a tree-like habit that is found in more basal genera of the "core Millettieae", e.g., *Lonchocarpus*, *Piscidia*, *Pongamiopsis* R. Viguier and *Neodunnia* R. Viguier. The evolutionary sequence cannot be reconstructed unequivocally for *Brachypterum* clade as tree and liana members are part of an unresolved trichotomy, though the liana habit is probably the derived state as the tree-like condition is present in the local outgroup for *Brachypterum*, the *Millettia pinnata-Fordia* clade. The tree-like habit is associated with the presence of chartaceous leaves and a preference for a more, at least during part of the year, arid habitat where generally deciduous taxa occur, whereas the lianas show a correlation with a sub-coriaceous to distinctly coriaceous leaf texture and presence in a more humid evergreen habitat (first author's observations).

An opposite leaflet arrangement (character 2, state 1; not shown) is present in the majority of Legumes (Adema's personal observation), as also found in the tribe Millettieae [alternate leaflets are found in *Craibia* and *Schefflerodendron* (Geesink, 1984), but they were not sampled in our study]. According to Hutchinson (1973), this state was considered as derived from the alternate condition. In this case, the tribe Dalbergieae, which has alternate leaflets was used as an only outgroup of Millettieae and, therefore, it is likely that Hutchinson is correct, and the opposite position in the present study may be a secondary reversal and as such an apomorphy, because when the Papilionaceae as a whole are considered, then the opposite leaflet arrangement is more likely to be an ancestral condition, because it is present in the early derived groups, Caesalpinioideae to Sophoreae of Papilionoideae, as well as the immediate sister groups of the Core-Millettieae (according to Hu et al., 2002, 2002), such as *Canavalia*, *Clitoria*, and Abreae. The adaptive significance of changes in the arrangement is obscure (Cronquist, 1988).

The presence of stipellae (character 3, state 0; Fig. 4-3A) is a derived state, which independently evolved several times. It is a synapomophy for the African *Aganope* (*Ostryoderris*) subclade, *Leptoderris*, *Phileoptera*, *Piscidia* and *Brachypterum*.

The presence of reddish or brownish young leaves (character 4, state 0; not shown) also evolved several times. The production of new leaves with distinctive colours other than green is particularly common in Millettieae, especially in *Derris* (incl. *Paraderris*; Sirichamorn et al., 2012a). Anthocyanins are pigments responsible for red and purple colours. As physiological reason for delayed greening it was initially hypothesised that anyhocyanin pigments are protectants against strong irradiation (Bornman et al., 1997). However, the observation that coloured young leaves are commoner among understory species than elsewhere (Kursar et Coley, 1992) refutes the argument, because the character appears to be independent of the sunlight intensity that reaches the plants (Sirichamorn et al., 2012a). Another theory to explain delayed chlorophyll production is herbivore pressure (Kursar and Coley, 1992; Turner, 2001). Chlorophyll is a nutritious molecule and the colour adds to its attractiveness for herbivores. Therefore, delayed greening may be a plant strategy to reduce the risk from herbivory (Turner, 2001). Anthocyanins are possibly anti-fungal compounds and might serve as a chemical defense for plants to protect their young leaves from pathogens (Coley and Aide, 1989). Unfortunately, our datamatrix shows a lot of missing data for this character as the colour requires observation on fresh material.

Another character which is phylogenetically informative and possibly related to the defense mechanism of the plants is the presence of a dark colour of dried specimens (character 26, state 0; appearing in both vegetative and reproductive parts), which is a synapomorphy for *Ostryocarpus* and *Aganope* (although not distinct in *A. impressa* (Dunn) Polhill; Fig. 4-3A). The exact chemical compounds responsible for the blackish colour are still unknown, but they are presumably phenolic molecules (e.g., tannins) that rapidly yield a dark-coloured polyphenolic substance by oxidation and polymerization (Queiroz et al., 2008; Parveen et al., 2010). Moreover, Bate-Smith and Metcalfe (1957) also mentioned that the capacity to synthesise tannins is a primitive character state, which tends to be lost during increasing phylogenetic specialisation. This is more or less congruent with our results, because *Ostryocarpus* and *Aganope*, earlier derived taxa in the phylogeny of the Millettieae, are the only genera with a blackish colour. It is absent in all other, later derived taxa in the core Millettieae sampled in this study. An indigo producing plant, *Philenoptera cyanescens* (Schum. & Thonn.) Roberty, actually shows a dark blue colour when dried, but this is another character state than the "blackish dry specimens" found in *Ostryocarpus* or *Aganope*.

— *Reproductive characters*: The type of inflorescence (character 5) is one of the main characters, which Geesink (1984) used for generic delimitation within tribe Millettieae. A paniculate inflorescence was suggested to be the most primitive type of inflorescence in the Dalbergieae-Millettieae group (Geesink, 1984). Our character reconstruction (Fig. 4-3B) indeed shows that true panicles were present early in the phylogeny of the tribe. Pseudoracemes-pseudopanicles, characterised by bearing flowers on vegetative short shoots called "brachyblasts" instead of elongated axes (Geesink, 1984; Tucker, 1987a, 1987b), are reconstructed as derived from the true panicle, whereas intermediate forms are supposed to be transitions between these two types of inflorescences. Character reconstruction also reveals that reversals to true panicles occured quite often during the evolution of the tribe. Brachyblasts are considered to be homologous to the lateral axes of the inflorescences as they are axillary to bracts (Geesink, 1984). Their shapes vary from wart- or knob-like to elongated cylindrical. In Millettieae, wart- or knob-like brachyblasts (character 6, state 1) are more commonly found and are reconstructed as the plesiomorphic condition (Fig. 4-3B), while the elongated cylindrical brachyblasts (state 2) are derived and form a synapomorphy for *Lonchocarpus* and the *Paraderris* subclade of *Derris*.

The brachyblast shapes (character 6) are correlated with the flower position (character 7), because the reconstructions of these two characters show similar patterns. The wart- or knob-like brachyblasts usually have flowers scattered throughout, whereas the long cylindrical brachyblasts have flowers apically. Less than (or up to) five flowers

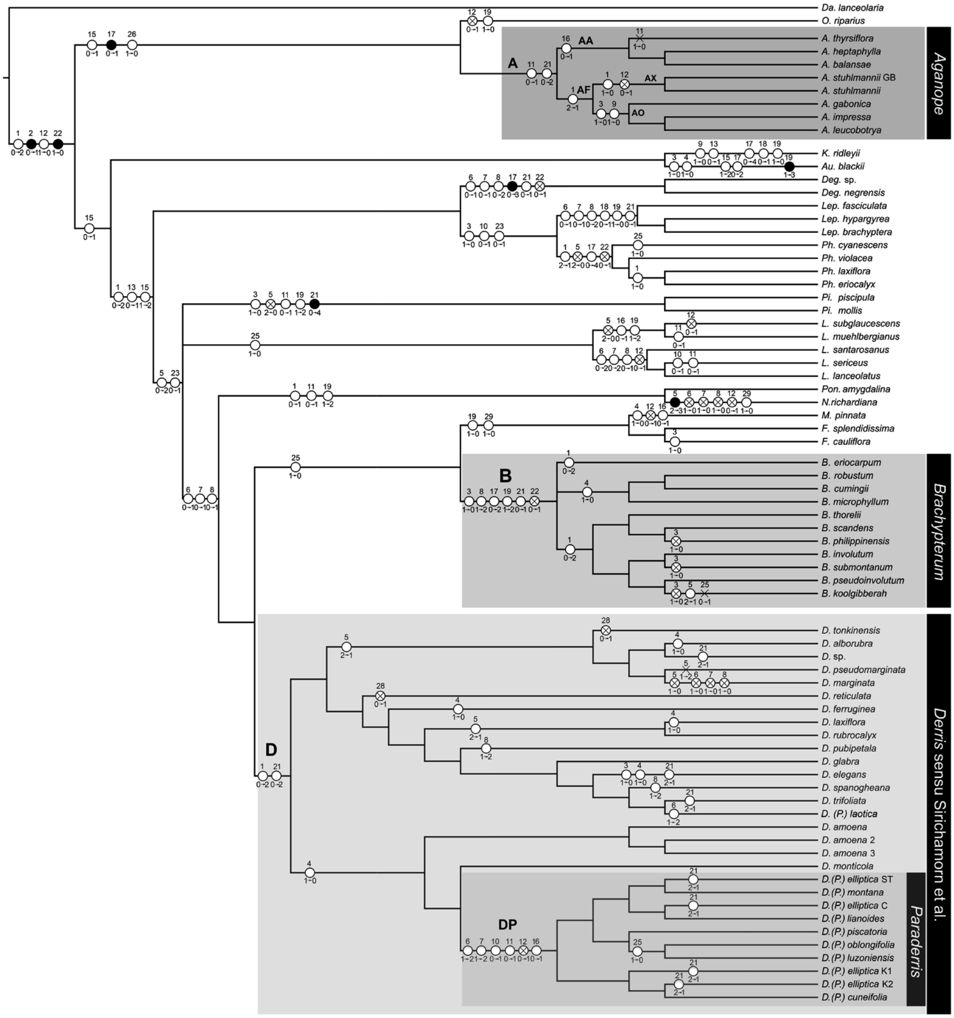


Fig. 4-2. The character state changes of the morphological characters traced on the majority rule consensus Bayesian tree of all molecular data (Fig. 1B). Legends:● = unique apomorphy; ○= parallelism; ✕ = reversal; ⊗= parallel reversal. Characters 20, 24 and 27 are not shown here. Abbreviations of genera are the same as mentioned in the legend to Fig. 1; A = *Aganope* main clade, AA = Asiatic *Aganope* subclade, AF = African *Aganope* subclade, AO = *Aganope-Ostryoderris* subclade, AX = *Aganope-Xeroderris* subclade, B = *Brachypterum* clade; D = *Derrris* s.s. clade and DP = *Paraderris* subclade [except *D.* (*P.*) *laotica*].

per brachyblast (character 8, state 1) is plesiomorphic and present in the majority of the core Millettieae and the *Derris* major clade (Fig. 4-3B). Brachyblasts with more than five flowers (state 2) present in *Deguelia* and *Leptoderris* show the derived condition from absent brachyblasts (state 0, found in paniculate inflorescences). The parallel condition but derived from less than 5 flowers (state 1) is present in

Brachypterum and a few species of *Derris* (Fig. 4-3B). This also implies that addition or reduction of the number of flowers on brachyblasts did not evolve in an one-way direction, reversals occur, similar to what was found in the evolution of the inflorescence type (character 5, Fig. 4-3B).

Flower bract larger than its subtended flower buds (character 9, state 0) is a synapomorphy for the African clade of *Aganope* (former *Ostryoderris*). *Kunstleria* was also reported to have slightly longer flower bracts (Geesink, 1984), however, its flower bracts are early caducous and are usually absent in herbarium specimens.

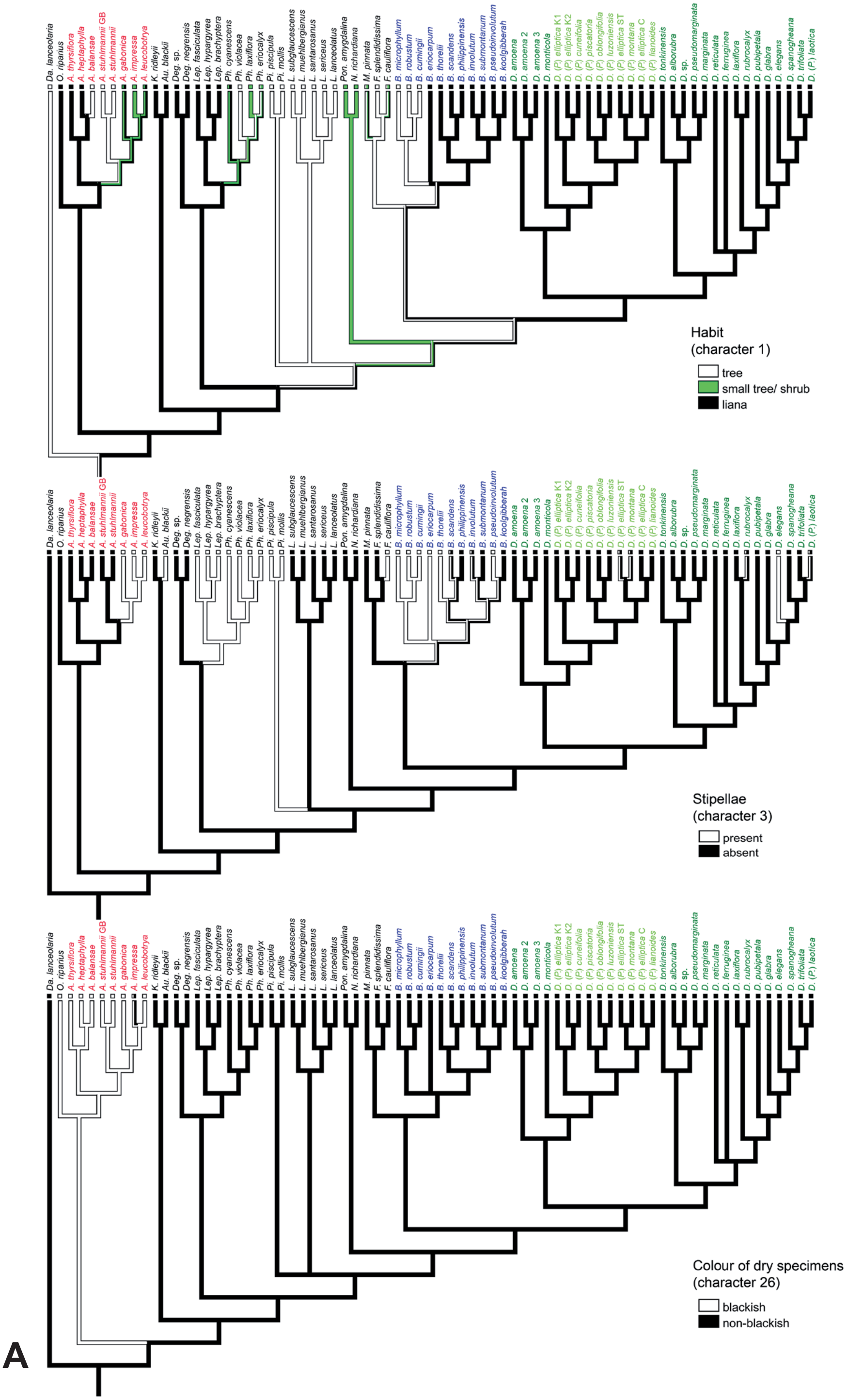
A hairy inner surface of the calyx (character 10, state 1) is apomorphic to a glabrous calyx inner surface. This character evolved independently in *Ostryocarpus*, *Leptoderris*, *Philenoptera*, *Lonchocarpus* (some species) and *Derris* subclade *Paraderris*.

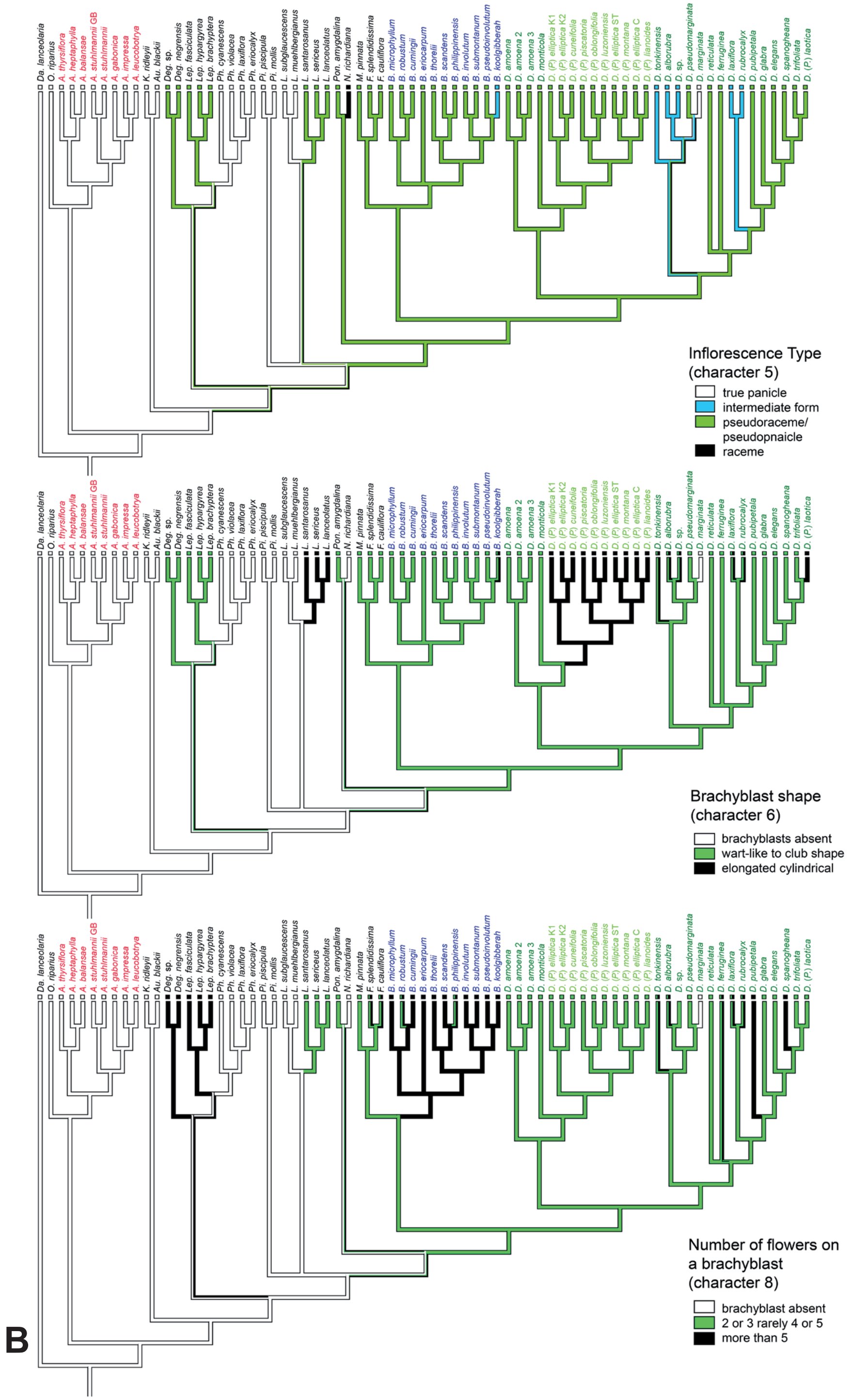
A standard petal (character 11) shorter than 10 mm (state 0) is the plesiomorphy; the apomorphy, standards longer than 10 mm (state 1) evolved more than once. This is, among others, typical for *Derris* subclade *Paraderris*.

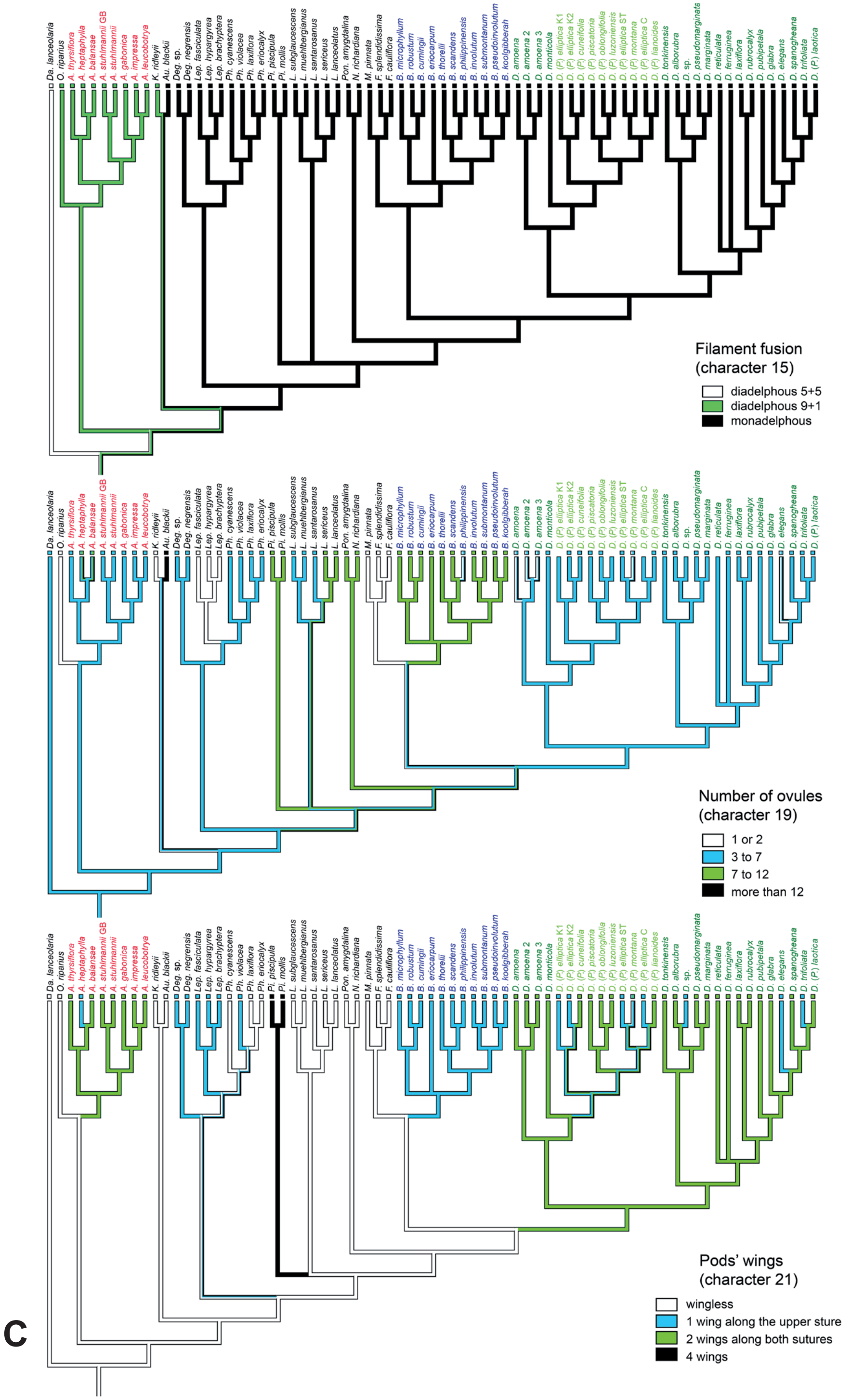
The basal callosities of the standard function as lids for the basal fenestrae of the staminal tube, thus possibly preventing desiccation of the floral disk (Geesink, 1984) or as tongue guide for pollinators. Their presence (character 12, state 1) is an apomorphy for *Derris* subclade *Paraderris* and *Lonchocarpus*.

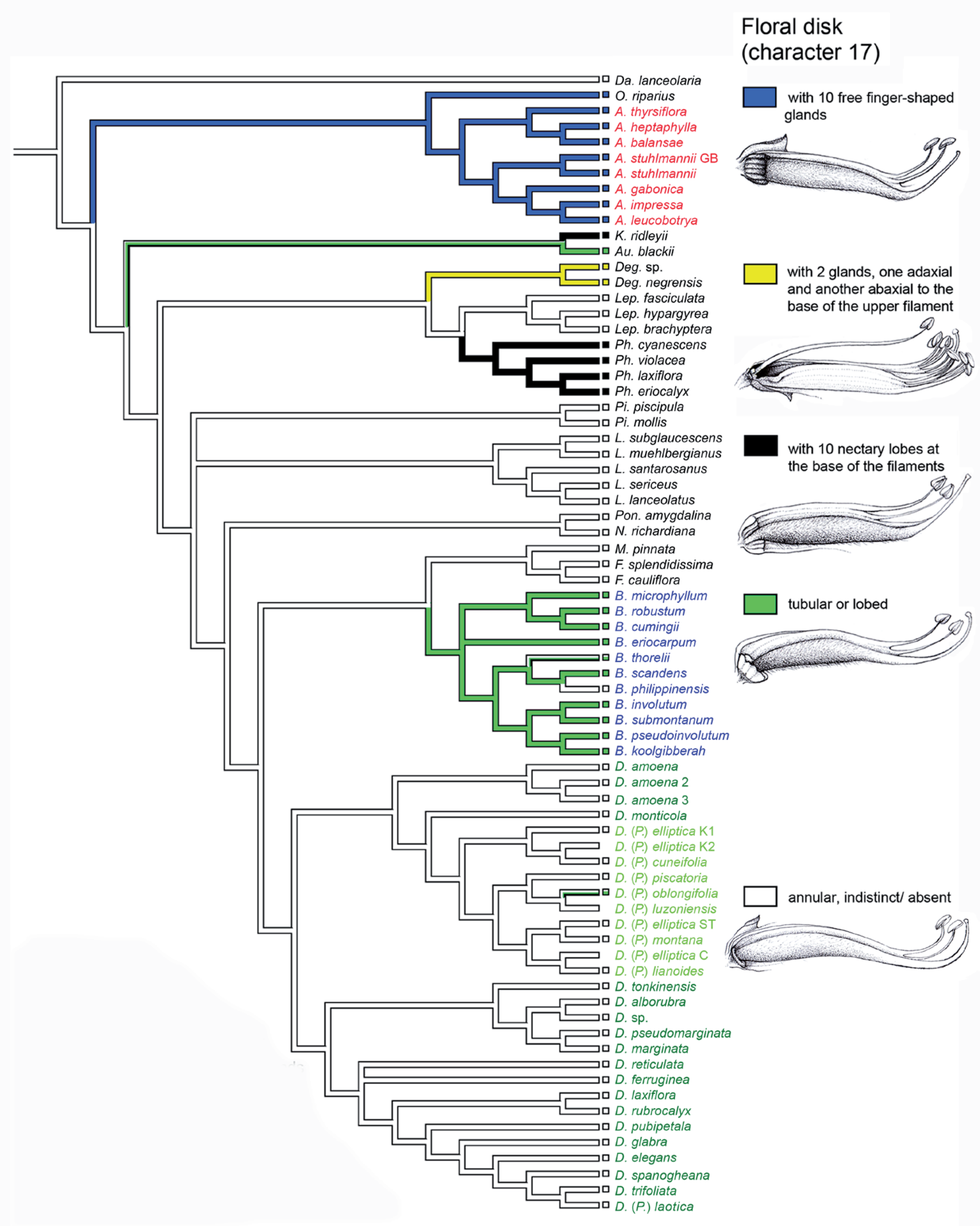
Wing petals show a general tendency to change from free or irregularly adherent to the keel petals (character 13, state 0), as found in the Basal Millettioid and Phaseoloid group (e.g. *Aganope* and *Ostryocarpus*), to distinctly adnate to the keel petals, as found in all sampled taxa of the core Millettieae. Sirichamorn et al. (2012a) mentioned that the lateral pockets of the wings and keels, which are hooked together by auricles or twisted claws (or any combination), are responsible for the adhesion between wings and keels. However, lateral pockets are present (character 14, state 1) in all sampled taxa, even in *Aganope* and *Ostryocarpus*, which have free or irregulary adnate wings. The adhesion between the two kinds of petals, on the other hand, might be a result of the adhesive excretion of the sculptured part of the wing blade, where excretory glandular tissue occurs (Geesink, 1984; Tewari and Nair, 1987). Wing

Fig. 4-3. Evolution of some selected morphological characters optimized onto the molecular phylogeny (Fig. 4-1: B) using Mesquite v.2.7.1. **A**: Habit (character 1), presence of stipellae (character 3) and colour of dry specimens (character 26).). **B**: Type of inflorescence (character 5), brachyblast shape (character 6) and number of flowers per brachyblast (character 8). **C**: Filament fusion (character 15), number of ovules (character 19) and number of pod wings (character 21). **D**: Shape of floral disk (character 17) and **E**: Presence of seed chambers (character 22). Double or triple coloured lines represent multistate characters. Species names of *Aganope* are presented in red. Species proposed to be transferred to *Brachypterum* are presented in blue. *Derris* + *D.* (*P.*) *laotica* and previous *Paraderris* are shown in dark green and light green, respectively.

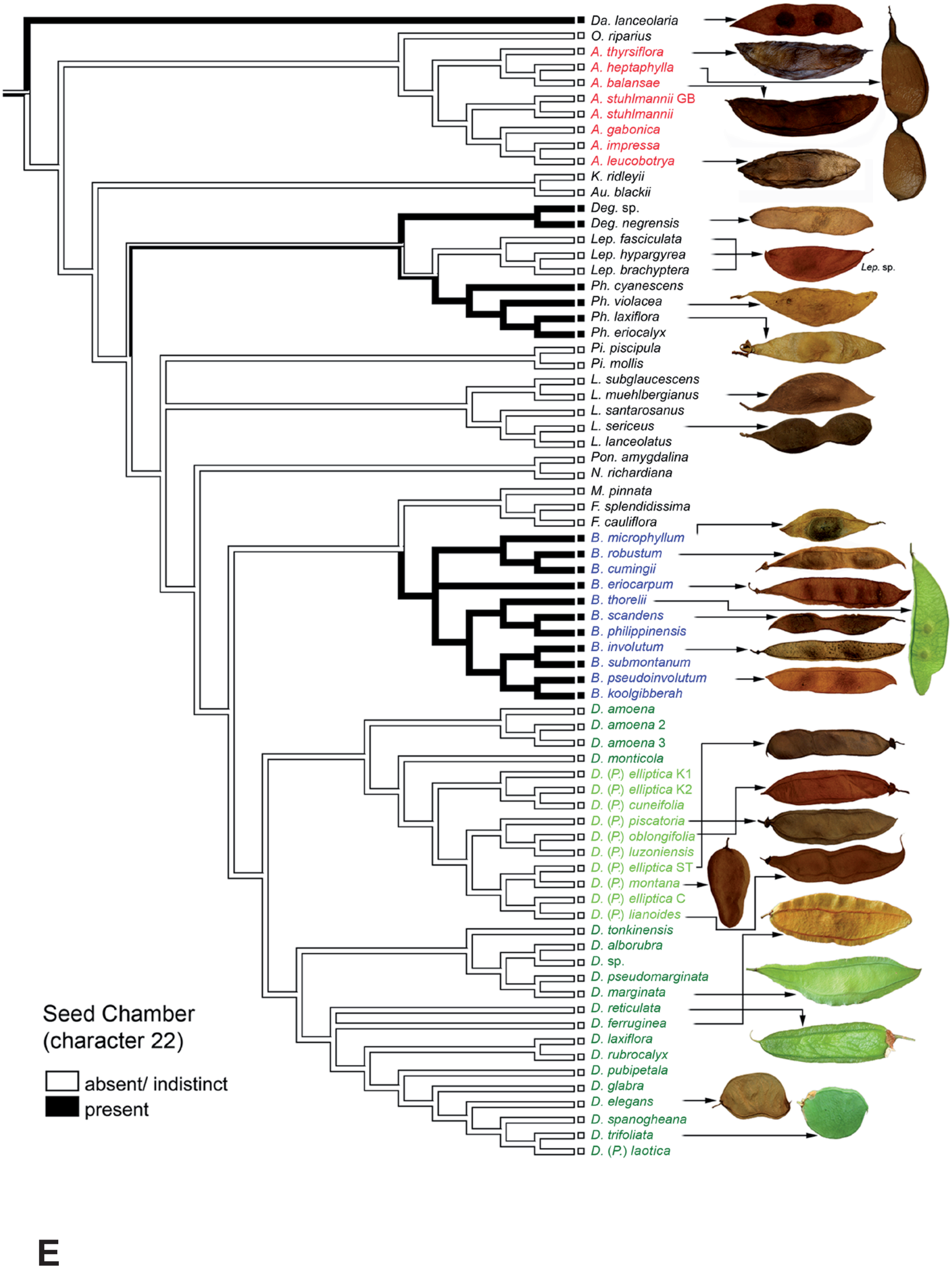

Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
Habit
(character 1)
☐ tree
🟩 small tree/ shrub
■ liana
Stipellae
(character 3)
☐ present
■ absent
Colour of dry specimens
(character 26)
☐ blackish
■ non-blackish
A


Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
Inflorescence Type
(character 5)
☐ true panicle
🟦 intermediate form
🟩 pseudoraceme/ pseudopnaicle
■ raceme
Brachyblast shape
(character 6)
☐ brachyblasts absent
🟩 wart-like to club shape
■ elongated cylindrical
Number of flowers on a brachyblast
(character 8)
☐ brachyblast absent
🟩 2 or 3 rarely 4 or 5
■ more than 5
B


Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
Filament fusion
(character 15)
☐ diadelphous 5+5
🟩 diadelphous 9+1
■ monadelphous
Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
Number of ovules
(character 19)
☐ 1 or 2
🟦 3 to 7
🟩 7 to 12
■ more than 12
Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
C
Pods' wings
(character 21)
☐ wingless
🟦 1 wing along the upper sture
🟩 2 wings along both sutures
■ 4 wings


Floral disk
(character 17)
with 10 free finger-shaped glands
with 2 glands, one adaxial and another abaxial to the base of the upper filament
with 10 nectary lobes at the base of the filaments
tubular or lobed
annular, indistinct/ absent
Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica

D


Da. lanceolaria
O. riparius
A. thyrsiflora
A. heptaphylla
A. balansae
A. stuhlmannii GB
A. stuhlmannii
A. gabonica
A. impressa
A. leucobotrya
K. ridleyii
Au. blackii
Deg. sp.
Deg. negrensis
Lep. fasciculata
Lep. hypargyrea
Lep. brachyptera
Lep. sp.
Ph. cyanescens
Ph. violacea
Ph. laxiflora
Ph. eriocalyx
Pi. piscipula
Pi. mollis
L. subglaucescens
L. muehlbergianus
L. santarosanus
L. sericeus
L. lanceolatus
Pon. amygdalina
N. richardiana
M. pinnata
F. splendidissima
F. cauliflora
B. microphyllum
B. robustum
B. cumingii
B. eriocarpum
B. thorelii
B. scandens
B. philippinensis
B. involutum
B. submontanum
B. pseudoinvolutum
B. koolgibberah
D. amoena
D. amoena 2
D. amoena 3
D. monticola
D. (P.) elliptica K1
D. (P.) elliptica K2
D. (P.) cuneifolia
D. (P.) piscatoria
D. (P.) oblongifolia
D. (P.) luzoniensis
D. (P.) elliptica ST
D. (P.) montana
D. (P.) elliptica C
D. (P.) lianoides
D. tonkinensis
D. alborubra
D. sp.
D. pseudomarginata
D. marginata
D. reticulata
D. ferruginea
D. laxiflora
D. rubrocalyx
D. pubipetala
D. glabra
D. elegans
D. spanogheana
D. trifoliata
D. (P.) laotica
Seed Chamber
(character 22)
☐ absent/ indistinct
■ present
E

petals have a threefold function. They serve as attractants, as a landing stage for bees and levers to depress and raise the keel (Knuth, 1908). In the major clade of *Derris*, the revolute wing petals (character 28, state 1) can be found in some species [e.g., *D. marginata* (Roxb.) Benth., *D. reticulata* Craib] and strongly revolute wing petals are found in *D. tonkinensis*. The character evolved independently more than once. Because only one living specimen was observed for each species, it is still unknown whether or not this character is constant or that the degree of revolution is effected by different environmental factors in different habitats.

Fusion of organs is common in legumes, especially in the androecium (Rodríguez-Riaño et al., 1999). Both adnation (fusion of different organs, e.g., stamens and petals) or connation (fusion of the same organs) are found among legume species (Tucker, 1987a). Stamens are always initially free in the early stage of development and different degrees of filament fusion takes place later. Developmentally, a fused androecium is thus always to be considered as derived from the free state (Tucker, 1987a). In older floras only two types of fusion, i.e., diadelphy and monadelphy, have been recognized. However, in more recent ontogenic studies of Tucker (1987a, 1989) pseudomonadelphy has been described for an initially diadelphous (9+1) androecium in young buds, but in older ones or in mature flowers the upper filament attaches itself to the adjacent filaments by surface fusion at the margin, while leaving a pair of basal fenestrae. A pseudomonadelphous androecium with basal fenestrae commonly occurs in many genera of Millettieae (Tucker, 1989). In this study degrees of filament fusion (character 15) were observed on fully opened mature flowers. As the ontogenic observations were not carried out intensively in this study, we still regard the pseudomonadelphy with basal fenestrae according to Tucker's definition as just monadelphy (state 2 of the character 15). This state was found in the majority of sampled Millettieae taxa in our study. The "equal diadelphy" can be found in species of *Dalbergia* (also in *Dalbergia lanceolaria*, the outgroup in this study) in which there are two groups of five (5+5) (Tucker, 1987a). According to the character reconstruction (Fig. 4-3C) the filament fusion changes from diadelphous (9+1) in the basal Millettioid taxa to monadelphous (= pseudomonadelphous with basal fenestrae according to Tucker, 1987a) in the more advanced core Millettieae. The filament fusion is an important adaptive advantage, specially associated with pollination mechanisms and possibly the result of coevolution (Tucker, 1987a). Although the diadelphous and pseudomonadelphous androecium with basal fenestrae were considered functionally equivalent, the later type of androecium provides adaptive advantages over the diadelphous androecium by forming the staminal column which protects the ovary and ovules against insect attack and prevents desiccation of the intrastaminal nectary, and, limits the range of pollinators that can work the flowers (Rodríguez-Riaño et al., 1999). Adnation of the vexillary (upper) filament (character 18, state 1) to the standard petal is derived from a free upper filament (state 0) and forms a synapomorphy for *Leptoderris* and *Kunstleria*. Stamens bearing hairs are relatively infrequent among legumes (Tucker, 1987a). The presence of hairs on anthers and connectives (character 16, state 1) is a synapomorphy for the Asiatic clade of *Aganope* [*A. balansae* (Gagnep.) P.K. Lôc, *A. heptaphylla* and *A. thyrsiflora*], for *Dahlstedtia* Malme (*Lonchocarpus muehlbergianus* Hassl. and *L. subglucescens* Mart. ex Benth.) and *Derris* subclade *Paraderris*.

Interestingly, the intrastaminal floral disks (character 17) in the various palaeotropic *Derris*-like genera are quite different (see Fig. 4-3D). A floral disk consisting of ten free finger-like glands (state 1) is synapomorphic for *Ostryocarpus* and *Aganope*. This character state is also present in *Platycyamus* Benth. (not sampled in this study), another genus in the basal Millettioid and Phaseoloid group, and also in several Phaseoleae such as *Spatholobus* and *Mucuna* (Adema, personal observation). *Brachypterum* has as apomorphy a disk that is distinctly tubular or lobed (state 2, but indistinct in a few species). A synapomorphy for *Deguelia* is a floral disk formed by two glands, one adaxial and another abaxial to the base of the upper filament (state 3, see Fig. 4-3D). The disc of *Philenoptera* consists of ten nectary lobes adnate to the base of the filaments (state 4 of Fig. 4-3D), also an apomorphy. An annular or indistinct floral disk (state 0) is present in the majority of the Millettieae, also in the major clade of *Derris*, and is plesiomorphic.

The majority of the taxa of Millettieae have three to seven ovules per ovary, which is the plesiomorphic character state (state 1 of the character 19, see Fig. 4-3C). More than seven but less than 12 ovules is more derived and synapomorphous for the *Piscidia*, *Dahlstedtia*, *Pongamiopsis*+*Neodunia* and *Brachypterum* clade.

Characters related to pods were thought to be of little value in the classification of Millettieae (Hu et al., 2000). This is re-examined here. The shape of the pods (character 20) is a sometimes difficult character, because assigning states is not easy, as there is a large percentage of intermediate conditions and many taxa are polymorphic (showing more than one state). The elliptic pod (state 1) is plesiomorphic, whereas rounded pods (state 0) and elongated strap-like pods (state 2) are apomorphic, but evolved several times in the Millettieae. The shape of the pods is highly associated with the number of seeds in the pods (character 24); the round pods usually carry a single, centred seed, while seeds scattered along the length of pods are found in the elliptic and strap-shaped pods.

Winged pods (character 21) are derived from a wingless condition. The presence of only one wing along the upper suture (state 1) is a synapomorpy for *Brachypterum, Deguelia* and *Leptoderris*. The presence of two wings along both sutures (state 2) is a synapomorpy for *Aganope* and *Derris*, however, reduction to one wing has evolved several times in the *Derris* major clade (Fig. 4-3C). The wing of the pods is presumed to be a general adaptation to wind dispersal (Hu et al., 2000). However, according to the first author's opinion, the thinness, papery texture and low mass of the *Derris*-like pods itself, as mentioned in Jayasuriya et al. (2012), might be a more significant factor to facilitate wind dispersal than the wings, which are generally narrow (not more than 15 mm wide, Sirichamorn et al., 2012a). The same pod characters may also help *Brachypterum scandens* (Roxb.) Benth., *Derris trifoliata*, and other species for their dispersion by water, as Jayasuriya et al. (2012) reported that their pods are buoyant; therefore, they can also float and may thus be water-dispersed even by sea (several species are correlated with mangroves).

The most striking characteristic of the pods are the seed chambers (character 22), a character that might be phylogenetically informative. Seed chambers are the hard, darker coloured (when dry) areas around seeds formed by the thickenings of endocarp and mesocarp (Polhill, 1981). Geesink (1984) mentioned it as a unique character for *Brachypterum*. However, Adema (2000) stated that it was also found in other genera of Millettieae (e.g., *Aganope*) with different degrees of endo-mesocarp thickening. Three species of Thai *Aganope* were later reported to lack visible seed chambers (Sirichamorn et al., 2012a). Kirkbride et al. (2003), in their studies on fruits and seeds of Fabaceae genera, indicated that 260 genera, including many more genera of Millettieae have externally visible seed chambers. Obivously, there is no clear definition of seed chambers and it might be dependent on the observers. Thus, more intensive anatomical studies of the percicarp are to be followed by precise definitions. In this study the first author has defined presence of the seed chambers by two aspects: 1) they are distinctly externally visible in dry pods and more importantly, 2) they are formed by a thickening of the peri- and mesocarp, so that the pericarp around seeds must be obviously thicker than other areas of the pod. In some species of *Aganope* and *Derris* s.s., a darker coloured area around seeds is sometimes found, but without the thickening of the pericarp, or sometimes the thickened areas around seeds are formed by the reticulation of the vascular bundles, not truly by the pericarp itself. In these cases the first author did not consider them as a "real" seed chamber and they were all coded as absent/ indistinct seed chambers (state 0 of character 22). The presence of the seed chambers (Fig. 4-3E) is derived from seed chambers lacking and it is a synapomorphy not only for *Brachypterum*, but also for *Deguelia* and *Philenoptera*.

The position of the seed hilum (character 23) changes from a distinctly eccentric hilum (deviating more than 45 degrees from the equatorial plane of the seed), found in the basal group of Millettieae, to slightly eccentric (deviating less than 45 degrees) or central (at the equatorial plane of seed), found in the majority of taxa of the core Millettieae. Seed dormancy and storage behaviour of *Derris* and *Brachypterum* have been reported to be different (Jayasuriya et al., 2012), but they are not included in our analyses due to lack of data on the other genera.

Comparing phylogenetic classification with traditional classification and implication for taxonomy of Asiatic *Derris*-like taxa—Our total evidence phylogenetic reconstruction does not support the recognition of all *Derris*-like taxa as a single, widely defined genus *Derris* sensu lato (s.l.) as proposed by Bentham (1860), because such a genus would be clearly polyphyletic. Two of Bentham's sections, section *Aganope* and section *Brachypterum* should be reinstated to generic level as proposed by Geesink (1984). Two other sections, i.e. section *Derris* (*Euderris*) and section *Dipteroderris*, are unresolved, not recognisable and should, therefore, be abolished. Section *Paraderris*, which was raised to genus level and accepted by various authors (Geesink, 1984; Adema, 2000, 2003; Wei et al., 2008; Sirichamorn et al., 2012a), is a monophyletic group within the major clade of *Derris*. However, recognition of *Paraderris* as a genus will make *Derris* s.s. paraphyletic. Therefore, we will synonymise *Paraderris* with *Derris* s.s. without any infrageneric recognition, because some typical *Derris*-like taxa are part of the *Paraderris* clade. This is unfortunate, because *Paraderris* is a morphologically distinct group (DP in Fig. 4-2) for which bootstrap support rose from 50% to 92% when morphological data were added (Fig. 4-1A). Synapomorphies of the *Paraderris* clade are the long and slender brachyblasts bearing flowers apically, large standard petals with basal callosities and hairy anthers. The genus *Derris* always lacked distinct morphological characters, and its circumscription was based on a combination of plesiomorphic characters such as a pseudoraceme-pseudopanicle, adnate wing and keel petals, monadelphous stamens and absent or annular floral disks. Only the liana habit in combination with two-winged pods are synapomorphies of *Derris* s.s. (including *Paraderris*; Fig. 4-2). However, these two characters have evolved several times independently in the phylogeny of the tribe. A formal infrageneric classification for *Derris* s.s. will not be proposed, because the two clades (Fig. 4-1) are not completely sampled, nor well supported, or recognisable.

Systematic treatment and nomenclatural changes

Our results from both previous molecular research (Sirichamorn et al., 2012b) and the total evidence phylogeny presented here show that *Derris* s.s. is either paraphyletic (circumscription by Geesink, 1984) or polyphyletic (circumscriptions by Adema, 2000, and Sirichamorn et al., 2012a). A monophyletic *Derris* is defined here by reinstating *Brachypterum* and by synonymising *Paraderris* with *Derris* s.s. The new combinations for Brachypterum and former Paraderris are presented here, together with a new formal description of the genera.

KEY TO THE GENERA OF ASIATIC *DERRIS*-LIKE PLANTS

1. Flowers solitary per node. Wings free from keel petals. Stamens diadelphous. Disks consisting of 10 free finger-shaped glands. Seeds with a distinctly eccentric hilum. Specimens usually turn blackish when dry...*Aganope*

1. Flowers clustered on reduced lateral axes (brachyblasts), rarely solitary. Wings adnate to keel petals. Stamens monadelphous. Disks annular, short tubular or five to 10-lobed, sometimes hardly visible or absent. Seeds with central or slightly eccentric hilum. Specimens not turning blackish when dry 2

2. Trees or lianas. Stipellae generally present. Leaflets generally more than 7, up to 41 (or more in some cases) per leaf. Inflorescences pseudoracemes or pseudopanicles, rarely intermediate forms (*B. koolgibberah*). Brachyblasts wart-like or club-shaped, bearing usually more than 5 flowers. Standard without distinct basal callosities. Floral disks generally tubular or cylindric or 10-lobed. Pods usually narrowly elliptic or strap-like, with one wing along the upper suture only and distinct seed chamber when dry...............................*Brachypterum*

2. Lianas. Stipellae generally absent. Leaflets generally 3–9, rarely up to 15 per leaf. Inflorescences pseudoraceme-pseudopanicles or intermediate forms, rarely true panicles (*D. marginata*). Brachyblasts wart-like or club-shaped to elongated cylindrical, bearing generally less than 5 flowers. Standard with or without basal callosities. Floral disks generally annular, indistinct or absent. Pods rounded, elliptic to narrowly elliptic or strap-like, with one wing along the upper suture or two wings along both sutures, rarely wingless, without thickening of pericarp around seed (dark-coloured parts around the seeds can be found in some cases)...*Derris*

BRACHYPTERUM (Wight & Arn.) Benth., Comm. Legum. Gen.: 37. 1837. ≡ *Dalbergia* L.f. subgen. *Brachypterum* Wight & Arn., Prod. Fl. Ind. Or. 1: 264. 1834. ≡ *Derris* Lour. sect. *Brachypterum* (Wight & Arn.) Benth., J. Proc. Linn. Soc., Bot. 4 (Suppl.): 101. 1860. ≡ *Deguelia* Aubl. sect. *Brachypterum* (Wight & Arn.) Taub. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 3, 3: 345. 1894 — TYPE: *Brachypterum scandens* (Roxb.) Miq. [based on *Dalbergia scandens* Roxb., Pl. Corom. 2: pl. 192. 1805. = *Derris scandens* (Roxb.) Benth.].

= *Solori* Adans., Fam. 2: 327. 1763, *nom. rejic. prop.* — TYPE: "H.M. 6, T. 22" [= *B. scandens* (Roxb.) Miq., but heterotypic under the present Art. 10, ICBN].

Lianas or trees. Twigs usually lenticellate. Leaves imparipinnate; stipules present, persistent or caducous; stipellae generally present or sometimes reduced, persistent. Leaflets generally more than 7, up to 41 (or more) per leaf, opposite, entire. Inflorescences axillary pseudoracemes, often combined with terminal or axillary pseudopanicles, intermediates only in *B. koolgibberah*. Flowers usually more than 5, fascicled on (or rarely on top of) callose, knob-like or club-shaped brachyblasts. Bracts subtending brachyblasts and flowers persistent or caducous, shorter than flower buds; bracteoles present, usually at apex of pedicel or at base of calyx. Calyx cup-shaped, often greenish or slightly reddish, bilabiate, upper lip 2-lobed, often indistinctly so; lower lip 3-lobed. Corolla whitish, pinkish or purplish; standard without distinct basal callosities, reflexed at base; wings approximately as long as keel petals and adherent by lateral pockets or hooked together by auricles or twisted claws. Stamens 10, monadelphous, with basal fenestrae; anthers all equal, fertile, glabrous. Disc distinct, tubular, cylindric or 10-lobed. Ovary with 7–12 ovules. Pods indehiscent, thin and stiff, usually narrowly elliptic or strap-shaped, with a wing along the upper suture only. Seed chambers distinct. Seeds bean-shaped, 1–4 or 7; hilum usually central.

Distribution—This genus comprises about 11 species. The type species, *B. scandens* is a common and widespread species ranging from Reunion island to India, Sri Lanka, Bangladesh, Myanmar, throughout Indochina, throughout *Malesia*, to N. Australia. *Brachypterum eriocarpum* occurs in S. and SE. China and N. of Laos and Vietnam (Thailand?). *Brachypterum microphyllum* is also cultivated in Madagascar. *Brachypterum cumingii* and *B. philippinensis* are endemic to the Philippines. Three species, *B. koolgibberah*, *B. pseudoinvolutum* and *B. submontanum* are endemic to Papua New Guinea and *B. involutum* is endemic to Australia.

Habitat and Ecology—Primary and secondary forest, in mixed deciduous forest or at the edge of dry evergreen forest, in fully exposed or semi-shaded, disturbed or degraded areas, along roads or rivers.

Note—The type specimen of *B. philippinensis* is only flowering and without fruits. The fruiting specimens that have been included by Merrill (1923) are slightly more hairy than the flowering specimens, especially the leaflets are thinly strigose at the lower surface. One of three fruiting specimens deposited in L., *Elmer 14373*, is used as a source of molecular data because the DNA extraction of the flowering type specimen was unsuccessful. The fruits of the three fruiting specimens clearly show fruit characteristics of *Brachypterum*. Compared with the leaflets of the type specimen, the leaflets of the three fruiting specimens in L are smaller, but they all have the same shape and distinct acuminate apex. Flowers of the type specimen show annular or inconspicuous floral disks, which is uncommon for *Brachypterum* of which the floral disks are usually tubular or lobed. However, an indistinct floral disk is also observed in *B. thorelii.*

Brachypterum cumingii (Benth.) Sirich., Adema & Welzen, **comb. nov.** ≡ *Derris cumingii* Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 104. 1860 — TYPE: PHILIPPINES, *Cuming 1208* (isotypes: L!, MO!).

Brachypterum eriocarpum (F.C. How) Sirich., Adema & Welzen, **comb. nov.** ≡ *Derris eriocarpa* F.C. How, Acta Phytotax Sin. 3: 233. 1954 — TYPE: CHINA. Guangxi, Lung Chow, *S. P. Ko 55325* (holotype: IBSC, n.v.).

Brachypterum involutum (Sprague) Sirich., Adema & Welzen, **comb. nov.** ≡ *Wisteria involuta* Sprague, Gard. Chron. 3: 36. 1904 ≡ *Derris involuta* (Sprague) Sprague, Gard. Chron. 3: 38. 1905 — TYPE: cultivated in the Temperate-house of the Royal Botanic Garden Kew.

Brachypterum koolgibberah (F.M. Bailey) Sirich., Adema & Welzen, **comb. nov.** ≡ *Derris koolgibberah* F.M. Bailey, Rep. Exeped. Bellenden-Ker 38. 1884 — TYPE: AUSTRALIA, Queensland, *F.M. Bailey s.n.* (holotype: BRI, isotype: K!).

Brachypterum microphyllum Miq., Fl. Ned. Ind., Eerste bijv.: 296. 1860. ≡ *Derris microphylla* (Miq.) B.D. Jacks., Index Kewensis 1: 332. 1895 — TYPE: INDONESIA. Sumatra: Palembang, *Teijsmann s.n.* (holotype: L!; isotype: U!).

= *Derris dalbergioides* Baker in Hook.f., Fl. Brit Ind. 2: 241. 1878 — TYPE:

MALAYSIA. Malacca, *Maingay s.n.* (lectotype designated by Sirichamorn et al. in *Syst. Bot.* 37: 418. 2012: K!).

Brachypterum philippinensis (Merr.) Sirich., Adema & Welzen, **comb. nov.** ≡ *Derris philippinensis* Merr., Philip. J. Sc. 5: 104. 1910. ≡ *Derris multiflora* Benth. var. *longifolia* Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 108. 1860 — TYPE: PHILIPPINES. Luzon, *Cuming 1162* (isotype: L!).

Brachypterum pseudoinvolutum (Verdc.) Sirich., Adema & Welzen, **comb. nov.** ≡ *Derris koolgibberah* F.M. Bailey subsp. *pseudoinvoluta* Verdc., Kew Bull. 32: 469. 1978 ≡ *Derris pseudoinvoluta* (Verdc.) Adema, Thai For. Bull. Bot. 28: 11. 2000 — TYPE: PAPUA NEW GUINEA, Lae, *Womersley NGF 15395* (holotype: K, isotypes: L!, LAE).

Brachypterum robustum (Roxb. ex DC.) Dalzell & A.Gibson, Bombay Fl. 77. 1861. ≡ *Dalbergia robusta* Roxb. [Hort. Beng. 53. 1814, nom. nud.] ex DC., Prodr. 2: 417. 1825. ≡ *Derris robusta* (Roxb. ex DC.) Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 104. 1860. ≡ *Deguelia robusta* (Roxb. ex DC.) Taub., Bot. Centralbl. 47: 388. 1891 — TYPE: INDIA. Silhet, *Wallich 5849B* (lectotype designated by Thothathri in Fasc. Fl. India 8: 26. 1982: CAL; isolectotype: K!).

= *Brachypterum polyphyllum* Miq., Fl. Ned. Ind. 1: 139. 1855. ≡ *Derris polyphylla* (Miq.) Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 104. 1860 — TYPE: INDONESIA. Java, Soerakarta, *Horsfield s.n. (L16)* (holotype: U!; isotypes: CAL, K!,).

Brachypterum scandens (Roxb.) Benth., Ann. Wien. Mus. 2: 101. 1837. ≡ *Dalbergia scandens* Roxb., Pl. Coromandel 2: 49, pl. 192. 1805. ≡ *Derris scandens* (Roxb.) Benth., Proc. Linn. Soc., Bot. 4, (Suppl.): 103. 1860 — TYPE: INDIA. Roxburgh, Pl. Coromandel 2: 49, *pl. 192.* 1805 (lectotype designated by Thothathri in Fasc. Fl. India 8: 27. 1982: CAL).

= *Dalbergia timoriensis* DC., Prod. 2: 417. 1825. ≡ *Brachypterum timoriensis* (DC.) Benth. ex Miq., Fl. Ned. Ind. 1: 138. 1855. ≡ *Derris timoriensis* (DC.) Pittier, Contr. U.S. Nat. Herb. 20: 41. 1917 — TYPE: not indicated (P or G-DC).

= *Dalbergia venusta* Zipp. ex Spanoghe, Linnaea 15: 197. 1841 — TYPE: INDONESIA. Lesser Sunda Islands, Timor, *Zippelius s. n.* (holotype: L!; isotype: L!).

= *Millettia litoralis* Dunn, Philip. J. Sci., C., Bot. 6: 316. 1911 — TYPE: PHILIPPINES. Mindanao, St. Cruz, *DeVore & Hoove 250* (holotype: K!).

Brachypterum submontanum (Verdc.) Sirich., Adema & Welzen, **comb. nov.** ≡ *Derris submontana* Verdc., Kew Bull. 32: 465. 1978 — TYPE: PAPUA NEW GUINEA. *Clemens 8162* (holotype: B, isotypes: A, L!).

Brachypterum thorelii (Gagnep.) Sirich., Adema & Welzen, **comb. nov.** ≡ *Millettia thorelii* Gagnep., Not. Syst. (Paris) 2: 365. 1913. ≡ *Derris thorelii* (Gagnep.) Craib, Fl. Siam. Enum. 1: 435, 493. 1928 — TYPE: LAOS. De Xieng Khouang à Pak Lai, 1866-1868, *Thorel s. n.* (lectyotype designated by Phan in Phan and Vidal, Fl. Cambodge, Laos and Vietnam 30: 58. 2001: P!; isolectotype: P!).

DERRIS Lour., Fl. Cochin. 432. 1790, nom. cons. — TYPE: *Derris trifoliata* Lour. (Typ. cons.).

= *Derris* Lour. sect. *Dipteroderris* Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 102. 1860 —TYPE: *Derris ferruginea* (Roxb.) Benth. (lectotype designated by Sirichamorn et al., 2012a).

= *Derris* Lour. sect. *Paraderris* Miq., Fl. Ind. Bat. 1: 145. 1855. Benth. ≡ *Deguelia* Aubl. sect. *Paradeguelia* Taub. in Engl. & Prantl., Nat. Pflanzenfam. ser. 2, 3: 345. 1894, nom illeg. ≡ *Paraderris* (Miq.) Geesink, Leiden Bot. Ser. 8: 109. 1984 — TYPE: *Derris cuneifolia* Benth. (lectotype designated by Geesink in Leiden Bot. Ser. 8: 109. 1984). [= *Paraderris cuneifolia* (Benth.) Geesink].

= *Salken* Adans., Fam. 2. 322. 1763, nom. rejic. — TYPE: "H.M. 8, t. 46" (= *D. trifoliata Lour.*)

Lianas. Twigs usually lenticellate. Leaves imparipinnate; stipules present, persistent or caducous; stipellae absent or present, persistent. Leaflets generally 3–9, rarely up to 15 per leaf, opposite, entire, variable in shape and size. Inflorescences axillary pseudoracemes, often combined with terminal or axillary pseudopanicles, rarely true panicles, sometimes an intermediate form present: a panicle in the lower part and a pseudoraceme in the upper part, or, a pseudoraceme in the lower part and flowers solitary in the upper part. Flowers usually 2–5(–7) scattered throughout or on the top of knob-like, club-shaped to long and slender brachyblasts. Bracts subtending brachyblasts and flowers persistent or caducous, shorter than the corresponding flower buds; bracteoles present, usually at the apex of the pedicel or at the base of the calyx. Calyx cup-shaped, often maroonish or reddish, bilabiate, upper lip 2-lobed, often indistinctly so; lower lip 3-lobed. Corolla generally whitish or pinkish; standard reflexed at base, without or with distinct basal callosities; wings approximately as long as keel petals, in some species curved backward towards the calyx, wings and keel petals adherent by lateral pockets or hooked together by auricles or twisted claws (or any combination). Stamens 10, monadelphous, with basal fenestrae; anthers all equal, fertile, glabrous or hairy. Disc generally inconspicuous or annular. Ovary with 2–5 (rarely up to 7) ovules. Pods indehiscent, thin and stiff, with a wing along both sutures or along the upper suture only, rarely wingless. Seed chambers absent but sometimes seeds surrounded by a thickening of the pod's vascular bundles. Seeds bean-shaped, 1 or 2(–3) to rarely more per pod; hilum usually central.

Distribution—This genus comprises about 50 species, mainly in SE Asia, one species extending from East Africa to Australia and W. Pacific (*D. trifoliata*, a mangrove species).

Habitat and Ecology—Species of *Derris* s.s. prefer sunlight and water, and are, therefore, usually found in fully exposed or semi-shaded areas along streams or rivers, sometimes in mixed deciduous forests or at the edge of dry evergreen forests, also found in disturbed or degraded areas; *D. trifoliata* is typical for the mangrove; while *D. tonkinensis* only occurs on limestone.

Only the taxa previously referred to *Paraderris* and here synonymised with *Derris* (again) are mentioned here.

Derris canarensis (Dalzell) Baker in Hook.f., Fl. Brit. India 2: 246. 1878. ≡ *Pongamia canarensis* Dalzell, Hooker's J. Bot. Kew Gard. Misc. 2: 37. 1850. ≡ *Paraderris canarensis* (Dalzell) Adema, Blumea 48: 137. 2003 — TYPE: INDIA. Kanara, Mysore, Kassaleh, *Ritchie 1720* (neotype designated by Thothathri in Fasc. Fl. India 8: 12. 1982: CAL).

= *Derris oblonga* Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 112. 1860. ≡ *Deguelia oblonga* (Benth.) Taub., Bot. Centralbl. 47: 387. 1891 — TYPE: INDIA. Konkan, *Stocks s.n.*; SRI LANKA, *Gardner 476*, *Walker s.n.* and *Thwaites 1493* [all syntypes listed by Adema, in Blumea 48: 137. 2003 (n.v.)].

Derris cuneifolia Benth. in Miq., Pl. Jungh. 253. 1852. ≡ *Deguelia cuneifolia* (Benth.) Taub., Bot. Centralbl. 47: 386. 1891. ≡ *Paraderris cuneifolia* (Benth.) Geesink, Leiden Bot. Ser. 8: 109. 1984 — TYPE: NEPAL. Nookate, *Wallich Cat. 5887* (lectotype designated by Thothathri in Fasc. Fl. India 8: 13. 1982: CAL; isolectotypes: K!; BM, LE).

= *Galedupa marginata* Roxb. [Hort. Bengal. 53. 1814 (nom. nud.)], Fl. Ind. 3: 241. 1832 — TYPE: INDIA. Silhet, *Wallich Cat. 5896A* (holotype: K-W; isotype: P!).

= *Derris discolor* Benth., Proc. Linn. Soc., Bot. 4 (Suppl.): 111. 1860 — TYPE: INDIA. Sikkim: Terai, lower hill, *J.D. Hooker s. n.* (holotype: K!; isotypes: K!, P!).

= *Derris hancei* Hemsl., Bot. Mag. t. 8008 (after *D. alborubra* Hemsl.): 131. 1905 — TYPE: CHINA. Canton: along the river, *Sampson* in herb. *Hance 9920* (holotype: K!).

= *Derris glauca* Merr. & Chun, Sunyattsenia 2: 246. 1953 — TYPE: CHINA. Hainan: Ngai Yuen, 4 Jun 1933, *F.C. How 70860* (holotype: NY!, photo; isotypes: US!, A).

= *Derris truncata* Craib, Kew Bull. 385. 1927 — TYPE: THAILAND. Phitsanulok: Nakhawn Tai, 3 Apr 1924, *Kerr 8898* (holotype: K!; isotype: BK!).

= *Derris cuneifolia* Benth. var. *longipedicellata* Thoth., Bull. Bot. Surv. India 3: 191. 1961 — TYPE: INDIA. Sikkim: *Sivoke, Ribu 760* (holotype: CAL).

= *Derris cuneifolia* Benth. f. *assamica* Thoth., Bull. Bot. Surv. India 3: 192. 1961 — TYPE: INDIA. Assam: Cachar, Bishnupur, *U. Kanjilal 4835* (holotype: CAL).

Derris elliptica (Wall.) Benth., J. Proc. Linn. Soc., Bot. 4 (Suppl.): 111. 1860. ≡ *Pongamia elliptica* Wall., Pl. Asiat. Rar. 3: 20, t. 237. 1832. ≡ *Paraderris elliptica* (Wall.) Adema, Thai. For. Bull., Bot. 28: 11. 2001 — TYPE: INDIA. Hort. Bot. Calcutta (originally from Ambon), *Wallich 5881A* (holotype: K!; isotype: CAL, fragments).

= *Dalbergia purpurea* Reinw. ex Hassk., Flora 25, Beibl. 2: 53. 1842 — TYPE: INDONESIA. Java, *Blume s.n.* (holotype: L!).

= *Pongamia hypoleuca* Miq., Fl. Ned. Ind. 1: 148. 1855 — TYPE: BORNEO. *Korthals s.n.* (lectotype designated by Adema in Blumea 48: 137. 2003: L!).

= *Pongamia volubilis* Zoll. & Mor. var *glaucophylla* Miq., Fl. Ned. Ind. 1: 149. 1855. ≡ *Derris elliptica* (Wall.) Benth. var. *glaucophylla* (Miq.) Kaneh. & Hatus., Bot. Mag. Tokyo 56: 364. 1942 — TYPE: INDONESIA. Java, *Anonymous s.n.* (lectotype designated by Adema in Blumea 48: 137. 2003: L!).

= *Derris elliptica* (Wall.) Benth. var. *chittagongensis* Thoth., Bull. Bot. Surv. India 3: 195. 1961. ≡ *Paraderris elliptica* (Wall.) Adema var. *chittagongensis* (Thoth.) Adema, Blumea 48: 137. 2003 — TYPE: INDIA. Chittagong: Kodla, *Baldal Khan 450 (C)* (holotype: CAL!; isotype: CAL, photo K!).

Derris hainanensis Hayata, Icon. Pl. Formosan. 3: 77. 1913. ≡ *Paraderris hainanensis* (Hayata) Adema, Blumea 48: 138. 2003 — TYPE: CHINA. Hainan, *K. Katsumada s.n.* (n.v.).

Derris lacei Dunn, Kew Bull. 206. 1914. ≡ *Paraderris lacei* (Dunn) Adema, Blumea 48: 138. 2003 — TYPE: MYANMAR. Maymyo Plateau, *Lace 6115* (lectotype designated by Adema in Blumea 48: 138. 2003: K, isolectotype: CAL).

Derris laotica Gagnep., Not. Syst. 2: 348. 1911. ≡ *Paraderris laotica* (Gagnep.) Adema, Blumea 48: 138. 2003 — TYPE: CAMBODIA. Bhâklon, *Magnen et al. s.n.* (lectotype designated by Phan in Phan and Vidal, Fl. Cambodge, Laos & Vietnam 30: 68. 2001: P!; isolectotype: K, fragments).

= *Derris laotica* Gagnep var. *virens* Gagnep, Not. Syst. 2: 348. 1911 — TYPE: CAMBODIA. Siem-reap, *Godefroi 686* (lectotype designated by Phan in Phan and Vidal, Fl. Cambodge, Laos & Vietnam 30: 68. 2001: P!; isolectotype: P!).

Derris lianoides Elmer, Leafl. Philipp. Bot. 1: 228. 1907. ≡ *Paraderris lianoides* (Elmer) Adema, Blumea 48: 138. 2003 — TYPE: PHILIPPINES. Luzon, Prov. Taybas, Luchon, *Elmer 7443* (holotype: PNH, probably lost, isotypes CAL, K).

Derris lushaiensis Thoth., Bull. Bot. Surv. India 12: 104. 1972. ≡ *Paraderris lushaiensis* (Thoth.) Adema, Blumea 48: 138. 2003.— TYPE: INDIA, *Gage 23D (A)* (holotype: CAL).

Derris luzoniensis (Adema) Sirich., Adema & Welzen, **comb. nov.** ≡ *Paraderris luzoniensis* Adema, Blumea 48: 134. 2003 — TYPE: PHILIPPINES. Luzon, Palanan area, Dimpnat, *Ridsdale et al. ISU 564* (holotype: L!, isotype: K).

Derris montana Benth. in Miq., Pl. Jungh. 253. 1852 ≡ *Paraderris montana* (Benth.) Adema, Blumea 48: 139. 2003 —TYPE: INDONESIA. Java, Dieng, *Junghunh s.n.* (holotype: BO).

= *Derris cuneifolia* Benth. var. *malaccensis* Benth., J. Proc. Linn. Soc., Bot. 4 (Suppl.): 112. 1860. ≡ *Derris malaccensis* (Benth.) Prain, J. Asiat. Soc. Beng. 66, 2: 107. 1897. ≡ *Paraderris malaccensis* (Benth.) Adema, Thai For. Bull., Bot. 28: 11. 2001 — TYPE: MALAYSIA. Malacca, *Griffith KD 1774* (holotype: K!; isotype: CAL).

= *Derris malaccensis* (Benth.) Prain var. *aptera* Prain, J. Asiat. Soc. Beng. 66, 2: 108. 1897 — TYPE: MALAYSIA. Perak, *King's coll. 4518* (lectotype designated by Adema in Blumea 48: 139. 2003: K!; isolectotypes: A, CAL).

Derris oblongifolia Merr., Philipp. J. Sci., C 7: 82. 1912. ≡ *Paraderris oblongifolia* (Merr.) Adema, Blumea 48: 139. 2003 — TYPE: PHILIPPINES. Luzon, Subprov. Bauco, Bontoc, *Vanoverberg 280*.

Derris ornithocephala (Adema) Sirich., Adema & Welzen, **comb. nov.** ≡ *Paraderris ornithocephala* Adema, Blumea 48: 134. 2003 — TYPE: INDONESIA. Papua, NE Kepala Burung, Manokwari, Numi, Sungai Asai, *Dransfield et al. 7554* (holotype: K, isotype: L!).

Derris piscatoria (Blanco) Sirich., Adema & Welzen **comb. nov.** ≡ *Cylista piscatoria* Blanco, Fl. Filip.: 589. 1837. ≡ *Millettia piscatoria* (Blanco) Merr., Publ. Bur. Sci. Gov. Lab. 27: 37. 1905. ≡ *Paraderris piscatoria* (Blanco) Adema, Blumea 48: 139. 2003 — TYPE: PHILIPPINES. Luzon, Batangas Prov., Mt Batulo, *Merrill Spec. Blanc. 469* (neotype designated by Adema in Blumea 48: 139. 2003: L!, neoisotypes: A, K).

Acknowledgements

The authors wish to express their sincere thanks to all curators and staff of BCU, BK, BKF, CMU, K, L, P and WAG for permission to examine herbarium material, specimen loans, and various kinds of support. B. Gravendeel, M.C.M. Eurlings and other staff of the DNA Markerpoint Facility of Leiden University and Naturalis Biodiversity Center are thanked for kindly providing assistance, laboratory training, and facilities as well as helpful suggestions on molecular issues. The authors are very grateful to J.F. Veldkamp for his useful advice on nomenclatural issues and D.C. Thomas for the use of the Mesquite program. The first author also thanks the Royal Thai Government for financial support of his PhD study.

APPENDIX 4-1. Species, voucher specimen, and GenBank information for sequence data reported in the study. Herbarium abbreviations (explained in http://sciweb.nybg.org/science2/IndexHerbariorum.asp) are given between parentheses. SLR = Suan Luang Rama IX Park and Botanic Garden, Bangkok, Thailand. Accession numbers for sequences taken from Genbank are shown in italics. Species names are according to the classification presented here with *Brachypterum* recognised as genus, and *Paraderris* synonimised with *Derris* (name *Paraderris* between brackets to show its origin).

Species; *Voucher* or plant register (if from a living collection), Source and Geographic regions, GenBank accession (*trnK-matK*, ITS/5.8S, *trnL-F* IGS, *psbA-trnH* IGS).

Aganope balansae (Gagnep.) P.K.Lôc; *Poilane 26751* (P), Vietnam: Tonkin, JX506601, JX506433, JX506489, JX506544. ***Aganope gabonica*** (Baill.) Polhill; *Karmann s.n.* (L), Gabon: Franceville, JX506605, JX506438, –, JX506548. ***Aganope heptaphylla*** (L.) Polhill; *Santisuk 688* (L), Thailand: Ranong, JX506600, JX506432, JX506488, JX506543. ***Aganope impressa*** (Dunn) Polhill; *Dubois s.n.* (L), Congo: Luki, JX506604, JX506436, JX506492, JX506547. ***Aganope leucobotrya*** (Dunn) Polhill; *Versteegh et al. 150* (L), Ivory Coast: Grand Bassam, –, JX506437, –, –. ***Aganope stuhlmannii*** (Taub.) Adema (code name in this study = *A. stuhlmannii* GB); *Corby 2162* (K), Africa, *AF142708*, *AF467485*, –, –. ***Aganope stuhlmannii*** (Taub.) Adema (code name in this study = *A. stuhlmanii*); *Versteegh et al. 456* (L), Ivory Coast: Korhogo, JX506603, JX506435, JX506491, JX506546. ***Aganope thyrsiflora*** (Benth.) Polhill; *Sirichamorn YSM 2009-22* (L), Thailand: Songkhla, JX506602, JX506434, JX506490, JX506545.

Austrosteenisia blackii (F.Muell.) Geesink; *Pedley 5005* (K), Australia, *AF142707*, *AF467020*, –, –.

Brachypterum cumingii (Benth.) Sirich., Adema & Welzen; *Gaerlan et al. PPI 10368* (L), Philippines: Luzon, JX506618, JX506447, JX506505, JX506561. ***Brachypterum eriocarpum*** (F.C.How) Sirich., Adema & Welzen; *Wang Hong 7673* (QBG), China: Yunnan, JX506625, JX506454, JX506512, JX506568. ***Brachypterum involutum*** (Sprague) Sirich., Adema & Welzen; *Murray, Coveny & Bishop* s.n., sheet no. *NSW 409439* (L), Australia: North coast, JX506622, JX506451, JX506509, JX506565. ***Brachypterum koolgibberah*** (F.M.Bailey) Sirich., Adema & Welzen; *Brass 8205* (L), Papua New Guinea: Sturt Island, JX506624, JX506453, JX506511, JX506567. ***Brachypterum microphyllum*** Miq.; *Sirichamorn YSM 2009-16* (L), Thailand: Chumphon, JX506619, JX506448, JX506506, JX506562. ***Brachypterum philippinensis*** (Merr.) Sirich., Adema & Welzen; *Elmer 14373* (L), Philippines: Sorsogon, JX506627, JX506455, –, –. ***Brachypterum pseudoinvolutum*** (Verdc.) Sirich., Adema & Welzen; *Streimann & Kairo NGF27776* (L), Papua New Guinea: Morobe, JX506623, JX506452, JX506510, JX506566. ***Brachypterum robustum*** (Roxb. ex DC.) Dalzell & A.Gibson; *Sirichamorn YSM 2009-09* (L), Thailand: Lampang, JX506617, JX506446, JX506504, JX506560. ***Brachypterum scandens*** (Roxb.) Benth.; *Sirichamorn YSM 2009-01* (L), Thailand: Chon Buri, JX506621, JX506450, JX506508, JX506564. ***Brachypterum submontanum*** (Verdc.) Sirich., Adema & Welzen; *Takeuchi et al. 4349* (L), Papua New Guinea: Morobe, JX506626, –, JX506513, JX506569. ***Brachypterum thorelii*** (Gagnep.) Sirich., Adema & Welzen; *Sirichamorn YSM 2009-03* (L), Thailand: Phrae, JX506620, JX506449, JX506507, JX506563.

Dalbergia lanceolaria L.f.; *Sirichamorn YSM 2009-02* (L), Thailand: Phrae, JX506655, JX506484, JX506541, JX506597.

Deguelia negrensis (Benth.) Taub.; *C. & F. Sastre152* (L), Brazil, JX506607, JX506441, –, –. ***Deguelia* sp.**; *Granville et al. 10075* (L), French Guiana: Hautmaroni, JX506608, JX506440, JX506495, JX506551.

Derris alborubra Hemsl.; *Sirichamorn YSM 2009-14* (L), Thailand: Nakhon Nayok, JX506638, JX506466, JX506524, JX506580. ***Derris amoena*** Benth. (code name in this study: *D. amoena*); *Sirichamorn YSM 2009-20* (L), Thailand: Surat Thani, JX506628, JX506456, JX506514, JX506570. ***Derris amoena*** Benth. (code name in this study: *D. amoena* 2); *Kerr 13700* (L), Thailand: Satun, JX506629, JX506457, JX506515, JX506571. ***Derris amoena*** Benth. (code name in this study: *D. amoena* 3); *Maxwell 83-11* (L), Singapore, JX506630, JX506458, JX506516, JX506572. ***Derris (Paraderris) cuneifolia*** Benth.; *Lei 612* (L), China: Hainan, JX506649, JX506478, JX506535, JX506591. ***Derris elegans*** Graham ex Benth. var. *elegans*; *K. & S. Larsen KL 32828* (L), Thailand: Narathiwat, JX506641, JX506469, JX506527, JX506583. ***Derris (Paraderris) elliptica*** (Wall.) Benth. [code name in this study: *D. (P.) elliptica* C]; living collection: *Sirichamorn YSM 2012-01* (SLR), Thailand: Bangkok (cutivated), JX506647, JX506475, JX506533, JX506589. ***Derris (Paraderris) elliptica*** (Wall.) Benth. [code name in this study: *D. (P.) elliptica* K1]; *Kostermans 260* (L), Thailand: Kanchanaburi, JX506648, JX506477, JX506534, JX506590. ***Derris (Paraderris) elliptica*** (Wall.) Benth. [code name in this study: *D. (P.) elliptica* K2]; *Kantchai 101* (L), Thailand: Kanchanaburi, –, JX506476, –, –. ***Derris (Paraderris) elliptica*** (Wall.) Benth. [code name in this study: *D. (P.) elliptica* ST]; *Sirichamorn YSM 2009-19* (L), Thailand: Surat Thani, JX506646, JX506474, JX506532, JX506588. ***Derris ferruginea*** (Roxb.) Benth.; *Sirichamorn YSM 2009-13* (L), Thailand: Udon Thani, JX506633, JX506461, JX506519, JX506575. ***Derris glabra*** Sirich.; *Sirichamorn YSM 2009-23* (L), Thailand: Songkhla, JX506635, JX506463, JX506521, JX506577. ***Derris (Paraderris) laotica*** Gagnep.; *Magnen, Gourgand and Châtillon s.n.* (P), Cambodia, JX506645, JX506473, JX506531, JX506587. ***Derris laxiflora*** Benth.; *Hu 1081*, Taiwan, *AF142715*, *AF467046*, –, –. ***Derris (Paraderris) lianoides*** Elmer; *Ridsdale SMHI 1863* (L), Philippines: Palawan, JX506653, JX506482, JX506539, JX506595. ***Derris (Paraderris) luzoniensis*** (Adema) Sirich., Adema & Welzen; *Ridsdale, Baquiran et al. ISU 564* (L), Philippines: Luzon, JX506654, JX506483, JX506540, JX506596. ***Derris marginata*** (Roxb.) Benth.; *Pierre s.n.* (L), India, JX506643, JX506471, JX506529, JX506585. ***Derris (Paraderris) montana*** Benth.; *Sirichamorn YSM 2009-21* (L), Thailand: Songkhla, JX506650, JX506479, JX506536, JX506592. ***Derris monticola*** (Kurz) Prain; *Kerr 1731* (L), Thailand: Chiang Mai, JX506637, JX506465, JX506523, JX506579. ***Derris (Paraderris) oblongifolia*** Merr.; *Sulit PNH 21618* (L), Philippines: Biliran island, JX506652, JX506481, JX506538, JX506594. ***Derris (Paraderris) piscatoria*** (Blanco) Sirich., Adema & Welzen; *Sulit PNH 14411* (L), Philippines: Samar, JX506651, JX506480, JX506537, JX506593. ***Derris pseudomarginata*** Sirich.; *Maxwell 76-31* (L), Thailand: Chon Buri, JX506639, JX506467, JX506525, JX506581. ***Derris pubipetala*** Miq.; *Maxwell 85-370* (L), Thailand: Pattani, JX506634, JX506462, JX506520, JX506576. ***Derris reticulata*** Craib; *Sirichamorn YSM 2009-18* (L), Thailand: Nakhon Ratchasima, JX506632, JX506460, JX506518, JX506574. ***Derris rubrocalyx*** Verdc.; *Davis 567* (L), Indonesia: Irian Jaya, JX506644, JX506472, JX506530, JX506586. ***Derris* sp.**; *Maxwell 50-75* (L), Thailand: Nakhon Sawan, JX506640, JX506468, JX506526, JX506582. ***Derris spanogheana*** Blume ex Miq.; *De Vogel 5788* (L), Indonesia: Sulawesi, JX506636, JX506464, JX506522, JX506578. ***Derris tonkinensis*** Gagnep.; *Sirichamorn YSM 2009-11* (L), Thailand: Lampang, JX506631, JX506459, JX506517, JX506573. ***Derris trifoliata*** Lour.; *Sirichamorn YSM 2009-06* (L), Thailand: Samut Prakan, JX506642, JX506470, JX506528, JX506584.

Fordia cauliflora Hemsl.; *voucher PS0230MT01*, unknown, *HM049511*, *GQ434352*, –, *GU396708*. ***Fordia splendidissima*** (Blume ex Miq.) Buijsen; *Tangah s.n.*, Malaysia: Sabah, *AF142718, AF467048*, –, –.

Kunstleria ridleyi Prain; *Ambriansyah et al. 951* (L), Indonesia: Berau, JX506598, –, JX506486, –.

Leptoderris brachyptera (Benth.) Dunn; *Herbarium Berolinense 403* (L), Cameroon: Limbe, JX506611, JX506444, JX506498, JX506554. ***Leptoderris fasciculata*** (Benth.) Dunn; *Serg. Romyn s.n.* (L), Cameroon: Lolodorf, JX506609, JX506442, JX506496, JX506552. ***Leptoderris hypargyrea*** (Harms) Dunn; *Zenker 3645* (L), Cameroon: Bipinde, JX506610, JX506443, JX506497, JX506553.

Lonchocarpus lanceolatus Benth.; *Hughes 144/92-1* (FHO), Mexico, *AF142717*, *AF467057*, –, –. ***Lonchocarpus muehlbergianus*** Hassl.; *Hanh 2258* (L), Paraguay: Guairá, *JX506615*, –, JX506502, JX506558. ***Lonchocarpus muehlbergianus*** Hassl.; *Tressens et al. 1992*, Argentina: Corrientes, –, *AF467059*, –, –. ***Lonchocarpus santarosanus*** Donn.Sm.; *Cabrera 1964* (L), México: Chiapas, JX506613, –, JX506500, JX506556. ***Lonchocarpus santarosanus*** Donn.Sm; *Hughes 1229*, El Salvador: Sonsonate, –, *AF467063*, –, –. ***Lonchocarpus sericeus*** (Poir.) Kunth ex DC.; *Fuerter s.n.*, Dominican Republic: Barahona, JX506612, JX506485, JX506499, JX506555. ***Lonchocarpus subglaucescens*** Mart. ex Benth.; *Hatschbach 18025* (L), Brazil: Paraná, *JX506614*, –, JX506501, JX506557. ***Lonchocarpus subglaucescens*** Mart. ex Benth.; *Hatschbach 41090*, Brazil, –, *AF467066*, –, –.

Millettia pinnata (L.) Panigrahi; *Sirichamorn YSM 2009-25* (L), Thailand: Surat Thani, JX506616, JX506445, JX506503, JX506559.

Neodunnia richardiana (Baillon) Geesink; *Schrire 2555* (K), Madagascar, *AF142713*, *AF467483*, –, –.

Ostryocarpus riparius Hook.f.; *Maesen 7524* (WAG), Benin: Ouémé, JX506599, JX506431, JX506487, JX506542.

Philenoptera cyanescens (Schum. & Thonn.) Roberty; Unknown, –, *AF534802*, –, –. ***Philenoptera eriocalyx*** (Harms) Geesink subsp. *wankiensis* (Mend. & Sousa) Geesink; *Hu 1090*, Zimbabwe, *AF142720*, *AF467487*, –, –. ***Philenoptera laxiflora*** (Guill. & Perr.) Rob.; *Hu 1117*, Senegal, –, *AF467488*, –, –. ***Philenoptera laxiflora*** (Guill. & Perr.) Rob.; *Hu 1126*, Senegal, *AF142721*, –, –, –. ***Philenoptera laxiflora*** (Guill. & Perr.) Rob.; *Lykke et al 856* (L), Senegal: Sine Saloum, –, –, JX506494, JX506550. ***Philenoptera violacea*** (Klotzsch) Schrire; *Busse 530* (L), German East Africa (Tanzania), JX506606, JX506439, JX506493, JX506549.

Piscidia mollis Rose; *Hu 1117* (DAV), México: Sonora, –, *AF467489*, –, –. ***Piscidia piscipula*** (L.) Sarg.; *Lavin & Luckow 5793* (TEX), México: Veracruz, *AF142710*, *AF467490*, –, –.

Pongamiopsis amygdalina (Baill.) R. Vig.; *DuPuy M575* (K), Madagascar, *AF142711*, *AF467494*, –, –.

APPENDIX 4-2. Data matrix of 29 morphological characters scored for the phylogenetic analyses and character reconstruction. Polymorphisms are indicated by all states present separated by a comma, and inapplicable or unknown characters by "–". Details of characters and states are also listed below. Abbreviation of genera: A. = *Aganope*, Au. = *Austrosteenisia*, B. = *Brachypterum*, D. = *Derris*, Da. = *Dalbergia*, Deg. = *Deguelia*, F. = *Fordia*, K. = *Kunstleria*, L. = *Lonchocarpus,* Lep. = *Leptoderris*, M. = *Millettia*, N. = *Neodunnia*, O. = *Ostryocarpus*, P. = *Paraderris*, Ph. = *Philenoptera*, Pi. = *Piscidia*, and Pon. = *Pongamiopsis*.

***Taxon*/character**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
A. balansae	0	1	1	-	0	0	0	0	1	0	1	0	0	1	1	1	1	0	1,2	2	2	0	0	1	1	0	0	0	1
A. gabonica	1,2	1	0	-	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	2	2	0	0	1	1	0	0	0	1
A. heptaphylla	2	1	1	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	1,2	2	1	0	0	1	1	0	0	0	1
A. impressa	1	1	0	-	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	2	2	0	0	1	1	0,1	0	0	1
A. leucobotrya	1,2	1	0	-	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	2	2	0	0	1	1	0	0	0	1
A. stuhlmannii	0	1	1	1	0	0	0	0	1	0	1	1	0	1	1	0	1	0	1	2	2	0	0	1	1	0	0	0	1
A. thyrsiflora	2	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1	2	2	0	0,1	1	1	0	0	0	1
Au. blackii	2	1	0	0	0	0	0	0	1	0	0	0	0	1	2	0	2	0	3	1,2	0	0	0	1	1	1	0	0	1
B. cumingii	0	1	0	1	2	1	1,2	2	1	0	0	0	1	1	2	0	2	0	2	2	1	1	1	1	0	1	0	0	1
B. eriocarpum	2	1	0	1	2	1	1	2	1	0	0	0	1	1	2	0	2	0	2	2	1	1	1	1	0	1	0	-	1
B. involutum	2	1	0,1	-	2	1	1	2	1	0	0	0	1	1	2	0	2	0	2	2	1	1	1	1	0	1	0	0	1
B. koolgibberah	2	1	1	-	1	1,2	1	2	1	0	0	0	1	1	2	0,1	2	0	2	2	1	1	1	1	1	1	0	-	1
B. microphyllum	0	1	0	1	2	1	1	2	1	0	0	0	1	1	2	0	2	0	2	2	1	1	1	1	0	1	0	0	1
B. philippinensis	2	1	1	-	2	1	1	1,2	1	0	0	0	1	0,1	2	0	0	0	0,1	2	1	1	1	1	0	1	0	-	1
B. pseudoinvolutum	2	1	0	-	2	1	1	2	1	0	0	0	1	1	2	0	2	0	2	1,2	1	1	1	1	0	1	0	-	1
B. robustum	0	1	0	1	2	1	1,2	1,2	1	0	0	0	1	1	2	0	2	0	2	2	1	1	1	1	0	1	0	0	1
B. scandens	2	1	0,1	1	2	1	1	2	1	0	0	0	1	1	2	0	2	0	2	2	1	1	1	1	0,1	1	0	0	1
B. submontanum	2	1	1	-	2	1	1	2	1	0	0	0	1	1	2	0	2	0	2	1,2	1	1	1	1	0,1	1	0	-	1
B. thorelii	2	1	0	1	2	1	1	2	1	0	0	0	1	1	2	0	0,2	0	2	2	1	1	1	1	0,1	1	0	0	1
Da. lanceolaria	0	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0,1	0	1	0	0,1	0,1	1	0	0	1
Deg. negrensis	2	1	1	-	2	1	1	2	1	0	0	0	1	1	2	0	3	0	1	1	1	1	0	1	1	1	0	0	1
Deg. sp.	2	1	1	-	2	1	1	2	1	0	1	0	1	1	2	0	3	0	1	2	1	1	0	1	1	1	0	0	1
D. alborubra	2	1	1	0	1	1,2	1	1,2	1	0	0	0	1	1	2	0	0	0	1	0,1	2	0	1	0	1	1	0	0	1
D. amoena	2	1	1	0	2	1	1	1	1	0	0	0	1	1	2	0	0	0	0,1	2	2	0	1	1	1	1	1	-	1
D. amoena 2	2	1	1	0	2	1	1	1	1	0	0	0	1	1	2	0	0	0	0,1	2	2	0	1	1	1	1	1	-	1
D. amoena 3	2	1	1	0	2	1	1	1	1	0	0	0	1	1	2	0	0	0	0,1	2	2	0	1	1	1	1	1	-	1
D. (*P.*) *cuneifolia*	2	1	1	0	2	2	2	1	1	1	1	1	1	1	2	0,1	2	0	1	0,1	2	0	-	0	0,1	1	0,1	0	1
D. (*P.*) *elliptica* C	2	1	1	0	2	2	2	1	1	1	1	1	-	-	2	-	-	0	-	1,2	1	0	1	1	0,1	1	0	0	1

***Taxon*/character**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
D. (*P.*) *elliptica* K1	2	1	1	-	2	2	2	1	1	1	1	1	-	-	2	-	-	0	-	2	1	0	1	1	0,1	1	0	0	1
D. (*P.*) *elliptica* K2	2	1	1	-	2	2	2	1	1	1	1	1	-	-	2	1	-	0	1	2	1	0	1	1	0,1	1	0	0	1
D. (*P.*) *elliptica* ST	2	1	0,1	0	2	2	2	1	1	1	1	1	1	1	2	1	0	0	1	1,2	1	0	1	1	0,1	1	0	0	1
D. elegans	2	1	0	-	2	1	1	1	1	0	0	0	1	1	2	0	0	0	0,1	0	1	0	1	0,1	0,1	1	0	0	1
D. ferruginea	2	1	1	0	2	1	1	1,2	1	0	0	0	1	1	2	0	0	0	1	1,2	2	0	1	1	1	1	0	0	1
D. glabra	2	1	1	1	2	1	1	1	1	0	0	0	1	1	2	0	2	0	1	2	2	0	1	1	1	1	0	0	1
D. (*P.*) *laotica*	2	1	0,1	-	2	2	1,2	1	1	0	0	0	1	1	2	0	0	0	1	1	2	0	-	0	1	1	0	0	1
D. laxiflora	2	1	1	0	1	1,2	1	1,2	1	0	0	0	1	-	2	0	0	0	1	1	2	0	1	0,1	1	1	0	0	1
D. (*P.*) *lianoides*	2	1	1	-	2	2	2	1	1	0,1	1	1	1	1	2	0,1	0	0	1	2	2	0	1	1	0,1	1	0	0	1
D. (*P.*) *luzoniensis*	2	1	1	-	2	2	2	1	1	-	-	-	-	-	2	-	-	0	-	2	2	0	1	1	0	1	0	0	1
D. marginata	2	1	1	1	0	0	1	0	1	0	0	0	1	1	2	0	0	0	1	1,2	2	0	1	0,1	1	1	0	0,1	1
D. (*P.*) *montana*	2	1	0,1	0	2	2	2	1	1	0,1	1	1	1	1	2	0,1	0	0	0,1	0,1	0,1,2	0	1	1	0,1	1	0	0	1
D. monticola	2	1	1	-	2	1	1	1	1	0	0,1	0	1	1	2	0	0	0	1	1,2	2	0	1	1	1	1	0	-	1
D. (*P.*) *oblongifolia*	2	1	1	-	2	2	2	1	1	0,1	1	1	1	1	2	0,1	0	0	1	2	2	0	1	1	0	1	0	0	1
D. (*P.*) *piscatoria*	2	1	1	-	2	2	2	1	1	1	1	1	1	1	2	1	2	0	1	2	2	0	1	1	0,1	1	0	0	1
D. pseudomarginata	2	1	1	-	2	1	1	1	1	0	0	0	1	1	2	0	0	0	1	1,2	1	0	1	1	1	1	0	-	1
D. pubipetala	2	1	1	-	2	1	1	2	1	0	0	0	1	1	2	0	0	0	1	0,1	2	0	1	1	1	1	0	0	1
D. reticulata	2	1	1	1	2	1	1	1	1	0	0	0	1	-	2	0	-	0	-	1,2	2	0	1	1	1	1	0	1	1
D. rubrocalyx	2	1	0,1	-	1	1,2	1	1,2	1	0	0	0	1	0,1	2	0	0	0	1	2	2	0	1	-	1	1	0	-	1
D. sp.	2	1	1	1	1	1,2	1	-	1	0	0	0	1	-	2	-	-	0	-	1,2	1	0	1	1	0,1	1	0	0	1
D. spanogheana	2	1	1	-	2	1	1	2	1	0	0	0	1	1	2	0	0	0	1	1	2	0	1	-	1	1	0	-	1
D. tonkinensis	2	1	1	1	1	1,2	1	1,2	1	0	0	0	1	0,1	2	0	0	0	1	1,2	2	0	1	1	1	1	0	1	1
D. trifoliata	2	1	1	1	2	1	1	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	1	0	1	1	0	0	1
F. splendidissima	0	1	1	-	2	1	1	1,2	1	0	0	0	1	1	2	0	0	0	0	1,2	0	0	1	1	0,1	1	0	0	0
F. cauliflora	0,1	1	0	-	2	1	1	1,2	1	0	0	0	1	1	2	0	0	0	0	1,2	0	0	1	1	0,1	1	0	0	0
K. ridleyii	2	1	1	-	0	0	0	0	0	0	0	0	1	1	1	0	4	1	0	2	0	0	0	0	0,1	1	0	-	1
L. lanceolatus	0	1	1	-	2	2	2	1	1	-	0	1	1	1	2	0	0	0	2	0,1,2	0	0	1	0,1	0	1	0	0	1
L. muehlbergianus	0	1	1	1	0	0	0	0	1	0	1	0	1	1	2	1	0	0	1	1,2	0	0	1	0	0	1	0	0	1
L. santarosanus	0	1	1	-	2	2	2	1	1	-	0	1	1	1	2	0	0	0	1	1,2	0	0	1	0	0	1	0	0	1

***Taxon*/character**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
L. sericeus	0	1	1	1	2	2	2	1	1	1	1	1	1	1	2	0	0	0	2	1,2	0	0	1	1	0	1	0	0	1
L. subglaucescens	0	1	1	-	0	0	0	0	1	0	0	1	1	1	2	1	0	0	1	1,2	0	0	1	-	0	1	0	0	1
Lep. brachyptera	2	1	0	1	2	1	1	2	1	1	0	0	1	1	2	0	0	1	0	1	1	0	1	0,1	1	1	0	0	1
Lep. fasciculata	2	1	0	1	2	1	1	2	1	1	0	0	1	1	2	0	0	1	0	1	1	0	1	0,1	1	1	0	0	1
Lep. hypargyrea	2	1	0	1	2	1	1	2	1	1	0	0	1	1	2	0	0	1	0	1	1	0	1	0,1	1	1	0	0	1
M. pinnata	0,1	1	1	0	2	1	1	1	1	0	0,1	1	1	1	2	1	0	0	0	0,1	0	0	1	0	0	1	0	0	0
N. richardiana	1	1	1	-	3	0	0	0	1	-	1	1	1	1	2	0	0	0	2	1,2	0	0	1	1	0,1	1	0	0	0
O. riparius	2	1	1	-	0	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0,1	0	0	0	0	1	0	0	0	1
Ph. cyanescens	1,2	1	0	1	0	0	0	0	1	1	0	0	1	1	2	0	4	0	1	1,2	0	1	1	1	0	1	0	0	1
Ph. eriocalyx	0,1	1	0	-	0	0	0	0	1	1	0	0	1	1	2	0	4	0	1	1,2	0	1	1	1	1	1	0	0	1
Ph. laxiflora	1	1	0	1	0	0	0	0	1	1	0	0	1	1	2	0	4	0	1	2	0	1	1	1	1	1	0	0	1
Ph. violacea	0	1	0	1	0	0	0	0	1	1	0,1	0	1	1	2	0	4	0	1	1,2	1	1	1	0,1	1	1	0	0	1
Pi. mollis	0	1	0	1	0	0	0	0	1	0	1	0	1	1	2	0	0	0	2	1	3	0	1	1	1	1	0	0	1
Pi. piscipula	0	1	0	1	0	0	0	0	1	0	1	0	1	1	2	0	0	0	2	1,2	3	0	1	1	1	1	0	0	1
Pon. amygdalina	1	1	1	-	2	1	1	1	1	0	0,1	0	1	1	2	0	0	0	2	0,1	0	0	1	0	1	1	0	0	1

APPENDIX 4-3. List of morphological characters used in phylogenetic analysis.

1. Habit: (0) tree; (1) small tree/shrub; (2) liana. **2. Leaflet arrangement**: (0) alternate; (1) opposite. **3. Stipellae**: (0) present; (1) absent. **4. Reddish pigments in young leaves**: (0) present; (1) absent. **5. Type of inflorescence**: (0) true panicle; (1) intermediate form between true panicle and pseudoraceme or pseudopanicle; (2) pseudoraceme or pseudopanicle; (3) simple raceme. **6. Shape of brachyblast**: (0) brachyblast absent; (1) knob-like to cylindrical; (2) elongate cylindrical. **7. Flower position on the brachyblast**: (0) brachyblast absent; (1) throughout the brachyblast; (2) at the apex of the brachyblast. **8. Number of flowers per brachyblast**: (0) brachyblast absent; (1) 2 or 3 per brachyblast, rarely 4 or 5; (2) more than 5 or up to 10 or more. **9. Flower bract**: (0) bigger than corresponding flower buds; (1) smaller than corresponding flower buds. **10. Indumentum of the calyx inside**: (0) glabrous; (1) with some hairs. **11. Length of standard petal**: (0) up to 10 mm; (1) more than 10 mm. **12. Presence of standard basal callosities**: (0) absent or indistinct; (1) present. **13. Adhesion of wings and keel petals**: (0) free or irregularly adherent; (1) adherent with sculptured part of the wing petals or with lateral pockets. **14. Presence of lateral pockets on wing or keel petals**: (0) absent; (1) present. **15. Degree of filament fusion**: (0) diadelphous 5+5; (1) diadelphous 9+1; (2) monadelphous. **16. Indumentum of the anther and connective tissue**: (0) glabrous; (1) hairy. **17. Floral disc shape**: (0) absent, indistinct or simply annular; (1) with 10 free finger-shaped glands; (2) tubular and/or lobed; (3) with 2 glands, one adaxial, one abaxial to the base of the upper filament; (4) with 10 nectary lobes at the base of the filaments. **18. Vexillary stamen**: (0) free from the standard; (1) adnate to the standard. **19. Number of ovules**: (0) 1 or 2; (1) 3 to 7; (2) 7 to 12; (3) more than 12. **20. Pod shape**: (0) round; (1) elliptic; (2) strap-like. **21. Pod wings**: (0) wingless; (1) wing along only the upper suture; (2) wings along both sutures; (3) 4 wings. **22. Seed chamber**: (0) absent/ indistinct; (1) present. **23. Position of seed hilum**: (0) distinctly eccentric: more than 45 degrees of the equatorial axis; (1) central or slightly eccentric: between 0 to 45 degrees of the equatorial axis. **24. Seed position in pod**: (0) in centre; (1) scattered. **25. Leaf texture**: (0) chartaceous; (1) subcoriacious to coriaceous. **26. Colour of dry specimens**: (0) usually turning blackish; (1): not turning blackish. **27. Lateral veins**: (0) anastomosing near the margin; (1) anastomosing in the margin. **28. Wing petal characteristics**: (0) not rolling backward; (1) rolling backward towards calyx. **29. Pod dehiscense**: (0) dehiscent; (1) indehiscent.