

Molecular and morphological phylogenetic reconstruction reveals a new generic delimitation of Asian *Derris* (Fabaceae): Reinstatement of *Solori* and synonymisation of *Paraderris* with *Derris*

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Abstract The genus *Derris* is a problematic taxon within 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 circumscription of *Derris* s.str. was also not monophyletic. In this study, 29 qualitative morphological characters were analyzed together with the molecular data of our earlier studies. The combined datasets confirmed the monophyly of *Solori* (also known as *Brachypterum*) and showed it to be distinct at the generic level with the following synapomorphies: presence of stipellae, more than five flowers per brachyblast, tubular and (or) lobed floral disk, seven to twelve ovules and one-winged pods with obvious seed chambers when dry. *Paraderris* appeared to be a well-supported monophyletic group, but nested within *Derris* s.str. In order to maintain the monophyly of *Derris* s.str., *Paraderris* is synonymised with *Derris* s.str., which broadens the generic circumscription for *Derris* s.str. This *Derris* s.str. only has two synapomorphies, the liana habit and two-winged pods. Other morphological characters used for previous generic circumscriptions of *Derris* s.str. appeared to be based on combinations of plesiomorphies. No infrageneric classification of *Derris* s.str. 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*; Asia; *Brachypterum*; character reconstruction; *Derris*; molecular and morphological phylogeny; *Paraderris*; *Solori*

Supplementary Material The Electronic Supplement (Figs. S1–S2, Table S1) is available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

Systematics of legumes is of major importance not only for 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, 1994). 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 provided 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 potentially can provide a greater number of informative characters (Hillis, 1987; Wortley & Scotland, 2006), which generally increase phylogenetic accuracy (Hillis, 1987, 1998). This does not mean that morphological data are meaningless, but sometimes in legume systematics, for example in 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 (1984a), whose study of this tribe is still the most comprehensive one 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 in 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 & 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 *Deguelia* Aublet, were once considered to be closely related

to or were even synonymised with *Derris*, here referred to as *Derris* s.l. (Bentham, 1860; Thothathri, 1961, 1982). However, recent molecular studies (Lavin & al., 1998; Hu & al., 2000, 2002; Kajita & al., 2001; Da Silva & al., 2012; Sirichamorn & al., 2012b) have shown that they are distantly related. These results confirmed the idea of Geesink (1984a), who proposed to raise many infrageneric taxa of *Derris* s.l. to generic level, e.g., *Brachypterum* (Wight & Arn.) Benth., *Deguelia*, *Ostryocarpus* and *Paraderris* (Miq.) Geesink. One remaining question is the relationship among the Asian *Derris*-like genera, i.e., *Brachypterum*, *Derris* s.str. and *Paraderris*, because only insufficient samples of these taxa were included in molecular phylogenetic reconstructions. Sirichamorn & al. (2012b) presented a more comprehensive phylogenetic analysis 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* (*Paraderris*) *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 latest generic concepts as proposed by Adema (2000) and followed by Sirichamorn & al. (2012a), who recognised *Derris* and *Paraderris* as distinct genera but *Brachypterum* as a part of *Derris*.

The generic name *Brachypterum* was established by Wight & Arnott (1834: 264) as a subgenus of *Dalbergia* L.f. containing only *D. scandens* Roxb. The name is later generally treated as the section *Brachypterum* of *Derris* Lour. s.l. (Bentham, 1860) and also occasionally as a genus (Bentham, 1837; Miquel, 1855). Geesink (1984a), in his attempt to reinstate *Brachypterum* into generic rank, had found that the species that includes the type of *Brachypterum*, *Derris scandens* (Roxb.) Benth. (= *Brachypterum scandens* (Roxb.) Miq.), also included the type of the older, long-unused and unknown generic name *Solori* Adans., which was already rejected against *Derris* but not against *Brachypterum* (*Vienna Code*, McNeill & al., 2006). Thus, Geesink (1984b) proposed to conserve *Brachypterum* against *Solori*. Unfortunately, the proposal was not recommended (Brummitt, 1987), chiefly because *Brachypterum* had been seldom used at generic rank up to then. The second attempt to conserve the now more commonly used name *Brachypterum* against the forgotten name *Solori* was re-proposed by Sirichamorn & al. (2013), but the nomenclatural committee still did not recommend the proposal for the same reasons (Applequist, 2013). As a consequence *Solori* will be proposed and used in this article instead of *Brachypterum*.

Although DNA sequence data have resolved phylogenetic relationships, the inclusion of morphological data in phylogenetic analyses is still necessary, or at least desirable (Queiroz & al., 1995) to be used as a “reality check” for molecular results (Wiens, 2004), 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 examine the phylogenetic relationships of Asian *Derris* as proposed by Sirichamorn & 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 by Sirichamorn & 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 taxa are phylogenetically far apart. The specimen vouchers with GenBank accession numbers, the list of morphological characters and the morphological data matrix are shown in Appendices 1–2 and in Table S1 (Electr. Suppl.), respectively.

Molecular and morphological data. — Four molecular markers were sequenced, chloroplast *trnL-F* IGS, *psbA-trnH* IGS and *trnK-matK* and nuclear ITS/5.8S. See Sirichamorn & al. (2012b) for details about DNA extraction, sequencing, and alignment (TreeBase submission ID: 15913; study accession URL: <http://purl.org/phylo/treebase/phyloids/study/TB2:SI5913>).

In total 29 morphological characters representing 6 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, 1984a; Ridder-Numan & Kornet, 1994; Dixon, 1997; Schrire, 2000) and also data from Floras (Miquel, 1855; Baker, 1878; Ridley, 1922; Rudd, 1991; Phan & Vidal, 2001; Wei & 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 multi-state 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 parsimony (Fitch, 1971). DNA sequence alignments were made with BioEdit v.7.0.9 (Hall, 1999) using CLUSTAL W Multiple alignment (default settings; Thompson & al., 1994) with subsequent manual adjustment. Gaps were coded as present/absent (1/0) characters, following the simple coding model of Simmons & Ochoterena (2000) and ambiguously aligned nucleotides were excluded. *Dalbergia lanceolaria* L.f. was specified as outgroup (Sirichamorn & 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 tree bisection-reconnection 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 maximum parsimony 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*) and Bayesian inference (MrBayes v.3.1.2; Ronquist & Huelsenbeck, 2003). All settings were as in Sirichamorn & al. (2012b). The results of the combined, total-evidence data were compared with the purely molecular-based phylogeny by Sirichamorn & al. (2012b).

Mesquite v.2.7.5 (Maddison & Maddison, 2011) was used to map morphological characters on the majority-rule consensus tree of all post-burn-in trees from the Bayesian analysis of the combined molecular datasets (Fig. 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 the combined morphological and molecular dataset. — The combined matrix yielded two most parsimonious cladograms of 5192 steps, with a consistency index of 0.56 and retention index of 0.76 (Table 1). The strict consensus tree (not shown) of the combined morphological and molecular dataset showed a topology and branch support similar to those found in the molecular analysis by Sirichamorn & al. (2012b), although bootstrap support for the *Paraderris* subclade, “DP”, was much higher (compare Fig. 1A and 1B). The majority-rule consensus Bayesian tree of the combined dataset is shown in Fig. 1A. This tree is slightly more resolved than the one obtained from the Bayesian analysis of the molecular data (Fig. 1B) in Sirichamorn & al. (2012b) as recognizable in the *Solori* clade (indicated by “S” in Fig. 1). The parsimony and Bayesian cladograms of the combined data support the recognition of *Aganope*, *Deguelia*, *Leptoderris*, *Lonchocarpus*, *Philenoptera* and *Solori* as distinct genera clearly apart from *Derris* and *Paraderris* (indicated by “D” and “DP” respectively in Fig. 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. 2. Some characters that are considered phylogenetically and taxonomically important synapomorphies are presented in Fig. 3A–C; and in Figs. S1–S2 in the Electr. Suppl.

The *Aganope* clade (A in Fig. 2) is supported by the following apomorphies: large flowers, standard petals longer than 10 mm (char[acter]. 11, state 1, reversal in *A. thyrsiflora* (Benth.) Polhill) and 2-winged pods (char. 21, state 2; Fig. 3A, 1-winged parallel in *A. heptaphylla* (L.) Polhill). The character supporting the Asian *Aganope* subclade (AA in Fig. 2) is anthers and connective tissue with hairs (char. 16, state 1). The character supporting the African *Aganope* major subclade (AF in Fig. 2) is treelet- (or shrub-)like habit (char. 1, state 1; though multistate for *A. gabonica* (Baill.) Polhill and *A. leucobotrya* (Dunn) Polhill). The African *Aganope-Ostryoderris* subclade (AO in Fig. 2) is supported by the presence of stipellae (char. 3, state 0, Electr. Suppl.: Fig. S1) and flower bracts larger than flower buds (char. 9, state 0). The monotypic African *Aganope-Xeroderris* (AX in Fig. 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 *Solori* clade (S in Fig. 2) are the presence of stipellae (char. 3, state 0, Electr. Suppl.: Fig. S1, with three times a parallel reversal), more than 5 flowers per brachyblast (char. 8, state 2, Electr. Suppl. Fig. S2), tubular or 10-lobed floral disks (char. 17, state 2, Fig. 3B, with a reversal in *S. philippinensis*), 8–12 ovules (char. 19, state 3, Fig. 3A), 1-winged pods (char. 21, state 1, Fig. 3A), and the presence of a seed chamber (char. 22, state 1, Fig. 3C).

The *Derris* major clade (D in Fig. 2) is supported by a liana habit (char. 1 state 2, Electr. Suppl.: Fig. S1) and pods having two wings along both sutures (char. 21, state 2, Fig. 3A, 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. 2) is supported by elongated brachyblasts (char. 6, state 2; Electr. Suppl.: Fig. S2) 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).

Table 1. Tree information and statistics from MP analyses of morphological, molecular (Sirichamorn & al., 2012b) and combined data.

	Phylogeny based on		
	Morphology	Molecular data	Combined data
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 most parsimonious trees	>50,000	2	2
Most parsimonious tree length	126	5024	5192
Consistency index, all characters	0.34	0.57	0.56
Consistency index, only informative characters	0.34	0.46	0.45
Retention index	0.80	0.76	0.76

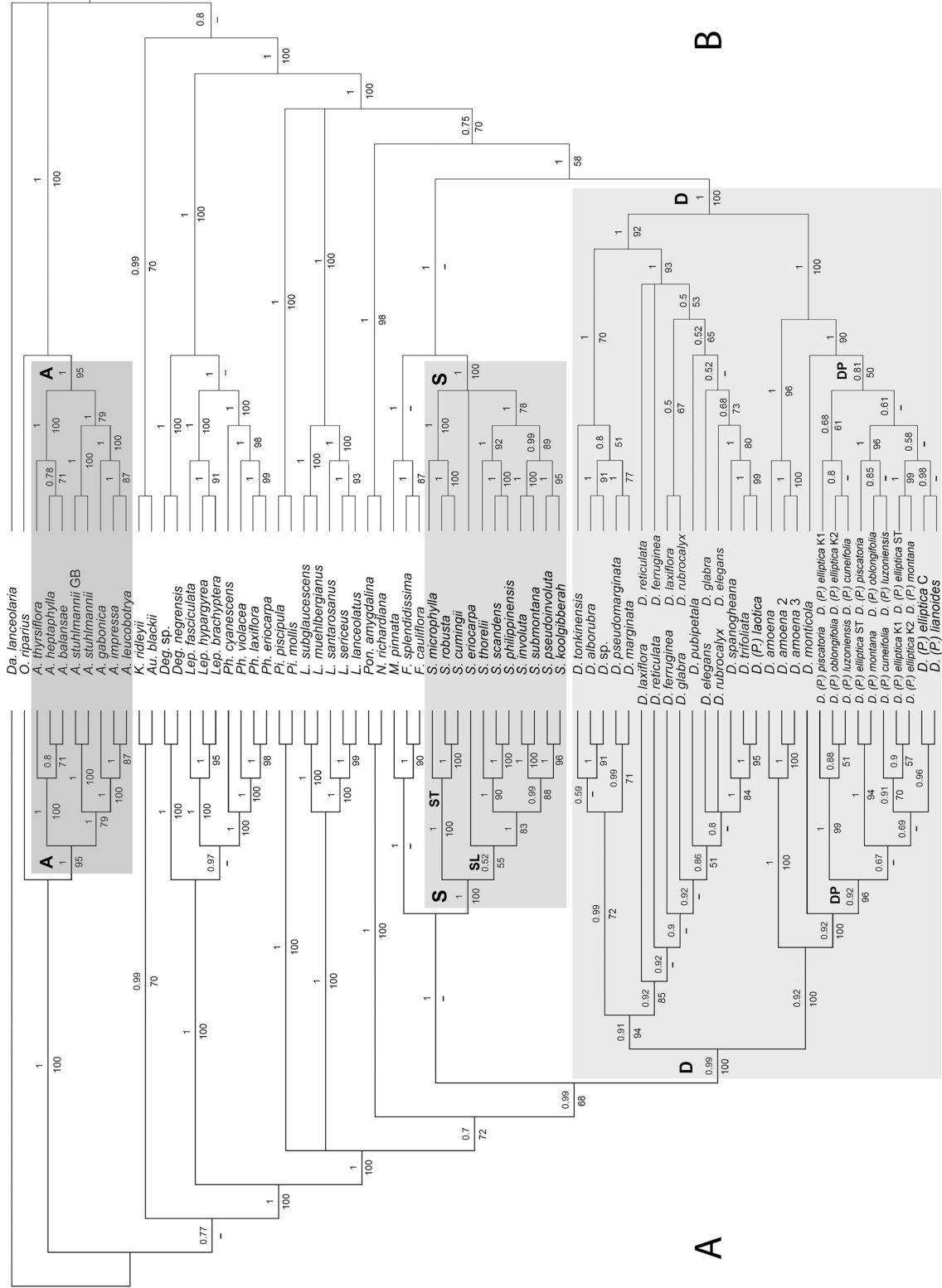


Fig. 1. A, majority-rule consensus tree from Bayesian analysis of all combined molecular and morphological datasets; **B**, majority-rule consensus tree from Bayesian analysis of the complete molecular dataset from a previous study (Sirichamorn & al., 2012b). — Numbers below branches are bootstrap support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

DISCUSSION

Morphological characters in phylogeny reconstruction of Asian *Derris* and other genera of tribe Millettieae. — Former phylogenetic analyses based on morphological characters only, either showed low resolution (Geesink, 1984a), 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 was low (see Table 1), which indicated the presence of many homoplastic

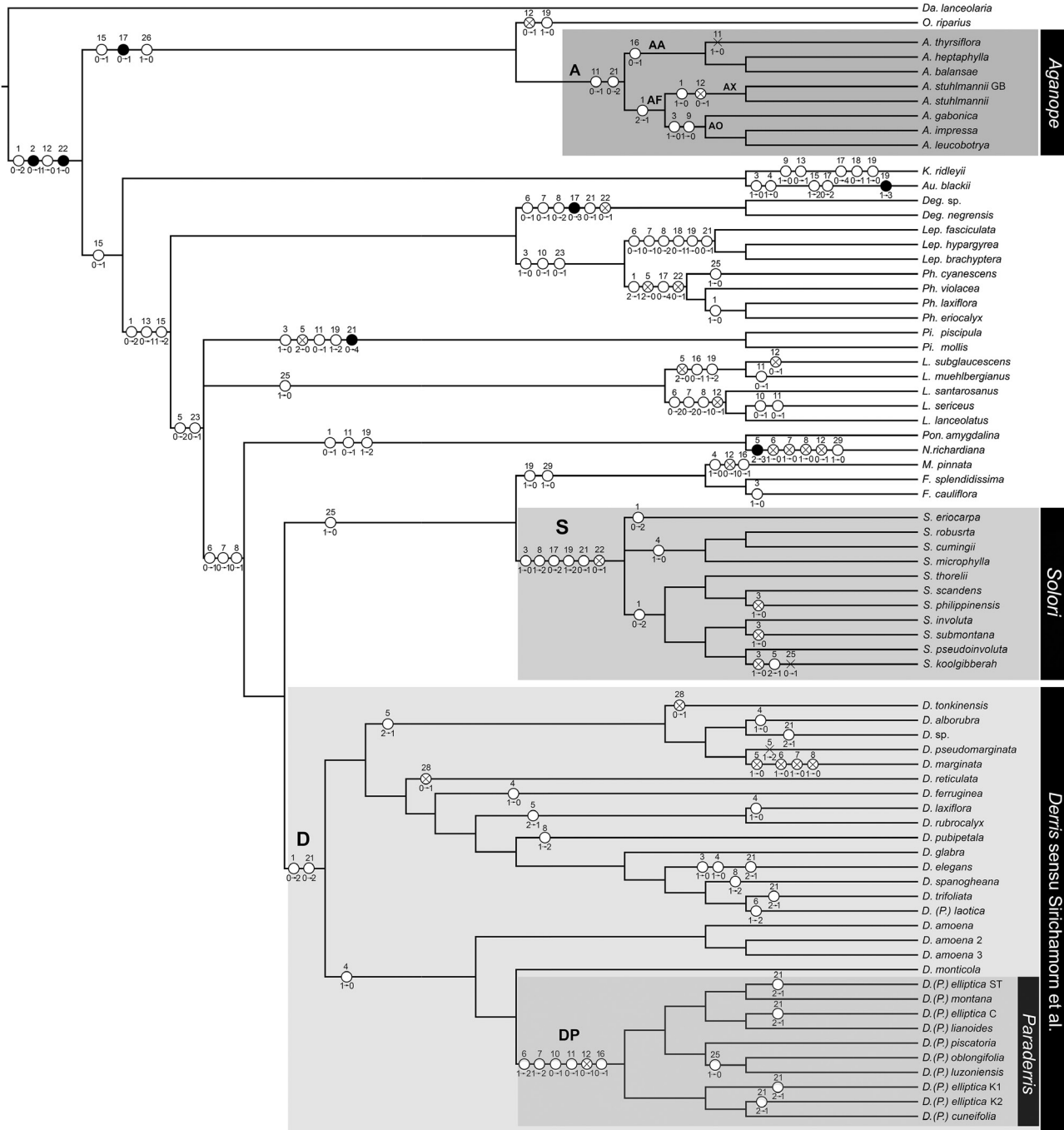
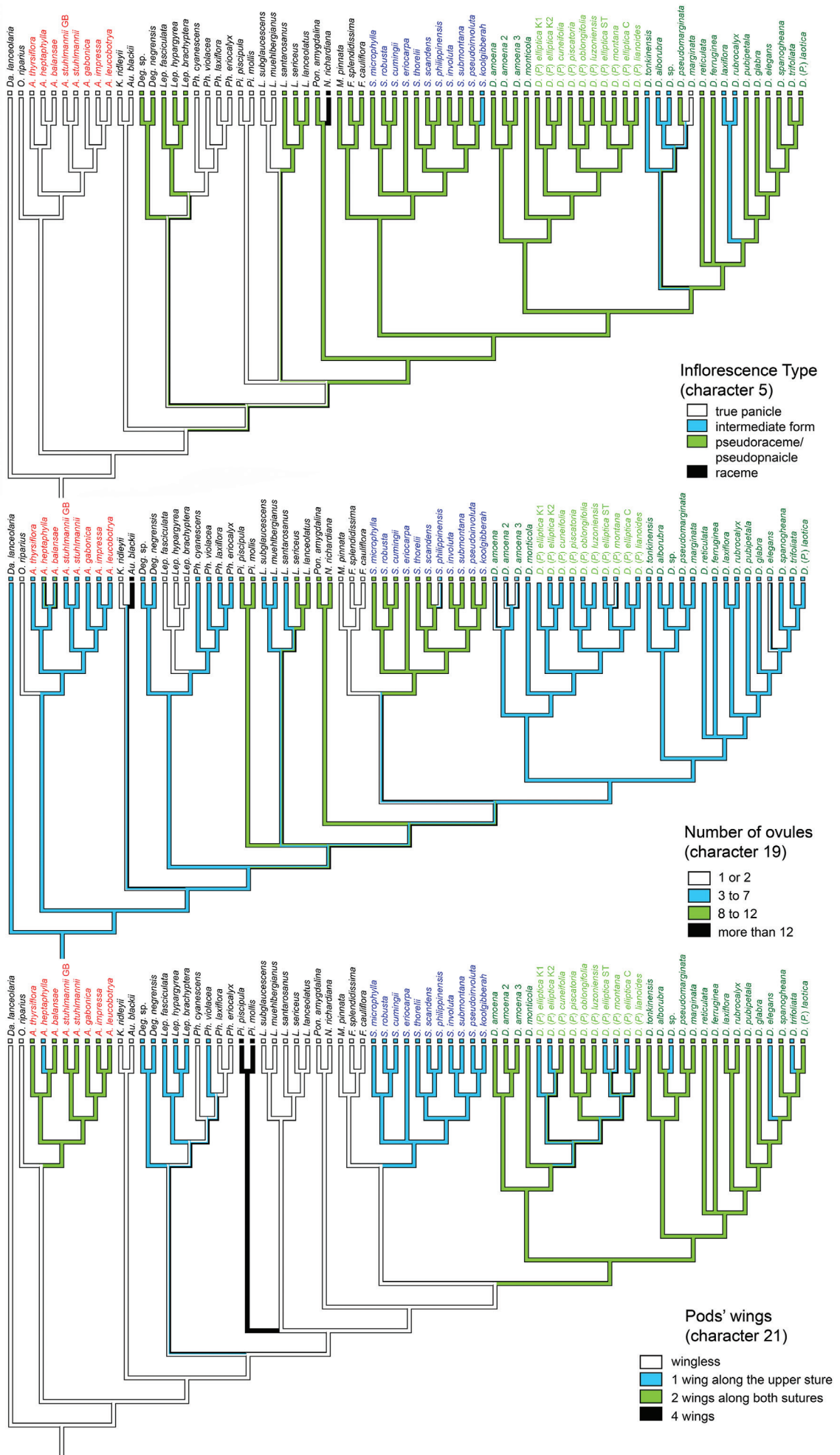


Fig. 2. Character state changes of the morphological characters traced on the majority-rule consensus Bayesian tree of all molecular data (Fig. 1B). Legends: ● = unique apomorphy; ○ = parallelism; × = reversal; ⊗ = parallel reversal. Characters 20, 24 and 27 are not shown here. Abbreviations of genera are the same as in Fig. 1. Capital letters: A, *Aganope* main clade; AA, Asiatic *Aganope* subclade; AF, African *Aganope* subclade; AO, *Aganope-Ostryoderris* subclade; AX, *Aganope-Xeroderris* subclade; D, *Derris* s.str. clade; DP, *Paraderris* subclade (except *D. (P.) laotica*) and S = *Solori* clade.

Fig. 3A



characters. We used as many morphological characters as possible that were presumed to be phylogenetically informative or important for taxonomy (Wiens, 2004). However, they were not very helpful in phylogenetic reconstruction. This is not surprising, because character coding, character conceptualisation and homology assessment are known problems when

reconstructing phylogenies using only morphology (Scotland & al., 2003) and often involve subjectivity. In *Derris* and *Solori* 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 *Solori koolgibberah* (F.M.Bailey)

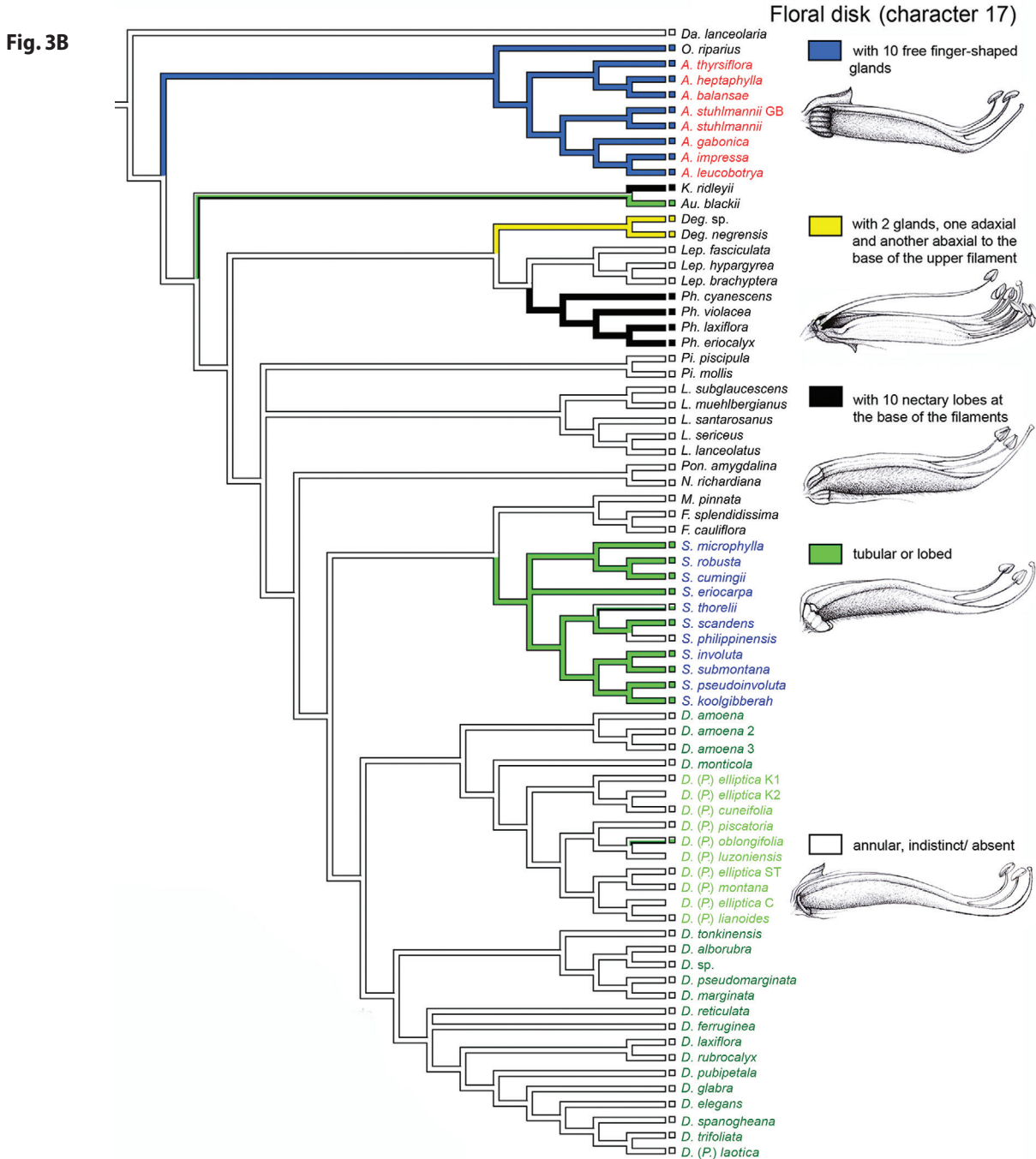


Fig. 3. Evolution of some diagnostic morphological characters optimised onto the molecular phylogeny (Fig. 1B) using Mesquite v.2.7.1. **A**, type of inflorescence (char. 5), number of ovules (char. 19) and number of pod wings (char. 21); **B**, shape of floral disk (char. 17); **C**, presence of seed chambers (char. 22). — Double or triple coloured lines represent multistate characters. Species names of *Aganope* are presented in red. Species proposed to be transferred to *Solori* are presented in blue. *Derris* + *D. (P) laotica* and previous *Paraderris* are shown in dark green and light green, respectively.

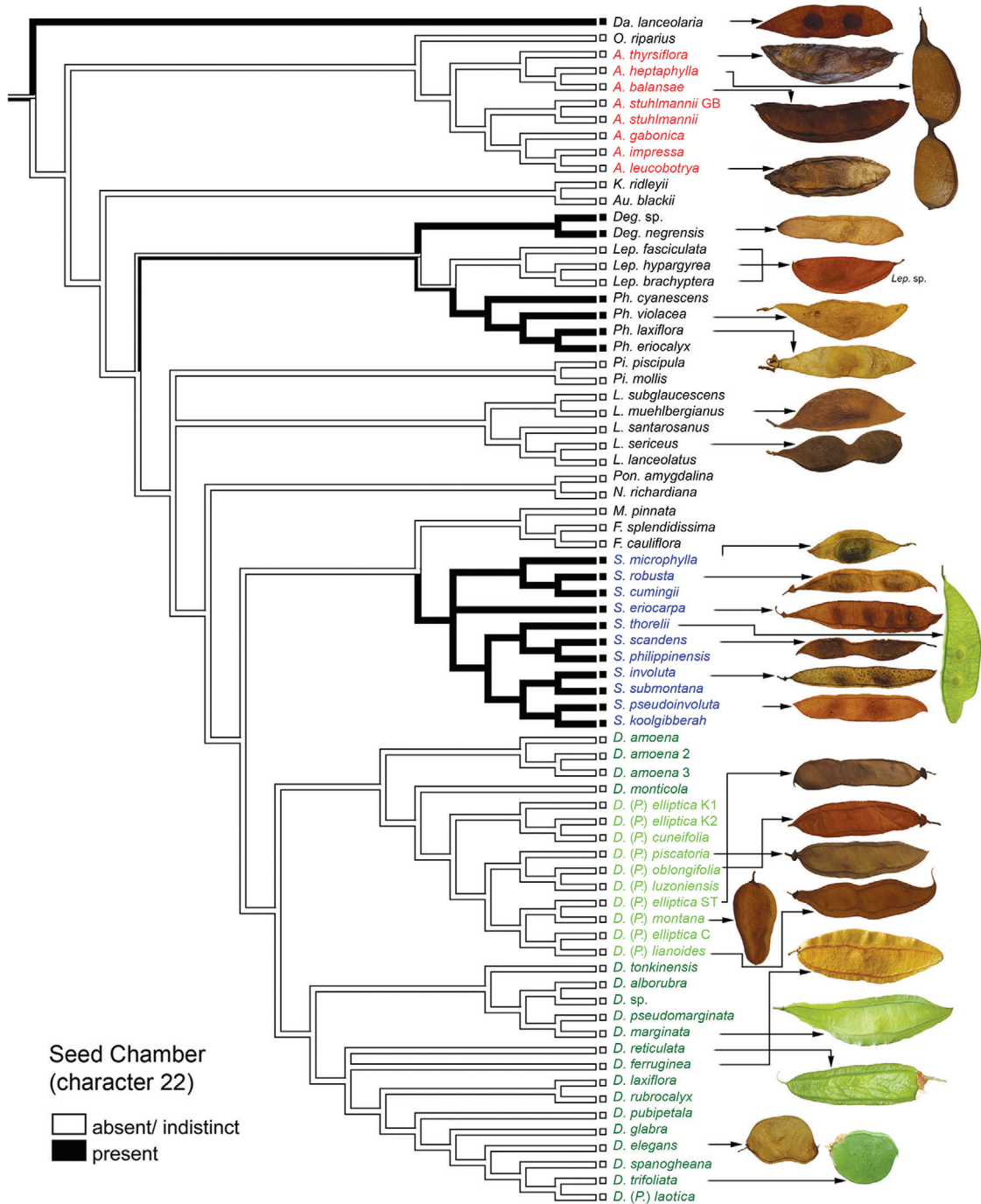
Sirich. & Adema, *Derris alborubra* Hemsl., *D. laxiflora* Benth. and *D. rubrocalyx* Verdc.) or with brachyblasts apically absent (*D. tonkinensis* Gagnep.). These indistinguishable intermediates received the same coding, but are quite likely the result of different, parallel reductions. Moreover, the 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, 1984a).

Recent studies have shown that morphology may either be convergent and misleading, thus creating “noise” that blurs phylogenetic signal (Gaubert & al., 2005), or it may provide

Fig. 3C



important support for new clades (Wahlberg & al., 2005; Sierra & al., 2010). Our study showed that combined molecular and morphological analyses resulted in better-resolved cladograms (Fig. 1A) than the analysis of only molecular datasets (Fig. 1B), e.g., the relationships between tree and liana species of *Solori* were slightly less resolved in the molecular phylogeny (Fig. 1B) than in the total-evidence cladogram (Fig. 1A); the latter showed a clear separation of the two subclades containing tree (ST) and liana species (SL), 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. 1A, BS 96%). 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 & 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. — The changes in several characters important for recognition of the taxa are discussed here; all changes are summarised in Fig. 2.

Vegetative characters. — The evolution of some vegetative characters is presented in Figs. S1–S2 (Electr. Suppl.). Hutchinson (1973) considered the “tree-like” habit more primitive than the liana habit. Within Millettieae the liana habit (char. 1, state 2) seems to have originated early, but it is difficult to decide which type is more plesiomorphic, because not many taxa with a tree-like habit were sampled here. Figures S1 and S2 (Electr. Suppl.) show that it is most parsimonious to consider the liana habit as a synapomorphy of the *Derris* major clade (+*Paraderris*) derived from a tree-like habit 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 *Solori* as tree and liana species are part of an unresolved trichotomy, although the liana habit is probably the derived state as the tree-like condition is present in the sister group, the *Millettia pinnata*–*Fordia* clade.

The presence of stipellae (char. 3, Electr. Suppl.: Fig. S1) is a derived state, which independently evolved several times. It is a synapomorphy for the subclade “*Ostryoderris*” (AO in Fig. 2) of the African *Aganope*, *Leptoderris*, *Philenoptera*, *Piscidia* and *Solori*.

The presence of reddish or brownish young leaves (char. 4, state 0) also evolved several times. The production of new leaves with anthocyanins is particularly common in Millettieae, especially in *Derris* (incl. *Paraderris*; Sirichamorn & al., 2012a). Bornman & al. (1997) hypothesized that anthocyanin pigments were protectants against strong irradiation. However, the observation that coloured young leaves are more common among understory species that receive less sunlight than elsewhere (Kursar & Coley, 1992) refuted the argument. Another theory to explain delayed chlorophyll production is herbivore pressure (Kursar & 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 & Aide, 1989).

Another phylogenetically informative character possibly related to the defense of the plants is the presence of a dark colour in dried specimens (char. 26; Electr. Suppl.: Fig. S1). The presence of this may be a synapomorphy of *Ostryocarpus* and *Aganope* (not distinct in some specimens of *A. impressa* (Dunn) Polhill). Phenolic molecules (e.g., tannins), which rapidly yield a dark-coloured polyphenolic substance by oxidation and polymerization (Queiroz & al., 2008; Parveen & al., 2010), are possibly responsible for the blackish colour.

Reproductive characters. — The type of inflorescence (char. 5, Fig. 3A) is one of the main characters which Geesink (1984a) 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, 1984a). Our character reconstruction indeed showed 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, 1984a; Tucker, 1987a, b), were reconstructed as derived from the true panicle, whereas intermediate forms were supposed to be transitions between these two types of inflorescences. However, reversals to true panicles occurred quite often during the evolution of the tribe. The shape of the brachyblasts varies from wart- or knob-like to elongated cylindrical. In Millettieae, wart- or knob-like brachyblasts (char. 6, state 1) are reconstructed as the plesiomorphic condition, while the elongated cylindrical brachyblasts (state 2) are derived and form a synapomorphy of *Lonchocarpus* and the *Paraderris* subclade of *Derris* (Electr. Suppl.: Fig. S2). The brachyblast shape correlates with the flower position (char. 7): the wart- or knob-like brachyblasts usually have flowers scattered throughout, whereas the long cylindrical brachyblasts bear flowers apically. The absence of the brachyblasts (state 0, in paniculate inflorescences) is the plesiomorphic condition from which many flowers (more than five, state 2) or up to five flowers (state 1) developed. The latter is present in the majority of the core Millettieae and the *Derris* major clade (Electr. Suppl.: Fig. S2) with further evolution to brachyblasts with many flowers. Reversals occurred regularly.

Fusion of organs is common in legumes, especially in the androecium (Rodríguez-Riaño & al., 1999). Both adnation (fusion of different organs, e.g., stamens and petals) and 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 take place later. Developmentally, a fused androecium was thus always to be considered as derived from the free state (Tucker, 1987a). In older Floras only two types of fusion, i.e., diadelphly and monadelphly, were recognized. However, in more recent ontogenic studies by Tucker (1987a, 1989), the term pseudomonadelphly was introduced for an initially diadelphous (9+1) androecium in young buds, where 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 (char. 15) were observed in fully opened mature flowers, but by lack of ontogenic observations, pseudomonadelphous is still coded as monadelphous (state 2 of char. 15). This state was found in the majority of sampled Millettieae taxa in our study. “Equal diadelphous” (Tucker, 1987a), with two groups of five stamens (5+5), can be found in species of *Dalbergia lanceolaria*, the outgroup in this study. Figure S2 (Electr. Suppl.) shows that the filament fusion changes from diadelphous (9+1) in the basal Millettoid 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 latter type of androecium provides adaptive advantages over the diadelphous androecium by forming the staminal column which protects the ovary and ovules against insect attack, prevents desiccation of the intrastaminal nectary, and limits the range of pollinators that can work the flowers (Rodríguez-Riaño & al., 1999).

Interestingly, the intrastaminal floral disks (char. 17, Fig. 3B) in the various palaeotropic *Derris*-like genera are quite different. An annular or indistinct floral disk (state 0) is present in the majority of Millettieae, also *Derris*, and is plesiomorphic, all other states are derived from it: (1). Ten free finger-like glands (state 1) are present in *Ostryocarpus* and *Aganope*. (2). The disk of *Solori* is usually tubular or lobed (state 2). (3). *Deguelia* has a floral disk formed by two glands, one adaxial and one abaxial to the base of the upper filament (state 3). (4). The disk of *Philenoptera* consists of ten nectary lobes adnate to the base of the filaments (state 4).

The majority of the taxa of Millettieae have three to seven ovules per ovary, which is the plesiomorphic character state (state 1 of char. 19, see Fig. 3A). More than seven ovules is more derived and synapomorphic for *Piscidia*, *Dahlstedtia* (2 species treated here under *Lonchocarpus*, i.e., *L. muehlbergianus* Hassl. and *L. subglaucescens* Mart. ex Benth.), *Pongamiopsis* + *Neodunia* and *Solori* clade.

Winged pods (char. 21) are derived from a wingless condition. The presence of only one wing along the upper suture (state 1) is a synapomorphy of *Solori*, *Deguelia* and *Leptoderris*. The presence of two wings along both sutures (state 2) is a synapomorphy of *Aganope* and *Derris* (with reversals to one wing; Fig. 3A). The wings are presumed to be a general adaptation to wind dispersal (Hu & al., 2000), though they are generally narrow (not more than 15 mm wide, Sirichamorn & al., 2012a). However, the thinness, papery texture and low mass of the *Derris*-like pods, as mentioned in Jayasuriya & al. (2012), indicates that probably the complete pod acts as wing. The same pod characters may also facilitate floating on water, especially important in species associated with mangroves, like *Derris scandens* (= *Solori scandens* (Roxb.) Sirich. & Adema)

and *D. trifoliata*. Jayasuriya & al. (2012) reported that the pods are buoyant and survive sea water.

The most striking characteristic of the pods are the seed chambers (char. 22, Fig. 3C). When dry, seed chambers are the hard, darker coloured areas around seeds formed by the thickenings of endocarp and mesocarp (Polhill, 1981). Geesink (1984a) listed it as a unique character for *Brachypterum* (= *Solori*). 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 & al., 2012a). Kirkbride & 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. Obviously, there is no clear definition of seed chambers. More intensive anatomical studies of the pericarp are to be followed by precise definitions. In this study seed chambers are defined as: (1) distinctly externally visible in dry pods and, more importantly, (2) formed by a thickening of the endo- and mesocarp. As such they are parallel synapomorphies of *Solori*, *Deguelia* and *Philenoptera* (Fig. 3C). In some species of *Aganope* and *Derris* s.str., a darker coloured area around seeds is sometimes found, but without the thickening of the endo- and mesocarp, or sometimes the thickened areas around seeds are formed by reticulation of the vascular bundles, not truly by the endo- and mesocarp itself. These are considered as seed chambers absent/indistinct (state 0 of char. 22).

Comparing phylogenetic and traditional classification and implications for the taxonomy of Asian *Derris*-like taxa.

— Our total-evidence phylogenetic reconstruction did not support the recognition of all *Derris*-like taxa as a single, widely defined genus *Derris* s.l. as proposed by Bentham (1860), because such a genus would be clearly polyphyletic. Two of Bentham’s sections, section *Aganope* and section *Solori* should be reinstated at generic level as proposed by Geesink (1984a). Two other sections, i.e., section *Derris* (*Euderris*) and section *Dipteroderris*, were unresolved, not recognisable and should, therefore, be abolished. Section *Paraderris*, which was raised to genus level and accepted by various authors (Geesink, 1984a; Adema, 2000, 2003a; Wei & al., 2008; Sirichamorn & al., 2012a), was a monophyletic group within the major clade of *Derris*. However, recognition of *Paraderris* as a genus would make *Derris* s.str. paraphyletic. Therefore, we will synonymise *Paraderris* with *Derris* s.str. 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. 2) for which bootstrap support rose from 50% to 96% when morphological data were added (Fig. 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* lacked distinct morphological characters, and its circumscription was based on a combination of plesiomorphic characters such as a pseudoraceme-pseudopanicule, 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.str. (including *Paraderris*). However, these two characters have evolved several times independently in the phylogeny of the tribe. A formal infrageneric classification for *Derris* s.str. will not be proposed, because the two clades (Fig. 1) were not completely sampled, nor well supported, or recognisable.

■ SYSTEMATIC TREATMENT AND NOMENCLATURAL CHANGES

A monophyletic *Derris* is defined here by reinstating *Solori* and by synonymising *Paraderris* with *Derris* s.str. The new combinations for *Solori* and former *Paraderris* are presented here, together with a new formal description of the genera.

Key to the Asian *Derris*-like genera

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 turning 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 5- to 10-lobed, sometimes hardly visible or absent. Seeds with central or slightly eccentric hilum. Specimens not turning blackish when dry 2
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 (seed chamber) around seed (dark-coloured parts around the seeds can be found in some cases) *Derris*
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 (*B. koolgibberah*). Brachyblasts wart-like or club-shaped, bearing usually more than 5 flowers. Standard without distinct basal callosities. Floral disks generally tubular or cylindrical or 10-lobed. Pods usually narrowly elliptic or strap-shaped, with one wing along the upper suture only and a distinct seed chamber when dry *Solori*

Solori Adans., Fam. Pl. 2: 327. 1763 ≡ *Dalbergia* subg. *Brachypterum* Wight & Arn., Prodr. Fl. Ind. Orient.: 264. 1834 ≡ *Brachypterum* (Wight & Arn.) Benth., Comm. Legum. Gen.: 37. 1837 ≡ *Derris* sect. *Brachypterum* (Wight & Arn.) Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 101. 1860 ≡ *Deguelia* sect. *Brachypterum* (Wight & Arn.) Taub.

in Engler & Prantl, Nat. Pflanzenfam. 3, 3: 345. 1894 – **Type (designated here for *Solori*):** *Solori scandens* (Roxb.) Sirich. & Adema (≡ *Dalbergia scandens* Roxb. ≡ *Brachypterum scandens* (Roxb.) Miq.).

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 throughout (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, cylindrical 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.

Solori cumingii (Benth.) Sirich. & Adema, **comb. nov.** ≡ *Derris cumingii* Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 104. 1860 ≡ *Deguelia cumingii* (Benth.) Taub. in Bot. Centralbl. 47: 386. 1891 ≡ *Pterocarpus cumingii* (Benth.) Kuntze, Revis. Gen. Pl. 1: 203. 1891 – Holotype: PHILIPPINES. *Cuming 1208* (K barcode K000898322!; isotypes: K!, L!, MO!).

Solori eriocarpa (F.C.How) Sirich. & Adema, **comb. nov.** ≡ *Derris eriocarpa* F.C.How in Acta Phytotax. Sin. 3: 233. 1954 – Holotype: CHINA. Guangxi, Lung Chow, *S.P. Ko 55325* (IBSC n.v.).

Solori involuta (Sprague) Sirich. & Adema, **comb. nov.** ≡ *Wisteria involuta* Sprague in Gard. Chron., ser. 3, 36: 141. 1904 ≡ *Derris involuta* (Sprague) Sprague in Gard. Chron., ser. 3, 38: 3. 1905 – Holotype: England, Royal Botanic Gardens, Kew, Temperate House [cultivated from material collected in Australia, New South Wales, Richmond River], 15 Jul 1904, *Sprague s.n.* (K barcode K000898356 [photo!]).

Solori koolgibberah (F.M.Bailey) Sirich. & Adema, **comb. nov.** ≡ *Derris koolgibberah* F.M.Bailey, Rep. Bellenden-Ker Range: 38. 1889 – Holotype: AUSTRALIA. Queensland, along the Mulgrave River, *F.M. Bailey s.n.* (BRI, n.v.; isotype: K!).

Solori microphylla (Miq.) Sirich. & Adema, **comb. nov.** ≡ *Brachypterum microphyllum* Miq., Fl. Ned. Ind., Eerste

- Bijv.: 296. 1861 = *Derris microphylla* (Miq.) B.D.Jacks., Index Kew. 1: 332. 1895 – Holotype: INDONESIA. Sumatra, Palembang, *Teijsmann s.n.* (L!; isotype: U!).
- = *Derris dalbergioides* Baker in Hooker, Fl. Brit. India 2: 241. 1878 – Lectotype (designated by Sirichamorn & al. in Syst. Bot. 37: 418. 2012): MALAYSIA. Malacca, *Maingay s.n.* (K!).
- Solori philippinensis*** (Merr.) Sirich. & Adema, **comb. nov.** = *Derris philippinensis* Merr. in Philipp. J. Sci., C 5: 104. 1910 = *Derris multiflora* var. *longifolia* Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 108. 1860 – **Lectotype (designated here for *Derris philippinensis*):** PHILIPPINES. Luzon, *Cuming 1162* (K!; isotypes: E!, L!).
- The lectotype of *Derris philippinensis* is also the holotype of *D. multiflora* var. *longifolia*. Syntypes of *D. philippinensis* include: PHILIPPINES, *BS 7635*, *Elmer 6177*, *Merrill 1969*, *5045*, *Williams 714* (all US [photos!]), *Topping 535* (unknown).
- Solori pseudoinvoluta*** (Verdc.) Sirich. & Adema, **comb. nov.** = *Derris koolgibberah* subsp. *pseudoinvoluta* Verdc. in Kew Bull. 32: 469. 1978 = *Derris pseudoinvoluta* (Verdc.) Adema in Thai Forest Bull., Bot. 28: 11. 2000 – Holotype: PAPUA NEW GUINEA. Lae, *Womersley NGF 15395* (K!, isotypes: L!, LAE n.v.).
- Solori pseudorobusta*** (Thoth.) Sirich. & Adema, **comb. nov.** = *Derris pseudorobusta* Thoth. in Bull. Bot. Surv. India 3: 181. 1962 – Holotype: INDIA. North-East Frontier Agency, *Panigrahi 14550A* (CAL n.v.; isotype: BSI n.v.).
- Solori robusta*** (Roxb. ex DC.) Sirich. & Adema, **comb. nov.** = *Dalbergia robusta* Roxb. ex DC., Prodr. 2: 417. 1825 (Hort. Bengal.: 53. 1814, nom. nud.) = *Derris robusta* (Roxb. ex DC.) Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 104. 1860 = *Brachypterum robustum* (Roxb. ex DC.) Dalzell & A.Gibson, Bombay Fl.: 77. 1861 = *Deguelia robusta* (Roxb. ex DC.) Taub. in Bot. Centralbl. 47: 388. 1891 – Lectotype (designated by Thothathri, Fasc. Fl. India 8: 26. 1982): INDIA. Silhet, *Wallich 5849B* (CAL n.v.; isolectotype: K!).
- = *Brachypterum polyphyllum* Miq., Fl. Ned. Ind. 1: 139. 1855 = *Derris polyphylla* (Miq.) Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 104. 1860 – Holotype: INDONESIA. Java, Soerakarta, *Horsfield s.n.* (U!; isotypes: CAL n.v., K!).
- Solori scandens*** (Roxb.) Sirich. & Adema, **comb. nov.** = *Dalbergia scandens* Roxb., Pl. Coromandel 2: 49, t. 192. 1805 = *Brachypterum scandens* (Roxb.) Benth. in Comm. Legum. Gen.: 37. 1837 = *Derris scandens* (Roxb.) Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 103. 1860 – Lectotype (designated by Thothathri, Fasc. Fl. India 8: 27. 1982): [Illustration] “*Dalbergia scandens*” in Roxburgh, Pl. Coromandel 2: t. 192. 1805.
- = *Dalbergia timoriensis* DC., Prodr. 2: 417. 1825 = *Brachypterum timoriense* (DC.) Benth. ex Miq., Fl. Ned. Ind. 1: 138. 1855 (“*timorensis*”) = *Derris timoriensis* (DC.) Pittier in Contr. U.S. Natl. Herb. 20: 41. 1917 – Type: not indicated (P or G-DC, both n.v.).
- = *Dalbergia venusta* Zipp. ex Span. in Linnaea 15: 197. 1841 – Holotype: INDONESIA. Lesser Sunda Islands, Timor, *Zippelius s.n.* (L barcode 0475849!; isotype: L barcode 0475873!).
- = *Millettia litoralis* Dunn in Philipp. J. Sci., C. 6: 316. 1911 – Holotype: PHILIPPINES. Mindanao, St. Cruz, *DeVore & Hoove 250* (K!).
- Solori submontana*** (Verdc.) Sirich. & Adema, **comb. nov.** = *Derris submontana* Verdc. in Kew Bull. 32: 465. 1978 – Holotype: PAPUA NEW GUINEA. *Clemens 8162* (B; isotypes: A n.v., L!).
- Solori thorelii*** (Gagnep.) Sirich. & Adema, **comb. nov.** = *Millettia thorelii* Gagnep. in Not. Syst. (Paris) 2: 365. 1913 = *Derris thorelii* (Gagnep.) Craib, Fl. Siam. 1: 435, 493. 1928 – Lectotype (designated by Phan in Phan & Vidal, Fl. Cambodge, Laos & Vietnam 30: 58. 2001): LAOS. De Xieng Khouang à Pak Lai, 1866–1868, *Thorel s.n.* (P!).
- Derris*** Lour., Fl. Cochinch.: 432. 1790, nom. cons. – Type: *Derris trifoliata* Lour., typ. cons.
- = *Derris* sect. *Dipteroderris* Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 102. 1860 – Type (designated by Sirichamorn & al., 2012a): *Derris ferruginea* (Roxb.) Benth.
- = *Derris* sect. *Paraderris* Miq., Fl. Ned. Ind. 1: 145. 1855 = *Deguelia* sect. *Paradeguelia* Taub. in Engler & Prantl, Nat. Pflanzenfam. 3, 3: 345. 1894 = *Paraderris* (Miq.) R.Geesink in Leiden Bot. Ser. 8: 109. 1984 – Type (designated by Geesink for *Derris* sect. *Paraderris* and *Deguelia* sect. *Paradeguelia* in Leiden Bot. Ser. 8: 109. 1984): *Paraderris cuneifolia* (Benth.) R.Geesink (= *Derris cuneifolia* Benth.).
- = *Salken* Adans., Fam. Pl. 2: 322. 1763, nom. rej. – Type: not designated.
- Lianas. Twigs usually lenticellate. Leaves imparipinnate; stipules present, persistent or caducous; stipellae absent or present, persistent. Leaflets generally 3–9(–15) per leaf, opposite, entire. Inflorescences axillary pseudoracemes, often combined with terminal or axillary pseudopanicles, rarely true panicles, sometimes intermediate forms like panicle in the lower part and pseudoraceme in the upper part, or, pseudoraceme in the lower part and flowers solitary in the upper part. Flowers usually 2–5(–7) scattered throughout or on top of knob-like, club-shaped to long and slender 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 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 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. Stamens 10, monadelphous, with basal fenestrae; anthers all equal, fertile, glabrous or hairy. Disc generally inconspicuous

or annular. Ovary with 2–5(–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.

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

= *Derris oblonga* Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 112. 1860 ≡ *Deguelia oblonga* (Benth.) Taub. in Bot. Centralbl. 47: 387. 1891 – Syntypes: INDIA. Konkan, *Stocks s.n.*; SRI LANKA. *Gardner 476*, *Walker s.n.* and *Thwaites 1493* (K, all n.v.).

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

= *Derris cuneifolia* f. *assamica* Thoth. in Bull. Bot. Surv. India 3: 192. 1961 – Holotype: INDIA. Assam, Cachar, Bishnupur, *U. Kanjilal 4835* (CAL n.v.).

= *Derris cuneifolia* var. *longipedicellata* Thoth. in Bull. Bot. Surv. India 3: 191. 1961 – Holotype: INDIA. Sikkim, *Sivoke, Ribu 760* (CAL n.v.).

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

= *Derris glauca* Merr. & Chun in Sunyatsenia 2: 246. 1935 – Holotype: CHINA. Hainan, Ngai Yuen, 4 Jun 1933, *F.C. How 70860* (NY [photo!]; isotypes: A [photo!], K!, P!, US [photo!]).

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

= *Derris truncata* Craib in Bull. Misc. Inform. Kew 1927: 385. 1927 – Holotype: THAILAND. Phitsanulok, Nakhawn Tai, 3 Apr 1924, *Kerr 8898* (K!; isotype: BK!).

= *Galedupa marginata* Roxb., Fl. Ind., ed. 1832: 3: 241. 1832 (as nom. nud. in Hort. Bengal.: 53. 1814) – Holotype: INDIA. Silhet, *Wallich Cat. 5896A* (K-W n.v.; isotype: P!).

Derris elliptica (Wall.) Benth. in J. Proc. Linn. Soc., Bot. 4 (Suppl.): 111. 1860 ≡ *Pongamia elliptica* [Sweet, Hort. Brit.: 131. 1826, nom. nud.] Wall., Pl. Asiat. Rar. 3: 20, t. 237. 1832 ≡ *Paraderris elliptica* (Wall.) Adema in Thai Forest Bull., Bot. 28: 11. 2001 (“2000”) – Holotype: INDIA. Hort. Bot. Calcutta (originally from Ambon), *Wallich 5881A* (K!; isotype: CAL, fragments, n.v.).

= *Dalbergia purpurea* Reinw. [ex Blume, Catalogus: 90. 1823,

nom. nud.] ex Hassk. in Flora 25(Beibl. 2): 53. 1842 – Holotype: INDONESIA. Java, *Blume s.n.* (L!).

= *Derris elliptica* var. *chittagongensis* Thoth. in Bull. Bot. Surv. India 3: 195. 1961 ≡ *Paraderris elliptica* var. *chittagongensis* (Thoth.) Adema in Blumea 48: 137. 2003 – Holotype: INDIA. Chittagong, Kodla, *Baldal Khan 450(C)* (CAL n.v.; isotypes: CAL n.v., K [photo!]).

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

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

Derris hainanensis Hayata, Icon. Pl. Formos. 3: 77. 1913 ≡ *Paraderris hainanensis* (Hayata) Adema in Blumea 48: 138. 2003 – Holotype: CHINA. Hainan, *K. Katsumada s.n.* (location unknown).

Derris lacei Dunn in Bull. Misc. Inform. Kew 1914: 206. 1914 ≡ *Paraderris lacei* (Dunn) Adema in Blumea 48: 138. 2003 – Lectotype (designated by Adema in Blumea 48: 138. 2003): MYANMAR. Maymyo Plateau, *Lace 6115* (K!; isolectotype: CAL n.v.).

Derris laotica Gagnep. in Not. Syst. (Paris) 2: 348. 1913 ≡ *Paraderris laotica* (Gagnep.) Adema in Blumea 48: 138. 2003 – Lectotype (designated by Phan in Phan & Vidal, Fl. Cambodge, Laos & Vietnam 30: 68. 2001): CAMBODIA. Bâklon, *Magnen & al. s.n.* (P!; isolectotype: K, fragments, n.v.).

= *Derris laotica* var. *virens* Gagnep. in Notul. Syst. (Paris) 2: 348. 1913 – Lectotype (designated by Phan in Phan & Vidal, Fl. Cambodge, Laos & Vietnam 30: 68. 2001): CAMBODIA. Siem-reap, *Godefroy 686* (P!).

Derris lianoides Elmer in Leaflet. Philipp. Bot. 1: 228. 1907 ≡ *Paraderris lianoides* (Elmer) Adema in Blumea 48: 138. 2003 – Holotype: PHILIPPINES. Luzon, Prov. Taybas, Luchon, *Elmer 7443* (PNH, probably lost; isotypes CAL n.v., K!).

Derris lushaiensis Thoth. in Bull. Bot. Surv. India 12: 104. 1972 ≡ *Paraderris lushaiensis* (Thoth.) Adema in Blumea 48: 138. 2003 – Holotype: INDIA, *Gage 23A-C* (CAL n.v.).

Derris luzoniensis (Adema) Sirich. & Adema, **comb. nov.** ≡ *Paraderris luzoniensis* Adema in Blumea 48: 134. 2003 – Holotype: PHILIPPINES. Luzon, Palanan area, Dimpnat, *Ridsdale & al. ISU 564* (L!; isotype: K n.v.).

Derris montana Benth. in Miquel, Pl. Jungh.: 253. 1852 ≡ *Deguelia montana* (Benth.) Taub. in Bot. Centralbl. 47: 387. 1891 ≡ *Pterocarpus montanus* (Benth.) Kuntze in Revis. Gen. Pl. 1: 203. 1891 ≡ *Paraderris montana* (Benth.) Adema

- in *Blumea* 48: 139. 2003 – Holotype: INDONESIA. Java, Dieng, *Junghuh s.n.* (BO n.v.).
- = *Derris caudata* Backer in *Blumea* 5: 513. 1945 – Holotype: INDONESIA. Java, Bantam, *Backer 7061* (BO? n.v.; isotype: L!).
- = *Derris cuneifolia* var. *malaccensis* Benth. in J. Proc. Linn. Soc., Bot. 4(Suppl.): 112. 1860 = *Derris malaccensis* (Benth.) Prain in J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 66: 107. 1897 = *Paraderris malaccensis* (Benth.) Adema in Thai Forest Bull., Bot. 28: 11. 2001 – Holotype: MALAYSIA. Malacca, *Griffith KD 1774* (K!; isotype: CAL n.v.).
- = *Derris danauensis* Backer in *Blumea* 5: 513. 1945 – Holotype: INDONESIA. Java, Rawah Danau, *Steenis 10539* (BO? n.v.; isotype: L!).
- = *Derris malaccensis* var. *aptera* Prain in J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 66: 108. 1897 – Lectotype (designated by Adema in *Blumea* 48: 139. 2003): MALAYSIA. Perak, *King's coll. 4518* (K!; isolectotypes: A n.v., CAL n.v.).
- = *Derris pachycarpa* Merr. in J. Straits Branch Roy. Asiat. Soc. 86: 312. 1922 – Holotype: MALAYSIA. Borneo, Sabah, *BS 1250 (Ramos)* (PNH†; isotype: K n.v.).

Derris oblongifolia Merr. in Philipp. J. Sci., C 7: 82. 1912 = *Paraderris oblongifolia* (Merr.) Adema in *Blumea* 48: 139. 2003 – Holotype: PHILIPPINES. Luzon, Subprov. Bauco, Bontoc, *Vanoverberg 280* (PNH†).

Derris ornithocephala (Adema) Sirich. & Adema, **comb. nov.** = *Paraderris ornithocephala* Adema in *Blumea* 48: 134. 2003 – Holotype: INDONESIA. Papua, NE Kepala Burung, Manokwari, Numi, Sungai Asai, *Dransfield & al. 7554* (K n.v.; isotype: L!).

Derris piscatoria (Blanco) Sirich. & Adema **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 in *Blumea* 48: 139. 2003 – Neotype (designated by Adema in *Blumea* 48: 139. 2003): PHILIPPINES. Luzon, Batangas Prov., Mt. Batulo, *Merrill Spec. Blanc. 469* (L!; isoneotypes: A n.v., K n.v.).

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Appendix 1. Species, voucher specimen, and GenBank information for sequence data reported in the study. Herbarium abbreviations 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 *Solori* recognised as genus, and *Paraderris* synonymised 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 & 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. stuhlmannii*); *Versteegh & al. 456* (L), Ivory Coast: Korhogo, JX506603, JX506435, JX506491, JX506546. *Aganope thyrsoflora* (Benth.) Polhill; *Sirichamorn YSM 2009-22* (L), Thailand: Songkhla, JX506602, JX506434, JX506490, JX506545. *Austrostenisia blackii* (F.Muell.) Geesink; *Pedley 5005* (K), Australia, *AF142707*, *AF467020*, –, –, *Dalbergia lanceolaria* L.f.; *Sirichamorn YSM 2009-02* (L), Thailand: Bangkok (cultivated), JX506655, JX506484, JX506541, JX506597. *Deguelia negrensis* (Benth.) Taub.; *C. & F. Sastrel 152* (L), Brazil, JX506607, JX506441, –, –, *Deguelia* sp.; *Granville & al. 10075* (L), French Guiana: Haut-maroni, 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 (cultivated), 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*]; *Kanchai 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: Udun 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; *Ridsdale, Baquiran & 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) piscatorica* (Blanco) Sirich. & Adema; *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 splendissima* (Blume ex Miq.) Buijsen; *Tangah s.n.*, Malaysia: Sabah, *AF142718*, *AF467048*, –, –, *Kunstleria ridleyi* Prain; *Ambriansyah & 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 & 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.; *Fuertes 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*, –, –, *Milletia 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 & 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* (DAY), México: Sonora, –, *AF467489*, –, –, *Piscidia piscipula* (L.) Sarg.; *Lavin & Luckow 5793* (TEX), México: Veracruz, *AF142710*,

Appendix 1. Continued.

AF467490, –, –, *Pongamiopsis amygdalina* (Baill.) R.Vig.; *DuPuy* M575 (K), Madagascar, AF142711, AF467494, –, –, *Solori cumingii* (Benth.) Sirich. & Adema; *Gaerlan & al. PPI 10368* (L), Philippines: Luzon, JX506618, JX506447, JX506505, JX506561. *Solori eriocarpa* (F.C.How) Sirich. & Adema; *Wang Hong 7673* (QBG), China: Yunnan, JX506625, JX506454, JX506512, JX506568. *Solori involuta* (Sprague) Sirich. & Adema; *Murray, Coveny & Bishop* s.n., sheet no. *NSW 409439* (L), Australia: North coast, JX506622, JX506451, JX506509, JX506565. *Solori koolgibberah* (F.M.Bailey) Sirich. & Adema; *Brass 8205* (L), Papua New Guinea: Sturt Island, JX506624, JX506453, JX506511, JX506567. *Solori microphylla* (Miq.) Sirich. & Adema; *Sirichamorn YSM 2009-16* (L), Thailand: Chumphon, JX506619, JX506448, JX506506, JX506562. *Solori philippinensis* (Merr.) Sirich. & Adema; *Elmer 14373* (L), Philippines: Sorsogon, JX506627, JX506455, –, –, *Solori pseudoinvoluta* (Verdc.) Sirich. & Adema; *Streimann & Kairo NGF 27776* (L), Papua New Guinea: Morobe, JX506623, JX506452, JX506510, JX506566. *Solori robusta* (Roxb. ex DC.) Sirich. & Adema; *Sirichamorn YSM 2009-09* (L), Thailand: Lampang, JX506617, JX506446, JX506504, JX506560. *Solori scandens* (Roxb.) Sirich. & Adema; *Sirichamorn YSM 2009-01* (L), Thailand: Chon Buri, JX506621, JX506450, JX506508, JX506564. *Solori submontana* (Verdc.) Sirich. & Adema; *Takeuchi & al. 4349* (L), Papua New Guinea: Morobe, JX506626, –, JX506513, JX506569. *Solori thorelii* (Gagnep.) Sirich. & Adema; *Sirichamorn YSM 2009-03* (L), Thailand: Phrae, JX506620, JX506449, JX506507, JX506563.

Appendix 2. List of morphological characters used in phylogenetic analyses.

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 between true panicle and pseudoraceme or pseudopanicule; (2) pseudoraceme or pseudopanicule; (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. **9. Flower bract:** (0) larger than corresponding flower buds; (1) smaller than corresponding flower buds. **10. Indumentum of 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 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 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) 8 to 12; (3) more than 12. **20. Pod shape:** (0) round; (1) elliptic; (2) strap-like. **21. Pod wings:** (0) wingless; (1) wing only along 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 0–45 degrees of the equatorial axis. **24. Seed position in pod:** (0) central; (1) scattered. **25. Leaf texture:** (0) chartaceous; (1) subcoriaceous to coriaceous. **26. Colour of dry specimens:** (0) usually turning blackish; (1) not turning blackish. **27. Lateral veins:** (0) anastomosing near margin; (1) anastomosing in margin. **28. Wing petal characteristics:** (0) not rolling backward; (1) rolling backward towards calyx. **29. Pod dehiscence:** (0) dehiscent; (1) indehiscent.