Reconstructing the deep-branching relationships of the papilionoid legumes

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ABSTRACT

Resolving the phylogenetic relationships of the deep nodes of papilionoid legumes (Papilionoideae) is essential to understanding the evolutionary history and diversification of this economically and ecologically important legume subfamily. The early-branching papilionoids include mostly Neotropical trees traditionally circumscribed in the tribes Sophoreae and Swartzieae. They are more highly diverse in floral morphology than other groups of Papilionoideae. For many years, phylogenetic analyses of the Papilionoideae could not clearly resolve the relationships of the early-branching lineages due to limited sampling. In the eight years since the publication of *Legumes of the World*, we have seen an extraordinary wealth of new molecular data for the study of Papilionoideae phylogeny, enabling increasingly greater resolution and many surprises. This study draws on recent molecular phylogenetic studies and a new comprehensive Bayesian phylogenetic analysis of 668 plastid *matK* sequences. The present *matK* phylogeny resolves the deep-branching relationships of the papilionoids with increased support for many clades, and suggests that taxonomic realignments of some genera and of numerous tribes are necessary. The potentially earliest-branching papilionoids fall within an ADA clade, which includes the recircumscribed monophyletic tribes Angylocalyceae, Dipterygeae, and Amburanae. The genera *Aldina* and *Amphimas* represent two of the nine main but as yet unresolved lineages comprising the large 50-kb inversion clade. The quinolizidine-alkaloid-accumulating Genistoid s.l. clade is expanded to include *Dermatophyllum* and a strongly supported and newly circumscribed tribe Ormosieae. Sophoreae and Swartzieae are dramatically reorganized so as to comprise monophyletic groups within the Core Genistoid clade and outside the 50-kb inversion clade, respectively. *Acosmium* is excluded from the Genistoids s.l. and strongly resolved within the newly circumscribed tribe Dalbergieae. By providing a better resolved phylogeny of the earliest-branching papilionoids, this study, in combination with other recent evidence, will lead to a more stable phylogenetic classification of the Papilionoideae.

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1. Introduction

The spectacular radiation of the papilionoid legumes (Papilionoideae) across an estimated 13 800 species, 478 genera, and 28 tribes is a legacy of their extraordinarily broad ecological and biogeographical range largely associated with diversifications in tropical rain forests, savannas, seasonally dry forests, and temperate regions worldwide (Lavin et al., 2005; Lewis et al., 2005; Schrire et al., 2005). Papilionoids are also well known for their unprecedented economic importance to agriculture and the food industry, as they include pulse legume crops such as soybean [*Glycine max* (L.) Merr.], culinary beans (*Phaseolus* L. spp. and *Vicia faba* L.), groundnut (*Arachis hypogaea* L.), lentil (*Lens culinarius* Medik.), pea (*Pisum sativum* L.), and the important forage crop alfalfa (*Medicago sativa* L.).

A highly specialized papilionate flower is the most distinctive morphological feature used to characterize and common to nearly all Papilionoideae. It is typically distinguished from the mostly radially symmetrical mimosoid and the generally bilateral but non-papilionate caesalpinioid flowers by having petals clearly differentiated into a standard (or banner), wings, and a keel, and partially fused stamens enveloping the ovary. This floral organization involves a strong bilateral symmetry and three-dimensional depth that often limit access to the nectar and pollen, and is intimately associated with bee pollination (Arroyo, 1981; Westerkamp and Claßen-Bockhoff, 2007). Variation in this floral architecture has greatly influenced the taxonomy of the Papilionoideae. A high degree of floral connation, especially of the staminal filaments, and keel and wing petals, has traditionally marked the putative "advanced" papilionoid tribes (e.g., Polhill, 1981a). Genera exhibiting flowers with greater radial symmetry than bilateral symmetry, or with incompletely differentiated petals and free stamens, in contrast, have

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been classified into the "primitive" or "basal" tribes Sophoreae and Swartzieae (e.g., Cowan, 1981; Polhill, 1981a, 1994).

The monophyly of the Papilionoideae has been consistently resolved in family-wide molecular phylogenetic analyses (Doyle, 1995; Käss and Wink, 1995, 1996, 1997; Doyle et al., 1997, 2000; Kajita et al., 2001; Wojciechowski et al., 2004; Lavin et al., 2005; McMahon and Sanderson, 2006; Cardoso et al., 2012a; LPWG, 2013). Perhaps the most unexpected finding stemming from the increasing interest in the Papilionoideae phylogeny was the broad polyphyly of the putatively "primitive" tribes, with elements of each scattered widely across the tree (Pennington et al., 2001; Wojciechowski, 2003; Wojciechowski et al., 2004; Cardoso et al., 2012a, 2012b). The landmark publication of *Legumes of the World* (Lewis et al., 2005) that summarized taxonomic and molecular phylogenetic advances to date represented a big step towards a phylogeny-based classification of the whole legume family. Radical shifts in inter and intra-tribal relationships within Papilionoideae were suggested, but the majority of the tribes remained defined in the traditional sense (Polhill, 1981a, 1981b, 1981c; Polhill, 1994), recognizing the need for more robustly supported phylogenies and better taxon sampling (Lewis et al., 2005). This was particularly true for the relationships among the earliest-branching papilionoids, where resolution was poor, and where phylogenies failed to sample several unusual, non-papilionate-flowered genera traditionally classified in Sophoreae and Swartzieae (Cardoso et al., 2012a). Indeed, that the early-branching papilionoids were problematic in this, and other ways, was emphasized earlier by the prominent legume taxonomist Roger Polhill of the Royal Botanic Gardens, Kew. In 1981 Polhill recognized the heterogeneous nature of the Sophoreae: "The Sophoreae s.l. is a tribe of convenience between the Caesalpinioideae and the bulk of the Papilionoideae, sharply defined from neither" (Polhill, 1981a: 213). Then later in 1994 he pointed out in his revised legume classification that "Considerable emphasis has been made on the analysis of basal groups in the Caesalpinioideae and Papilionoideae, but further studies here are critical if groups with derived features are to be defined clearly" (Polhill, 1994: xlii).

The molecular phylogenies derived from the *trnL* intron (Pennington et al., 2001) and *matK* (Wojciechowski et al., 2004) sequences were the first to focus on the unusual lineages of papilionoid legumes marked by radial floral symmetry or non-papilionate flowers. These studies provided a starting point for subsequent clade-specific phylogenetic studies involving non-papilionate flowered lineages, such as the Amorpheae (McMahon and Hufford, 2004), Lecointeoids (Mansano et al., 2004), Vataireoids (Cardoso et al., 2013a), Dalbergioids (Lavin et al., 2001; Cardoso et al., 2012b), and Genistoids (Boatwright et al., 2008a; Cardoso et al., 2012c). Recently, a renewed interest in the early-branching papilionoid phylogeny involving the most comprehensive sampling from within Sophoreae and Swartzieae has shed more light on the obscure position of several genera and relationships of many clades (Cardoso et al., 2012a). A recurrent result emerging from phylogenetic studies of the early-branching papilionoids is the evolutionary reversions from a papilionate flower to one with radial or undifferentiated architecture (Pennington et al., 2000; McMahon and Hufford, 2004; Cardoso et al., 2012a, 2012b, 2012c, 2013a). The high integration of floral parts in the papilionate flower has clearly been evolutionarily labile, thus rejecting the traditional view that non-papilionate flowers marked the "primitive" groups of Papilionoideae or in some manner represented signatures of antiquity (e.g., Arroyo, 1981; Polhill, 1981a, 1994; Tucker and Douglas, 1994). The taxon sampling of Cardoso et al. (2012a) was, however, intentionally sparse within the non-protein–amino-acid-accumulating (NPAAA) papilionoid lineages, and so they left significant implications with regard to the systematics of several early-branching clades to be further investigated in a more complete phylogeny.

To gain more insights into the evolution and phylogenetic classification of the Papilionoideae requires a robust taxon sampling that integrates the wealth of available molecular data (e.g., Hu et al., 2000; Lavin et al., 2001, 2003; Steele and Wojciechowski, 2003; McMahon and Hufford, 2004; Wojciechowski et al., 2004; Bruneau et al., 2008; Egan and Crandall, 2008; Stefanović et al., 2009; Delgado-Salinas et al., 2011; Cardoso et al., 2012a, 2012b, 2013a; Sirichamorn et al., 2012). A more comprehensive phylogeny of the Papilionoideae is pivotal for understanding the evolution of the dramatic floral diversity among the early-branching clades (Figs. 2–5; Pennington et al., 2000), the timing of diversification (Lavin et al., 2005), biogeography (Schrire et al., 2005), and the origin of the complex symbiotic association with root-nodulating bacteria in the whole subfamily (Doyle et al., 1997; Doyle and Luckow, 2003; Doyle, 2011). A better sampled phylogeny can also lead to a new opportunity to address the question of why the deep-nodes of the papilionoids are so poorly resolved (Lavin et al., 2005; Cardoso et al., 2012a). Why are the early-branching genera so prone to changes in floral symmetry (Pennington et al., 2000; Cardoso et al., 2012a, 2012b) or to the lack of the ability to nodulate (Sprent, 2001; J. Sprent, pers. comm.)? In the present study, however, we focus on questions related to a new phylogeny-based classification of the Papilionoideae to set the stage for future taxonomic, biogeographical, evolutionary, and ecological research. The most densely-sampled *matK* phylogeny at generic level of the Papilionoideae is analyzed to review the systematics of the early-branching clades. We set out to facilitate the formalization of a new phylogenetic classification of the Papilionoideae, where most informally named clades (sensu Wojciechowski et al., 2004; Cardoso et al., 2012a) are reported as potential candidates to be recognized at tribal rank. Finally, we address some key challenges for the path toward reconstructing the deep-branching relationships of the Papilionoideae.

2. Materials and methods

Taxon sampling and molecular data

The complete plastid *matK* protein-coding gene (Hilu and Liang, 1997) was selected because it has been widely used in legume phylogenetics and revealed excellent resolution at many taxonomic levels (e.g., Hu et al., 2000; Lavin et al., 2001; Steele and Wojciechowski, 2003; McMahon and Hufford, 2004; Wojciechowski et al., 2004; Bruneau et al., 2008; Pennington et al., 2010; Delgado-Salinas et al., 2011; Cardoso et al., 2012a, 2013a). Comparative analyses of the *matK* and *rbcL* genes have shown levels of sequence divergence up to ninefold higher for *matK* than for *rbcL*, and substitutions are distributed more uniformly among the three codon positions in *matK* (Lavin et al., 2005). We screened GenBank for all available *matK* sequences of legumes. Our strategy was aimed at sampling as many genera as possible across all major lineages of the Papilionoideae as guided by the previous phylogenies of Wojciechowski et al. (2004) and Cardoso et al. (2012a). Because the phylogenetic analysis of Cardoso et al. (2012a) focusing on the early-branching clades used a too sparse taxon sampling from within the NPAAA clade, the present more densely-sampled analysis can validate the clades that emerged from that study. Also, a comprehensive taxon sampling potentially improves phylogenetic accuracy because of the increased probability of subdividing long branches (e.g., Graybeal, 1998; Pollock et al., 2002; Zwickl and Hillis, 2002; Heath et al., 2008).

Our *matK* data set includes 668 accessions, of which 535 are from Papilionoideae, representing 507 species and 323 of the 478 currently recognized genera within the subfamily (Lewis et al., 2005). The early-branching clades accounted for 352 accessions from 325 species and 145 genera. Some early-branching genera are for the first time evaluated in a *matK* family-level phylogeny: *Ammopiptanthus* S.H.Cheng, *Aspalathus* L., *Argyrolobium* Eckl. & Zeyh., *Bocoa* Aubl., *Bolusia* Benth., *Dichilus* DC., *Euchlora* Eckl. & Zeyh., *Laburnum* Fabr., *Lebeckia* Thunb., *Rafnia* Thunb., and *Steinbachiella* Harms. Nearly all genera (49 out of 62) of the traditionally circumscribed tribes Sophoreae and Swartzieae have been sampled, except for representatives of the

following: *Ammothamnus* Bunge, *Dalhousiea* Wall. ex Benth., *Fairchildia* Britton & Rose, *Haplormosia* Harms, *Leucomphalos* Benth. ex Planch., *Mildbraediodendron* Harms, *Neoharmsia* R.Vig., *Pericopsis* Thwaites, *Petaladenium* Ducke, *Platycelyphium* Harms, *Sakoanala* R.Vig., *Salweenia* Baker, and *Uleanthus* Harms. Nevertheless, we can tentatively place most of these genera in some major branch of the papilionoid tree based on different DNA sequence data, chemistry or morphology. Most sequences used in the present data set are from our ongoing phylogenetic studies on the early-branching papilionoids (de Queiroz et al., 2010; Cardoso et al., 2012a, 2012b, 2013a; Le Roux et al., in press; Wojciechowski, 2013), which provided 181 accessions. Significant efforts of others added considerably to our broad taxon coverage (e.g., Hu et al., 2000; Lavin et al., 2001, 2003; Steele and Wojciechowski, 2003; McMahon and Hufford, 2004; Wojciechowski et al., 2004; Bruneau et al., 2008; Egan and Crandall, 2008; Stefanović et al., 2009; Delgado-Salinas et al., 2011; Lewis et al., 2012; Sirichamorn et al., 2012; L.P. de Queiroz et al., unpubl.; M.F. Wojciechowski, unpubl.).

We selected seven taxa from Polygalaceae, Surianaceae, and Quillajaceae, and 84 caesalpinioid and 42 mimosoid taxa representing all constituent main lineages as the outgroups (Luckow et al., 2003; Lewis et al., 2005; Bruneau et al., 2008; Bello et al., 2009, 2012).

Alignment and phylogenetic analysis

The *matK* sequences were aligned manually in Se-Al v2.0a11 (Rambaut, 1996) using the similarity criterion of Simmons (2004) and following the suggestions of Wojciechowski et al. (2004) in order to avoid inconsistencies derived from automated multiple alignments. These involved translating the DNA sequences to their corresponding amino acid sequences to accurately align the DNA sequences with insertions and deletions (indels) at equivalent positions. This procedure resulted in numerous, but unambiguous, indels with respect to their placement in the aligned data set. All sequences were complete except for 60 accessions that had 100 or more missing nucleotides at one of the ends, most of these however from the mimosoids or the NPAAA papilionoids. The *matK* data set of 668 aligned sequences of 1785 nucleotide characters is publicly available at http://www.montana.edu/mlavin/data/papilionoid6ilc.txt.

The *matK* phylogenetic tree was inferred using Bayesian inference (Yang and Rannala, 1997; Lewis, 2001) as implemented in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003) using the Cyberinfrastructure for Phylogenetic Research (CIPRES) Portal 2.0 (Miller et al., 2010). The best-fitting nucleotide substitution model GTR + I + Γ with base frequency, substitution rates, and among-site variation variables was estimated from the data via the Akaike information criterion (AIC) (Akaike, 1974) as implemented in ModelTest 3.7 (Posada and Crandall, 1998). Two separate runs of a Metropolis-coupled Markov Chain Monte Carlo (MCMC) permutation of parameters were each initiated with a random tree and eight simultaneous chains set at default temperatures (Huelsenbeck et al., 2001). Markov chains were run for 28 190 000 generations and sampled every 10 000th generation such that 2220 nonautocorrelated Bayesian trees were sampled broadly from likelihood stationarity for each of the two runs after a burn-in of 6 000 000 generations. The program Tracer v1.3 (Rambaut and Drummond, 2004) was used to assess the convergence of the MCMC run and the adequacy of the burn-in length. Trees sampled from post burn-in generations were summarized in a majority rule consensus tree that included posterior probabilities as branch support estimates. The Bayesian majority-rule consensus was then visualized and partially edited using FigTree v1.4.0 (Rambaut, 2012).

Clade nomenclature and classification

We followed the criteria of Wojciechowski et al. (2004) for recognizing major papilionoid clades, which are consistent with formal node-based definitions under a system of phylogenetic nomenclature (de Queiroz and Gauthier, 1994). These involved the definition of strongly supported monophyletic groups that are congruent with other studies based on different molecular markers. We give suggestions for future renaming of clades with available previously published names of papilionoid tribes. Formal taxonomic changes will be the focus of a more complete treatment for the whole family authored by the Legume Phylogeny Working Group (LPWG). We advocate that alongside a future new Linnean classification the informally named clades, especially more inclusive ones such as the Genistoids s.l., Dalbergioids s.l., Millettioids or Robinioids should be maintained in a new phylogenetic classification of legumes (Wojciechowski, 2013). Without grouping the tribes under such consistently supported clades the legume classification will be just a collection of tribes without implicit information of phylogenetic relationships between them. Such inclusive informal clades are not only taxonomically informative, but also bring a phylogenetic dimension for the practical purpose of classification. We recommend that phylogenetically unresolved genera should not be formally classified in a Linnean rank-based classification as distinct monotypic tribes at this stage when our phylogenetic estimates are based fundamentally on a few chloroplast loci. They should be recognized as incertae sedis until better resolved phylogenies, based upon multiple loci, including nuclear regions, are available (LPWG, 2013).

3. Results

The *matK* Bayesian majority-rule consensus tree was highly resolved and well supported with respect to the relationships for the major clades of the papilionoid legumes (Fig. 1; Appendix S1, see Supplemental data with the online version of this article). The monophyly of the Leguminosae is corroborated (Fig. 2). The Papilionoideae and Mimosoideae, excluding *Dinizia* Ducke, were each strongly supported as monophyletic and nested within a paraphyletic Caesalpinioideae (Fig. 2). Within the Papilionoideae, deep-branching relationships had increased support for many clades, and taxonomic realignments of some genera and of numerous tribes are necessary. The earliest dichotomy subtends two clades, one of which we term the ADA clade and it includes three lineages: the Angylocalyceae, Dipterygeae, and Amburaneae clades (Fig. 2). The ADA clade is sister to a weakly supported clade comprising the newly circumscribed tribe Swartzieae and a clade that includes the *Cladrastis* clade and the rest of the papilionoid legumes in the strongly-supported 50-kb inversion clade (Figs. 2–3). Nine strongly supported constituent clades within the 50-kb inversion clade were resolved as a polytomy: the genera *Amphimas* Pierre ex Dalla Torre & Harms, *Aldina* Endl., and *Dermatophyllum* Scheele, the newly circumscribed Exostyleae, the Vataireoid, *Andira*, and Genistoid s.l. clades, the Dalbergioid s.l. clade comprising tribes Amorpheae and the newly circumscribed Dalbergieae, and a large clade containing the newly circumscribed monophyletic Baphieae and the remaining papilionoids from within the NPAAA clade, namely the Hypocalypteae, Mirbelioids, Indigoferae, Millettioids, and the predominantly temperate Hologalegina clade (Figs. 3–5; Appendix S1).

The non-monophyly of several genera was also confirmed: *Aeschynomene* L., *Baphia* Afzel. ex Lodd., *Cladrastis* Raf., *Clathrotropis* Harms, *Myrocarpus* Allemão, *Psorothamnus* Rydb., *Sophora* L., and *Thermopsis* R.Br. The large Genistoid s.l. clade is strongly supported and fully resolved, and includes the monophyletic Brongniartieae, Crotalarieae, Genisteae, Podalyrieae with the inclusion of the morphologically unusual genus *Cadia* Forssk., and the resurrected tribes Leptolobieae and Ormosieae, which is strongly supported as sister to all Genistoids (Fig. 4). *Camoensia* Welw. ex Benth. & Hook.f., which has morphologically anomalous flowers, is the first-branching genus of the Core Genistoids and placed in its own monotypic tribe Camoensieae. Sophoreae is now dramatically reorganized to encompass only a small clade within the Core Genistoids (Fig. 4). A putative new genus to be segregated from *Clathrotropis* is not resolved with respect to any of the aforementioned main Genistoid subclades (Fig. 4). The genus *Acosmium* Schott is
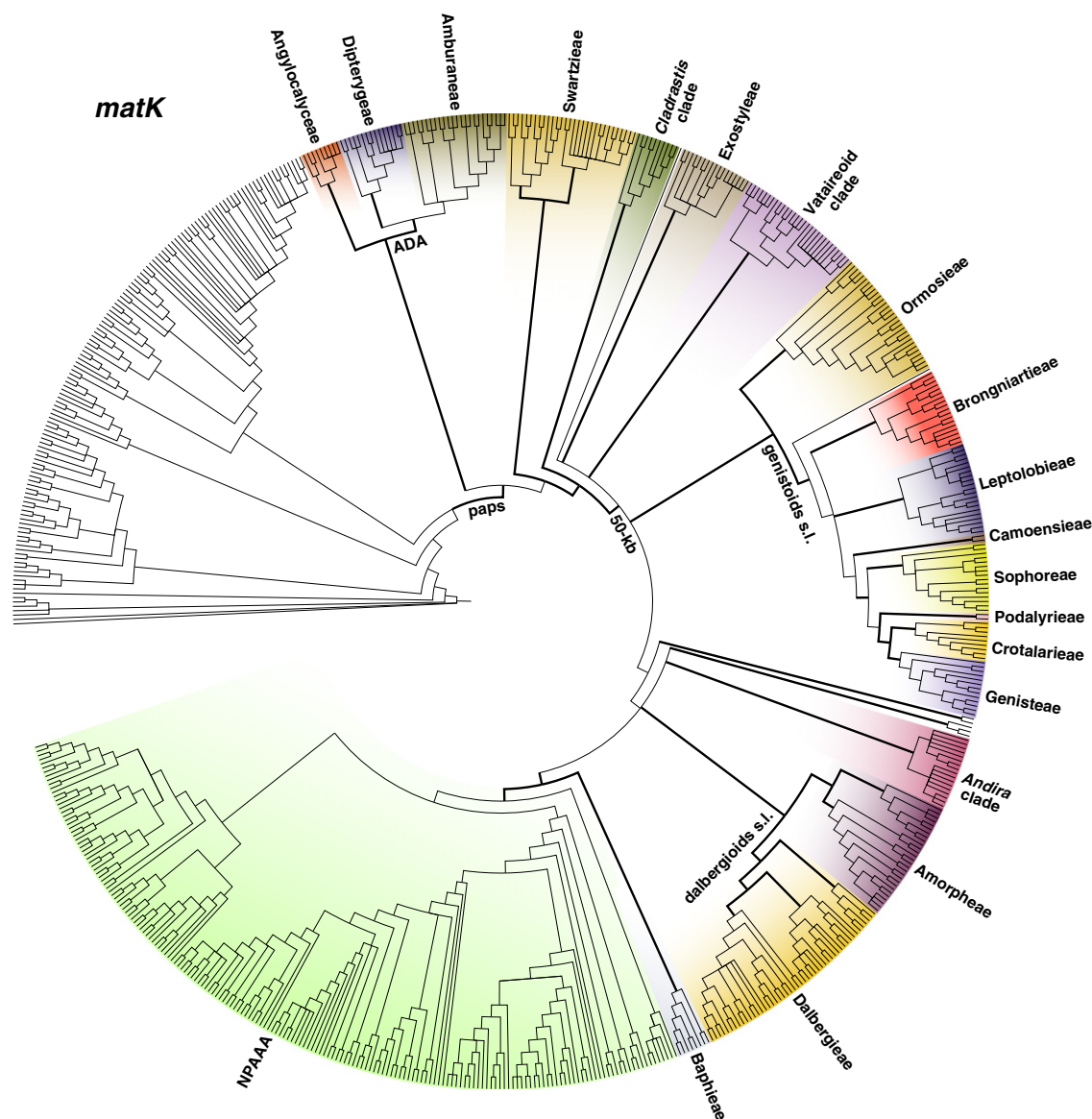
Fig. 1. Summary of the *matK* Bayesian majority-rule consensus tree of legumes showing the main early-branching papilionoid clades that are the focus of this study. The focus is set on the clades outside the large and diverse non-protein–amino-acid-accumulating (NPAAA) clade. Branches in bold are those supported by a posterior probability of 0.99–1.0.

excluded from the Genistoids s.l. and strongly confirmed within the newly circumscribed Dalbergieae (Fig. 5).

4. Discussion

The present *matK* phylogenetic analysis (Fig. 2) corroborates the monophyly of the subfamilies Mimosoideae and Papilionoideae nested within a paraphyletic Caesalpinioideae (Doyle et al., 1997, 2000; Luckow et al., 2003; Bruneau et al., 2008; Kajita et al., 2001; Pennington et al., 2001; Wojciechowski et al., 2004; Lavin et al., 2005; Cardoso et al., 2012a; LPWG, 2013). Relationships among the early-branching papilionoid lineages that fall outside of the non-protein–amino-acid-accumulating (NPAAA) clade (Fig. 1) were recently well resolved in phylogenetic analyses of *matK* and *trnL* intron sequences (Cardoso et al., 2012a). That study revealed the identity, generic composition and realignments, and inter-relationships of several new clades, which were largely unresolved in previous analyses (e.g., Doyle et al., 1997; Kajita et al., 2001; Pennington et al., 2001;

Wojciechowski et al., 2004; McMahon and Sanderson, 2006). The present study confirms the same deep-node relationships revealed by the parsimony and Bayesian phylogenetic analyses of Cardoso et al. (2012a) (Figs. 1–5), as well as the subclades within the large NPAAA clade as revealed by the first most comprehensive family-level phylogeny of Wojciechowski et al. (2004) (Appendix S1), demonstrating the value of the *matK* gene in resolving legume relationships. Dense sampling of taxa for *matK* provided resolution of the early-branching papilionoids even when preliminary studies suggested that resolution would be difficult to obtain.

When the latest tribal legume classification was published (Lewis et al., 2005), adequate genus-level sampling was not yet available to embark upon formal changes to the taxonomic scheme of Polhill (1994). The accumulation of new molecular data in recent years, especially with respect to the use of the *matK* gene (e.g., Bruneau et al., 2008; Egan and Crandall, 2008; Stefanović et al., 2009; Delgado-Salinas et al., 2011; Cardoso et al., 2012a, 2012b, 2013a; Sirichamorn et al., 2012) has provided the impetus to move Papilionoideae systematics forward toward a
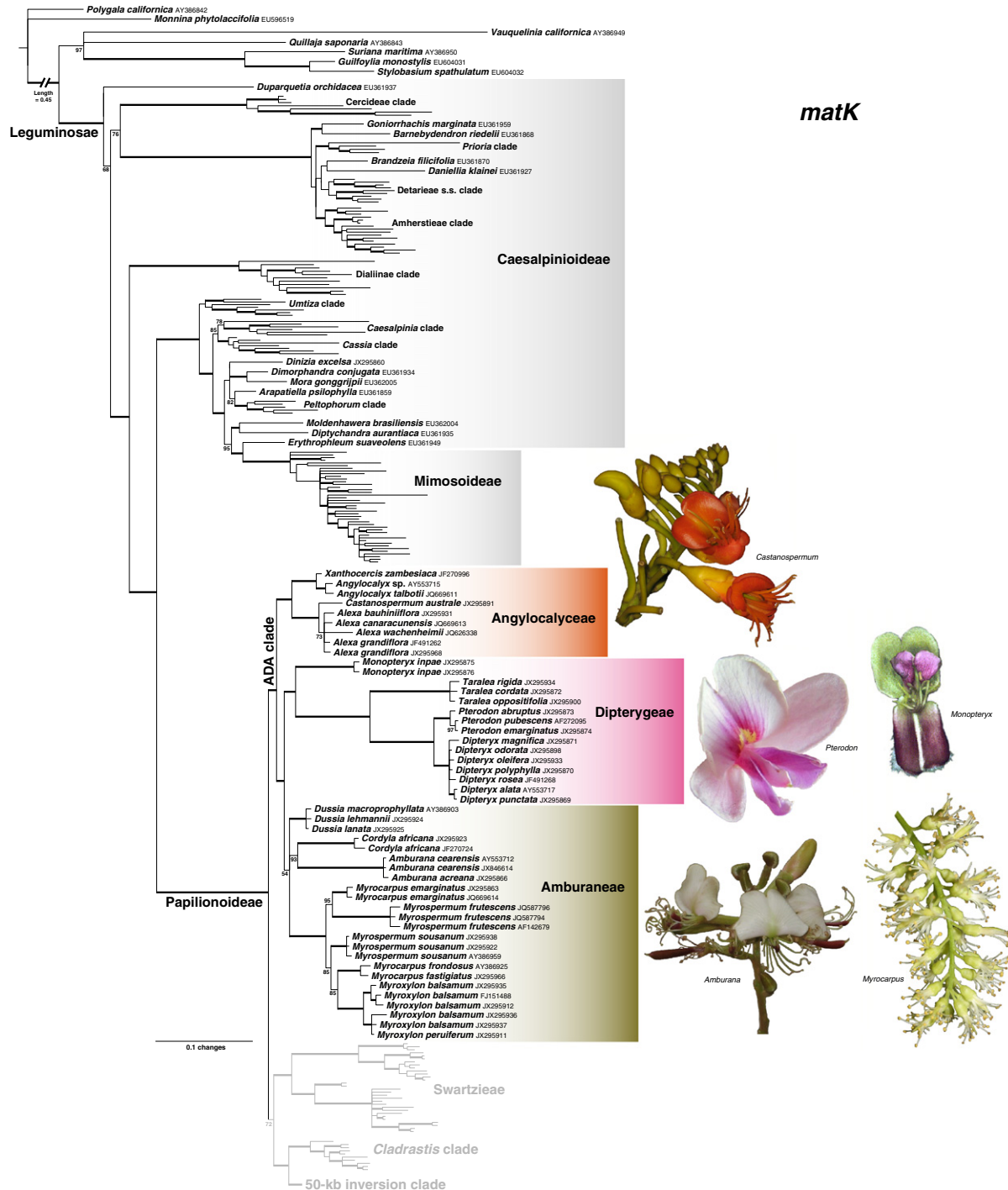
Fig. 2. Majority-rule consensus tree derived from the *matK* Bayesian analysis of the legumes with emphasis on the early-branching papilionoid clades. This portion of the tree highlights the relationships and generic composition of the first-branching ADA lineage. Representative outgroups from within mimosoids and caesalpinioids were comprehensively sampled. Most taxon names of mimosoids and caesalpinioids as well as of the non-protein–amino-acid-accumulating (NPAAA) papilionoids are omitted to focus on clades of interest. Numbers on branches are Bayesian posterior probabilities. Posterior probabilities are not given for the resolved branches weakly supported by 0.50–0.79. Branches in bold are those supported by a posterior probability of 0.99 or 1.0. GenBank accession numbers are provided after taxon names. Photos: Domingos Cardoso [*Amburana cearensis* (Allemão) A.C.Sm., *Castanospermum australe* A.Cunn. & C.Fraser ex Hook., and *Myrocarpus fastigiatus* Allemão], Mauricio Mercadante (*Pterodon pubescens* Benth.), and Scott Mori (*Monopteryx inpae* W.A.Rodrigues).

more stable higher-level classification of the entire family that reflects phylogeny. We provide below an overview of the relationships and generic composition of the early-branching clades, most of which are readily distinguished by non-molecular synapomorphies, and which might be recognized at tribal level in a new phylogenetically based Linnean classification. In terms of species diversity, from the currently recognized 196 early-branching genera (Table 1), it is noteworthy that more than 70% are species-poor (48 genera are
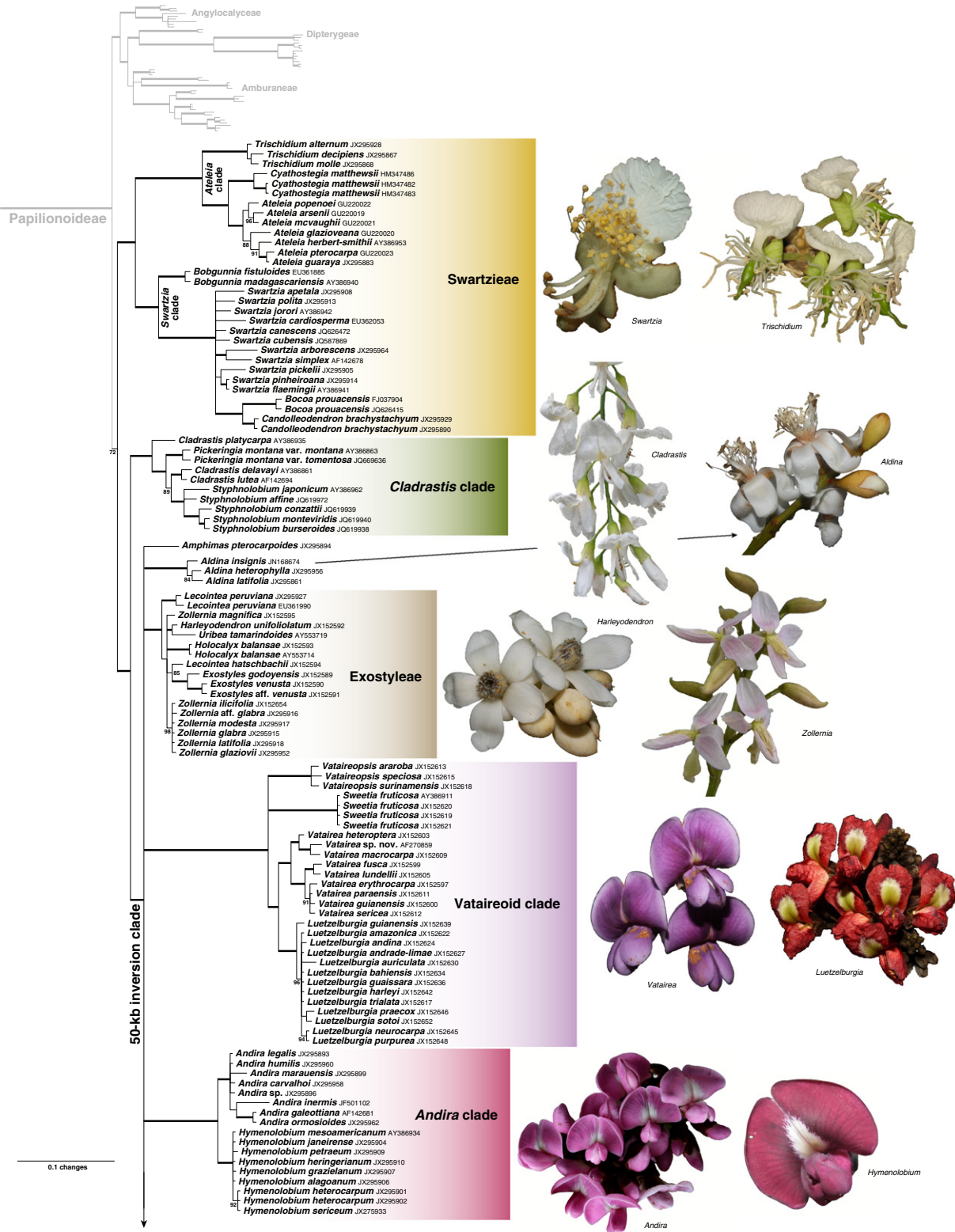
Fig. 3. Continuation of the *matK* Bayesian majority-rule consensus tree of the early-branching papilionoids. This portion shows the first-branching Swartzieae and *Cladrastis* clades, as well as some isolated, unresolved genera, the Exostyleae, Vataireoid, and *Andira* clades from the large 50-kb inversion clade. See Fig. 2 for details. Photos: Cecília de Azevedo (*Andira fraxinifolia* Benth.), Domingos Cardoso [*Aldina latifolia* Benth., *Harleyodendron unifoliolatum* R.S.Cowan, *Luetzelburgia sotoi* D.B.O.S.Cardoso, L.P.Queiroz & H.C.Lima, *Swartzia macrostachya* Benth., *Trischidium molle* (Benth.) H.E.Ireland, and *Vatairea guianensis* Aubl.] Alan Cressler [*Cladrastis kentukea* (Dum.Cours.) Rudd], Vinícius Dittrich (*Hymenolobium alagoanum* Ducke), and Gustavo Shimizu (*Zollernia ilicifolia* Vogel).

monospecific and 92 have 2–10 species) and mostly non-papilionate-flowered, whereas only 10 genera can be considered species rich (>100 species). All together these genera contribute towards making the early radiation of papilionoid legumes one of the most striking examples of unparalleled evolution of flower diversity among the flowering plants (Figs. 2–5).
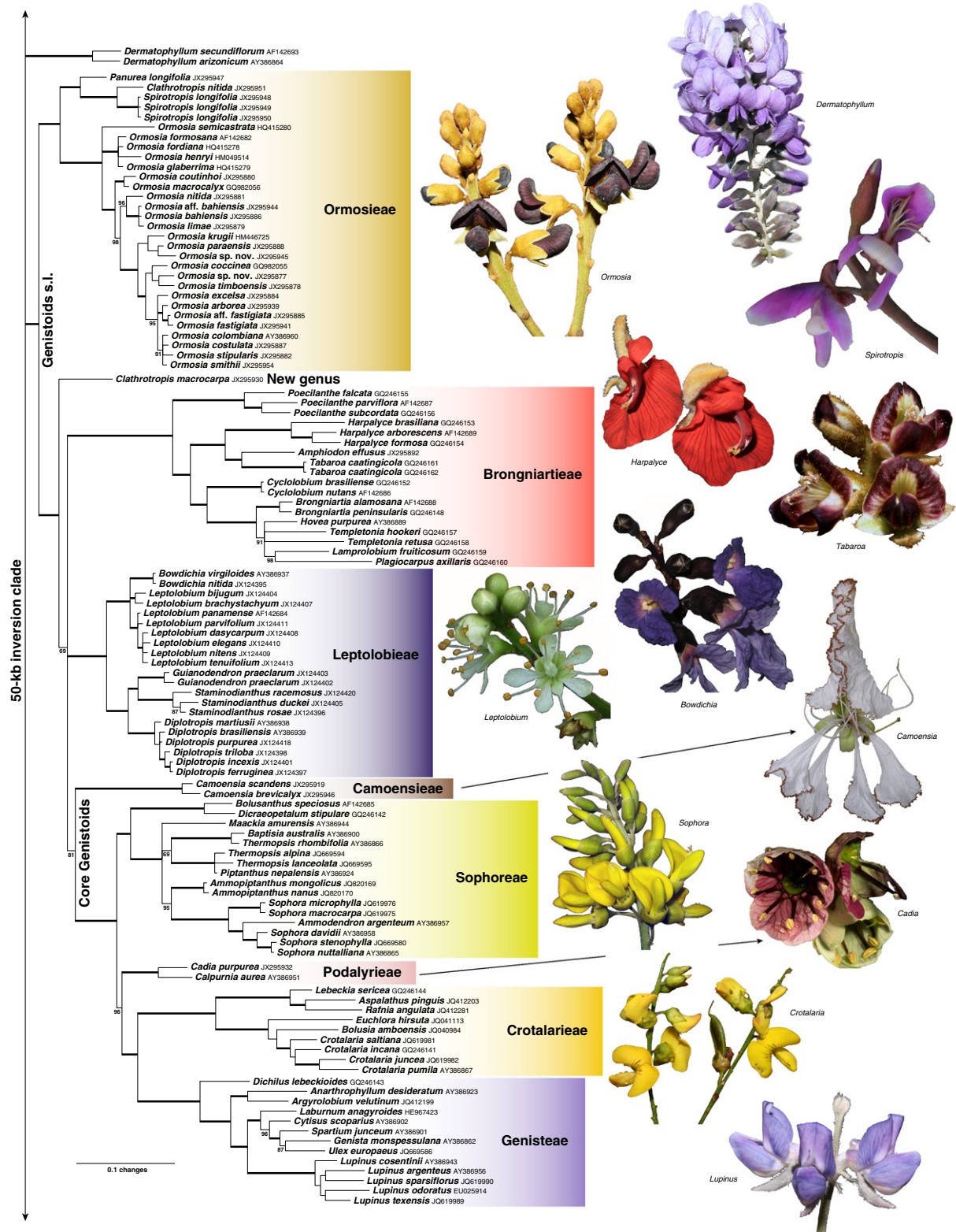
Fig. 4. Continuation of the *matK* Bayesian majority-rule consensus tree of the early-branching papilionoids. This portion shows the large Genistoid s.l. clade and its putative related, yet unresolved genus *Dermatophyllum*. See Fig. 2 for details. Photos: Domingos Cardoso [*Bowdichia virgilioides* Kunth, *Camoensia scandens* (Welw.) J.B.Gillett, *Crotalaria maypurensis* Kunth, *Harpalyce lanata* L.P.Queiroz, *Leptolobium dasycarpum* Vogel, *Lupinus sericeus* Pursh, *Ormosia* sp. nov., and *Sophora tomentosa* L.], Émile Fonty [*Spirotropis longifolia* (DC.) Baill.], Mark Olson (*Cadia purpurea* Forssk.), Luciano P. de Queiroz (*Tabaroa caatingicola* L.P.Queiroz, G.P.Lewis & M.F.Wojc.), and Martin Wojciechowski [*Dermatophyllum secundiflorum* (Ortega) Gandhi & Reveal].

Earliest-branching papilionoid clades

We have identified 26 morphologically disparate and mostly species-poor woody genera, traditionally classified into the tribes Swartzieae, Sophoreae, and Dipterygeae, as comprising the first-branching papilionoids. They fall into three strongly supported lineages, a large ADA clade of morphologically eclectic genera, which is weakly supported as sister to all remaining papilionoids, the newly
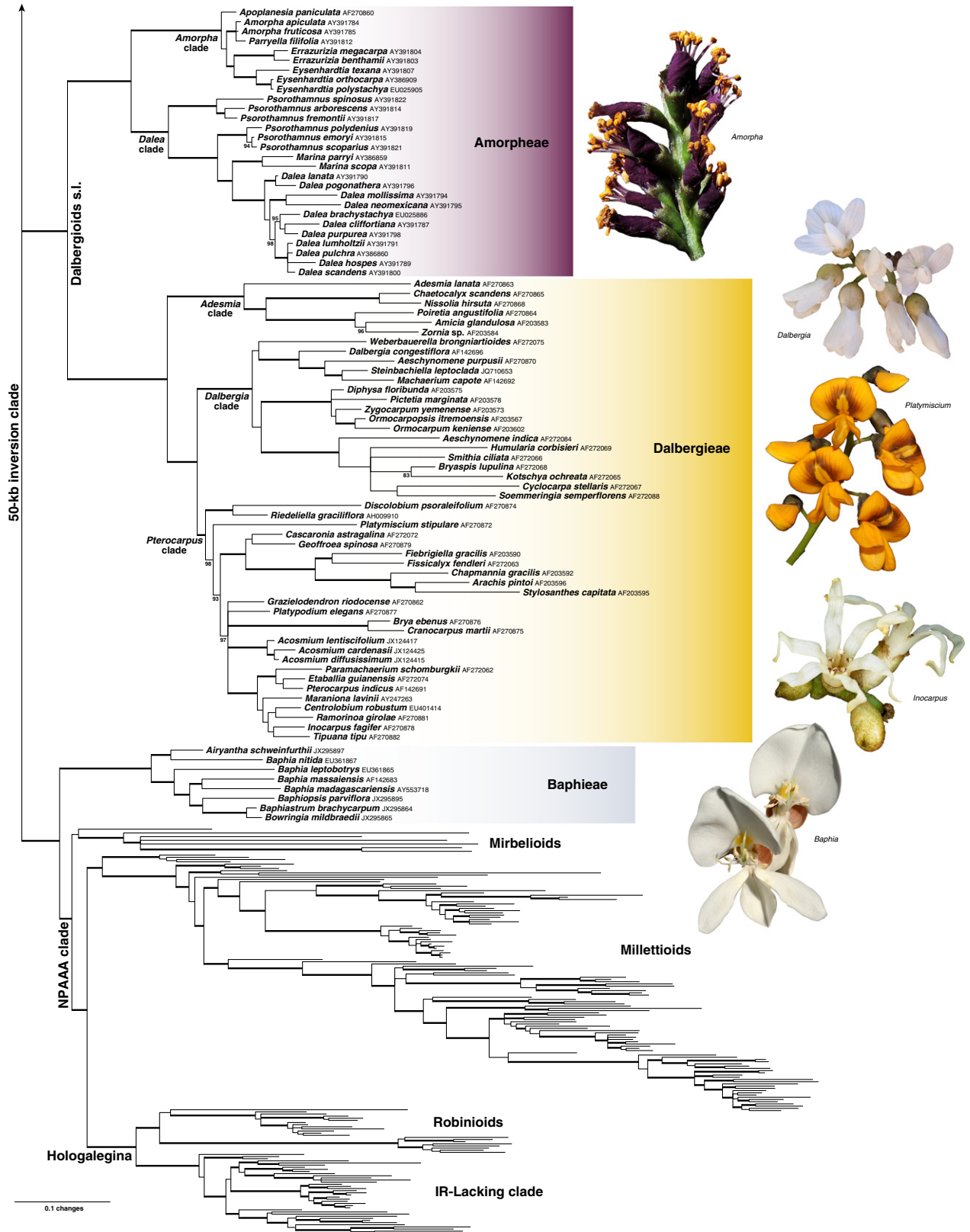
Fig. 5. Continuation of the *matK* Bayesian majority-rule consensus tree of the early-branching papilionoids. This portion shows relationships and generic composition of the Amorpheae, Dalbergieae, Baphieae, and the remaining papilionoids within the large non-protein–amino-acid-accumulating (NPAAA) clade. See Fig. 2 for details. Photos: Domingos Cardoso [*Dalbergia ecastaphyllum* (L.) Taub. and *Platymiscium floribundum* Vogel], Thomas Palmer (*Amorpha fruticosa* L.), Gerald Carr (*Inocarpus edulis* J.R.Forst. & G.Forst.), and Mark Hyde and Bart Wursten (*Baphia massaiensis* Taub., available at www.zimbabweflora.co.zw).

recircumscribed Swartzieae, and the *Cladrastis* clade (Figs. 1–3; Table 1). All earliest-branching genera that have been screened for the 50-kb in-version in the plastid DNA genome lack this feature (Doyle et al.,

1996). Our analysis is consistent with previous results (Wojciechowski et al., 2004; McMahon and Sanderson, 2006; Cardoso et al., 2012a; LPWG, 2013) in that the *Cladrastis* clade is strongly resolved as sister

Table 1

The early-branching clades of papilionoid legumes and constituent genera as recognized in the present study. Estimated numbers of species diversity (from Lewis et al., 2005 and augmented from our review of recent literature) are provided. Genera marked by an asterisk (*) were not sampled in any *matK* phylogeny, but for which there is information from other molecular markers (e.g., ITS, *rbcL* or *trnL* intron). Genera marked by two asterisks (**) were never sampled in a molecular phylogeny, but for which the morphology and chemistry may tentatively suggest their phylogenetic position. The plus sign (+) highlights the non-monophyletic genera as suggested by preliminary molecular evidences discussed in the text.

	Clade/Genus	No. spp.
ADA clade	**Angylocalyceae**	**21**
	Alexa	9
	Angylocalyx	7
	Castanospermum	1
	*Uleanthus***	1
	Xanthocercis	3
	Dipterygeae	**25**
	Dipteryx	12
	Monopteryx	3
	Pterodon	3
	Taralea	7
	Amburaneae	**29**
	Amburana	2
	Cordyla	7
	Dussia	9
	*Mildbraediodendron**	1
	Myrocarpus+	5
	Myrospermum	2
	Myroxylon	3
	Swartzieae*	**213**
	Ateleia	20
	Bobgunnia	2
	Bocoa	3
	Candolleodendron	1
	Cyathostegia	1
	*Fairchildia**	1
	Swartzia	180
	Trischidium	5
	Cladrastis clade	**17**
	Cladrastis+	7
	Styphnolobium	9
	Pickeringia	1
	Exostyleae	**21**
	Exostyles	4
	Harleyodendron	1
	Holocalyx	1
	Lecointea	4
	Uribea	1
	Zollernia	10
	Vataireoid clade	**27**
	Luetzelburgia	13
	Sweetia	1
	Vatairea	9
	Vataireopsis	4
	Andira clade	**46**
	Andira	29
	Hymenolobium	17
Genistoids s.l.	**Ormosieae**	**139**
	Clathrotropis	2
	*Haplormosia***	1
	Ormosia	130
	Panurea	2
	*Petaladenium***	1
	Spirotropis	3
	Brongniartieae	**153**
	Amphiodon	2
	Brongniartia	63
	*Cristonia**	1
	Cyclolobium	1
	Harpalyce	25
	Hovea	37
	Lamprolobium	2
	Plagiocarpus	1
	Poecilanthe	7
	Tabaroa	1
	Templetonia	10
	*Thinicola**	1
	New genus[a]	2
	Leptolobieae	**29**
	Bowdichia	2
	Diplotropis	10

Table 1 (*continued*)

	Clade/Genus	No. spp.
Genistoids s.l.	*Guianodendron*	1
	Leptolobium	13
	Staminodianthus[b]	3
	Camoensieae	**2**
	Camoensia	2
	Core Genistoids	
	Sophoreae	**122**
	Ammodendron	5
	Ammopiptanthus	2
	*Ammothamnus***	2
	*Anagyris**	2
	Baptisia	17
	Bolusanthus	1
	Dicrae opetalum	3
	*Euchresta**	4
	Maackia	8
	Piptanthus	2
	*Platycelyphium**	1
	*Salweenia**	2
	Sophora+	50
	Thermopsis+	23
	Podalyrieae	**130**
	*Amphithalea**	42
	Cadia	7
	Calpurnia	7
	*Cyclopia**	23
	Liparia+**	20
	*Podalyria**	17
	*Stirtonanthus**	3
	*Virgilia**	2
	*Xiphoteca**	9
	Crotalarieae	**1221**
	Aspalathus	280
	Bolusia	5
	*Calobota**	16
	Crotalaria	700
	Euchlora	1
	*Ezoloba**	1
	*Lebeckia**	14
	*Leobordea**	51
	*Listia**	7
	*Lotononis**	91
	*Pearsonia**	13
	Rafnia	19
	*Robynsiophyton**	1
	*Rothia**	2
	*Wiborgia**	10
	*Wiborgiella**	10
	Genisteae	**618**
	*Adenocarpus**	15
	Anarthrophyllum	15
	*Argyrocytisus**	1
	Argyrolobium+	80
	*Calicotome**	3
	*Cytisophyllum**	1
	Cytisus	65
	Dichilus	5
	*Echinospartum**	5
	*Erinacea**	1
	Genista+	90
	*Gonocytisus**	3
	*Hesperolaburnum**	1
	Laburnum	2
	*Lembotropis**	2
	Lupinus	275
	*Melolobium**	15
	*Petteria**	1
	*Podocytisus**	1
	*Polhillia**	8
	*Retama**	4
	*Sellocharis**	1

Table 1 (continued)

	Clade/Genus	No. spp.
Genistoids s.l.	*Spartium*	1
	*Stauracanthus**	3
	Ulex	20
	Unresolved Genistoids	
	Dermatophyllum	4
	*Neoharmsia***	2
	*Pericopsis**	4
	*Sakoanala***	2
	New genus[c]	5
Dalbergioids s.l.	**Amorpheae**	**247**
	Amorpha	15
	Apoplanesia	1
	Dalea	165
	Errazurizia	3
	Eysenhardtia	15
	Marina	38
	Parryella	1
	Psorothamnus[+]	9
	Dalbergieae	**1367**
	Adesmia **clade**	
	Adesmia	240
	Amicia	6
	Chaetocalyx	13
	Nissolia	13
	Poiretia	11
	Zornia	75
	Dalbergia **clade**	
	Aeschynomene[+]	250
	Bryaspis	2
	Cyclocarpa	1
	Dalbergia	250
	Diphysa	14
	*Geissaspis**	2
	Humularia	35
	Kotschya	31
	Machaerium	130
	Ormocarpopsis	8
	Ormocarpum	18
	Pictetia	8
	Smithia	20
	Soemmeringia	1
	Steinbachiella	1
	Weberbauerella	2
	Zygocarpum	6
	Pterocarpus **clade**	
	Acosmium	3
	Arachis	69
	Brya	4
	Cascaronia	1
	Centrolobium	7
	Chapmannia	7
	Cranocarpus	3
	Discolobium	8
	Etaballia	1
	Fiebrigiella	1
	Fissicalyx	1
	Geoffroea	2
	Grazielodendron	1
	Inocarpus	3
	Maraniona	1
	Paramachaerium	5
	Platymiscium	19
	Platypodium	2
	Pterocarpus[+]	40
	Ramorinoa	1
	Riedeliella	3
	Stylosanthes	48
	Tipuana	1
	Baphieae	**57**
	Airyantha	2
	Baphia[+]	47

Table 1 (continued)

Clade/Genus	No. spp.
Baphiastrum	1
Baphiopsis	1
Bowringia	4
*Dalhousiea**	3
*Leucomphalos***	1
Unresolved genera	
Aldina	22
Amphimas	4

[a] New genus to accommodate two Amazonian mostly unifoliolate species from *Poecilanthe* s.l. (J.E. Meireles, unpubl.).
[b] Segregated genus from within *Diplotropis* s.l. to accommodate *D.* sect. *Racemosae* (Cardoso et al., 2012a; 2013b).
[c] New genus to accommodate *Clathrotropis macrocarpa* and related species with large elastically dehiscent pods mostly with thickened and dilated upper sutures (Cardoso et al., 2012a; D. Cardoso, unpubl.).

to a well-supported 50-kb inversion clade (Figs. 1–3). This clade is marked by a structural rearrangement within the large single copy region of the plastid genome (Doyle et al., 1996) and includes the bulk of Papilionoideae (LPWG, 2013).

The Angylocalyceae clade

The Angylocalyceae includes ca. 21 species and five genera (Fig. 2; Table 1), but the putatively related monospecific Amazonian genus *Uleanthus* remains to be studied further. Although we were not able to generate DNA sequences of *Uleanthus*, floral and pod morphologies suggest it might well belong here (Yakovlev, 1972; Povydysh et al., 2011). This clade is strongly marked by an ornithophilous floral syndrome in which the calyx and hypanthium are enlarged, the petals thickened and often red or orange, the standard often distinctly large, the lower petals undifferentiated or sometimes highly reduced, and the stamens and gynoecium exserted. The mostly white flowers of *Alexa*, however, have also been reported to be pollinated by phyllostomatid bats (Ramirez, 1995). The Angylocalyceae is biogeographically interesting for studies of long-distance dispersal as its constituent genera are widely disjunct: *Angylocalyx* Taub. and *Xanthocercis* Baill. occur in Africa and Madagascar, the monospecific *Castanospermum* A.Cunn. ex Hook. is endemic to Australia, and *Alexa* and *Uleanthus* are distributed only in the northern South American rain forests (Pennington et al., 2005).

The Dipterygeae clade

This is an exclusively Neotropical clade of ca. 25 woody species in four genera (Fig. 2; Table 1), of which *Dipteryx* Schreb., *Pterodon* Vogel, and *Taralea* Aubl. have consistently appeared in the same clade (Pennington et al., 2001; Wojciechowski et al., 2004). The morphologically disparate *Monopteryx* Spruce ex Benth. was previously classified in Sophoreae (Polhill, 1981a), but the *matK* and *trnL* intron phylogenies of Cardoso et al. (2012a) resolved the genus as sister to the rest of the Dipterygeae. The non-papilionate flowers of *Monopteryx*, in which the wing petals are much reduced and the keel petals are connate and open out exposing the free stamens, greatly contrasts with the truly papilionate flowers with fused stamens of the other Dipterygeae genera (Fig. 2). Despite the contrasting petal morphology, a synapomorphy of the Dipterygeae that encompasses *Monopteryx* is an unusual two-lipped calyx in which the two upper lobes are much enlarged and the three lower lobes are reduced to small teeth (Polhill, 1981a, 1981b). The two upper enlarged lobes of *Dipteryx*, *Pterodon*, and *Taralea* are petaloid and completely free to their base so that they resemble additional lateral wing petals. In *Monopteryx* the upper lobes are connate and assume a standard-like position. The monophyly and inter-relationships of the Dipterygeae genera are also strongly supported by floral and fruit traits (Cardoso et al., 2012a).

The Amburaneae clade

This is a mostly Neotropical clade comprising ca. 29 species and seven morphologically eclectic genera in terms of floral morphology (Fig. 2; Table 1). *Dussia* Krug & Urb. ex Taub. and *Myrospermum* Jacq. have strongly differentiated papilionate flowers, while *Myroxylon* L.f. has a well-differentiated standard, but the remaining petals are undifferentiated and much reduced. *Myrocarpus* Allemão has radially symmetrical, mimosoid-like flowers, whereas *Amburana* Schwacke & Taub. has only one petal and a long hypanthium (Fig. 2). The African genera *Cordyla* Lour. and *Mildbraediodendron* have a swartzioid-like floral morphology in which the flowers have an entire calyx, no petals, and numerous exserted stamens. The Amburaneae has been unresolved or only poorly supported in phylogenetic analyses of individual molecular data (e.g., Doyle et al., 1997; Pennington et al., 2001; Cardoso et al., 2012a), but its monophyly was better supported in the recent combined analysis of *matK* and *trnL* intron sequences (Cardoso et al., 2012a). We have added a few more taxa in the present *matK* analysis to challenge the monophyly of Amburaneae, which was maintained, yet with poor support (Fig. 2). We suggest recognizing Amburaneae as a new monophyletic tribe of the Papilionoideae because the poor support is only from a weak phylogenetic signal, not a strongly conflicting one. Branch lengths are short for most internodes that separate the three main ADA lineages (Fig. 2). Despite the lack of a clear non-molecular synapomorphy for the Amburaneae and the high level of floral diversity, resin chemistry marks the monophyly of this clade. This includes the production of balsams (*Myrocarpus*, *Myrospermum*, *Myroxylon*), coumarins (*Amburana*), abundant red resin from cut bark and twigs (*Dussia*), and the glandular punctate leaves of several genera (*Cordyla*, *Mildbraediodendron*, *Myrocarpus*, *Myrospermum*, *Myroxylon*). Some of these features, however, are shared with genera of its sister Dipterygeae clade (Pennington et al., 2001; Cardoso et al., 2012a).

The Swartzieae clade

The realignment of Swartzieae with the consistently resolved Swartzioid clade (Ireland et al., 2000; Pennington et al., 2001; Wojciechowski et al., 2004; Lavin et al., 2005; Torke and Schaal, 2008; Cardoso et al., 2012a; LPWG, 2013) is necessary because the current tribe (Cowan, 1981; see also Ireland, 2005) is polyphyletic. The Swartzieae as here circumscribed comprises ca. 213 species and eight genera, most of which are monospecific or weakly diversified (Fig. 3; Table 1). *Swartzia* Schreb. is exceptional in this clade in being the most diverse and species-rich papilionoid genus of Neotropical rain forests (Torke and Schaal, 2008). The non-papilionate swartzioid flowers are largely characterized by a tendency to lack petals combined with a profusion and elaboration of free stamens (Fig. 3). The relationships and monophyly of each of the constituent genera of this clade were better resolved in the comprehensive combined phylogeny of Torke and Schaal (2008). The present *matK* analysis included most Swartzieae genera, except for the re-established monospecific *Fairchildia* (Torke and Schaal, 2008), and recovered two well-supported subclades with contrasting internal resolution and ecological structuring. The *Swartzia* clade comprises mostly Neotropical genera and the African *Bobgunnia* J.H.Kirkbr. & Wiersema, all with a strong ecological predilection to lowland rain forests (Ireland, 2005; Schrire et al., 2005; Torke and Schaal, 2008). This subclade was however resolved as a polytomy (Fig. 3). The *Ateleia* clade was strongly resolved and ecologically concentrated in Neotropical seasonally dry woodlands (Schrire et al., 2005; Ireland, 2007; Ireland et al., 2010; Pennington et al., 2010). The highly resolved Ateleioid phylogeny represents a common pattern in legumes with predilection to the succulent biome (e.g., Pennington et al., 2009, 2010; de Queiroz and Lavin, 2011; Särkinen et al., 2012), which contrasts to the low resolution within the *Swartzia* clade and which is taken as evidence of rapid and recent diversification of the constituent genera expected for rain forest legumes (e.g., Richardson et al., 2001; Pennington et al., 2009).

The Cladrastis clade

The monophyly and inter-relationships of the *Cladrastis* clade have been consistently resolved in all molecular phylogenies (Figs. 1, 3; Wojciechowski et al., 2004; McMahon and Sanderson, 2006; LPWG, 2013; Cardoso et al., 2012a; Wojciechowski, 2013). The clade comprises 17 species in the papilionate-flowered genera *Cladrastis* Raf. and *Styphnolobium* Schott, which are disjunctly distributed in East Asia and North America, and the monospecific Californian chaparral endemic *Pickeringia* Nutt. ex Torr. & A.Gray (Wojciechowski et al., 2004; Wojciechowski, 2013). Both *Pickeringia* and *Styphnolobium* are individually strongly supported as monophyletic and nested within a paraphyletic *Cladrastis* (Fig. 3; Wojciechowski, 2013). The disjunct distribution of members of the clade in warm temperate to tropical regions of the Northern Hemisphere is a pattern common to many other legume genera, including the caesalpinioids *Gleditsia* L. and *Gymnocladus* Lam., as well as the species-rich papilionoids *Astragalus* L. and *Oxytropis* DC. (Schrire et al., 2005).

The Exostyleae clade

The Exostyleae corresponds to the Lecointeoid clade, first identified by morphological cladistic analysis (Herendeen, 1995) and later confirmed by molecular data (Fig. 3; Mansano et al., 2004; Cardoso et al., 2012a; LPWG, 2013). It is an exclusively Neotropical clade of ca. 21 woody species and six genera mostly from tropical rain forests. The non-papilionate Exostyleae flowers vary from truly radially symmetrical in most genera (*Lecointea* Ducke, *Exostyles* Schott, *Harleyodendron* R.S.Cowan, and *Holocalyx* Micheli) to bilaterally symmetrical in *Zollernia* Wied-Neuw. & Nees and *Uribea* Dugand & Romero. Likely synapomorphic morphological features for the Exostyleae are the serrate and sometimes spinescent leaflet or leaf margins, basifixed anthers, and drupaceous fruits (Herendeen, 1995; Mansano et al., 2004). The clade also shows a tendency towards unifoliolate or simple leaves (Mansano et al., 2004). Additionally, these taxa share some unique traits in wood anatomy (Gasson, 1996; Gasson and Webley, 1999) and floral ontogeny (Mansano et al., 2002). The ecological predilection and lack of resolution within the Exostyleae (Fig. 3) mirrors the phylogenetic pattern described for the predominantly rain forest-inhabiting *Swartzia* clade. Other sources of molecular data may help to resolve generic relationships within Exostyleae, although it is clear that the *trnL* intron also does not provide sufficient resolution (Mansano et al., 2002). A resolved phylogeny for the Exostyleae would be helpful to investigate the evolution of floral symmetry within this interesting early-branching clade.

The Vataireoid clade

The Vataireoids comprise ca. 27 woody species from the Neotropical genera *Luetzelburgia* Harms, *Vatairea* Aubl., *Vataireopsis* Ducke, and the monospecific *Sweetia* Spreng. (Fig. 3). The monophyly and internal relationships of the Vataireoid clade were strongly supported in a comprehensive seven-gene phylogeny (Cardoso et al., 2013a). An interesting result stemming from that study included the evidence of independent evolution of the undifferentiated, non-papilionate flowers of *Sweetia* and *Luetzelburgia*, both traditionally classified in Sophoreae (Polhill, 1981a). The Vataireoid clade is synapomorphically diagnosable by, among other characters, the highly congested leaves at the distal ends of fascicled branches and the samara-like fruit with a long distal wing arising from a basal seed-chamber (Cardoso et al., 2013a). The unusual small lateral wing attached to each side of the seed-chamber in most Vataireoids is closely similar only to the single-seeded pods of the South African Cape genus *Wiborgia* of Crotalarieae (Boatwright et al., 2008b). The sister-group relationship of the Vataireoids in the context of the Papilionoideae phylogeny remains unclear (Figs. 1, 3; Cardoso et al., 2012a). Lavin et al. (2005)

found representatives of the Exostyleae as a weakly supported sister to the Vataireoids. These two early-branching clades have many species unusually marked by leaves or leaflets with non-entire margins (Cardoso et al., 2013a). The congested leaves at the distal branch ends characterize not only the Vataireoids but also several species of *Hymenolobium* Benth. and *Andira* Lam. of the *Andira* clade. Despite the many similarities of the Vataireoids with other early-branching clades, all phylogenetic studies, not just the present one, did not resolve the sister relationship of the Vataireoid clade among the other main eight lineages of the 50-kb inversion clade.

The Andira clade

This clade includes ca. 46 species of predominantly Neotropical rain forest trees in the genera *Andira* and *Hymenolobium* (Fig. 3). The close relationship of these genera is suggested by their similar floral, vegetative, and root nodule morphologies, which include the mostly fascicled leaves and densely flowered paniculate inflorescences at distal branch ends, and the truly papilionate flowers involving petal differentiation and stamen connation (Pennington, 1995, 2003). The monophyly of both genera has been strongly supported by phylogenetic analyses of restriction sites and nrDNA ITS and plastid sequence data (Pennington, 1995; Simon et al., 2009; Cardoso et al., 2012a) and is further supported by the drupaceous fruits of *Andira* that greatly contrasts with the laterally compressed samaras of *Hymenolobium*. The *Andira* clade has remained unresolved within the 50-kb inversion clade in all broad-level phylogenies of Papilionoideae (e.g., Doyle et al., 1997; Pennington et al., 2001; Wojciechowski et al., 2004; Cardoso et al., 2012a; LPWG, 2013). Wojciechowski et al. (2004) found only a very weakly supported sister relationship of the *Andira* clade and Dalbergioids s.l. Indeed, mostly because of their indehiscent fruits *Andira* and *Hymenolobium* were long classified in the Dalbergieae (Polhill, 1981c, 1994; de Lima, 1990).

The Genistoid s.l. clade

The Genistoids s.l. are the most species-rich early-branching clade with over 2400 species (Table 1; Fig. 4). This clade was defined by Wojciechowski et al. (2004) and expanded by Cardoso et al. (2012a) to include a strongly supported *Ormosia* clade, which is here proposed to accommodate the resurrected tribe Ormosieae. The Genistoid s.l. clade includes the many papilionate-flowered genera from within the predominantly Southern Hemisphere tribes Brongniartieae, Crotalarieae, Genisteae, Podalyrieae, the recircumscribed Sophoreae, and the resurrected Camoensieae and Leptolobieae, in addition to Ormosieae. Genera also exhibiting radial floral symmetry and undifferentiated petals or free stamens, hitherto considered typical of the traditional circumscription of Sophoreae (Polhill, 1981a), are found dispersed across the clade. The Genistoid legumes are largely known to accumulate quinolizidine alkaloids (e.g., Hatfield et al., 1980; Waterman and Faulkner, 1982; Kinghorn et al., 1988; Ricker et al., 1994, 1999; Greinwald et al., 1995, 1996; Veitch et al., 1997; Van Wyk, 2003; Wink and Mohamed, 2003; Kite et al., 2013), although there exist examples of pyrrolizidine alkaloid-bearing genera [e.g., *Crotalaria* L., *Laburnum* Fabr., *Lotononis* (DC.) Eckl. & Zeyh., *Pericopsis*; Van Wyk, 2003; Wink and Mohamed, 2003] or taxa exhibiting a total absence of alkaloids (e.g., *Cyclopia* Vent.; Boatwright et al., 2008a). Relationships within the Genistoids s.l. are generally well resolved, except for the placement of *Dermatophyllum*, *Neoharmsia*, *Pericopsis*, *Sakoanala*, and an undescribed new genus, as well as the relationships between Brongniartieae, Leptolobieae, and Core Genistoids (Fig. 4).

The early-branching-genistoid Ormosieae clade

The Ormosieae is sister to the rest of the Genistoids s.l. and includes six genera and ca. 138 species, of which the genus *Ormosia* Jacks. alone accounts for ca. 130 species (Fig. 4; Table 1). The Ormosieae has mainly

diversified in Neotropical rain forests of the Amazon basin, but the largest genus *Ormosia* also shows diversity in southeast Asia and northern Australia (Rudd, 1965; Pennington et al., 2005). The few Asian species of *Ormosia* (*Ormosia formosana* Kaneh., *Ormosia fordiana* Oliv., *Ormosia glaberrima* Y.C.Wu, *Ormosia henryi* Prain, and *Ormosia semicastrata* Hance) newly included in this study suggest the monophyly of the genus (Fig. 4). A robust generic circumscription within Ormosieae requires additional sampling of the morphological diversity of *Ormosia* (Rudd, 1965) and of the potentially related monospecific genera *Haplormosia* and *Petaladenium*. The African *Haplormosia*, unusually marked by simples leaves, and the enigmatic *Petaladenium* from Brazilian Amazonia have strong morphological ties to Ormosieae but they have never been sampled in any molecular phylogenies (Table 1; Pennington et al., 2005; Cardoso et al., 2012a). In addition to producing quinolizidine alkaloids (Kinghorn et al., 1988), *Haplormosia* is very similar to *Ormosia* with respect to floral and pod morphology and shares the simple leaves with *Panurea* Spruce ex Benth. & Hook.f. *Petaladenium* is distinctive among Papilionoideae in having fimbriate-glandular wing petals, but its overall vegetative and inflorescence morphology suggests some affinity to *Ormosia*, whereas the linear-oblong dehiscent pods are similar to *Panurea* and *Spirotropis*. Perhaps the clearest synapomorphy of Ormosieae as circumscribed here (to also include *Petaladenium* and *Haplormosia*) is the mostly dehiscent pods with woody valves.

The genistoid Brongniartieae clade

The Brongniartieae includes ca. 153 species and 13 genera (Table 1), among which the Neotropical *Harpalyce* D.Don is perhaps the most unusual because of the peltate glands and resupinate flowers with strongly bilabiate calyx and mostly helically contorted keel (Fig. 4). Three genera have been added after the latest circumscription of the tribe by Ross and Crisp (2005): the monospecific *Tabaroa* L.P.Queiroz, G.P.Lewis & M.F.Wojc. from the Brazilian Caatinga dry woodlands (de Queiroz et al., 2010), *Amphiodon* from the non-flooded Amazonian forest (Cardoso et al., 2012a; J.E. Meireles, unpubl.), and a new Amazonian genus with mostly unifoliolate leaves yet to be segregated from *Poecilanthe* s.l. (J.E. Meireles, unpubl.). Brongniartieae has been traditionally diagnosed by the dimorphic anthers that are alternately basifixed and dorsifixed. However, dimorphic anthers are also found variously among African Crotalarieae, Podalyrieae, and Genisteae of the Core Genistoids (Polhill, 1976). Phylogenetic analyses of *matK* sequences have consistently resolved all Australian genera (*Hovea* R.Br., *Lamprolobium* Benth., *Plagiocarpus* Benth., *Templetonia* R.Br.) nested within a paraphyletic group of American genera (Fig. 4; see also de Queiroz et al., 2010), in contrast with the results derived from ITS sequences, which did not resolve a clade of Australian genera (Thompson et al., 2001). A putative morphological synapomorphy for the Australian Brongniartieae clade is the simple or unifoliolate leaves, but this feature has also evolved independently in the Neotropical *Cyclolobium* Benth., *Poecilanthe* s.s., and the new segregate genus from *Poecilanthe* s.l. (J.E. Meireles, unpubl.; H.C. de Lima, pers. comm.). Generic relationships within Brongniartieae have also been strongly supported by individual analysis of *matK* data (Fig. 4; de Queiroz et al., 2010), except for *Templetonia* and the remaining Australian genera. Thompson et al. (2001) however found a strongly supported sister relationship between *Templetonia* and *Hovea*. The Australian genera *Cristonia* J.H.Ross with unusual features such as simple leaves that are distinctly bilobed apically and two upper calyx lobes that are united into a truncate limb, and *Thinicola* J.H.Ross with dense silvery indumentum, foliaceous stipules, and ornithophilous flowers, were not sampled in the present *matK* phylogeny, but they have been resolved close to *Lamprolobium* in the ITS phylogeny (Thompson et al., 2001). Most Brongniartieae genera are not only clearly distinguished based on molecular data, but also on exclusive morphological features (Ross and Crisp, 2005; de Queiroz et al., 2010).

The genistoid Leptolobieae clade

The resurrection of tribe Leptolobieae (Fig. 4; Table 1) should correspond to the recently recognized *Bowdichia* clade, which includes the papilionate-flowered *Bowdichia* Kunth, *Diplotropis* Benth., and *Staminodianthus* D.B.O.S.Cardoso, H.C.Lima & L.P.Queiroz gen. nov. ined., and the nearly-radial-flowered *Leptolobium* Vogel and *Guianodendron* Sch.Rodr. & A.M.G.Azevedo (Cardoso et al., 2012b, 2012c, 2013b). The Leptolobieae includes ca. 29 species of trees mostly from tropical rain forests and savannas of South America and only one species endemic to Central America. Notable morphological synapomorphies of this clade are the flowers with subequal and symmetric lower petals (wings and keel), lateral petals (wings) without sculpturing, staminal filaments free to the base, and compressed samaroid fruits with a narrow marginal wing (Cardoso et al., 2012c). Within Leptolobieae, the non-homology of traits involved in floral symmetry (Cardoso et al., 2012c) provides an example of the recurrent convergent floral evolution among the early-branching papilionoids (Pennington et al., 2000; McMahon, 2005; Cardoso et al., 2012b).

The genistoid Camoensieae clade

The Camoensieae includes only two species from the African genus *Camoensia*. This is perhaps the strangest genus of Papilionoideae because of its large flowers with a long hypanthium and free, weakly-differentiated, crimped petals that expose the stamens (Fig. 4). The distinctiveness of *Camoensia* also led Polhill (1981a) to classify the genus separately in its own group in Sophoreae. The phylogenetic position of *Camoensia* was only recently clarified in the *matK* phylogeny of Cardoso et al. (2012a). That study resolved the genus as sister to a strongly supported clade comprising the Core Genistoid lineages originally circumscribed by Crisp et al. (2000), a result also recovered in the present analysis, though only moderately supported (Fig. 4).

The genistoid Sophoreae clade

The monophyletic Sophoreae as circumscribed here is greatly narrowed to encompass ca. 122 species and 14 genera from a strongly supported clade within the Core Genistoids (Fig. 4; Table 1). The pantropical *Sophora tomentosa* L. with sea-drifted seeds is the most widespread species, but members of Sophoreae are distributed variously in Mediterranean and temperate regions of North America, the Mediterranean Basin, Africa, tropical regions of Australasia and the Pacific, and western South America. Our new circumscription of Sophoreae still includes the florally disparate *Dicraeopetalum* Harms marked by radially-symmetrical flowers and embraces the currently recognized tribes Thermopsideae and the monotypic Euchresteae (Lock, 2005; Ohashi, 2005). Free stamens, the hallmark morphology of Sophoreae, also characterize the Thermopsideae. If Thermopsideae and Euchresteae have to be maintained, new tribes would have to be created for some taxonomically small clades of genera traditionally classified in Sophoreae (Fig. 4) and even the non-monophyletic Thermopsideae would have to be recircumscribed (Wang et al., 2006). We suggest a more inclusive concept of Sophoreae, which is indeed an opinion shared by others (e.g., Lock, 2005; Ohashi, 2005; Wang et al., 2006; LPWG, 2013). The identification of morphological synapomorphies for a newly circumscribed Sophoreae is yet to be further investigated.

We might have resolved the long standing taxonomic puzzle surrounding the tribe Sophoreae, but the genus *Sophora* still reflects the problems of the tribe and is not monophyletic. Even with the dismembering of *Sophora* by the segregation of *Styphnolobium* and *Dermatophyllum*, which fall in two disparate clades outside the Genistoids (Figs. 3, 4; Cardoso et al., 2012a), the monophyly of *Sophora* still remains unclear with respect to the genera *Ammodendron* Fisch. ex DC., *Euchresta* Benn., *Maackia* Rupr., and *Salweenia* (Fig. 5; Kajita et al., 2001). The genera

Euchresta and *Salweenia* were never evaluated in a *matK* phylogeny, but phylogenetic analyses of other plastid genes have consistently placed them close to *Sophora* (Kajita et al., 2001; Yue et al., 2011). The mysterious African *Sophora inhambanensis* Klotzsch, once thought to be closely related to the Podalyrieae, was strongly resolved within *Sophora* by recent phylogenetic analysis of ITS sequences (Boatwright and Van Wyk, 2011). The East Asian and North American disjunct *Thermopsis* is also not monophyletic. Phylogenetic analysis of both *matK* and ITS sequences suggests a geographical division between the Old World and New World *Thermopsis*, but the East Asian *Thermopsis* species are still poorly resolved with respect to the genera *Piptanthus* Sweet and *Anagyris* L. (Fig. 4; Wang et al., 2006).

The genistoid Podalyrieae clade

The monophyly and generic composition of the Podalyrieae were defined in the comprehensive analysis of nrDNA ITS and *rbcL* sequences of Boatwright et al. (2008a). This clade comprises ca. 130 species and nine genera (Table 1), within which the florally anomalous genus *Cadia* has evolved, as also confirmed by analyses of *matK* sequences (Fig. 4; Cardoso et al., 2012a). Despite *Cadia* being the only genus with radially symmetrical flowers within a clade otherwise largely marked by papilionate flowers, it indeed shares several characters with members of the Podalyrieae, including the imparipinnately compound leaves, axillary racemose inflorescences, carboxylic acid esters of quinolizidine alkaloids, and the isoflavone 3-hydroxydaidzein as a major seed flavonoid (Van Wyk, 2003; Boatwright et al., 2008a). Most Podalyrieae genera can be recognized by the combination of an intrusive calyx base, weakly dimorphic anthers, and arillate seeds (Van Wyk and Schutte, 1995). Together with the majority of Crotalarieae genera (e.g., *Aspalathus* and *Rafnia*), the Podalyrieae is among the oldest radiations of the Cape floral clades largely endemic to the mountain fynbos of South Africa (Edwards and Hawkins, 2007).

The genistoid Crotalarieae clade

The Crotalarieae is mostly endemic to Africa and by far the largest subclade within the Genistoids s.l., with ca. 1221 species and 16 genera. Over 80% of the species diversity of Crotalarieae comes from only two genera, *Crotalaria* and *Aspalathus* (Table 1). All Crotalarieae genera bear the typical papilionate flowers, but *Bolusia* has more elaborate resupinate flowers with the keel helically coiled through several turns (Polhill, 1976; Le Roux and Van Wyk, 2012). The re-circumscription of the Crotalarieae and the transfer of *Argyrolobium*, *Dichilus*, *Melolobium* Eckl. & Zeyh., and *Polhillia* C.H.Stirt. to the tribe Genisteae (Van Wyk and Schutte, 1995) agree with the complete generic phylogeny of the tribe Crotalarieae (Boatwright et al., 2008b), which has led to ongoing taxonomic revision and delimitation of all Crotalarieae genera (Boatwright et al., 2008c; Boatwright and Van Wyk, 2009, 2011; Boatwright et al., 2009, 2010, 2011; Van Wyk et al., 2010; Le Roux et al., in press). The present *matK* phylogeny agrees with the more comprehensive analysis of ITS and *rbcL* sequences of Boatwright et al. (2008b) in revealing well-supported generic relationships in two main subclades (Fig. 4). Among the close relatives from within the Core Genistoids, the Crotalarieae has been strongly resolved as sister to the Genisteae (Fig. 4). Indeed, both tribes are the only Genistoids accumulating pyrrolizidine alkaloids, although the Genisteae is primarily known to accumulate quinolizidine alkaloids of the α-pyridone type (Van Wyk, 2003; Wink and Mohamed, 2003). Despite a lack of defining morphological synapomorphies, the Crotalarieae is easily distinguished from the Genisteae by the absence of bilabiate calyces with a bifid upper lip and a trifid lower lip, which is a potential synapomorphy for the Genisteae (Van Wyk, 2005; Boatwright et al., 2008b).

The genistoid Genisteae clade

The Genisteae includes ca. 618 papilionate-flowered species in 25 genera (Table 1; Polhill and Van Wyk, 2005) that are largely confined to the temperate biome (Schrire et al., 2005). The genus *Lupinus* L., one of the most spectacular plant radiations (Hughes and Eastwood, 2006), is also the most diverse within the clade. All molecular phylogenies that have comprehensively sampled within the Genisteae have strongly resolved its monophyly (Käss and Wink, 1997; Kajita et al., 2001). The small African genus *Dichilus* that was transferred from the Crotalarieae (Polhill, 1976; Bisby, 1981) to the Genisteae by Van Wyk and Schutte (1995) is for the first time sampled in a *matK* phylogeny. Our results confirm the analysis of *rbcL* sequences that place the genus as closely related to the Genisteae (Fig. 5; Kajita et al., 2001). Morphological features that traditionally distinguished the tribe (e.g., the lack of an aril, or the presence of an aril but on the short side of the seed, and stamen filaments fused in a closed tube with markedly dimorphic anthers; Polhill, 1976; Bisby, 1981) might be synapomorphies, to which can be added the bilabiate calyx and presence of α-pyridone alkaloids (Polhill and Van Wyk, 2005). Noteworthy, the rare isoflavone 5-O-methylgenistein that has been reported in the leaves of most Genisteae genera is very likely a synapomorphy of the whole clade (Van Wyk, 2003). Previous molecular phylogenies indicate several generic recircumscriptions yet are poorly resolved (Kajita et al., 2001; Wink and Mohamed, 2003; Pardo et al., 2004). The *matK* gene provided excellent resolution for the few accessions included in the present study (Fig. 5). Perhaps, the inclusion of the many genera for which *matK* data are still lacking (Table 1), as well as the broad morphological diversity of putatively non-monophyletic genera (Wink and Mohamed, 2003; Pardo et al., 2004), can help to resolve relationships within Genisteae.

Unplaced genistoid genera

Five genera with strongly bilaterally-symmetrical papilionate flowers still remain unresolved within the Genistoid s.l. clade with respect to the previously described lineages (Table 1). The genus *Dermatophyllum* comprises only four species from warm temperate woodlands, chaparral, and deserts of southern United States to central Mexico (Fig. 4; Pennington et al., 2005). Its phylogenetic position has not yet been resolved within the 50-kb inversion clade (Fig. 4; Cardoso et al., 2012a), but because it also accumulates a range of quinolizidine alkaloids (Kite and Pennington, 2003) and has some morphological similarity to *Sophora* L. (Polhill, 1981a), we follow the suggestion of LPWG (2013) who indicated that this genus might be a sister to the Genistoid s.l. clade.

Cardoso et al. (2012a) suggested the segregation of five Neotropical species of the *Clathrotropis macrocarpa* group into a separate genus, which is distinguished by leaflets with prominent venation and larger elastically dehiscent pods that are sometimes thickened and dilated along the upper sutures. This new genus is also known to bear quinolizidine alkaloids (Ricker et al., 1994; Sagen et al., 2002) and its relationship is still elusive with respect to the Brongniartieae, Leptolobieae, and Core Genistoids (Fig. 4).

The small African genus *Pericopsis*, which also accumulates quinolizidine alkaloids (Kinghorn et al., 1988), is strongly supported within the Genistoids s.l., but unresolved with respect to the *C. macrocarpa* group, Brongniartieae, Leptolobieae, and Core Genistoids based on our preliminary analysis of *trnL* intron sequences (R.T. Pennington and D. Cardoso, unpubl.), a result also consistent with phylogenetic analysis of *rbcL* sequences (Doyle et al., 1997). The alternate leaflets, colleter-like glands in the axils of bract and bracteoles, and the characteristic compressed samaroid fruits with marginal narrow wings of *Pericopsis* suggest an affinity to the Leptolobieae genera (Cardoso et al., 2012c).

The small Malagasy genera *Sakoanala* and *Neoharmsia* were never sampled in molecular phylogenies, but their overall morphology indicates more similarity with Genistoid genera than any other major early-branching papilionoid lineage (Pennington et al., 2005; P. Herendeen, pers. comm.). Additionally, quinolizidine alkaloids have been reported for *Sakoanala* (Van Wyk et al., 1993).

The Amorpheae clade

This is a predominantly North American temperate clade of eight genera and ca. 247 species, most of which belong to the species-rich genus *Dalea* L. (Table 1). The Amorpheae is remarkably distinguished by the evolution of radial symmetry or the simplification of the papilionate flowers in most genera (Fig. 5; McMahon and Hufford, 2004; McMahon, 2005). The Amorpheae has been resolved as monophyletic in all previous molecular phylogenies (McMahon and Hufford, 2004; Wojciechowski et al., 2004; Cardoso et al., 2012a). These studies also show Amorpheae as sister to the Dalbergioid legumes (Lavin et al., 2001), herein Dalbergieae, in a well-supported more inclusive clade that has been collectively referred to as the Dalbergioid s.l. clade (Fig. 5). The Amorpheae has been diagnosed morphologically by synapomorphies that include the punctate glands throughout the plant body, indehiscent, single-seeded fruits, and terminal inflorescences (Barneby, 1977; McMahon and Hufford, 2004) but these features are found variously among the Dalbergieae genera (Lavin et al., 2001). Indeed, the indehiscent pods probably constitute a good synapomorphy for the larger Dalbergioid s.l. clade. Two main subclades and generic relationships within Amorpheae were strongly resolved in the comprehensively-sampled phylogeny of McMahon and Hufford (2004) (see Fig. 5), who first suggested a more narrowly circumscribed *Psorothamnus* Rydb. to include only the species with sessile or nearly sessile flowers, non-exserted pods, and non-spiny inflorescences. The genus *Psorodendron* Rydb. should be reestablished to accommodate the species with stout woody branches, spiny inflorescences and/or exserted pods that hitherto formed part of the non-monophyletic *Psorothamnus* (McMahon and Hufford, 2004).

The Dalbergieae clade

This is a mostly pantropical clade of 46 genera and ca. 1367 species, of which more than 60% belong to only the four species-rich genera *Adesmia* DC., *Aeschynomene* L., *Dalbergia* L.f., and *Machaerium* Pers. (Fig. 5; Table 1). The Dalbergieae corresponds to the Dalbergioid legumes largely defined by Lavin et al. (2001) with phylogenetic analyses of molecular and morphological data. The distinctive aeschynomenoid root nodule of the Dalbergieae (Lavin et al., 2001) makes this one of the very few large clades of Papilionoideae that are defined by a morphological synapomorphy (LPWG, 2013). Three main Dalbergioid lineages of morphologically eclectic genera, the *Adesmia*, *Dalbergia*, and *Pterocarpus* clades have been consistently resolved (Fig. 5; Lavin et al., 2001; Cardoso et al., 2012a, 2012b). The Dalbergieae is also marked by independent evolution of non-papilionate flowers in the small genera *Acosmium*, *Etaballia* Benth., *Inocarpus* J.R.Forst. & G.Forst., *Riedeliella* Harms, and some *Pictetia* DC. species (Fig. 5; Lavin et al., 2001; Cardoso et al., 2012b).

In the last ten years after the publication of Lavin et al. (2001), we have seen three unexpected additions to the Dalbergieae: the monospecific genus *Maraniona* C.E.Hughes, G.P.Lewis, Daza & Reynel, a completely new discovery arising from fieldwork (Hughes et al., 2004); the radially-symmetrical-flowered *Acosmium*, which was thought to belong to the Genistoids (Cardoso et al., 2012b); and more recently, *Steinbachiella* Harms. Lewis et al. (2012) clarified the taxonomic identity of this orphaned monospecific taxon by showing it to be a clearly defined genus, phylogenetically close to *Machaerium* (Fig. 5). Other recent advances within Dalbergieae include an attempt to elucidate inter-relationships between *Aeschynomene* s.l., *Dalbergia*, and *Machaerium* (Ribeiro et al., 2007), and the phylogenies of

individual genera, such as *Platymiscium* (Saslis-Lagoudakis et al., 2008), *Centrolobium* Mart. ex Benth. (Pirie et al., 2009), *Arachis* L. (Bechara et al., 2010), and *Pterocarpus* Jacq. (Saslis-Lagoudakis et al., 2011). Studies are already underway or about to be published that provide new results concerning the phylogeny and biogeography of *Adesmia* (Iganci et al., 2013), *Amicia* (T. Särkinen & C. Hughes, unpubl.), *Dalbergia* (Vatanparast et al., 2013), *Machaerium* (F. Filardi et al., unpubl.), and *Zornia* (A.P. Fortuna-Perez et al., unpubl.). Additionally, a new assessment of relationships among the Malagasy endemic *Ormocarpopsis* R.Vig. and allies suggests a broader circumscription of *Ormocarpopsis* to encompass the monospecific *Peltiera* Du Puy & Labat (Thulin et al., 2013). Substantial progress also needs to be made with respect to the poorly resolved relationships among the mostly monospecific or species-poor genera of the *Pterocarpus* clade (Fig. 5; Lavin et al., 2001; Saslis-Lagoudakis et al., 2008; Cardoso et al., 2012b). A better sampling would be important for the large genus *Aeschynomene* s.l., which clearly comprises two disparate clades that are also morphologically, ecologically, and biogeographically distinct (Fig. 5; Lavin et al., 2001; Ribeiro et al., 2007; M. Lavin, unpubl.). *Aeschynomene* sect. *Aeschynomene* is paraphyletic with respect to the genera *Kotschya* Endl., *Smithia* Aiton, *Humularia* P.A.Duvign., *Bryaspis* P.A.Duvign., *Geissaspis* Wight & Arn., *Cyclocarpa* Afzel. ex Urb., and *Soemmeringia* Mart., and its constituent species have medifixed stipules and are primarily distributed in wet forests and savannas, where they have broad geographic ranges. The monophyletic *Aeschynomene* sect. *Ochopodium* Vogel is closer to *Machaerium* and its members have basifixed stipules and are primarily inhabiting seasonally dry forests, with individual species narrowly distributed (M. Lavin, unpubl.). Further taxonomic changes to the delimitation of *Aeschynomene* will inevitably require a comprehensive phylogenetic analysis and sampling which will also have to include much of the diversity of the large genus *Machaerium*, as well as the recently reestablished *Steinbachiella*.

The Baphieae clade

The Baphioid legumes, first defined in the *trnL* intron phylogeny of Pennington et al. (2001) and confirmed in the *matK* phylogeny of Cardoso et al. (2012a) could be clearly distinguished as a separate papilionoid tribe that is sister to the species-rich NPAAA clade (Fig. 5; Appendix S1). The Baphieae comprises ca. 57 species largely from Africa and southern Asia and includes the genera *Airyantha* Brummitt, *Baphia* Afzel. ex Lodd., *Baphiastrum* Harms, *Bowringia* Champ. ex Benth., *Dalhousiea*, and *Leucomphalos* traditionally classified in Sophoreae (Polhill, 1981a), plus *Baphiopsis* Benth. ex Baker of Swartzieae (Polhill, 1994). In addition to the free stamens and poorly differentiated lower petals, or flowers sometimes appearing radially symmetrical, Baphieae is characterized by having simple or unifoliolate leaves, anthers more or less basifixed, and the calyx splitting to the base either down one side only and therefore appearing spathaceous, or down both sides and thus becoming bilabiate (Brummitt, 1968; Polhill, 1981a). Taxonomic and phylogenetic progress is yet to be made with respect to the non-monophyletic large genus *Baphia*, and to evaluate the relationship and generic status of *Bowringia* and the monospecific *Baphiastrum* and *Leucomphalos*.

Unresolved early-branching genera

Tribal designations for two unresolved early-branching genera remain uncertain and depend on whether monotypic tribes should be recognized or not. The phylogenetically isolated and radially-symmetrical-flowered genus *Amphimas* from lowland rain and seasonally dry tropical forests of west and central Africa is one of the nine unresolved lineages of the large 50-kb inversion clade (Fig. 3; Cardoso et al., 2012a). In addition to its non-papilionate flowers with free stamens and unusually feature of

having only three petals that are each deeply two-lobed, *Amphimas* is known to produce balsam (Polhill, 1981a; Pennington et al., 2005).

The South American *Aldina* is also phylogenetically isolated within 50-kb inversion clade (Fig. 3; Cardoso et al., 2012a). Traditionally, this genus was included in the tribe Swartzieae (Cowan, 1981) because of its non-papilionate, radially symmetrical flowers with entire calyces and numerous stamens (Fig. 5). *Aldina* includes ca. 22 species primarily in the rain forest biome, including habitats such as tropical montane and lowland Amazonian forests and white sand savannas (Stergios and Cowan, 1999; Ireland, 2005).

The NPAAA clade

The non-protein–amino-acid-accumulating (NPAAA) clade (Fig. 5; Appendix S1) is not the focus of the present study, although we also have comprehensively sampled genera within this clade. The NPAAA clade is species-rich and comprises about 9464 species and 305 genera, representing almost 70% of the species and more than 60% of the genera in the Papilionoideae, and almost 50% of the species and genus diversity of the whole legume family (Lewis et al., 2005). All NPAAA lineages are predominantly marked by the evolution of highly specialized papilionate flowers (Lewis et al., 2005). Detailed taxonomic, biogeographical, and phylogenetic accounts of many NPAAA papilionoids are addressed elsewhere (Hu et al., 2000; Wojciechowski et al., 2000, 2004; Allan et al., 2003; Crisp and Cook, 2003; Lavin et al., 2003; Steele and Wojciechowski., 2003; Lewis et al., 2005; Schrire et al., 2009; Stefanović et al., 2009; Sirichamorn et al., 2012) and recently reviewed by the LPWG (2013). The present *matK* phylogeny resolved many well-supported major clades within the NPAAA papilionoids (Appendix S1), such as the Mirbelioids, Indigofereae, Millettioids, Robinioids, and the inverted-repeat-lacking clade (IR-Lacking clade), which are also consistent with those resolved by Wojciechowski et al. (2004) and McMahon and Sanderson (2006), the latter of which involved an analysis of more than two thousand sequences in a supermatrix framework. However, it is clear that greater phylogenetic resolution is yet to be achieved among the early-branching genera of the Millettioids and IR-Lacking clade, and within the Phaseoloid subclades (Appendix S1; Wojciechowski et al., 2004; Stefanović et al., 2009).

Challenges in reconstructing the Papilionoideae phylogeny

The challenge of reconstructing the deep-branching history of the papilionoid legumes has been addressed numerous times in the last decades (Doyle et al., 1997; Käss and Wink, 1995, 1996, 1997; Doyle et al., 1997, 2000; Kajita et al., 2001; Pennington et al., 2001; Wojciechowski et al., 2004; McMahon and Sanderson, 2006; Cardoso et al., 2012a). Although we have revealed many strongly supported and well-resolved clades within Papilionoideae, relationships among the first-diverging clades and the main lineages within the 50-kb inversion clade still remain unresolved (Fig. 1). Because our analyses are based upon a single gene, this is not surprising, and the addition of more loci is necessary. Furthermore, much is yet to be accomplished on integrating data on the incredible morphological and chemical diversity of legumes into our phylogenetic estimates, and to sample the many genera for which molecular data are still lacking (LPWG, 2013). Many promising opportunities are now possible by the increasing development of cost-effective high-throughput next generation sequencing (e.g., Harrison and Kidner, 2011; Egan et al., 2012; LPWG, 2013). Although next-gen technologies may eventually help, given the excellent phylogenetic resolution obtained with the *matK* gene, we make a plea that future efforts on Papilionoideae phylogenetics should focus more on those genera for which the *matK* sequences are still lacking. We do not have *matK* sequences for 52 of the 196 early-branching papilionoid genera (Table 1). At least for most of them we have fairly reliable information from other DNA markers, but unfortunately no molecular data are

available for some key genera, such as *Haplormosia*, *Neoharmsia*, *Petaladenium*, *Sakoanala*, and *Uleanthus* (Table 1). More thorough sampling is also needed to resolve the taxonomy of non-monophyletic genera, such as *Aeschynomene*, *Baphia*, *Clathrotropis*, *Myrocarpus*, and *Sophora* (Table 1). We must also devote our attention to morphologically heterogeneous species-rich genera, such as *Crotalaria*, *Dalea*, *Machaerium*, and *Ormosia*.

The recent formation of the Legume Phylogeny Working Group holds out hopes of integrating legume expertise worldwide to take advantage of sharing data and new approaches in phylogenetics (LPWG, 2013). Under such a collaborative effort, a complete generic phylogeny and revised clade-based classification of the whole legume family should be feasible in the near future (LPWG, 2013). Certainly, by having a more complete and resolved Papilionoideae phylogeny, we will be able to further explore the evolution of other features, particularly those that vary in the early-branching clades. An excellent example of this is the recurrent convergent evolution of non-papilionate floral morphologies (Figs. 2–5; Pennington et al., 2000; McMahon, 2005; Boatwright et al., 2008a; Cardoso et al., 2012a, 2012b, 2013a). An exciting research direction would be to explore the interplay between floral morphology and species diversification that have ultimately resulted in the predominance of species-rich papilionoid clades.

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