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A dated phylogeny of the Neotropical Dipterygeae clade reveals 30 million years of winged papilionate floral conservatism in the otherwise florally labile early-branching papilionoid legumes

CATARINA S. CARVALHO[1,2,3,*], HAROLDO CAVALCANTE DE LIMA[2,3,4], MARISTERRA RODRIGUES LEMES[1], CHARLES E. ZARTMAN[1], CÁSSIO VAN DEN BERG[5], CARMEN ROSA GARCÍA-DÁVILA[6], EURÍDICE N. HONORIO CORONADO [7], MALTE MADER[8], KATHELYN PAREDES-VILLANUEVA[9], NIKLAS TYSKLIND[10] and DOMINGOS CARDOSO[2,11,*]

[1]*Instituto Nacional de Pesquisas da Amazônia (INPA), Coordenação de Biodiversidade, Av. André Araújo, 2936, Petrópolis, 69060-001, Manaus, Amazonas, Brazil*
[2]*Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão, 915, 22460-030, Rio de Janeiro, RJ, Brazil*
[3]*Escola Nacional de Botânica Tropical, Rua Pacheco Leão, 2040, Horto, 22460-030, Rio de Janeiro, RJ, Brazil*
[4]*Instituto Nacional da Mata Atlântica / INMA-MCTI, Av. José Ruschi, 4, Centro, 29650-000, Santa Teresa, Espírito Santo, Brazil*
[5]*Programa de Pós-Graduação em Botânica (PPGBot), Universidade Estadual de Feira de Santana, Av. Transnordestina, s.n., Novo Horizonte, 44036-900, Feira de Santana, Bahia, Brazil*
[6]*Instituto de Investigaciones de la Amazonía Peruana (IIAP), Av. José A. Quiñones km 2.5, Iquitos, Peru*
[7]*School of Geography and Sustainable Development, University of St Andrews, St Andrews, KY16 9AL, UK*
[8]*Thünen Institute of Forest Genetics, Sieker Landstrasse 2, 22927 Grosshansdorf, Germany*
[9]*Carrera de Ingeniería Forestal, Laboratorio de Dendrocronología, Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno, Km 9 carretera al Norte, El Vallecito, Santa Cruz, Bolivia*
[10]*National Research Institute for Agriculture, Food and Environment, UMR0745 EcoFoG, AgroParisTech, Cirad, CNRS, Université des Antilles, Université de Guyane, Campus Agronomique, Avenue de France, BP97387 Kourou Cedex, France*
[11]*Programa de Pós-Graduação em Biodiversidade e Evolução (PPGBioEvo), Instituto de Biologia, Universidade Federal da Bahia, Rua Barão de Jeremoabo, s.n., Ondina, 40170-115, Salvador, Bahia, Brazil*

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The early-branching clades of Fabaceae subfamily Papilionoideae are characterized by their remarkable lability in floral architecture. In contrast, more derived papilionoid lineages are marked by evolutionary conservatism towards strongly bilateral, papilionate flowers. Here, we show an unexpected example of conservatism of a unique floral architecture during the early diversification history of the papilionoids. We built the most comprehensively sampled molecular phylogenetic tree with a focus on the early-diverging papilionoid Dipterygeae clade to evaluate conservatism of the winged papilionate architecture and associated traits related to flower specialization (e.g. zygomorphy, petal differentiation, stable stamen number and stamen sheath). Dipterygeae comprise *c.* 22 species of mostly giant trees from across tropical forests in Central America and the Amazon, but they are also ecologically dominant in the savannas of the Brazilian Central Plateau. Phylogenetic analyses of nuclear ribosomal ITS/5.8S and

*Corresponding authors. E-mail: carvalho_catarina@outlook.com; cardosobot@gmail.com

plastid *matK* and *trnL* intron sequences strongly supported inter-relationships and the monophyly of each genus (*Dipteryx*, *Monopteryx*, *Pterodon* and *Taralea*). Bayesian relaxed-clock dating and a Bayesian model of ancestral character estimation revealed *c*. 30 Myr of conservatism of all winged papilionate-related flower traits in a clade comprising the most recent common ancestor of *Dipteryx*, *Pterodon* and *Taralea*, but lability in fruit morphology during the diversification of the entire Dipterygeae clade. Despite *Monopteryx* and remaining Dipterygeae being florally discrepant, they are collectively defined by a floral synapomorphy that is unique among all papilionoid Fabaceae: the highly differentiated calyx, where the two upper lobes are enlarged and wing-like, whereas the other three lower lobes are reduced. We suggest that the different dispersal strategies and the ancient winged papilionate floral conservatism in Dipterygeae, which has maintained effective ecological interactions with specialized pollinators and ensured the protection of young flower buds and developing fruits, may explain successful evolutionary and ecological persistence of the clade across the main Neotropical biomes.

ADDITIONAL KEYWORDS: Fabaceae – floral evolution – Leguminosae – molecular phylogenetics – Papilionoideae.

INTRODUCTION

Fabaceae exhibit a broad diversity of flower architecture. The associated flower traits are taxonomically informative, and, combined with molecular data across many clades, have advanced our understanding of their evolutionary history (Marazzi *et al.*, 2012; Leite, Mansano & Teixeira, 2014; Paulino *et al.*, 2014; Leite *et al.*, 2015; Prenner & Cardoso, 2017) and phylogenetic classification (e.g. Cardoso *et al.*, 2013a; LPWG, 2013, 2017). The early diversification history of Fabaceae is generally marked by clades with floral evolutionary lability, resulting in a dramatic diversity of flower architectures (e.g. Cronk & Möller, 1997; Pennington *et al.*, 2000; Prenner & Klitgaard, 2008; Cardoso *et al*., 2012a, 2012b, 2013a, 2013b; Leite *et al.*, 2015; Prenner *et al.*, 2015; Prenner & Cardoso, 2017). Flowers of Fabaceae may vary from a basic radially symmetrical rosid-like architecture, involving undifferentiated and free sepals and petals, and with free stamens, to the well-known papilionate flower, a highly specialized, bilaterally symmetrical flower with clearly differentiated petals, a varying degree of connation among all organs, and the reproductive organs often enclosed by the keel petals. Such floral heterogeneity is greatly pronounced, particularly in the early-branching lineages of Fabaceae subfamily Papilionoideae, possibly the result of a complex gene expression and ecological pressures imposed by specific pollination ecology during an ancient history of diversification (e.g. Arroyo, 1981; Citerne, Möller & Cronk, 2000; Theissen, 2001; Citerne *et al.*, 2003; Citerne, Pennington & Cronk, 2006; Feng *et al.*, 2006; Zhang, Kramer & Davis, 2010; Sinjushin & Karasyova, 2017).

The floral disparity among the papilionoid Fabaceae has been observed in the recently recircumscribed early-branching ADA (Angylocalyceae + Dipterygeae + Amburaneae) and Swartzieae clades (*sensu* Cardoso *et al.*, 2012a, 2013a). These lineages lack the 50-kb inversion in the large single copy (LSC) of the plastid DNA genome that is diagnostic for the large papilionoid 50-kb inversion clade (Doyle *et al.*, 1996; Cardoso *et al.*, 2012a; LPWG, 2017). They show great floral variation; some show radial symmetry, incompletely differentiated petals and free stamens (e.g. *Cordyla* Lour. and *Myrocarpus* Allem.; Amburaneae) while others are strongly bilateral and papilionate [e.g. *Dussia* Krug & Urb. ex Taub., *Petaladenium* Ducke (Amburaneae) and *Dipteryx* Schreb., *Pterodon* Vogel, and *Taralea* Aubl. (Dipterygeae)]. Despite the relationships between the early-diverging papilionoids still not being fully resolved (e.g. Zhao *et al.*, 2021; Choi *et al.*, 2022), the hypothesis that non-papilionate flowers appeared only in ancient lineages (e.g. Polhill, 1981a, 1994) has already been ruled out (e.g. Pennington *et al.*, 2001; Cardoso *et al.*, 2012a; Choi *et al.*, 2022). This new phylogenetic view has led to a better understanding of how the first-branching clades in Papilionoideae are related to each other and how many times the non-papilionate flowers have evolved from or reversed to the truly papilionate floral architecture (Pennington *et al*., 2000, 2001; Cardoso *et al*., 2013b, 2015).

Recent advances in the phylogeny of the early-branching lineages of Papilionoideae call our attention to the Dipterygeae (*sensu* Cardoso *et al.*, 2012a), a clade of *c*. 22 exclusively Neotropical tree species in the genera *Dipteryx*, *Monopteryx* Spruce ex Benth., *Pterodon* and *Taralea* (Fig. 1), most of which are marked by a unique winged papilionate floral morphology. Because of their strongly papilionate flowers with enclosed fused stamens and expanded upper calyx lobes often assuming a wing-shaped orientation (Fig. 1), *Dipteryx*, *Pterodon* and *Taralea* have long been recognized in the tribe Dipterygeae (Polhill, 1981b; Lewis *et al.*, 2005), which was later confirmed to be monophyletic (Pennington *et al.*, 2001; Wojciechowski, Lavin & Sanderson, 2004; Cardoso *et al*., 2012a, 2015). Traditionally classified in Sophoreae (Polhill, 1981a), *Monopteryx* was resolved, however, as sister to the remainder of Dipterygeae (Cardoso *et al*., 2012a, 2015), despite having free stamens and a non-winged floral architecture which greatly contrast with the flowers

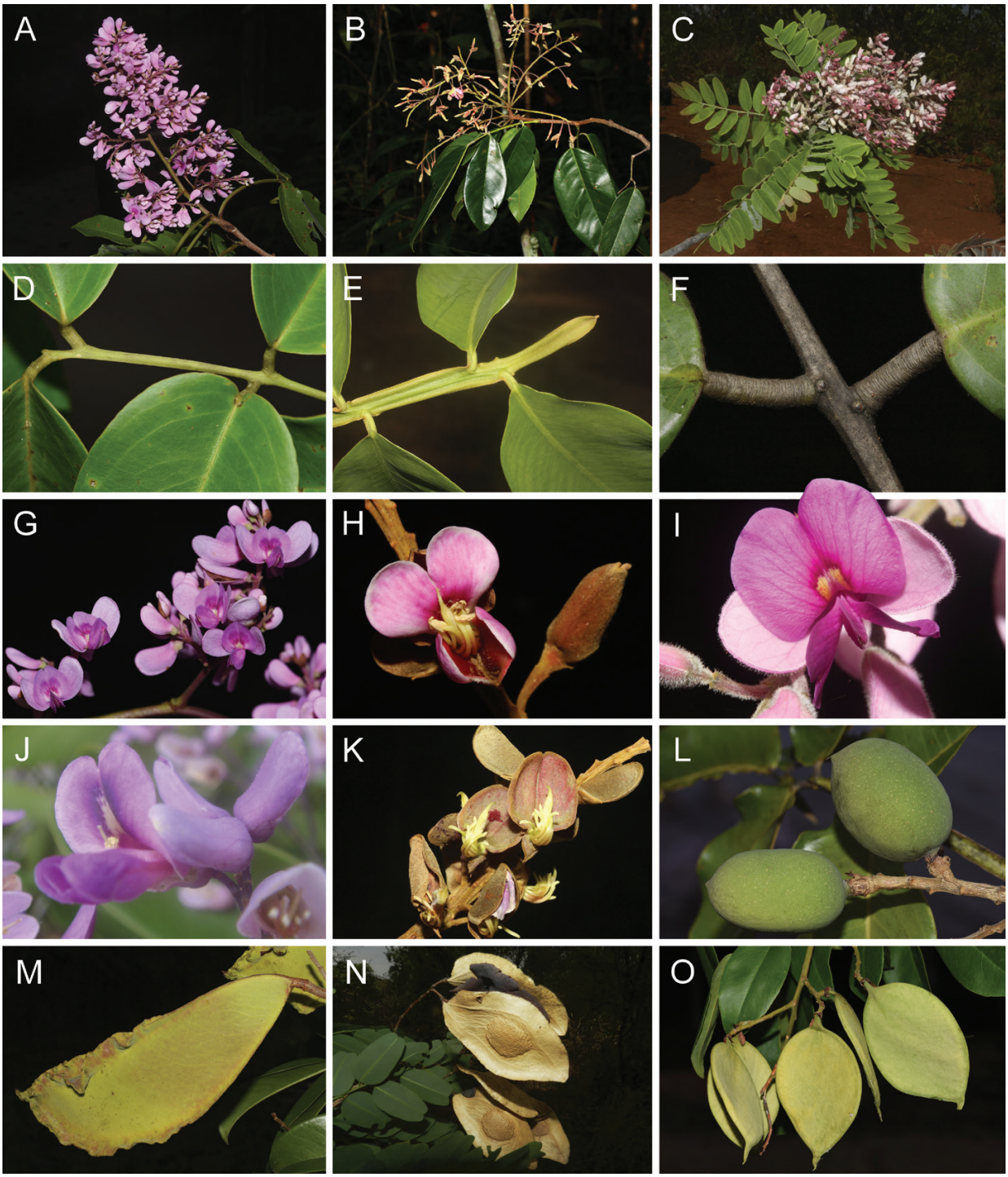

Figure 1. Morphological diversity in the early-branching Dipterygeae clade of papilionoid Fabaceae. A, inflorescence of *Dipteryx magnifica*. B, inflorescence of *Monopteryx uaucu*. C, inflorescence of *Pterodon pubescens*. *Taralea oppositifolia* (D) and *D. odorata* (E) showing the flattened leaf rachis. F, terete leaf rachis of *M. angustifolia* with extrafloral nectaries. G, the winged papilionate floral architecture of *D. magnifica* showing the wing-oriented expanded, petaloid upper calyx lobes. H, the non-winged bilaterally symmetrical flower of *M. angustifolia* with exposed free stamens. I, winged papilionate flower of *P. abruptus* with wing-oriented upper calyx lobes. J, winged papilionate flower of *T. cordata* but with a hidden, standard-oriented expanded upper calyx lobes. K, fused upper calyx lobes of *M. angustifolia* enclosing the developing young fruit. L, drupes of *D. odorata*. M, legume of *M. uaucu*. N, cryptosamara of *P. emarginatus*. O, legumes of *T. oppositifolia*. All photographs by D. Cardoso, except C and N by C. S. Carvalho, and J by H. C. Lima.

of typical Dipterygeae. However, all share a common morphology: the two calyx upper lobes are evidently enlarged, whereas the three lower ones are reduced (Polhill, 1981b). The two upper lobes together with the petals seem to function as a pollinator attractor (Leite *et al.*, 2014). In flowers of *Monopteryx* spp., however, the two upper lobes are fused and perform a function similar to the standard petal (Polhill, 1981a; Cardoso *et al.*, 2013a), whereas in remaining Dipterygeae they are free and wing-like. The fruits also vary in the Dipterygeae clade: *Monopteryx* and *Taralea* have the typically dehiscent pod or legume, whereas *Dipteryx* and *Pterodon* have an indehiscent drupe and cryptosamara, respectively (Polhill, 1981b; Kirkbride, Gunn & Weitzman, 2003; Pinto, Francisco & Mansano, 2014). This great morphological variation in the clade raises the question of how these quite contrasting fruit morphologies have evolved in Dipterygeae.

Most species of Dipterygeae are found in rainforests, from the Amazon basin and the Caribbean to the Brazilian Atlantic coastal forest (Carvalho *et al.*, 2022b), but species of the clade also occur in savannas (Cerrados in Brazil), and South American seasonal dry tropical forests (SDTFs) (the Caatinga of north-eastern Brazil; Simon *et al.*, 2009; Pennington & Lavin, 2016). Its occurrence across such a diversity of ecologically distinct environments or biomes makes the Dipterygeae clade an excellent model for understanding the patterns of colonization of Fabaceae in the Neotropics and their evolutionary and ecological persistence in biomes (Lavin *et al.*, 2004; Schrire, Lavin & Lewis, 2005; Oliveira-Filho *et al.*, 2013; Pennington & Lavin, 2016).

Although Dipterygeae have been repeatedly supported as a monophyletic group (Pennington *et al.*, 2001; Cardoso *et al.*, 2012a, 2013a, 2015; Honorio Coronado *et al.*, 2020), this is the first time that all currently known species of the clade, with the exception of *Taralea crassifolia* (Benth.) Ducke, have been sampled in a phylogenetic study. Molecular phylogenetic analyses with the most complete taxon sampling are crucial for constructing a solid phylogenetic classification (LPWG, 2013, 2017) and to understand floral evolution (Pennington *et al.*, 2000; Prenner & Klitgaard, 2008; Cardoso *et al.*, 2013a; Bruneau *et al.*, 2014; Prenner & Cardoso, 2017) and biogeographical diversification (Schrire *et al.*, 2005; Koenen *et al.*, 2013; Oliveira-Filho *et al.*, 2013). By analysing molecular data from nuclear ribosomal (ITS/5.8S) and plastid (*matK* and *trnL* intron) DNA sequences, we aim to investigate the phylogenetic relationships in the Dipterygeae clade and the evolution of floral morphology in the clade and its constituent genera. We also raised the question of whether evolutionary conservatism in the winged papilionate-related traits of flower architecture has marked the Dipterygeae clade in contrast to the early-branching papilionoid Fabaceae that are otherwise marked by the recurrent independent evolution of radial floral symmetry and lack of flower specialization (e.g. Pennington *et al.*, 2000; Cardoso *et al.*, 2012b).

MATERIAL AND METHODS

Taxon sampling and molecular data

Our sampling involved 40 species from the earliest branching lineages of Papilionoideae, most of which (21) belong to the ingroup, Dipterygeae. Whenever possible, multiple conspecific accessions of species of Dipterygeae were also included to evaluate the patterns of species monophyly that are common to rainforest-inhabiting plant clades (Pennington & Lavin, 2016). Our complete sampling involved 132 DNA sequences from the publicly available GenBank database (https://www.ncbi.nlm.nih.gov/genbank/), many of which come from our molecular phylogenetic studies with a focus on the early-branching papilionoids (e.g. Cardoso *et al.*, 2015). We also augmented the taxon and gene coverage by producing 97 new sequences, including accessions with previously developed genomic data using RADSeq and MiSeq (i.e. *Dipteryx punctata*; Honorio Coronado *et al.*, 2019) and from morphologically unique or enigmatic species never sampled before in molecular phylogenetic analyses, because their complex morphology and taxonomy precludes easy identification, and owing to their scarcity in herbarium collections or the difficulty in reaching them in remote areas [*Dipteryx hermetopascoaliana* C.S.Carvalho, H.C.Lima & D.B.O.S.Cardoso, *Dipteryx lacunifera* Ducke, *Monopteryx angustifolia* Spruce ex Benth., *Pterodon pubescens* (Benth.) Benth. and *Pterodon cipoensis* C.S.Carvalho, H.C.Lima & D.B.O.S.Cardoso]. Leaf samples for DNA extraction were sampled in the herbaria HUEFS, RB and UB, and during field expeditions in Central America (rainforests of Costa Rica and Panama) and South America (Amazonian rain forests of Bolivia, Brazil, French Guiana and Peru; Atlantic Coastal Rainforest of Brazil; savannas of Brazil and Bolivia; and the Caatinga seasonally dry forest of north-eastern Brazil).

The DNA datasets included the nuclear ribosomal ITS/5.8S and the plastid protein-coding *matK* and *trnL* intron, all of which are loci widely used to resolve relationships in Fabaceae and with successful implications for understanding their systematics, biogeography and morphological evolution (e.g. Cardoso *et al.*, 2015, 2017; Ramos *et al.*, 2016; de la Estrella *et al.*, 2018; Torke *et al.*, 2022). Our plastid datasets of *matK* and *trnL* intron each had 61 sequences. For the ITS/5.8S, 97 sequences were sampled, of which 78 belonged to Dipterygeae. For the

three gene (ITS/5.8S + *matK* + *trnL* intron) combined analysis, we sampled 41 sequences, including the 22 accessions of Dipterygeae. As outgroup taxa, we chose representative species of all genera from the Angylocalyceae, Amburaneae and Swartzieae clades, as guided by broad-level comprehensive phylogenetic analyses of Papilionoideae (Cardoso *et al.*, 2013a; Choi *et al.*, 2022).

DNA extraction, amplification and sequencing

DNA was extracted from silica-gel-dried leaf material or herbarium material following Doyle & Doyle (1987). Polymerase chain reactions (PCRs) were done with Top Taq Master Mix (Qiagen, Santa Clarita, CA, USA). Amplification primers, sequencing primers and reaction conditions for *matK* were described in Wojciechowski *et al.* (2004). The universal forward primer c (5′-CGAAATCGGTAGACGCTACG-3′) was used with the reverse primer d (5′-GGGGATAGAGGGACTTGAAC-3′) to amplify the *trnL* intron (Taberlet *et al.*, 1991). PCR conditions for the *trnL* intron included a 3-min denaturing step at 94 °C, followed by 40 cycles of 1 min at 94 °C (denaturation), 30 s at 55 °C (annealing) and 1 min at 72 °C (extension), and a further extension for 10 min at 72 °C. The forward primer 17SE (5′-ACGAATTCA TGGTCCGGTGAAGTGTTCG-3′) was used with the reverse primer 26SE (5′-TAGAATTCCCCGGTTCGCT CGCCGTTAC-3′) to amplify the ITS/5.8S region (Sun *et al.*, 1994). PCR involved a 5-min denaturing step at 94 °C, followed by 28–30 cycles of 1 min at 94 °C (denaturation), 1 min at 50–52 °C (annealing) and 3 min at 72 °C (extension), and further extension for 7 min at 72 °C. Amplified PCR products were purified using the Qiagen Kit or 11% solution of polyethylene glycol (PEG) 6000 macrogol. The same primers used for PCR were also used for sequencing, except for the ITS/5.8S region that was sequenced with the primers 92 (5′-AAGGTTTCCGTAGGTGAAC-3′) (Desfeux & Lejeune, 1996) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) and to flanked sequence ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′) and ITS 3 (5′-GCATCGATGAAGAACGCAGC-3′; White *et al.*, 1990). Sequencing reactions in both directions were done using the BigDye Terminator kit (v.3.1; Applied Biosystems/Life Technologies Corp., Carlsbad, CA, USA). The products of sequencing were analysed on a sequencer ABI3730XL (Applied Biosystems) of Fundação Oswaldo Cruz (FIOCRUZ-BA).

Alignment and phylogenetic analyses

The forward and reverse reads of the newly sequenced accessions were assembled into a contig with Geneious v.4.8.5 (Drummond *et al.*, 2009). Sequences were aligned with SeaView v.4 (Gouy, Guindon & Gascuel, 2009) using the similarity criterion of Kelchner (2000) and Simmons (2004) to avoid inconsistencies derived from automated multiple alignments. Voucher information and collecting locality for all newly generated sequences and the associated GenBank numbers are given in Table 1.

For phylogenetic reconstruction, we used two approaches: maximum likelihood (ML) and Bayesian inference (BI), as implemented in specific phylogenetic software in the CIPRES Science Gateway v.3.3 online portal (www.phylo.org) (Miller, Pfeiffer & Schwartz, 2010). We performed analyses for each individual gene and for all genes combined into a single matrix of nuclear and plastid data. ML reconstruction was performed in RAxML v.8 (Stamatakis, 2014), using the nucleotide substitution model GTR+GAMMA, with the gamma distribution and invariant sites estimated during running. Support values of the nodes were estimated with 1000 bootstrap replicates, for which values ≥0.95 were considered strong (Stamatakis, Hoover & Rougemont, 2008). The plastid regions and ITS/5.8S were analysed separately to identify any case of possible incongruence among partitions. The parsimony-based partition homogeneity test (incongruence length difference test; Farris *et al.*, 1994) was not used here because it has often generated misleading results (Dolphin *et al.*, 2000; Yoder, Irwin & Payseur, 2001; Barker & Lutzoni, 2002).

For BI (Lewis, 2001), the best-fitting nucleotide substitution model for each partition was selected via the Akaike and Bayesian information criteria (AIC and BIC), implemented in jModelTest2 v.2.1.6 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012), at CIPRES v.3.3 online (Miller *et al.*, 2010). The selected models were GTR+I+G for ITS/5.8S, GTR+G for *matK* and GTR+G for the *trnL* intron. BI was performed in MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003). 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 and trees sampled every 10 000th generation (Huelsenbeck *et al.*, 2001), with a burn-in of 25%. Posterior probability (PP) values ≥0.95 were considered strong. The remaining trees were summarized in a 50% majority-rule consensus tree that was visualized and partially edited for graphical presentation using FigTree v.1.4.3 (Rambaut, 2018).

Ancestral character estimation

To examine patterns of floral and fruit lability or conservatism during the evolution of Dipterygeae, we used the majority-rule consensus tree derived from the combined Bayesian analysis to estimate the evolution of ten key morphological characters that have been widely

Table 1. DNA sequences newly generated for this study, with a focus set on the Neotropical papilionoid legume tribe Dipterygeae (*Dipteryx*, *Monopteryx, Pterodon* and *Taralea*). Voucher specimen information, including collection locality, voucher collector and number, and herbarium acronym are provided

Species	Voucher details, herbarium	Country, locality	GenBank ITS	GenBank *matK*	GenBank *trnL* intron
Cordyla densiflora Milne-Redh.	*E.Mhoro 1211* (WAG)	Tanzania, Iringa, Iringa Rural District	OP099453		ON932469
Dipteryx alata Vogel	*G.Martinelli 18716* (HUEFS)	Brazil, Mato Grosso, Barão de Melgaço			ON932471
Dipteryx ferrea (Ducke) Ducke	*I.Huamantupa 19428* (CUZ)	Peru, Santa Cruz - Shintuya	OP099456		
Dipteryx hermetopascoalina C.S.Carvalho, H.C.Lima & D.B.O.S.Cardoso	*B.Schindler s.n.* (MAC 0064287)	Brazil, Alagoas, Branquinha	OP099467	ON932462	ON932481
Dipteryx lacunifera Ducke	*C.S.Carvalho 351 Ind2* (RB)	Brazil, Piauí, Ribeiro Gonçalves	OP099457		ON932473
Dipteryx lacunifera Ducke	*C.S.Carvalho 351 Ind3* (RB)	Brazil, Piauí, Ribeiro Gonçalves		ON932454	
Dipteryx lacunifera Ducke	*C.S.Carvalho 351 Ind4* (RB)	Brazil, Piauí, Ribeiro Gonçalves			ON932472
Dipteryx lacunifera Ducke	*F.C.L.Pinto 32* (ALCB)	Brazil, Piauí, Piripiri	OP099458		
Dipteryx magnifica (Ducke) Ducke	*D.Cardoso 4019* (HUEFS)	Brazil, Pará, Santarém		ON932455	ON932474
Dipteryx magnifica (Ducke) Ducke	*PPBIO 316* (PPBIO)	Brazil, Amazonas, BR 319, Manaus-Porto Velho	OP099459		
Dipteryx odorata (Aubl.) Forsyth f.	*C.S.Carvalho 311* (RB)	Brazil, Pará, Belém		ON932456	ON932475
Dipteryx odorata (Aubl.) Forsyth f.	*C.S.Carvalho et al. 340 Ind2* (RB)	Brazil, Pará, Pauapebas	OP099460		
Dipteryx odorata (Aubl.) Forsyth f.	*C.S.Carvalho 340 Ind3* (RB)	Brazil, Pará, Pauapebas			ON932476
Dipteryx odorata (Aubl.) Forsyth f.	*H.C.Lima 7570* (RB)	Brazil, Pará, Canaã dos Carajás	OP099464	ON932460	
Dipteryx odorata (Aubl.) Forsyth f.	*L.P.Queiroz 13062* (RB)	Brazil, Pará, Belém	OP099466		
Dipteryx odorata (Aubl.) Forsyth f.	*V.F.Paula 4* (HUEFS)	Brazil, Bahia, Jequié	OP099465	ON932461	ON932480
Dipteryx oleifera Benth.	*J.Carrión 1844* (RB)	Panamá, Colón, Colón	OP099468		ON932482
Dipteryx polyphylla Huber	*C.S.Carvalho 374* (RB)	Brazil, Amazonas, Manaus	OP099469		

Table 1. Continued

Species	Voucher details, herbarium	Country, locality	GenBank ITS	GenBank *matK*	GenBank *trnL* intron
Dipteryx polyphylla Huber	*PPBIO 506* (PPBIO)	Brazil, Amazonas, BR 319, Manaus-Porto Velho	OP099470		
Dipteryx polyphylla Huber	*PPBIO 546* (PPBIO)	Brazil, Amazonas, BR 319, Manaus-Porto Velho	OP099471		
Dipteryx punctata (Blake) Amshoff	*K.Paredes 689* (USZ)	Bolivia, Loma Alta	OP099463	ON932459	ON932479
Dipteryx punctata (Blake) Amshoff	*Tysklind 1* (-)	Frech Guiana, Paracou	OP099461	ON932457	ON932477
Dipteryx punctata (Blake) Amshoff	*Tysklind s.n.* (-)	Frech Guiana, Paracou	OP099462	ON932458	ON932478
Dipteryx rosea Spruce ex Benth.	*D.Cardoso 3430* (HUEFS)	Brazil, Amazonas, São Gabriel da Cachoeira			ON932483
Dipteryx rosea Spruce ex Benth.	*D.Cardoso 4214* (HUEFS)	Brazil, Amazonas, São Gabriel da Cachoeira	OP099472	ON932463	
Mildbraediodendron excelsum Harms	*G.Moukassa 4129* (E)	Republic of Congo, Sangha	OP099454		
Mildbraediodendron excelsum Harms	*R.Letouzey 5413* (WAG)	Cameroon, à 2 km à l'Ouest de Masea			ON932470
Monopteryx angustifolia Spruce ex Benth.	*D.Cardoso 4256* (HUEFS)	Brazil, Amazonas, São Gabriel da Cachoeira	OP099485	ON932464	
Monopteryx angustifolia Spruce ex Benth.	*D.Cardoso 4264* (HUEFS)	Brazil, Amazonas, São Gabriel da Cachoeira	OP099473	ON932465	ON932484
Monopteryx inpae W.A.Rodrigues	*C.S.Carvalho 381* (RB)	Brazil, Amazonas, Manaus	OP099474		
Monopteryx inpae W.A.Rodrigues	*PPBio 622* (PPBIO)	Brazil, Amazonas, BR 319, Manaus-Porto Velho	OP099475		
Monopteryx uaucu Spruce ex Benth.	*D.Cardoso 4210* (HUEFS)	Brazil, Amazonas, São Gabriel da Cachoeira	OP099476		
Myrocarpus frondosus Allem.	*D.Cardoso 2204* (HUEFS)	Cultivated at Rio de Janeiro Botanic Garden	OP099455		
Pterodon abruptus (Moric.) Benth.	*D.Cardoso 3685* (HUEFS)	Brazil, Minas Gerais, Manga		ON932466	
Pterodon cipoensis C.S.Carvalho, H.C.Lima & D.B.O.S.Cardoso	*C.W.Fagg 2390* (UB)	Brazil, Minas Gerais, Jaboticatubas			ON932485

Table 1. Continued

Species	Voucher details, herbarium	Country, locality	GenBank ITS	GenBank *matK*	GenBank *trnL* intron
Pterodon cipoensis C.S.Carvalho, H.C.Lima & D.B.O.S.Cardoso	*C.W.Fagg 2400* (UB)	Brazil, Minas Gerais, Diamantina		ON932467	ON932486
Pterodon cipoensis C.S.Carvalho, H.C.Lima & D.B.O.S.Cardoso	*D.Neves 1438* (HUEFS)	Brazil, Minas Gerais, Diamantina			OQ032674
Pterodon emarginatus Vogel	*C.S.Carvalho 366* (RB)	Brazil, Maranhão, Caxias	OP099479		
Pterodon emarginatus Vogel	*D.Cardoso 3977* (HUEFS)	Brazil, Minas Gerais, Santana de Pirapama	OP099480		
Pterodon emarginatus Vogel	*K.Dexter 7229* (RB)	Bolivia, Santa Cruz, Santa Cruz			ON932487
Pterodon pubescens (Benth.) Benth.	*C.S.Carvalho 358* (RB)	Brazil, Distrito Federal, Brasília	ON932478		
Pterodon pubescens (Benth.) Benth.	*C.S.Carvalho 362* (RB)	Brazil, Distrito Federal, Brasília			ON932488
Pterodon pubescens (Benth.) Benth.	*C.S.Carvalho 363* (RB)	Brazil, Distrito Federal, Brasília	OP099478		
Taralea cordata Ducke	*H.C.Lima 7208* (RB)	Brazil, Amazonas, Barcelos	OP099481		
Taralea cordata Ducke	*H.C.Lima 7368* (RB)	Brazil, Amazonas, Barcelos	OP099482		
Taralea cordata Ducke	*H.C.Lima 7370* (RB)	Brazil, Amazonas, Barcelos	OP099483		
Taralea cordata Ducke	*H.C.Lima 7372 Ind 7* (RB)	Brazil, Amazonas, Barcelos	OP099487		
Taralea cordata Ducke	*H.C.Lima 7372 Ind 8* (RB)	Brazil, Amazonas, Barcelos	OP099488		
Taralea cordata Ducke	*H.C.Lima 7372 Ind 9* (RB)	Brazil, Amazonas, Barcelos	OP099489		
Taralea cordata Ducke	*H.C.Lima 7372 Ind 11* (RB)	Brazil, Amazonas, Barcelos	OP099490		
Taralea cordata Ducke	*H.C.Lima 7386* (RB)	Brazil, Amazonas, Barcelos	OP099484		
Taralea cordata Ducke	*H.C.Lima 7390* (RB)	Brazil, Amazonas, Novo Airão	OP099486		
Taralea cordata Ducke	*H.C.Lima 8175 Ind1* (RB)	Brazil, Roraima, Caracaí		ON932468	ON932489
Taralea cordata Ducke	*H.C.Lima 8175 Ind2* (RB)	Brazil, Roraima, Caracaí	OP099491		
Taralea cordata Ducke	*H.C.Lima 8175 Ind3* (RB)	Brazil, Roraima, Caracaí	OP099492		
Taralea cordata Ducke	*H.C.Lima 8175 Ind4* (RB)	Brazil, Roraima, Caracaí	OP099493		
Taralea cordata Ducke	*H.C.Lima 8175 Ind5* (RB)	Brazil, Roraima, Caracaí	OP099494		
Taralea cordata Ducke	*H.C.Lima 8175 Ind6* (RB)	Brazil, Roraima, Caracaí	OP099495		

Table 1. Continued

Species	Voucher details, herbarium	Country, locality	GenBank ITS	GenBank *matK*	GenBank *trnL* intron
Taralea cordata Ducke	*H.C.Lima 8175 Ind8* (RB)	Brazil, Roraima, Caracaí	OP099496		
Taralea cordata Ducke	*H.C.Lima 8175 Ind10* (RB)	Brazil, Roraima, Caracaí	OP099497		
Taralea cordata Ducke	*H.C.Lima 8175 Ind12* (RB)	Brazil, Roraima, Caracaí	OP099498		
Taralea cordata Ducke	*H.C.Lima 8175 Ind13* (RB)	Brazil, Roraima, Caracaí	OP099499		
Taralea cordata Ducke	*H.C.Lima 8175 Ind14* (RB)	Brazil, Roraima, Caracaí	OP099500		
Taralea cordata Ducke	*H.C.Lima 8175 Ind15* (RB)	Brazil, Roraima, Caracaí	OP099501		
Taralea cordata Ducke	*PPBIO 526* (PPBIO)	Brazil, Amazonas, BR 319, Manaus-Porto Velho	OP099503		
Taralea cordata Ducke	*PPBIO 2010* (PPBIO)	Brazil, Amazonas, BR 319, Manaus-Porto Velho	OP099502		
Taralea oppositifolia Aubl.	*H.C.Lima 7396* (RB)	Brazil, Amazonas, Novo Airão	OP099504		
Taralea rigida Schery *t*	*G.Martinelli 17278* (RB)	Brazil, Amazonas, Barcelos	OP099514		
Taralea rigida Schery	*H.C.Lima 7283 Ind1* (RB)	Brazil, Amazonas, Barcelos	OP099505		
Taralea rigida Schery	*H.C.Lima 7283 Ind2* (RB)	Brazil, Amazonas, Barcelos	OP099506		
Taralea rigida Schery	*H.C.Lima 7283 Ind3* (RB)	Brazil, Amazonas, Barcelos	OP099507		
Taralea rigida Schery	*H.C.Lima 7283 Ind4* (RB)	Brazil, Amazonas, Barcelos	OP099508		
Taralea rigida Schery	*H.C.Lima 7283 Ind5* (RB)	Brazil, Amazonas, Barcelos	OP099509		
Taralea rigida Schery	*H.C.Lima 7283 Ind6* (RB)	Brazil, Amazonas, Barcelos	OP099510		
Taralea rigida Schery	*H.C.Lima 7283 Ind7* (RB)	Brazil, Amazonas, Barcelos	OP099511		
Taralea rigida Schery	*H.C.Lima 7283 Ind8* (RB)	Brazil, Amazonas, Barcelos	OP099512		
Taralea rigida Schery	*H.C.Lima 7283 Ind10* (RB)	Brazil, Amazonas, Barcelos	OP099513		

described as taxonomically useful in the tribe (Ducke, 1940; Polhill, 1981a, b; Lewis *et al.*, 2005): leaf extrafloral nectary, leaf rachis, floral symmetry, flower architecture, lobe connation, lobe expansion, lobe orientation, fertile stamen number, stamen connation and fruit type [the morphology terminology followed Beentje (2010); see Supporting Information, Appendix S1]. All traits were equally weighted and coded as discrete bistate or unordered multistate characters. We used a stochastic character mapping approach (Huelsenbeck, Nielsen & Bollback, 2003), which employs the MCMC algorithm to sample character histories from their posterior probability distribution. The best fit model of character evolution [ER (equal rates), ARD (all different rates) or SYM (symmetrical)] was tested using the *fitDiscrete* function of the R package geiger (Harmon *et al.*, 2008). The best model selected by Akaike weights was used as input in the function *make.simmap* from the R

package phytools (Revell, 2012) to execute the character mappings with 1000 simulations (Appendix S2). The resulting trait-mapped phylogenetic trees were plotted with the R package ggtree (Yu *et al.*, 2017).

Divergence time estimation

Molecular divergence times were estimated from the combined (ITS/5.8S, *matK* and *trnL* intron) dataset using a Bayesian uncorrelated lognormal relaxed-clock model (Drummond *et al.*, 2006) implemented in BEAST v.1.8.2 (Drummond *et al.*, 2012), via the CIPRES Science Gateway. The BEAST analysis incorporated the same substitution models used in the phylogenetic reconstruction, a random starting tree and a Yule speciation process. To obtain absolute ages, lognormal prior age distributions were used on two fossil-calibrated nodes (Ho, 2007), and we chose a normal prior distribution to estimate ages from a comprehensive study of Fabaceae (Lavin, Herendeen & Wojciechowski, 2005). The root was calibrated at 55 Mya (offset = 55.0 mean = 0.0 and SD = 1.0) based on fossil flowers representing *Barnebyanthus* Crepet & Herendeen from the USA (Crepet & Herendeen, 1992; Herendeen & Wing, 2001). Fossil fruits and leaves of the south-eastern USA suggesting an affinity with *Swartzia* Schreb. (Herendeen, 1992) were used to set a calibration of 45 Mya (offset = 45.0, mean = 0.0 and SD = 1.0) for the crown node of Swartzieae (*sensu* Cardoso *et al.*, 2013a). The ADA clade was calibrated (mean = 50.8 Mya, SD = 3.8) according to the estimated ages of Lavin *et al.* (2005). The priors for the parameter ucld mean gamma were shape = 0.001 and scale = 1000. The BEAST running file was generated in BEAUTI v.1.8.2 (Drummond *et al.*, 2012), by enforcing the main lineages, Dipterygeae and each of the constituent genera, to be monophyletic, as strongly supported by the Bayesian combined analysis. Two independent MCMC runs of 100 000 000 generations were run, sampling parameters every 10 000 generations after a 10% burn-in period. Convergence and stationarity were checked with TRACER v.1.6 (Rambaut & Drummond, 2013), and all parameter estimates had ESS (effective sample size) values > 200. Independent runs were combined in LogCombiner, and the maximum clade credibility (MCC) tree was generated using the TreeAnnotator. The MCC tree was annotated as a chronogram with median ages and 95% highest posterior density (HPD) intervals of node ages and visualized with FIGTREE v.1.4.4.

RESULTS

Phylogenetic relationships from the individual molecular datasets

The individual Bayesian and ML analyses of ITS/5.8S (Fig. 2) and *matK* (Supporting Information, Appendix S3) sequence data showed Dipterygeae as a strongly supported monophyletic group [1.0 PP and 98 bootstrap support (BS) in the ITS tree; 0.99 PP and 99 BS in the *matK* tree], whereas the *trnL* intron dataset only weakly supported the clade (0.73 PP and 66 BS; Appendix S4). The sister relationship of Dipterygeae with regard to the remaining lineages of the ADA clade was not robustly resolved in any individual Bayesian and ML analyses, except for Bayesian analysis of the *trnL* intron. The monophyly of all genera of Dipterygeae (*Dipteryx*, *Monopteryx*, *Pterodon* and *Taralea*) was demonstrated with maximum support in almost all individual Bayesian and ML analyses, except for *Pterodon* in the analysis of *trnL* intron sequences. *Monopteryx* was clearly resolved as sister to all remaining Dipterygeae genera in the analyses of ITS/5.8S (1.0 PP and 98 BS) and *matK* (1.0 PP and 76 BS), but only poorly supported with the *trnL* intron dataset. *Taralea* appeared as sister to the *Dipteryx* + *Pterodon* clade with maximum support values in all individual analyses, except with the ITS/5.8S dataset (0.83 PP and 74 BS). The sister relationship between *Dipteryx* and *Pterodon* was clearly resolved in all individual analyses, except in the *trnL* intron analysis.

Phylogenetic relationships from combined nuclear and plastid data

In the combined analyses, all species currently known for the genera of Dipterygeae were sampled, except for some *Taralea* spp. The Bayesian and ML analyses with these combined DNA sequences did not show any decrease in the support values that could stem from putative incongruence among partitions. Rather, they strongly resolved not just the monophyly and sister relationship of Dipterygeae with Amburaneae (0.97 PP and 90 BS), but also the monophyly and inter-relationships of all constituent genera of Dipterygeae. Again, *Monopteryx* appeared as sister to the remaining genera (1.0 PP and 99 BS), and *Taralea* received maximum support values as sister to the strongly supported clade comprising *Dipteryx* and *Pterodon* (Fig. 3).

Leaf, flower and fruit evolution

For the ancestral state estimation, SYM and ER were the models that best fitted the data and were used to perform the stochastic mappings (Supporting Information, Appendix S2). The ancestral state estimation of morphological characters (Figs 5–9) showed that the most recent common ancestor (MRCA) of Dipterygeae probably had leaflets > 5 cm long, whereas smaller leaflets, < 5 cm long, evolved as a synapomorphy of *Pterodon*, and also arose independently in one *Taralea* sp. (Fig. 5A). The

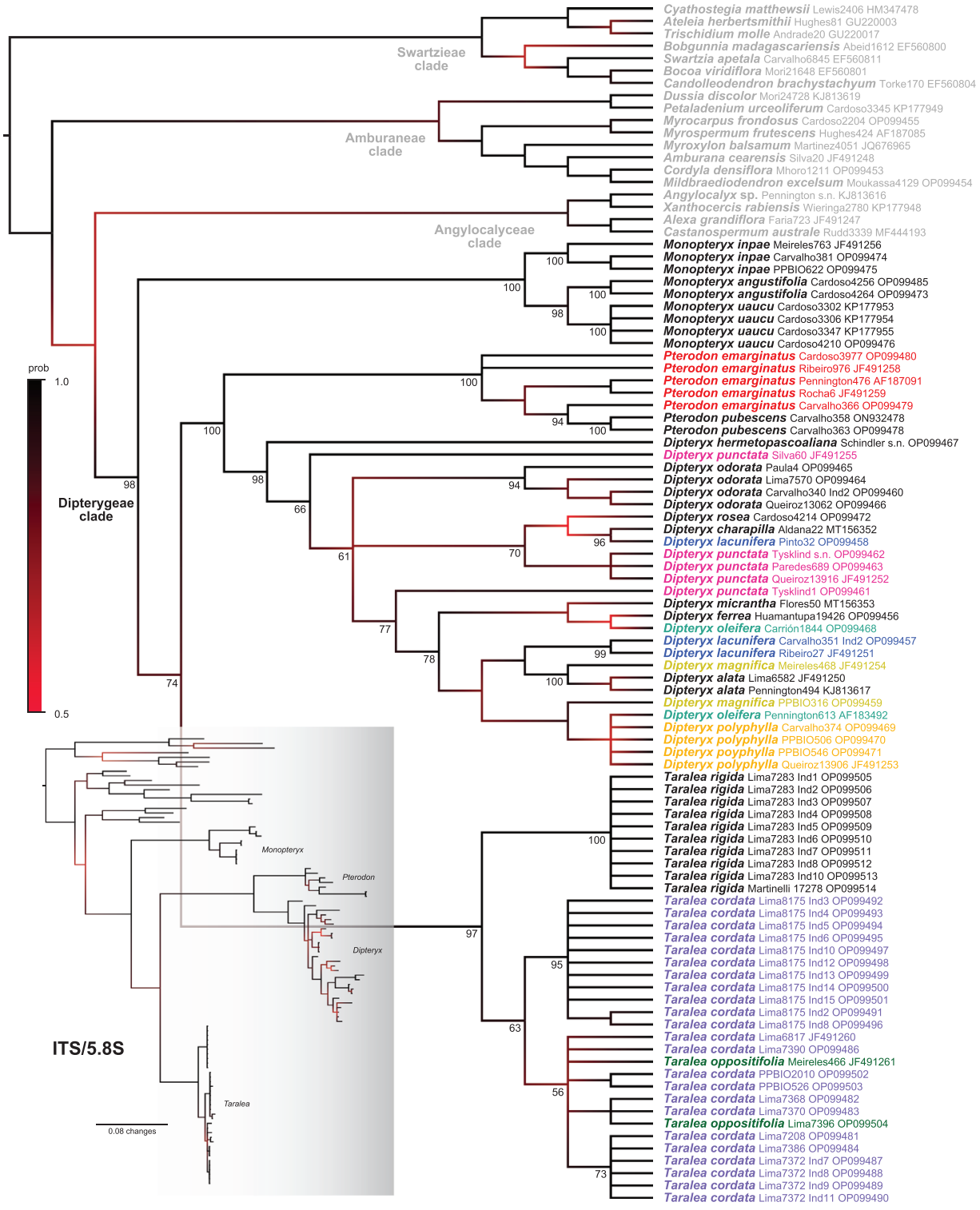

Figure 2. Majority-rule consensus tree derived from a Bayesian analysis of 97 ITS/5.8S accessions of the early-branching papilionoids, with a focus on Dipterygeae. Representative outgroups from Swartzieae, Angylocalyceae and Amburaneae were also comprehensively sampled and are shown in grey. The phylogram is presented on the left; branches in black are those supported by a posterior probability of 0.99–1.0, and the weakly supported branches are shown with a red gradient. The cladogram shows the multiple accessions of the species of Dipterygeae, and numbers below the branches are likelihood bootstrap support values. Accessions with the same non-black colour represent non-monophyletic species, probably due to incomplete lineage sorting. GenBank accession numbers are provided after taxon names.

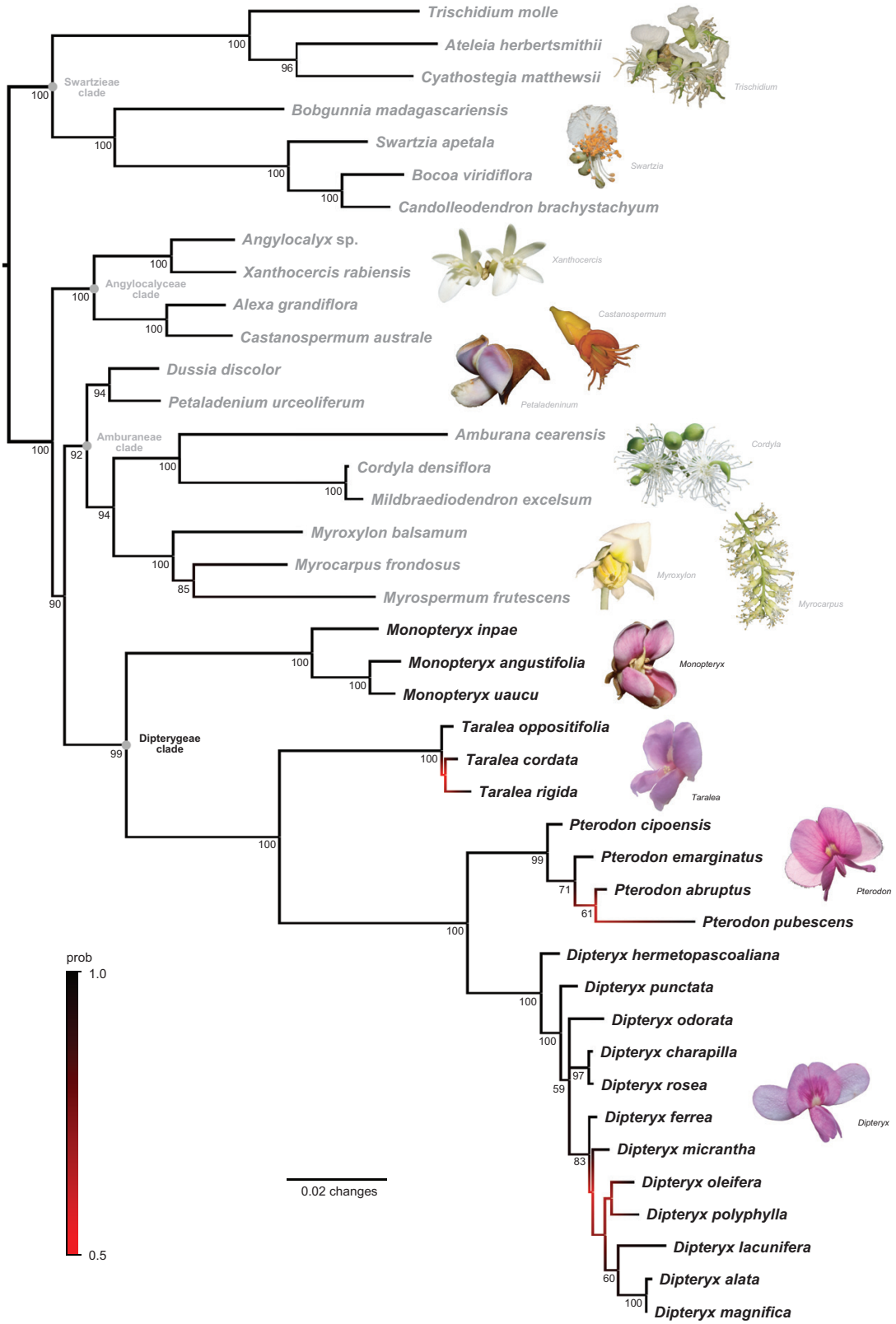

Figure 3. Majority-rule consensus phylogram derived from the combined nuclear (ITS/5.8S) and plastid (*matK* and *trnL* intron) Bayesian analysis of 41 accessions showing relationships among Swartzieae and Angylocalyceae, Dipterygeae and Amburaneae (ADA clade) (*sensu* Cardoso *et al.*, 2012a, 2013a). Representative sequences from Swartzieae and the ADA

MRCA of Dipterygeae had a terete leaf rachis, which shifted independently twice to flattened rachis in *Taralea* and *Dipteryx* (Figs 1D–E, 5B). The MRCA of Dipterygeae probably did not have winged papilionate flowers, but then this floral architecture arose and was evolutionarily maintained with the origin and diversification of *Taralea*, *Dipteryx* and *Pterodon*. (Figs 1G–J, 6A). Although *Monopteryx* does not have a papilionate floral architecture consisting of strongly differentiated petals enclosing the reproductive organs, its flowers are nevertheless bilaterally symmetrical, just as with those of the MRCA of Dipterygeae and extant genera of almost all lineages of the early-branching papilionoids analysed here; the typical radially symmetrical flowers evolved independently only in Swartzieae, Angylocalyceae and Amburaneae (Figs 1G–J, 6B). Reconstruction of the evolution of upper lobe expansion showed that expanded upper lobes evolved as an unequivocal synapomorphy of the Dipterygeae clade, a feature that is shared for all genera and without any example of secondary loss (Figs 1G–J, 7A). Like the majority of the papilionate-flowered lineages, all genera of Dipterygeae have the typical free upper calyx lobes (Figs 1G–J, 7B), except for *Monopteryx*, which is uniquely marked by apomorphic fused upper calyx lobes (Figs 1H, K, 7B). The MRCA of Dipterygeae had standard-oriented upper calyx lobes (Fig. 8A), like most Papilionoideae with strongly papilionate flowers. Such an orientation hides the upper calyx lobes on the back of the standard petal, even in *Monopteryx* and *Taralea*, in which they are greatly enlarged (Fig. 1G–J). This state, however, has shifted to the unique wing-oriented upper calyx lobes as synapomorphic for the clade comprising *Dipteryx* and *Pterodon*, where the expanded, petaloid lobes are not hidden by the standard petal and resemble the wing petals (Figs 1G–J, 8A). The dehiscent legume of the earliest-divergent *Monopteryx* and *Taralea* is plesiomorphic, but then the cryptosamara and drupe evolved later as synapomorphies of *Pterodon* and *Dipteryx*, respectively (Figs 1L–O, 8B). The ancestral state for stamen number in Dipterygeae was reconstructed as ten (Fig. 9A), which is in fact a plesiomorphic state because it has evolved earlier in the MRCA of the entire ADA clade. The MRCA of Dipterygeae was inferred as having free stamens, which was retained in *Monopteryx*, but then it changed into connate stamens as a synapomorphy for the clade including all remaining genera of Dipterygeae (Fig. 9B).

Divergence times

Divergence time analysis (Fig. 4; Table 2) showed that the Dipterygeae clade arose *c.* 46.10 Mya (52.99–38.59 HPD) and its MRCA started to diversify during the Middle Eocene *c.* 39.48 Mya (47.85–30.54 HPD), when the earliest-diverging genus *Monopteryx* also originated. Diversification in *Monopteryx* started only later *c.* 15.18 Mya (27.23–6.02 HPD). *Taralea* is the second most ancient Dipterygeae genus, having arisen during the Early Oligocene *c.* 29.77 Mya (38.33–20.88 HPD), but its long stem branch led to a more recent Pliocene radiation of the extant species only since 4.39 Mya (9.92–1.23 HPD). *Dipteryx* and *Pterodon* diverged from each other during the Early Miocene *c.* 20.01 Mya (28.00–13.03 HPD), but their MRCAs started to diversify *c.* 12.97 Mya (19.37–7.95 HPD) and 9.08 Mya (16.29–3.52 HPD), respectively.

DISCUSSION

Monophyly of the genera of Dipterygeae as supported by morphology and molecular data

Previous phylogenetic analyses of the early-branching Papilionoideae only sampled densely within *Dipteryx* only (e.g. Cardoso *et al.*, 2012a, 2015), thus leaving unanswered the generic identity or monophyly of all constituent genera of Dipterygeae. Here, by newly sampling almost all morphologically key, poorly collected and phylogenetically unplaced species of Dipterygeae, such as *Dipteryx charapilla*, *D. lacunifera*, *D. hermetopascoaliana*, *Pterodon cipoensis* and *Monopteryx angustifolia*, we were able to strongly demonstrate the monophyly of the currently recognized genera in the clade (Fig. 3). The geographically confined Amazonian *Monopteryx* was confirmed here as the earliest diverging genus of Dipterygeae (Fig. 3; Cardoso *et al.*, 2012a). Its non-papilionate flowers with the two upper calyx lobes almost completely fused and free stamens were used to place *Monopteryx* in the *Dussia* group of the traditional circumscription of Sophoreae (Polhill, 1981a; Pennington, Stirton & Schrire, 2005). However, the molecular and morphological data strongly support the unequivocal placement of *Monopteryx* as sister to the remaining genera of Dipterygeae, with which it shares bilaterally symmetrical (=zygomorphic) flowers, expanded upper calyx lobes and a fixed number of ten stamens (Figs 6, 7, 9).

clade used as outgroups are shown in grey. Numbers below the branches are likelihood bootstrap support values; branches in black are those supported by a posterior probability of 1.0, and the weakly supported branches are shown with a red gradient. The diversity of flowers among the genera of Swartzieae, Angylocalyceae, Dipterygeae and Amburaneae are highlighted by photographs. Photographs: *Castanospermum*, *Dipteryx*, *Monopteryx*, *Myrocarpus*, *Myroxylon*, *Petaladenium*, *Pterodon*, *Trischidium* and *Swartzia* by D. Cardoso; *Cordyla* and *Xanthocercis* by F. Ratovoson; *Taralea* by H. C. Lima.

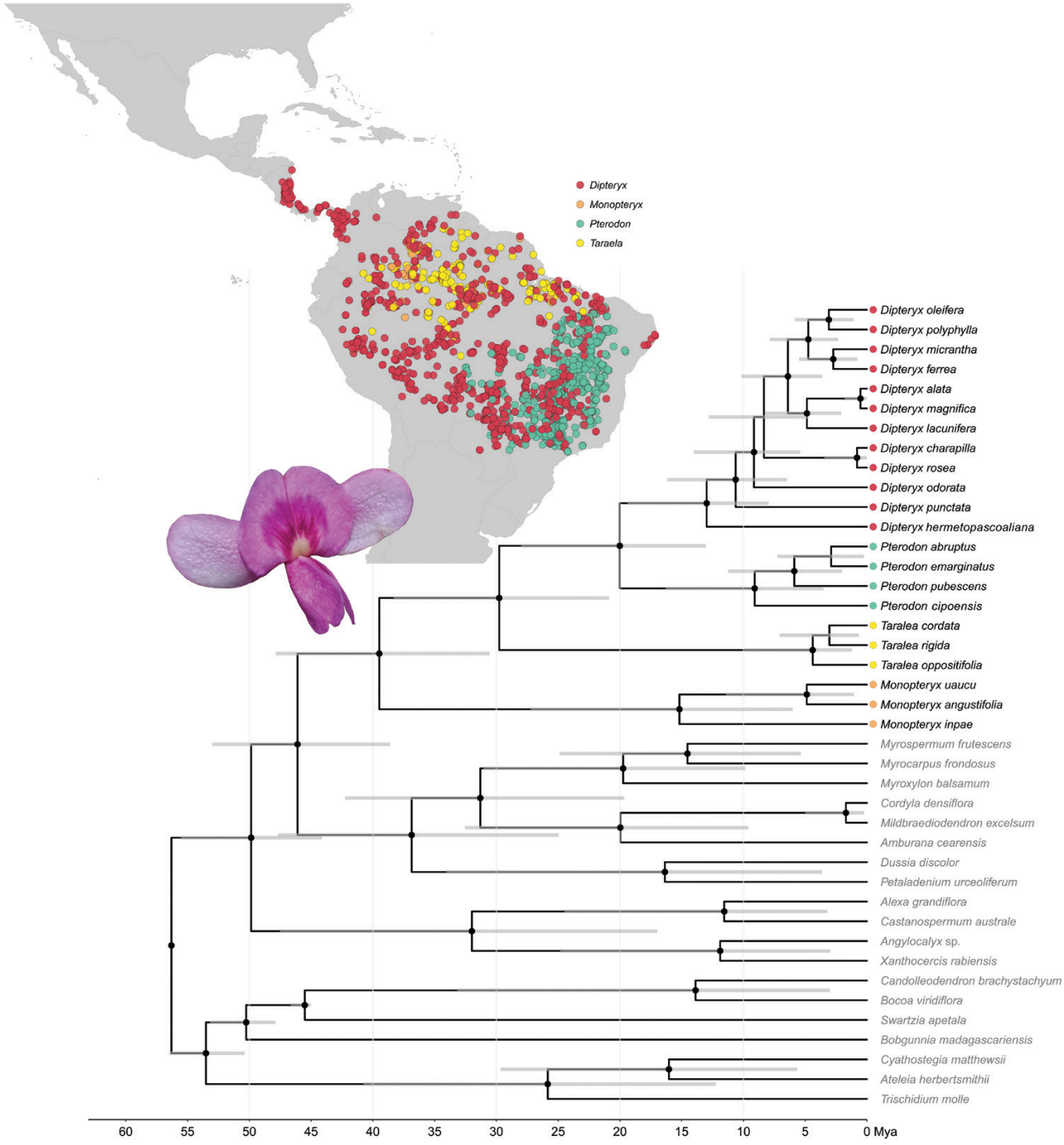

Figure 4. BEAST-derived chronogram of Dipterygeae (*Dipteryx*, *Monopteryx*, *Pterodon* and *Taralea*) and related early-branching papilionoid lineages as estimated from the combined nuclear (ITS/5.8S) and plastid (*matK* and *trnL* intron) DNA sequence data. Light grey bars on the nodes represent 95% of the high posterior density of divergence times. The map shows the distribution of all genera of Dipterygeae in the Neotropics.

As such, the previous view on the great importance given to the highly plesiomorphic free stamens (Fig. 9B) to genera of Sophoreae (Polhill, 1981a, 1994) is again shown here to hold no signal for indicating true evolutionary relationships in the context of the early diversification of Papilionoideae. The floral ontogeny of all genera of Dipterygeae except *Monopteryx* has already been described in detail (Leite *et al.*, 2014). Although we have revealed here the homology in some floral traits between *Monopteryx* and remaining

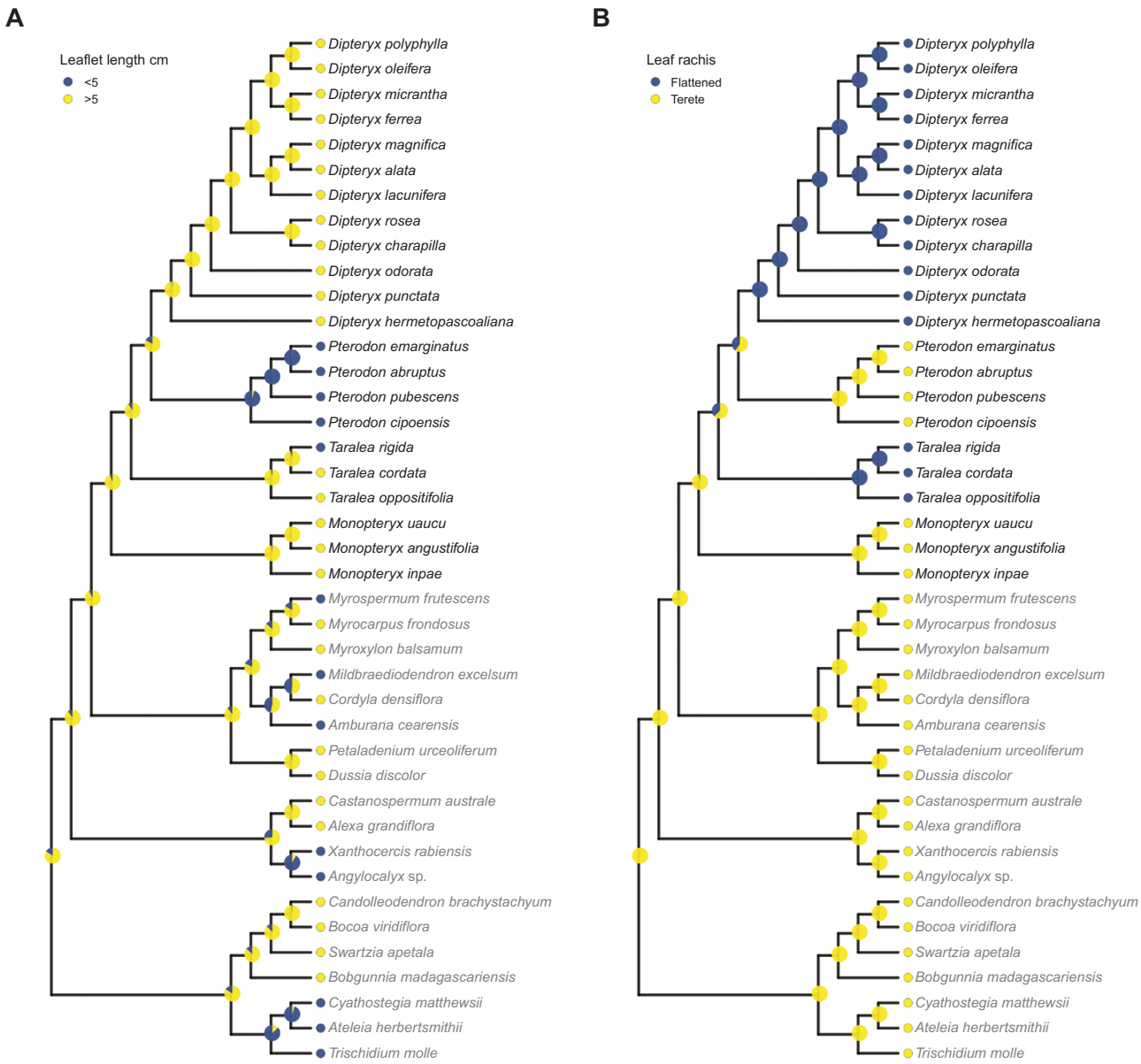

Figure 5. Posterior probabilities of character states derived from stochastic mapping of A, leaflet length (cm) and B, leaf rachis over a Bayesian majority-rule consensus tree of Dipterygeae.

Dipterygeae, despite their contrasting general flower architecture (Fig. 1G–J; Cardoso *et al.*, 2012a), a complete ontogenetic characterization of *Monopteryx* would help us to understand where and how in early development flowers in the genus greatly deviated.

Taralea and *Dipteryx* have a historical taxonomic confusion (e.g. Schreber, 1791; Bentham, 1860), because of their shared papilionate flowers with enlarged upper calyx lobes, fused ten stamens and sympatry of some Amazonian species. Individual and combined analyses of nuclear and plastid DNA sequences (Fig. 3; Cardoso *et al.*, 2015) and a plastid phylogenomic analysis (Choi *et al.*, 2022) have demonstrated strongly that they are not sister clades. *Taralea* has accumulated several plesiomorphic features that help to easily distinguish it from *Dipteryx*: the enlarged upper calyx lobes oriented behind the standard petal and the elastically dehiscent legume (Ducke, 1940; Polhill, 1981b; Kirkbride *et al.*, 2003; Leite *et al.*, 2014; Pinto *et al.*, 2014). Despite the recent radiation of *Taralea* since *c.* 4.9 Mya (Fig. 4; Table 2) largely associated with periodically floodable riverine vegetation, high mountaintops of the Guyana shield and white-sand Amazonian forests, it is an open question why the genus remained with a long stem

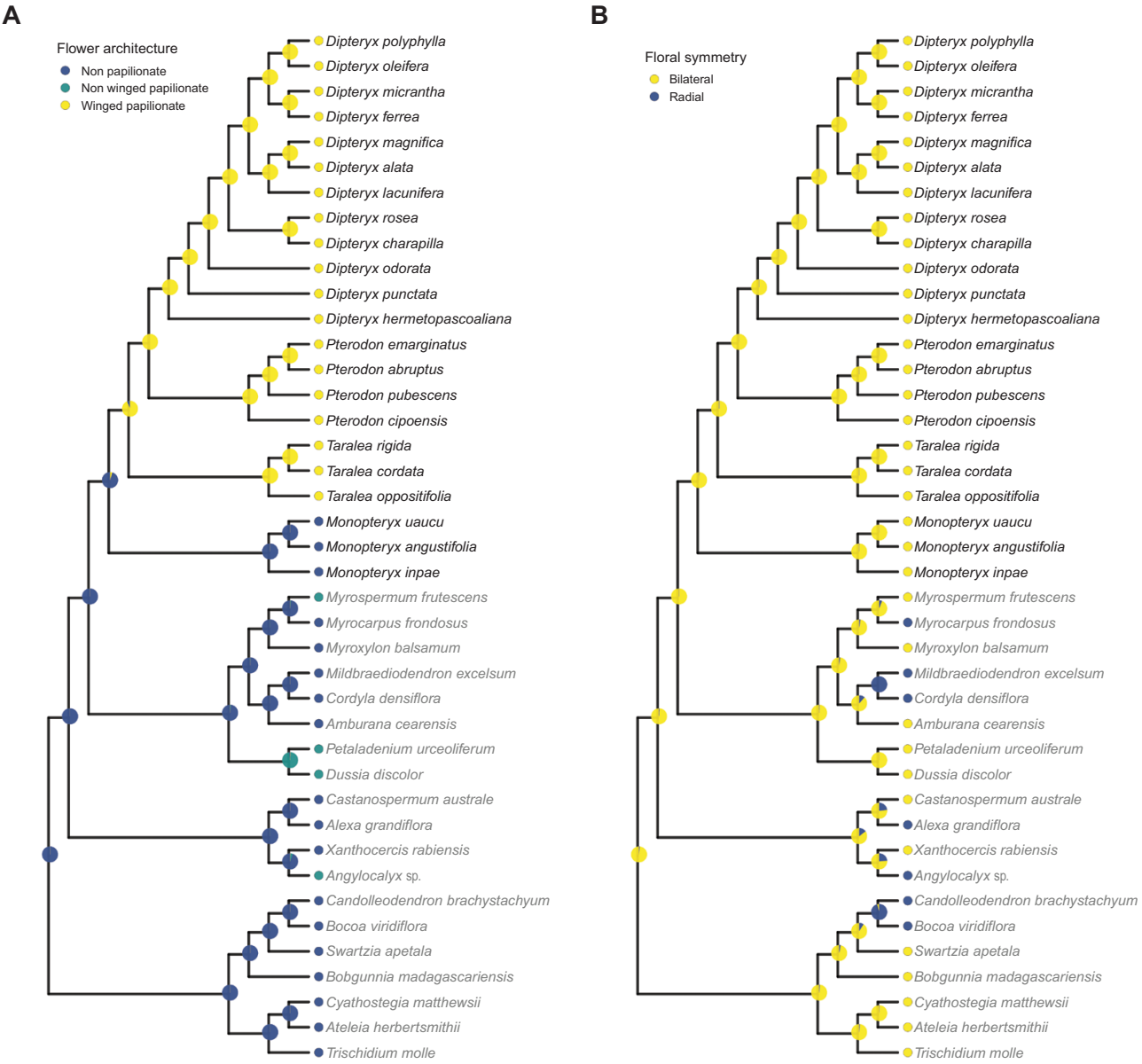

Figure 6. Posterior probabilities of character states derived from stochastic mapping of A, flower architecture and B, floral symmetry over a Bayesian majority-rule consensus tree of Dipterygeae.

branch since it diverged nearly 30 Mya from the MRCA of the *Dipteryx* + *Pterodon* clade. Given the greater predilection of most Amazonian species of Dipterygeae for the more ancient upland terra-firme rain forests (Burnham & Johnson, 2004; Hoorn *et al.*, 2010), the MRCA of the entire clade might have originated and flourished initially in such settings. This suggests that early ancestors of *Taralea* might have experienced a long biogeographical history in terra-firme forests before the extant species originated by habitat specialization. For example, the availability of the more recent archipelago of disjunct patches of white-sand habitats across the Amazon basin (Richards, 1941; Adeney *et al.*, 2016) might have opened new niches for the evolution of some extant *Taralea* spp. Although speciation by habitat specialization has been recurrent in Amazonian white-sand-affiliated plant lineages (Fine *et al.*, 2010; Fine & Baraloto, 2016; Guevara *et al.*, 2016; Capurucho *et al.*, 2020), a more detailed biogeographical investigation of biome switches and conservatism during the diversification of the Dipterygeae clade will be helpful to address such questions.

Even though *Dipteryx* and *Taralea* have been historically taxonomically associated, and indeed are still largely misidentified among herbarium

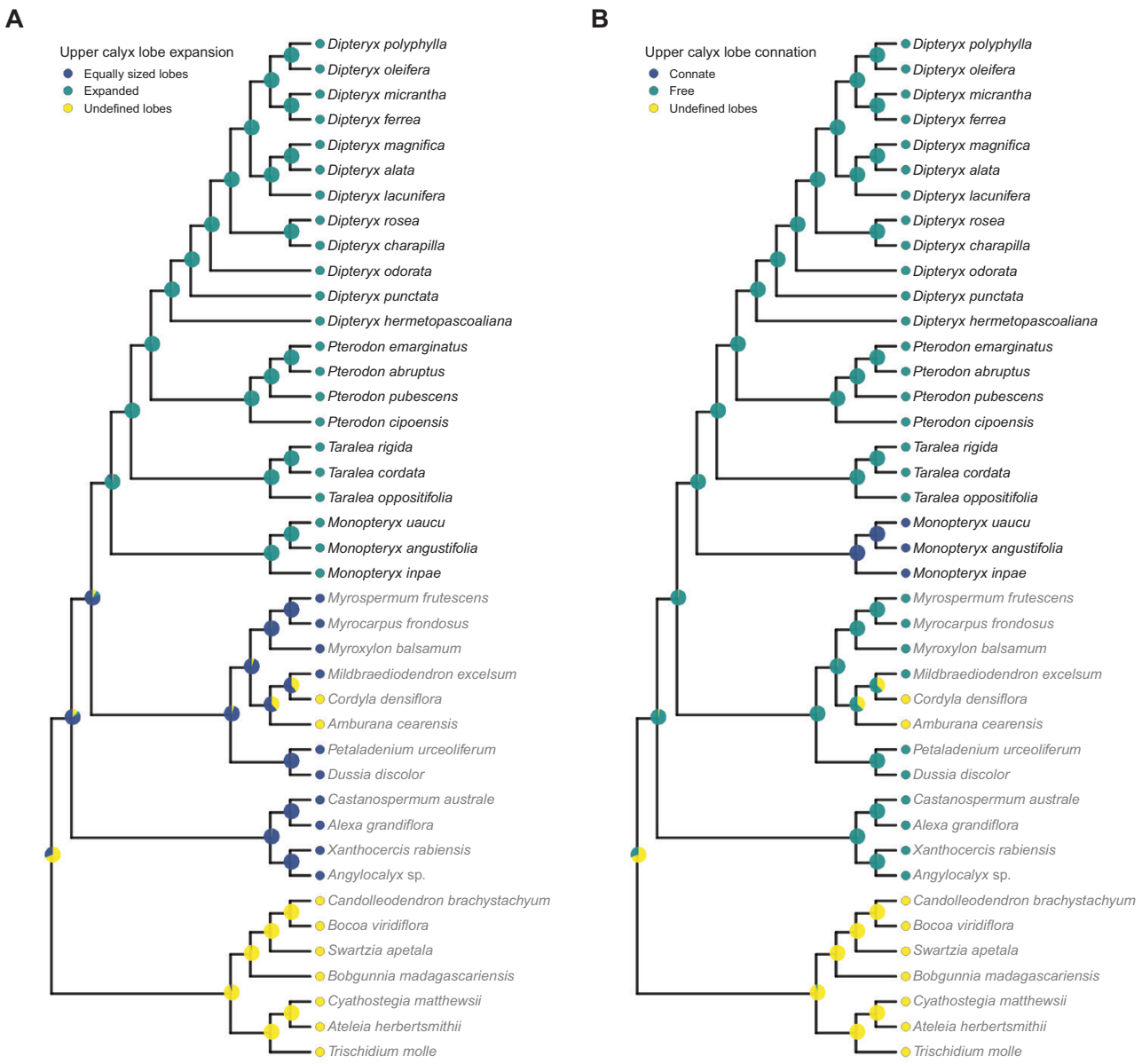

Figure 7. Posterior probabilities of character states derived from stochastic mapping of A, upper calyx lobe expansion and B, upper calyx lobe connation over a Bayesian majority-rule consensus tree of the Dipterygeae.

collections, the sister relationship of *Dipteryx* with *Pterodon* is strongly supported. This clade is marked by remarkable morphological synapomorphies [the upper lobes of the calyx in their papilionate flowers that are expanded and oriented to assume a wing-like shape (Figs 1G, I, 8A) and their shared indehiscent fruits (Fig. 8B)], although in each genus they are particularly distinct and recovered as synapomorphies, that is ovoid to fusiform drupes in *Dipteryx* and flattened cryptosamara in *Pterodon* (Figs 1L, N, 8B). The *Dipteryx* clade comprises 12 known species and has greatest diversity in the Neotropical rain forests. Only two species are widespread in other South America formations: savannas and SDTFs (C. S. Carvalho *et al.*, unpubl. data). The single savanna-affiliated species *Dipteryx alata* Vogel has been ecologically very successful, as observed by its widespread distribution all over central Brazil and western Bolivia, where it has been listed among the most dominant tree species (Ratter *et al.*, 2006). Likewise, the small genus *Pterodon*, consisting of only four species of medium-sized trees,

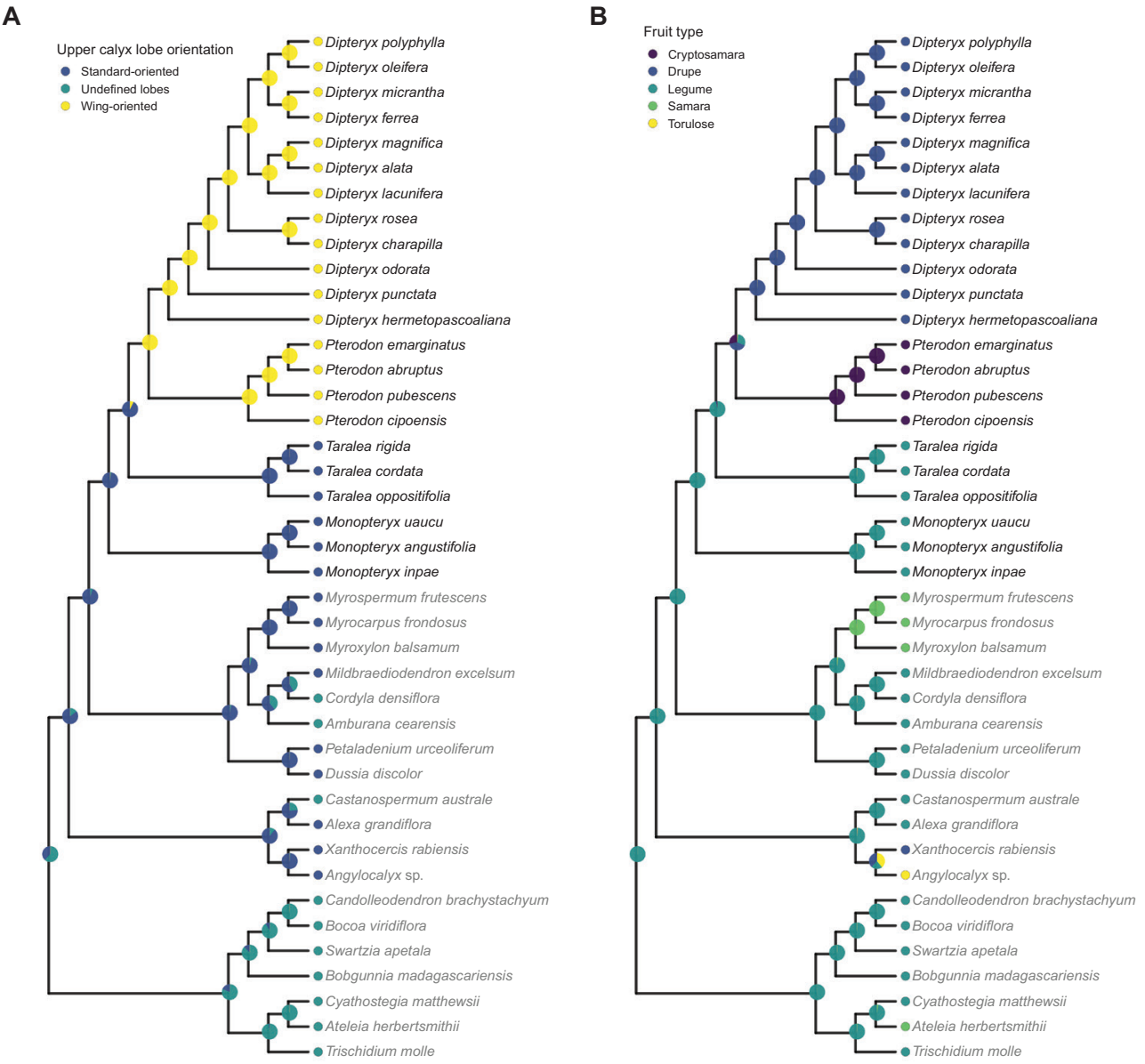

Figure 8. Posterior probabilities of character states derived from stochastic mapping of A, upper calyx lobe orientation and B, fruit type over a Bayesian majority-rule consensus tree of Dipterygeae.

has widely colonized the South American savannas and SDTFs (Ratter *et al.*, 2006; Carvalho, Cardoso & Lima, 2020; Carvalho *et al.*, 2022a).

All genera of Dipterygeae except *Monopteryx* included non-monophyletic species in the ITS/5.8S phylogenetic analysis that was densely sampled with multiple accessions (Fig. 2). The non-monophyly and recency of species have been found as common patterns in tree clades largely confined to Amazonian rain forests and savannas (Richardson *et al.*, 2001; Cardoso *et al.*, 2012c, 2013b; Pennington & Lavin, 2016). In contrast, monophyletic tree species with old stem ages are generally found in SDTF-confined clades (Pennington *et al.*, 2010; Queiroz & Lavin, 2011; Pennington & Lavin, 2016). The contrasting ecology in terms of dispersal limitation or successful immigration, niche conservatism and disturbance in these evolutionarily distinct Neotropical biomes are argued to explain the distinct nature of species in DNA-sequence-based phylogenetic trees (Pennington & Lavin, 2016). Whether the phylogenetic patterns of monophyly and paraphyly of species are biome-specific (Pennington & Lavin, 2016) or lineage-specific, as evidenced by recent counter-examples from dry-forest-inhabiting paraphyletic species such as in *Ceiba* Mill. (Pezzini *et al.*, 2021), *Luetzelburgia* Harms (Cardoso *et al.*, 2013b)

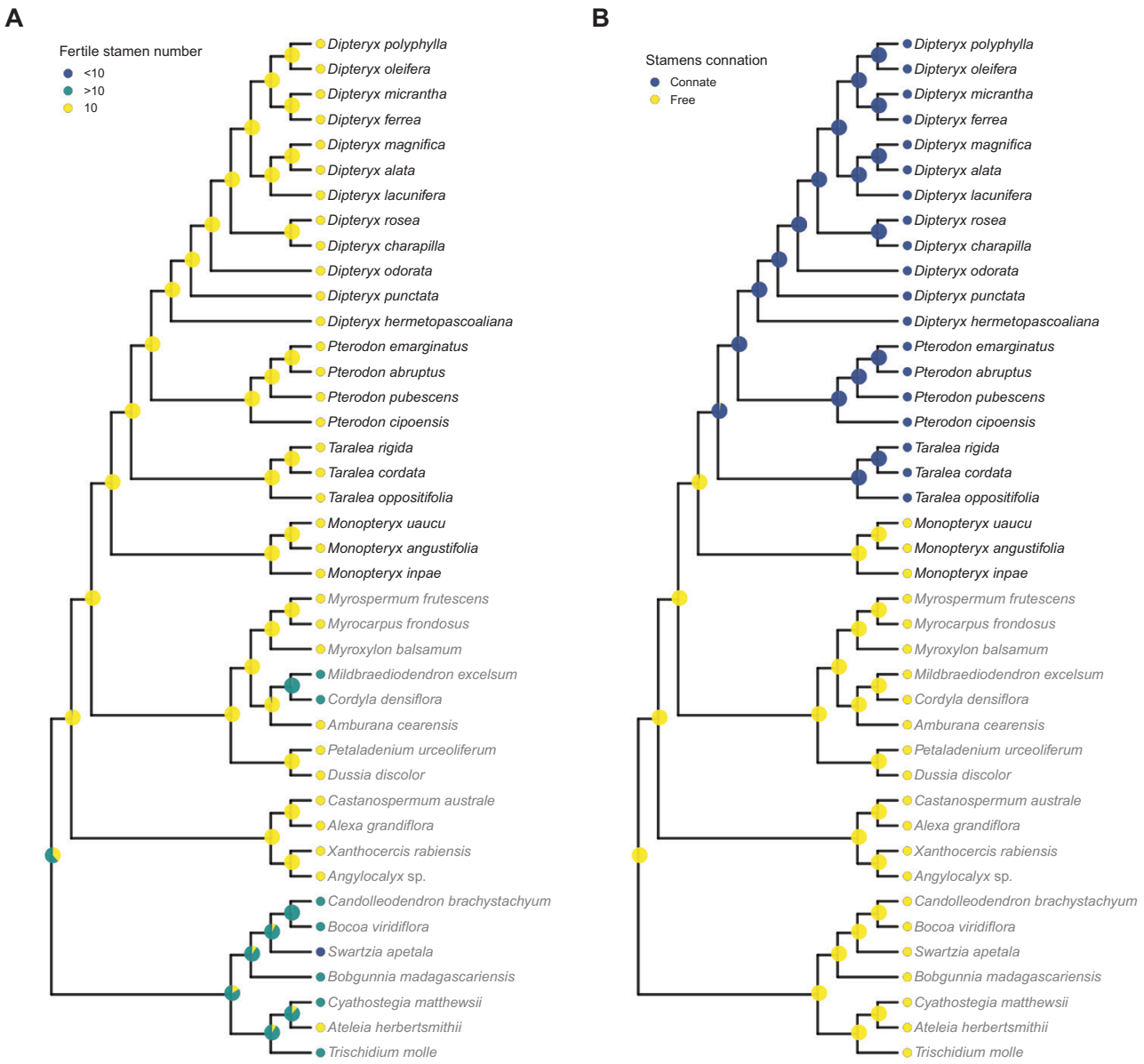

Figure 9. Posterior probabilities of character states derived from stochastic mapping of A, fertile stamen number and B, stamen connation over a Bayesian majority-rule consensus tree of Dipterygeae.

and *Dipteryx lacunifera*, or the rain-forest-inhabiting monophyletic *Monopteryx* spp. (Fig. 2), suggests that there are more complex underlying ecological and evolutionary processes constraining the phylogenetic nature of plant species across Neotropical biomes.

Evolutionary conservatism of winged papilionate flowers in Dipterygeae greatly contrasts with floral architectures across papilionoids

Almost all genera branching off at the earliest nodes of the phylogenetic tree of Papilionoideae each have their own set of floral traits that make up some of the most singular floral architectures in the subfamily. During their diversification history, high evolutionary lability in flower architecture has involved drastic changes in flower symmetry, calyx entirety and shape, petal number, and fusion and number of stamens (Fig. 3; Pennington *et al.*, 2000; Cardoso *et al.*, 2013a). Flowers of Papilionoideae to some degree mirror the early floral evolution of the angiosperms, in which virtually all early-branching families have a unique flower architecture (Endress, 1996; Sauquet *et al.*, 2017). In contrast, we have reported here a remarkable ancient

Table 2. Mean estimated ages and 95% confidence interval (HPD) bounds for nodes of the phylogeny of Dipterygeae referred to in the text, Figure 3 and in the BEAST chronogram with three calibrations: 55 Mya (offset = 55.0 mean = 0.0 and SD = 1.0) for root; 45 Mya (offset = 45.0, mean = 0.0 and SD = 1.0) for the crown node of Swartzieae; and 50.8 Mya (SD = 3.8) for the crown node of Dipterygeae

Node	Mean age (Mya)	HPD (Mya)
Dipteryx stem	20.01	28.00–13.03
Dipteryx crown	12.97	19.37–7.95
Pterodon stem	20.01	28.00–13.03
Pterodon crown	9.08	16.29–3.52
Taralea stem	29.77	38.33–20.88
Taralea crown	4.39	9.92–1.23
Monopteryx stem	39.48	47.85–30.54
Monopteryx crown	15.18	27.23–6.02
Dipteryx + *Pterodon* stem	29.77	38.33–20.88
Dipteryx + *Pterodon* crown	20.01	28.00–13.03
Taralea + *Pterodon* + *Dipteryx* stem	39.48	47.85–30.54
Taralea + *Pterodon* + *Dipteryx* crown	29.77	38.33–20.88
Dipterygeae stem	46.10	52.99–38.59
Dipterygeae crown	39.48	47.85–30.54

floral conservatism since nearly 30 Mya involving the stability of the winged papilionate flowers with fused stamens that underlines the radiation of three genera in the Dipterygeae clade (Fig. 3). Despite the inter-relationships between Swartzieae, the ADA clade and the remainder of the Papilionoideae still needing further resolution (Zhao *et al.*, 2021; Choi *et al.*, 2022), unveiling the most likely ancestral flower of Papilionoideae will not change our general conclusion on the evolutionary conservatism of the wing-shaped floral architecture in Dipterygeae.

Traditionally, the atypical floral morphologies in Papilionoideae were considered plesiomorphic and used to recognize members of the most 'primitive' tribes such as the Swartzieae and Sophoreae (Polhill & Raven, 1981c; Polhill, 1994). Since the first molecular studies with a focus on early-branching Papilionoideae, the above hypothesis was questioned, with wide taxonomic implications (e.g. Doyle *et al.*, 1997; Ireland, Pennington & Preston, 2000; Pennington *et al.*, 2000; Cardoso *et al.*, 2012a, 2013a, 2015; LPWG, 2013). The mostly radially symmetrical non-papilionate flowers with free stamens and undifferentiated petals that are found in Swartzieae and the ADA clade (Fig. 3), and in Exostyleae, genistoids, dalbergioids and Baphieae, probably reversed from papilionate forms multiple times in the subfamily (Pennington *et al.*, 2000; Cardoso *et al.*, 2013b). Such great floral diversity is also associated with varying floral syndromes and largely coincides with the rapid radiation during the rise of Papilionoideae (Lavin *et al.*, 2005; Cardoso *et al.*, 2013a; Choi *et al.*, 2022).

Ecological conditions may explain the floral conservatism described here in Dipterygeae. Indeed, the persistence of the markedly enlarged calyx genera in Dipterygeae may be related to the protection of the young buds during flower development, assuring their reproductive success. In earlier stages, the developing young flower buds (Fig. 1G) are protected by secretory canals (Leite *et al.*, 2014). In mature stages, the calyx persists after pollination and encloses and shuts the young fruit until total maturation (C. S. Carvalho *et al.*, unpubl. data). The calyx marcescence indicates that they may be co-opted for novel functions unrelated to pollination (Herrera, 2011). The calyx appears to provide heat to the fruit or protect it from herbivory by the larvae that feed from seeds in enclosed fruits (Sisterson & Gould, 1999; Herrera, 2010, 2011; Ida & Totland, 2014; Yongqian *et al.*, 2019). However, studies have not always indicated immediate adaptive value to the calyx persistence (Yonemori, Hirano & Sugiura, 1995; Nakano, Yonemori & Sugiura, 1997; Sisterson & Gould, 1999).

Some pollination studies (Perry & Starret, 1980; Martins & Batalha, 2007; Oliveira & Sigrist, 2008) reported that bees are the first pollinators of *Dipteryx* and *Pterodon*. With some exceptions, Fabaceae are mainly bee-pollinated, with the syndrome being more highly developed in Papilionoideae with truly papilionate flowers (Arroyo, 1981; Pennington *et al.*, 2000). According to Pennington *et al.* (2000) and Cronk & Möller (1997), the pressure to attract different pollinators or the lack of specialist pollinators may favour rapid evolution, as found in the early-branching Papilionoideae. In contrast, the winged papilionate flowers of Dipterygeae remained stable, perhaps explained mainly by their tight association with bee pollination.

Although the evolution of floral symmetry and architecture in Dipterygeae has been largely conserved, fruit evolution underwent remarkable morphological shifts across genera (Fig. 8B). Fruits vary from typically dehiscent pods with or without crimped wing-like crests along the upper sutures to indehiscent drupes and cryptosamaras (e.g. Ducke, 1940; Gunn, 1981; Van der Pijl, 1982). The four morphologically distinct fruits distinguish the four genera of Dipterygeae and, with their patterns of dispersal and seedling establishment, may explain the relative ease with which species of Dipterygeae can achieve success in colonizing different environments in the Neotropics. *Dipteryx* spp. are known to disperse by barochory, hydrochory or

zoochory (Almeida, Silva & Ribeiro, 1990; Vieira-Jr. *et al.*, 2007; Pinto *et al.*, 2014; C. S. Carvalho *et al.*, unpubl. data), all of which are dispersal syndromes that confer success in rain forests ('terra-firme' and periodically flooded lands), savannas and seasonally dry forests. The exclusively rain-forest-inhabiting *Monopteryx* and *Taralea* present mostly ballistic dispersal with their elastically dehiscent pods (Van der Pijl, 1982), but zoochoric and hydrochoric secondary dispersal have also been recorded in *Taralea* (Pinto *et al.*, 2014; pers. obs.). *Pterodon* spp. occur in savannas and seasonally dry forests, and their flattened cryptosamaras are primarily associated with anemochory (Janzen, 1980; Barroso *et al.*, 1999). Studies of long-term performance of seedlings in Dipterygeae have only been conducted in the economically important *Dipteryx*, and thus there is little information available. The seedling performance of the Mesoamerican *Dipteryx panamensis* Record & Mell (=*Dipteryx oleifera* Benth.) was strongly related to the availability of light inside the forest (Steven, 1988), where the seeds must maintain their viability during the shaded period for proper development of the seedlings. The seeds of *Dipteryx* are extremely vulnerable to weathering (Botezelli, Davide & Malavasi, 2000), but short-term studies of the savanna-inhabiting *D. alata* showed that once the seeds are maintained inside the hard and woody endocarp they are protected from herbivory and environmental water ingress (Melhem, 1972; Corrêa, Rocha & Naves, 2000). Despite the scarcity of physiological studies in Dipterygeae, the hard endocarp of *Dipteryx* drupes probably protects the seeds from adverse environmental conditions and the seedlings are able to endure harsh environmental conditions until establishment of the young trees.

CONCLUSIONS AND FUTURE PROSPECTS

The four main lineages of Dipterygeae match the four genera that are currently recognized (*Dipteryx*, *Monopteryx*, *Pterodon* and *Taralea*). Our results corroborate previous molecular phylogenetic studies (Cardoso *et al.*, 2012a, 2013a, 2015) that have shown *Monopteryx* to be sister to the clade comprising the remaining traditionally recognized genera of Dipterygeae. Thus, the new concept of Dipterygeae must encompass *Monopteryx*, despite this genus having a distinct flower architecture. The evolutionary history of Fabaceae is marked by early-branching clades displaying great lability in floral morphology (e.g. Pennington *et al.*, 2000; Prenner & Klitgaard, 2008; Cardoso *et al.*, 2013a; Bruneau *et al.*, 2014; Prenner *et al.*, 2015; LPWG, 2017; Prenner & Cardoso, 2017). Papilionoideae (Fig. 3; Lavin *et al.*, 2001; Cardoso *et al.*, 2012a, 2013b; Ramos *et al.* 2016) are no exception, but the early-diverging Dipterygeae clade shows an incredible evolutionary conservatism in floral morphology. Although the ontogenetic study conducted by Leite *et al.* (2014) explored flower development of three genera of Dipterygeae (*Dipteryx*, *Pterodon* and *Taralea*), the non-winged papilionate-flowered *Monopteryx* deserves more detailed study to understand better floral homology and the evolutionary pathway that led to the striking winged papilionate floral conservatism in Dipterygeae. Furthermore, unveiling the floral shifts and conservatism in Dipterygeae will require a comparative study across Dipterygeae and related lineages in the ADA clade and Swartzieae that describe the patterns of gene expression that regulate floral development and identity (e.g. Citerne *et al.*, 2000, 2003, 2006; Theissen, 2001; Feng *et al.*, 2006; Zhang *et al.*, 2010; Sinjushin & Karasyova, 2017). In addition, it is important to study floral biology, which could reveal the roles of the unique calyx shape of Dipterygeae, including the marcescence that encloses the developing fruits (e.g. Herrera, 2011). In contrast to the conservatism in floral traits, the fruits of Dipterygeae show high evolutionary lability in their morphologies, which is hypothesized here to explain why species of Dipterygeae have attained such a wide distribution across the main Neotropical biomes.

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AUTHOR CONTRIBUTIONS

C.S.C., H.C.L. and D.C. conceived the project. C.S.C., H.C.L., D.C., C.E.Z., C.R.G.D., E.N.H.C., K.P.V. and N.T. collected specimens in the field or contributed tissue samples. D.C., H.C.L., M.R.L., C.vdB. and M.M. contributed reagents. C.S.C., M.M. and D.C. obtained DNA sequences. C.S.C. and D.C. performed all analyses and prepared figures. C.S.C. and D.C. wrote the paper, and incorporated comments from all other co-authors.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher's website.

Appendix S1. Matrix of morphological characters and associated states that was used in the stochastic mapping estimations across a phylogenetic tree of the early-branching lineages of Papilionoideae with a focus on Dipterygeae (*Dipteryx*, *Monopteryx*, *Pterodon* and *Taralea*). The clades are in accordance with the combined analysis of ITS/5.8S, *matK* and *trnL* intron DNA sequences (see also Fig. 3). The morphology terminology followed Beentje (2010) and taxonomic studies of Fabaceae for specific terms.

Appendix S2. AICc values of evolutionary models from the tests to find which of the evolutionary models best fitted the data for the stochastic estimations. ER (equal rates), ARD (all different rates), SYM (symmetrical).
Appendix S3. A *matK*-based majority-rule consensus tree derived from a Bayesian analysis of 61 accessions of the earliest-branching papilionoid clades, with a focus on Dipterygeae. Representative outgroups from Swartzieae and from Amburaneae and Angylocalyceae of the ADA clade were also comprehensively sampled and are shown in grey. Branches in black are those supported by a posterior probability of 0.99–1.0, whereas the weakly supported branches are shown in red gradient; numbers below branches are likelihood bootstrap support values. GenBank accession numbers are provided after taxon names.
Appendix S4. A *trnL*-based majority-rule consensus tree derived from a Bayesian analysis of 61 accessions of the earliest-branching papilionoid clades, with a focus on Dipterygeae. Representative outgroups from Swartzieae and from Amburaneae and Angylocalyceae of the ADA clade were also comprehensively sampled and are shown in grey. Branches in black are those supported by a posterior probability of 0.99–1.0, whereas the weakly supported branches are shown in red gradient; numbers below branches are likelihood bootstrap support values. GenBank accession numbers are provided after taxon names.