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Re-delimitation of *Tinospora* (Menispermaceae): Implications for character evolution and historical biogeography

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Abstract

Traditional *Tinospora* is a heterogeneous genus, distributed in the African and Asian tropics as well as Australia and adjacent islands. Molecular phylogenetics has contributed greatly to improve our understanding of the genus over the past decade, however its circumscription is yet unresolved. In this study, we present a phylogenetic analysis of Burasaieae using six molecular markers (*rbcL*, *atpB*, *matK*, *ndhF*, *trnL-F*, ITS), with a focus on *Tinospora*. Our results indicate that sampled species of *Tinospora* are distributed in three different clades. *Tinospora tinoporoides*, endemic to Australasia, is strongly supported as sister to the South American *Borismene*. By integrating lines of evidence from molecular phylogeny and morphology, we resurrected the monotypic *Fawcettia* to include *F. tinoporoides*. Our estimated age for the split of *Fawcettia*-*Borismene* was ca. 29 Ma, suggesting that trans-Pacific long-distance dispersal may be the most feasible explanation for the Australasian–South American disjunction. *Tinospora oblongifolia* is a member of *Hyalosepalum*, characterized by three stamens with connate filaments, whereas *T. tenera*, once placed in *Hyalosepalum*, is recovered within *Tinospora*, characterized by six stamens. Evolutionary inferences of morphological characters indicate that the five selected characters, traditionally used to distinguish genera in Burasaieae, are highly homoplastic. Our molecular dating and ancestral range reconstruction suggest that *Tinospora* originated from Africa in the middle Oligocene (ca. 28 Ma) and expanded into Asia in the Early Miocene (ca. 21 Ma). Within *Tinospora*, a vicariance event occurred in the Middle Miocene (ca. 17 Ma) resulting in the split of African *T. tenera* and its Asian allies. One dispersal from Asia to Africa was inferred in the Late Miocene (ca. 10 Ma). Australian *T. smilacina* and *T. esiangkara* originated from Asia in the early Late Miocene (ca. 11 Ma). Thus, geodispersal and subsequent vicariance, as well as transoceanic long-distance dispersal, have been responsible for the present distribution of *Tinospora*.

Keywords biogeography; *Fawcettia*; geodispersal; Menispermaceae; phylogeny; tropical forests

INTRODUCTION

The genus *Tinospora* Miers (Menispermaceae), consisting of about 32 species, is disjunctly distributed in the African and Asian tropics, also in Australia and adjacent islands (Forman, 1986, 2007; Kessler, 1993). *Tinospora* species are main foodplants of larvae of fruit-piercing moths, and thus play an important role in the biological chain that results in extensive damage to certain fruit crops, such as longan, citrus, and mandarin (Bänziger, 1982). Some species, such as *T. crispa* (L.) Hook. f. & Thomson, *T. sinensis* (Lour.) Merr., and *T. sagittata* Gagnep. (= *Paratinospora sagittata* (Oliv.) Wei Wang), are utilized as traditional Chinese medicines (Luo, 1996). Nevertheless, traditional *Tinospora* is a heterogeneous assemblage. Based on molecular phylogenetic analyses, at least four species have been segregated from the genus. *Tinospora caffra* (Miers) Troupin (= *Desmonema caffra* Miers) was the first to be found not to cluster with other *Tinospora* (Ahmad & al., 2009; Hoot & al., 2009; Jacques & al., 2011; Wefferling & al., 2013; Ortiz & al., 2016). Wang & al. (2017) confirmed this result and resurrected *Hyalosepalum* Troupin to accommodate *H. caffrum* (Miers) Troupin (= *T. caffra*). *Tinospora sagittata* Gagnep. (= *Paratinospora sagittata* (Oliv.) Wei Wang) and *T. dentata* Diels (= *Paratinospora dentata* (Diels) Wei Wang) were excluded from *Tinospora* and placed into the newly described genus *Paratinospora* Wei Wang (Wang & al., 2017). *Tinospora uviforme* (Baill.) Troupin

was recovered as a member of *Chasmanthera* Hochst., i.e., *C. uviformis* Baill. (Ortiz & al., 2016). On the other hand, *Limacia esiangkara* F.M.Bailey was transferred to *Tinospora* by Forman (2007) as *T. esiangkara* (F.M.Bailey) Forman, and this placement was confirmed by subsequent molecular studies (Ortiz & al., 2007; Wang & al., 2012, 2017). Although tremendous progress has been made in our understanding of *Tinospora* over the past ten years, its circumscription has remained unresolved, mainly owing to the uncertain systematic position and taxonomic treatment of *Fawcettia* F.Muell.

Fawcettia with the sole species *F. tinosporoides* F.Muell. was first described by Mueller (1877) and was thought to be close to *Fibraureae* or *Tinospora* of *Burasaieae*. The genus was recognized by Bailey (1899) and was retained by Diels (1910) in his monograph of the family *Menispermaceae*, on the basis of the presence of a third whorl of outermost sepals. However, Forman (1981) argued that the presence of this third outermost whorl of sepals was not only inconsistent in *Fawcettia*, but that the difference in sepal whorls was too small to justify the recognition of the latter and therefore placed it in *Tinospora* as *T. tinosporoides* (F.Muell) Forman. Subsequent authors accepted its inclusion in *Tinospora* (Kessler, 1993; Forman, 2007; Mabberley, 2017). *Tinospora tinosporoides* is restricted to rainforests and complex notophyll vine forests in southeastern Queensland and northeastern New South Wales (Forman, 2007), and to date, this species has not been sampled in any molecular study.

Tinospora together with *Chasmanthera* Hochst. and *Jateorhiza* Miers was placed in a broad *Chasmanthera* by Baillon (1872). However, this broad *Chasmanthera* was not accepted by subsequent authors (e.g., Diels, 1910; Troupin, 1962; Kessler, 1993). Troupin (1962) argued, if Baillon's concept was adopted, *Kolobopetalum* Engl., *Leptoterantha* Louis ex Troupin, and *Syntriandrium* Engl. should also be reduced to the broad *Chasmanthera*. Similarly, *Odontocarya* Miers could also be placed in the broad *Chasmanthera* (Barneby, 1970). Sepals and stamens are considered the most important characters in keeping these genera separate (Troupin, 1962), yet to date, their taxonomic significance has never been discussed in comparison to molecular phylogeny. Recent phylogenetic analyses indicate that the aforementioned seven genera, as well as *Dialythea* Exell&Mendonça, *Hyalosepalum*, *Rhigiocarya* Miers, and *Sarclophium* Troupin, formed a monophyletic group with strong support (e.g., Wang & al., 2012, 2017; Ortiz & al., 2016). To shed light on the taxonomic status of these genera, the evolutionary patterns of some taxonomically relevant morphological characters, such as number of sepal whorls, stamen connation, and pollen aperture types (Diels, 1910; Troupin, 1962; Kessler, 1993), need to be evaluated in a broad phylogenetic context.

The objectives of this study are: (1) to re-delimitate *Tinospora* by clarifying the phylogenetic position and taxonomic treatment of *Fawcettia*, (2) to determine the evolutionary patterns of key morphological characters of *Burasaieae*, and (3) to investigate the historical biogeography of *Tinospora* s.str.

MATERIALS AND METHODS

Taxon sampling and DNA sequencing

We sampled 44 species, representing 22 of the 24 currently recognized genera in *Burasaieae* (Ortiz & al. 2016), and *Paratinospora* and *Hyalosepalum* recently described and resurrected by Wang & al. (2017), respectively. Our sampling includes 16 species still placed in *Tinospora*, 3 from Africa, 4 from Australasia, and 9 from Asia. Following the results of Wang & al. (2012) and Ortiz & al. (2016), we selected three species representing all three genera of *Coscinieae*, the other tribe of *Chasmantheroideae*, as outgroups. Species, vouchers and GenBank accession numbers are given in the Appendix 1.

We amplified six plastid (*rbcL*, *atpB*, *matK*, *ndhF*, *trnL-F*) and nuclear (ITS) markers. Laboratory procedures and sequence handling followed Wang & al. (2017). When ITS-A and ITS-B did not work for long ITS sequences, additional primers, ITSC and ITS-D, were used (Blattner, 1999). Sequences were aligned using Geneious v.10.1.3 (Kearse & al., 2012) based on the previous data matrices of Wang & al. (2017), and then adjusted manually in BioEdit v.7.0 (Hall, 1999). One polyAG region in the *trnL-F* matrix (representing 10 nucleotides) and four difficult-to-align regions in the ITS matrix (encompassing 126 nucleotides) were excluded from the analyses. The final lengths of these six marker datasets were: *rbcL*, 1385 bp; *atpB*, 1412 bp; *matK*, 1235 bp; *ndhF*, 2066 bp; *trnL-F*, 1133 bp; and ITS, 656 bp (suppl. Appendices S1–S6).

Phylogenetic analysis

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI) methods for the combined cpDNA (five plastid markers), ITS, and the combined cpDNA and ITS datasets. ML and BI analyses were conducted in RAxML v.7.2.6 (Stamatakis, 2006) and MrBayes v.3.2.5 (Ronquist & al., 2012), respectively. For ML analyses, RAxML was performed with the GTR + I + Γ substitution model for each DNA region, and nodal support was assessed using the fast bootstrap option with 1000 replicates. For BI analyses, each DNA region was assigned its own model of nucleotide substitution, as determined by the Akaike information criterion (AIC) via jModeltest v.2.1.4 (Posada, 2008). Two independent runs, each consisting of four Markov Chain Monte Carlo (MCMC) chains, were conducted with one tree sampled for every 1000 generations over 50 million generations, starting with a random tree. Stationarity was determined in Tracer v.1.6 (Rambaut & al., 2014). Majority-rule (>50%) consensus trees were constructed after removing the burn-in period samples (the first 25% of sampled trees). Based on Wang & al. (2014), we used the thresholds BS $\geq 70\%$ and PP ≥ 0.95 as an indication of significant conflict between the cpDNA and ITS datasets.

Analysis of character evolution

The distribution of five morphological characters, upon which the generic classification of Burasaieae, especially the broad Chasmanthera has traditionally been based, was investigated. Orthogynium sp. and Tinospora sp. were excluded from the analyses because the five characters evaluated here are still unknown in these two taxa. Information on morphological features was taken from the literature, particularly Diels (1910), Troupin (1962), Barneby (1970), Forman (1981), and Kessler (1993) for general morphological characters, and Thanikaimoni & al. (1984) for pollen aperture types. Patterns of evolution were inferred using the ML approach as implemented in Mesquite v.2.75 (Maddison & Maddison, 2011). The Markov k-state one-parameter model of evolution for discrete unordered characters (Lewis, 2001) was used.

Molecular dating analysis

We estimated the divergence times of Burasaieae using the uncorrelated lognormal Bayesian method in BEAST v.2.1.3 (Drummond & al., 2012). Following Wang & al. (2017), we used the cpDNA data for age estimates owing to the potential problems of recombination, incomplete concerted evolution, and high homoplasy in ITS sequences. Phylogenetic analyses (Ortiz & al., 2016; Wang & al., 2017; this study) indicate that the species of Tinospora are distributed in at least five clades. Thus, we did not use *T. excavata* Reid & Chandler from the Paleocene-Eocene transition of eastern Belgium (Fairon-Demaret & Smith, 2002) as a calibration point, as it is not possible to place it in the phylogenetic tree. Here we selected three fossils that can confidently be placed in our tree as internal calibration points. (1) A fossil endocarp of *Anamirta* Colebr. was used to constrain its stem age to at least 43.7 Ma (Manchester, 1994). (2) The stem age of *Parabaena* Miers was constrained to be at least 47.8 Ma based on the fossil *Parabaena bognoensis* Chandler from the London Clay (Chandler, 1964). (3) The stem group age of *Jateorhiza* was also constrained to be at least 47.8 Ma based on the fossil *Jateorhiza gilliamii* Chandler (Chandler, 1964). Following the suggestion of Parham & al. (2012), we used the uniform prior distributions for these three fossil calibration points. We set a 101 Ma maximum age for the root, which is the estimated crown age of the Chasmantheroideae (Wang & al., 2012), with a normal distribution and a standard deviation of three. A recent study reported a relatively younger age (80.14 Ma) for the crown age of the subfamily (Wefferling & Hoot, 2018). To explore the impact of the root age on the estimates, we also constrained the root to 80.14 Ma and reran the dating analysis using the cpDNA data.

Both dating analyses were carried out under the GTR + I + Γ model for each marker partition separately and with a Yule tree prior. The MCMC chains were run for 50 million generations, sampling every 5000 generations. Appropriate burn-in and the effective sample size value of each parameter (>200) were assessed in Tracer v.1.6 (Rambaut & al., 2014). The maximum clade credibility (MCC) tree with median branch lengths and 95% highest posterior density (HPD) intervals on nodes was built in TreeAnnotator v.1.8.4 (Drummond & al., 2012).

Biogeographical analysis

To infer range evolution of Tinospora, we focused on Tinospora and its closely related genera belonging to the broad Chasmanthera. The MCC tree obtained from the cpDNA data with the root set as 101 Ma was modified in Mesquite v.2.75 (Maddison & Maddison, 2011) and was accordingly used for biogeographical analysis in the R package BioGeoBEARS (Matzke, 2013). Following Ree & Sanmartín (2018), we used the dispersal-extinction-cladogenesis (DEC) model (Ree & Smith, 2008). Four major areas of distribution were categorized: Asia (A); Australasia (B); Africa (C); and South America (D). We allowed the inferred ancestors to occupy up to two areas (sampled tips occupy only one area). Dispersal probabilities between pairs of areas were specified based on Buerki & al. (2011).

RESULTS

Phylogenetic analyses

The cpDNA dataset comprised 7235 aligned nucleotides. ML and BI analyses yielded identical trees (Fig. 1). *Calyccarpum* Nutt. ex Torr. & A.Gray is the earliest-diverging lineage in Burasaieae, followed by the monophyletic group consisting of *Aspidocarya* Hook.f. & Thomson, *Disciphania* Eichler, and *Parabaena*, and then *Tinomiscium* Miers ex Hook.f. & Thomson. *Tinospora tinosporoides* and *Borismene* Barneby formed a clade with strong support (BS = 95%, PP = 1.0). *Dioscoreophyllum* Engl. is sister to the broad *Chasmanthera* (BS = 100%, PP = 1.0). *Jateorhiza* is sister to all other broad *Chasmanthera* (BS = 100%, PP = 1.0). *Tinospora* (excluding *T. oblongifolia* and *T. tinosporoides*) is sister to the clade I (BS = 90%, PP = 1.0). *Tinospora oblongifolia* (Engl.) Troupin is recovered as sister of *Hyalosepalum* (BS = 72%, PP = 0.96). *Rhigiocarya* groups with *Sarcophium* (BS = 97%, PP = 1.0). Relationships among the seven clades, *Borismene*–*Tinospora tinosporoides*, *Paratinospora*, *Penianthus longifolius*, *Penianthus patulinervis*–*Sphenocentrum jollyanum*, *Burasaia Thouars*–*Orthogynium* Baillon, *Fibraurea* Lour., and *Dioscoreophyllum*–broad *Chasmanthera* are not resolved.

The aligned matrix of ITS sequences was 657 characters in length. ML and BI analyses produced identical trees (Fig. 2). Comparing to the cpDNA topology, the ITS topology has lower resolution, but a distant relationship between *Tinospora oblongifolia* and other *Tinospora* is also recovered. *Tinospora* is sister to clade II (BS = 92%, PP = 1.0). *Rhigiocarya* and *Kolobopetalum* have a sister relationship with strong support (BS = 90%, PP = 0.99).

The combined cpDNA and ITS dataset comprised 7892 aligned nucleotides. ML and BI analyses resulted in highly congruent trees (suppl. Fig. S1). The topology from the combined cpDNA and ITS dataset (suppl. Fig. S1) is congruent with the cpDNA tree (Fig. 1), but the relationships within Burasaieae are usually resolved with greater support in the combined cpDNA and ITS tree except for the placement of *Rhigiocarya* (the BS and PP values were 35% and 0.02 lower, respectively).

Character evolution

A summary of character states that are relevant for the taxonomy of the group is shown in Fig. 3. Exploration of character changes and ancestral-state inference were undertaken using the tree from the combined cpDNA and ITS analysis. The ML tree was chosen based on its congruence with that obtained from BI (suppl. Fig. S1). Likelihood inferences of character states indicate that all five selected morphological characters (number of sepal whorls, number of stamens, stamen connation, dehiscence types of anthers, pollen aperture types) are homoplastic in Burasaieae. For example, three sepals seem to have evolved independently at least three times (Fig. 4A). Trace of the three states for stamen connation (no, yes, and outer whorl free and inner whorl connate) appears to be extremely complex (Fig. 4B).

Divergence time estimation and biogeographical reconstruction

The different ages of the root have no effect on divergence time estimates. A comparison of estimated times from the different ages of the root is shown in Fig. 5. The age estimation using the cpDNA data with the root set as 101 Ma is here reported and was used for biogeographical analysis. Ancestral area reconstruction for *Tinospora* is indicated in Fig. 6. The Australian *T. tinosporoides* split from its South American sister *Borismene* at about 29.05 Ma (95% HPD: 12.43– 47.44; node 1 in Fig. 5). *Tinospora* originated from Africa at 28.57 Ma (95% HPD: 22.67– 34.76; node 2), and its most recent common ancestor had already spread to Asia by 21.54 Ma (95% HPD: 15.63– 27.62; node 3). A vicariance event separated African *T. tenera* Miers and its Asian sister at about 17.53 Ma (95% HPD: 12.02– 23.39; node 4). One dispersal from Asia to Australia occurred at about 11.16 Ma (95% HPD: 7.15– 15.92; node 5). The African *T. bakis* (A.Rich.) Miers diverged from the ancestor of the Australian *T. esiangkara* and *T. smilacina* Benth. at about 9.71 Ma (95% HPD: 5.84– 14.61; node 6).

DISCUSSION

The trees resulting from the combined cpDNA and ITS dataset are congruent with those from the cpDNA dataset (suppl. Fig. S1 vs. Fig. 1), whereas the placements of *Tinospora* and *Rhigiocarya* are incongruent in the cpDNA and ITS trees (suppl. Fig. S2). The BS value the placement of *Tinospora* was increased from 90% in the cpDNA data to 100% in the combined cpDNA and ITS data. A similar case for *Tinospora* was also reported by Wang & al. (2017). Based on statistical tests, Wang & al. (2017) suggested that the conflict for the placement of *Tinospora* between the cpDNA and ITS data is artificial and resulted from high substitution rates and homoplasy in the ITS sequences. However, other causes, such as intergeneric hybridization or incomplete lineage sorting, cannot be ruled out. More nuclear DNA regions are needed to test these hypotheses in the future. For *Rhigiocarya*, the BS and PP values become lower in the combined cpDNA and ITS tree (Fig. 2 vs. suppl. Fig. S1). In the cpDNA tree, *Rhigiocarya* is sister to *Sarcophium*, with which it shares longitudinally dehiscent

anthers and pollen with tricolporate aperture. Conversely, the ITS data suggest *Rhigiocarya* as sister to *Kolobopetalum*, supported by outer free and inner connate stamens. Thus, *Rhigiocarya* might be a hybrid genus.

The intergeneric relationships within Burasaieae revealed by the cpDNA and combined cpDNA and ITS datasets are consistent with previous molecular studies (Wang & al., 2012, 2017; Wefferling & al., 2013; Ortiz & al., 2016). As shown by Wang & al. (2017), the topology was consistent with the separation of *Paratinospora*, *Hyalosepalum*, and *T. uviforme* from *Tinospora*. Moreover, we found that the *Tinospora* species sampled in this study are distributed in three different clades (Fig. 1, suppl. Fig. S1): *Tinospora tinosporoides* and *Borismene* formed a clade; *T. oblongifolia* clustered with *Hyalosepalum*; and the remaining *Tinospora* species formed a clade.

The resurrection of *Fawcettia* and the Australasian–South American disjunction

Because a third, outermost whorl of sepals is sometimes found in three *Tinospora* species, *T. cordifolia* (Willd.) Miers ex Hook.f. & Thomson (sampled in this study), *T. merrilliana* Diels, and *T. trilobata* Diels, Forman (1981) reduced the monotypic *Fawcettia* to *Tinospora*, where it was placed as *T. tinosporoides*. However, our phylogenetic analyses strongly suggest that *T. tinosporoides* has only a distant relationship with *Tinospora* s.str. (including *T. cordifolia*, the type of the genus; Fig. 1). Besides the difference in number of sepal whorls, *T. tinosporoides* markedly differs from other *Tinospora* species in having triangular to ovate leaves without glandular patches below the basal nerve-axils (vs. cordate or linear leaves with glandular patches), pseudopaniculate inflorescences (vs. racemose), sessile male flowers (vs. pedicellate), densely spinulose endocarp (vs. verrucose or tuberculate), continuous, not ruminant endosperm (vs. ruminant; continuous endosperm also occurs in the New Guinean *T. arfakiana* Becc., a species not sampled here) (Forman, 1981, 2007), and pollen with tricolpate aperture (vs. tricolporate) (Figs. 3, 4). The sister relationship between *Tinospora tinosporoides* and *Borismene* is strongly supported (BS = 95%, PP = 1.0). They share a three-whorled calyx (Fig. 3). Nevertheless, *T. tinosporoides* is distinguished from *Borismene* in many other morphological characters, such as inflexed petals (vs. not inflexed), carpophore present (vs. absent), papery endocarps with a smooth surface (vs. bony, densely spinulose), not ruminant endosperm (vs. ruminant), and tricolpate aperture (vs. tricolporate) (Barneby, 1972; Forman, 1981; Thanikaimoni & al., 1984). Thus, our analysis suggests that *Fawcettia* is a distinct genus in Burasaieae and is here resurrected.

The sister relationship between *Fawcettia* and *Borismene* recovered in this study results in an Australasian–South American genus pair. This amphi-Pacific tropical disjunction in the Southern Hemisphere is fascinating as it results in an explanatory challenge, and may shed light on the assembly of tropical floras in the past (Thorne, 1972; Givnish & Renner, 2004). Both *Fawcettia* and *Borismene* are restricted to tropical forests (Barneby, 1972; Forman, 2007). Our divergence time estimates indicate that the split of *Fawcettia* and *Borismene* occurred in the middle Oligocene, ca. 29 Ma (12.43– 47.44 Ma; node 1 in Fig. 5). This estimated age is partly consistent with the opening of the Drake Passage between South America and Antarctica (ca. 30– 35 Ma; Sáez & al., 1999; McLoughlin, 2001). It has been suggested that Antarctica may have served as a migration route for some megathermal lineages between Australasia and South America in the early Tertiary (Morley, 2003; Vicente & al., 2017). However, during the Oligocene, global climate was cooling (Zachos & al., 2001), which could have prevented migration of Menispermaceae through Antarctica. Molecular phylogenetic studies have indicated that migrations of megathermal lineages, such as Sapotaceae (Bartish & al., 2011), Loranthaceae (Liu & al., 2018), and Anomospermeae (Menispermaceae; Lian & al., 2019), through Antarctica mainly occurred in the Paleocene– early Eocene, a global warming period (Zachos & al., 2001). Thus, we hypothesize that trans-Pacific long-distance dispersal may explain the modern disjunct distribution of *Fawcettia* and *Borismene*. Fruits of both genera are red and fleshy drupes and may be favored by birds (Barneby, 1972). Trans-Pacific long-distance dispersal has been reported in some lineages, such as *Coriaria* L. (Coriariaceae; Yokoyama & al., 2000), *Nothofagus* Blume (Nothofagaceae; Knapp & al., 2005), and *Heterozostera nigricaulis* J.Kuo (Zosteraceae; Smith & al., 2018).

The circumscription of *Hyalosepalum*

Owing to the fact that the generic name *Desmonema* (Menispermaceae; Miers, 1867) was first used in Euphorbiaceae by Rafinesque (1833), Troupin (1949) provided a new generic name, *Hyalosepalum*, to accommodate eight African species. However, later, Troupin (1962) deemed that whether stamens were free or not was not enough to separate *Hyalosepalum* and *Tinospora*, and therefore reduced the former to the latter. Earlier phylogenetic analyses have indicated that *T. caffra* (= *H. caffrum*, the type of *Hyalosepalum*) has a distant relationship with *Tinospora* (Ahmad & al., 2009; Hoot & al., 2009; Jacques & al., 2011; Wefferling & al., 2013; Ortiz & al., 2016; Wang & al., 2017). Thus, Wang & al. (2017) resurrected *Hyalosepalum*; however, the circumscription of the resurrected genus has been challenging since only two out of the eight species of *Hyalosepalum* were sampled. *Hyalosepalum uviforme* (Baill.) Troupin (= *Tinospora uviforme*) has been

confirmed to be a member of Chasmanthera, i.e., *C. uviforme* Baill. (Ortiz & al., 2016; this study). Here, we included *T. oblongifolia* (= *H. oblongifolium* (Engl.) Troupin) and *T. tenera* Miers (= *H. tenerum* (Miers) Troupin) in molecular phylogenetic analyses for the first time. *Tinospora oblongifolia* groups with *H. caffrum* with moderate support (BS = 72%, PP = 0.96; Fig. 1). The two species share three stamens with connate filaments, whereas *Tinospora* species have six free stamens (Diels, 1910; Troupin, 1962). Conversely, *H. tenerum* was embedded within *Tinospora* with strong support (Fig. 1). In agreement with this relationship is the shared presence of six stamens (Diels, 1910; Troupin, 1962). The filaments of *H. tenerum* are only connate at the base, whereas the filaments of other *Hyalosepalum* are completely connate.

Evolution of morphological characters

Sepal and stamen characters, including number of sepal whorls, number of stamens, stamen connation, dehiscence type of anthers, and pollen aperture type, have traditionally been used for generic recognition within Burasaieae, especially for the delimitation of *Tinospora*. These characters are traced on the phylogeny of the combined cpDNA and ITS data (Fig. 3). Likelihood inference indicates evolutionary patterns of morphological characters (Fig. 4). The clade containing *Dioscoreophyllum* and the broad *Chasmanthera* has two whorls of sepals, a feature that is also found in *Paratinospora*, *Disciphania* and *Parabaena*. Most genera of Burasaieae have six stamens. In the broad *Chasmanthera*, the state “three stamens” originated once, and reversals to “six stamens” occurred in *Leptoterantha* and *Odontocarya truncata* Standl., respectively. Free stamens are the plesiomorphic state of Burasaieae, and connate stamens have evolved four times independently. In *Rhigiocarya*, *Kolobopetalum* and *Odontocarya truncata*, the outer three stamens are free and the inner three are connate. Our phylogenetic hypothesis suggests that the dehiscence of anthers and pollen aperture types are extremely complex in the broad *Chasmanthera*.

The number of stamens, the presence/absence of stamen connation, dehiscence type of anthers, and pollen aperture types are homoplastic in the broad *Chasmanthera*, but each genus of the broad *Chasmanthera* has at least one unique combination of these four morphological characters except for *Tinospora* and *Sarcophium* (Fig. 3). However, *Sarcophium* is distinguished from *Tinospora* by having an endocarp with erect processes (vs. verruca or tubercule; Kessler, 1993). Our phylogenetic analyses indicate that there are 11 genera in the broad *Chasmanthera* (Fig. 1, suppl. Fig. S1). If the broad generic concept of Baillon (1872) is accepted, it will be extremely disruptive for nomenclature because numerous new nomenclatural combinations will be required, especially since both *Tinospora* and *Odontocarya* contain more than 30 species (Ortiz & al., 2016). Considering phylogenetic and morphological evidence and the nomenclatural option, here we conclude that segregation of these 11 genera is strongly preferable, in agreement with earlier authors (e.g., Diels, 1910; Troupin, 1962; Kessler, 1993; Ortiz & al., 2016; Wang & al., 2017).

Biogeography of *Tinospora*

Our time estimates for Burasaieae are consistent with the results of previous studies (Wang & al., 2012, 2017). This was anticipated because the same calibration fossils were used. Our results indicate that *Tinospora* originated from Africa in the Oligocene (28.57 Ma, 95% HPD: 22.67–34.76; node 2 in Fig. 6), and its most recent common ancestor likely had spread into Asia in the Early Miocene (21.54 Ma, 95% HPD: 15.63–27.62; node 3). There are four main competing hypotheses to explain floristic exchanges between the African and Asian tropics: Gondwanan vicariance or Indian raft, boreotropical migration, Miocene geodispersal, and long-distance dispersal (reviewed in Thomas & al., 2015). Our estimated age for the dispersal from Africa to Asia is obviously younger than the timing of collision of India and continental Asia, ca. 50 Ma (Van Hinsbergen & al., 2012) or 35 Ma (Ali & Aitchison, 2008), and also younger than the timing of disruption of the boreotropical forests, ca. 34 Ma (Collinson, 1992; Wolfe, 1992; Morley, 2007). Thus, the Indian raft and boreotropical migration hypotheses were rejected, while the Miocene geodispersal hypothesis is temporally congruent with our inferences. During the Early to Middle Miocene, global climate was warming (Zachos & al., 2001). Moreover, due to the collision of the Afro-Arabian plate with the Iranian and Anatolian plates, land connections between Africa and Southwest Asia developed during this period (Rögl, 1998; Popov & al., 2004). Evidence from plant and vertebrate macrofossils and palynological data indicate that there were tropical forests in Arabia from the Early to Middle Miocene (Mandaville, 1984; Kürschner, 1998; Otero & Gayet, 2001; Ataabadi, 2010; Pound & al., 2012). *Tinospora* species primarily inhabit tropical rainforests, monsoon forests, and open woodlands (Troupin, 1962; Forman, 1986). Thus, the Arabian corridor during the Early to Middle Miocene may have facilitated the range expansion of *Tinospora*. Other tropical lineages, such as Annonaceae (Zhou & al., 2012; Thomas & al., 2015), *Isodon* (Schrad. ex Benth.) Spach (Lamiaceae; Yu & al., 2014), and *Searsia* F.A.Barkley (Anacardiaceae; Yang & al., 2016), have also migrated through Arabia during this period.

Our analyses indicate that *Tinospora* was widely distributed in Africa and Asia until a vicariance event occurred in the Middle Miocene (17.53 Ma, 12.02–23.39 Ma; node 4), which resulted in the divergence of the African *T.*

tenera and its Asian allies. After the late Middle Miocene, climate deterioration occurred (Zachos & al., 2001), which may have hampered the exchange of megathermal plants between Africa and Asia through Arabia.

The African *T. bakis* originated from Asia in the Late Miocene (9.71 Ma, 5.84– 14.61 Ma) with the extinction of its Asian ancestor (node 6 in Fig. 6). This age is younger than the disruption of the aforementioned Arabian Miocene corridor. Thus, transoceanic long-distance dispersal may be the most likely explanation for this colonization event. The fruits of *Tinospora* are brightly colored and fleshy drupes (Forman, 1986), which may be favored by birds. Transoceanic longdistance dispersal has been hypothesized to explain the Asian- African disjunction for other plant groups, such as *Adansonia* L. (Malvaceae; Baum&al., 1998), *Osbeckia* L. (Melastomataceae; Renner & Meyer, 2001), and *Loranthaceae* (Liu & al., 2018).

The clade including the Australian *T. smilacina* and *T. esiangkara* originated from Asia in early Late Miocene (11.16 Ma, 7.15– 15.92 Ma; node 5), obviously later than the convergence between Asia and New Guinea/Australian plates, ca. 25 Ma (Morley, 1998; Hall, 2002, 2009). This convergence led to the formation of the Wallacean transition zone between the Sunda and the Sahul shelves, and some taxa have dispersed from one side to the other (Richardson & al., 2012). The winteraceous fossil leaves collected from the Middle Miocene in Central Yunnan support the exchange of megathermal plants between Gondwana and Asia after the convergence (Liang & al., 2018). The “west-to-east” migration pattern in *Tinospora* is also found in some other plant taxa, such as *Pseuduvaria* Miq. (Annonaceae; Su & Saunders, 2009), *Alocasia* (Schott) G.Don (Araceae; Nauheimer & al., 2012), and *Begonia* L. (Begoniaceae; Thomas & al., 2012).

AUTHOR CONTRIBUTIONS

WW designed the research. LL performed the lab work and analyzed data. RDCO, FJ, ZDC and WW collected the materials. LL and WW interpreted the results and wrote the paper. All authors contributed with further discussion and writing of the manuscript. — RDCO, <https://orcid.org/0000-0002-4673-4347>; FJ, <https://orcid.org/0000-0002-7729-1067>; WW, <https://orcid.org/0000-0001-6901-6375>

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Appendix 1. Taxa, voucher identification and GenBank accession numbers for molecular analyses of the tribe Burasaieae.

Species, locality, voucher, and GenBank accession: ITS, trnL-F, matK, ndhF, rbcL, and atpB. An asterisk (*) indicates newly generated sequences in this study, a dash (–) denotes missing data.

INGROUPS: *Aspidocarya uvifera* Hook.f. & Thomson, China, Hong YP 99190 (PE), KY365639, EF143884, EF143853, JN051701, FJ626593, HQ260821. *Borismene japurensis* (Mart.) Barneby, cult. Belgium, D. Aplin S4033 (BR), KY365640, JN051746, JN051812, JN051702, JN051675, JN051871. *Burasaia madagascariensis* Thou., Madagascar, Rabenantoandro & al. 1262 (MO), KY365641, JN051747, JN051813, EF624272, HQ260767, HQ260823. *Calycocarpum lyonii* Nutt. ex A.Gray, U.S.A., Ortiz & al. 335 (MO), KY365642, JN051748, JN051814, EF624273, HQ260768, HQ260824. *Chasmanthera uviformis* Baill., Madagascar, P. Antilahimena 7571 (MO), MK670923*, KX384146, KX384083, KX384106, MK670938*, MK670944*. *Chasmanthera welwitschii* Troupin, cult. Belgium, D. Aplin S4040 (BR), KY365643, JN051751, JN051817, EF624277, EU526985, HQ260827. *Dialythea gossweileri* Exell & Mendonça, Gabon, F.J. Breteler 371 (MO), MK670924*, KX384130, KX384067, KX384098, MK670939*, –. *Dioscoreophyllum cumminsii* (Stapf) Diels, cult. Belgium, D. Aplin S4049 (BR), KY365644, JN051759, JN051825, EF624294, EU526988, EU526972. *Disciphania killipii* Diels, Peru, Ortiz & Zárate 310 (AMAZ, MO), KY365645, JN051760, JN051826, EF624295, HQ260779, HQ260835. *Fibraurea recisa* Pierre, China, Jin XH PT-2516 (PE), MK670925*, MK670931*, MK670934*, MK670936*, MK670940*, MK670945*. *Fibraurea tinctoria* Lour., cult. West Java, F. Jacques 04 (P), KY365646, JN051762, JN051828, EF624298, HQ260781, EU526970. *Hyalosepalum caffrum* (Miers) Troupin, Tanzania, Sitoni & al. 1257 (MO), –, –, KX384082, –, L37923, L37933. *Jateorhiza macrantha* (Hook.f.) Exell & Mendonça, Cameroon, Kenfack & Zapfack 2039 (MO), KY365647, JN051766, JN051832, EF624305, HQ260785, HQ260840. *Kolobopetalum leonense* Hutchinson & Dalziel, Ghana, Schmidt & al. 3435 (MO), KY365648, JN051767, JN051833, EF624306, HQ260786, HQ260841. *Leptoterantha mayumbensis* (Exell) Troupin, Congo, Ewango 3005 (MO), KY365649, JN051769, JN051835, EF624308, HQ260788, HQ260788. *Odontocarya tripetala* Diels, Peru, Ruiz 5601 (MO), KY365650, JN051772, JN051837, EF624316, HQ260789, HQ260845. *Odontocarya truncata* Standl., Costa Rica, Hammel & Perez 22567 (MO), KY365651, JN051773, JN051838, EF624317, HQ260790, HQ260846. *Orthogynium* sp., Madagascar, Birkinshaw & Rabenantoandro 549 (MO), KY365652, JN051774, JN051839, EF624318, JN051684, JN051880. *Parabaena sagittata* Miers ex Hook.f. & Thomson, China, Hong YP H346 (PE), KY365653, EF143885, EF143854, JN051714, FJ626597, HQ260849. *Paratinospora dentata* (Diels) Wei Wang, China, Chen & al. 20110517-1 (PE), KY365662, KY365726, KY365679, KY365695, KY365711, KY365627. *Paratinospora sagittata* (Oliv.) Wei Wang, China, Anonymous 1055 (PE), KY365665, KY365729, KY365682, KY365697, KY365713, KY365629. *Penianthus longifolius* Miers, Cameroon, Sweeney & al. 1436 (MO), KY365654, JN051779, JN051844, EF624323, HQ260794, HQ260850. *Penianthus patulinervis* Hutch. & Dalziel, Ivory Coast, M.T. Thijssen 378 (MO), MK670926*, KX384139, KX384076, –, FJ026500, FJ026440. *Rhigiocarya racemifera* Miers, Cameroon, Kenfack 1655 (MO), KY365655, JN051784, JN051849, EF624328, HQ260797, HQ260853. *Sarcophium suberosum* Troupin, Gabon, F.J. Breteler 12819 (MO), MK670927*, KX384141, –, KX384104, MK670941*, –. *Sphenocentrum jollyanum* Pierre, Nigeria, Daramota 30 (MO), KY365656, JN051787, JN051852, EF624334, JN051687, JN051885. *Syntriandrium preussii* Engl., Cameroon, Fernandez Casas MK 8407 (PE), KY365657, JN051794, JN051859, JN051729, HQ260804, HQ260860. *Tinomiscium petiolare* Hook.f. & Thomson, China, Hong YP H142 (PE), KY365658, EF143888, EF143857, JN051732, EF173675, HQ260863. *Tinospora baenzigeri* Forman, Thailand, Wang HC 108 (PE), KY365659, KY365723, KY365676, KY365692, KY365708, KY365624. *Tinospora bakis* (A.Rich.) Miers, cult. West Java, F. Jacques s.n. (P), KY365660, KY365724, KY365677, KY365693, KY365709, KY365625. *Tinospora cordifolia* (Willd.) Miers ex Hook.f. & Thomson, India, M. Immanuel Sagayaraj 56237 (RHJ) AY660534, KJ641530, JX193231, –,

DQ353864, DQ353860. *Tinospora crispa* (L.) Hook.f. & Thomson, cult. Singapore, Chen ZD s.n. (PE), KY365661, KY365725, KY365678, KY365694, KY365710, KY365626. *Tinospora esiangkara* (F.M. Bailey) Forman, Australia, Gray 8927 (MO), KY365663, KY365727, KY365680, EF624310, HQ260807, HQ260864. *Tinospora glabra* (Burm.f.) Merr., cult. West Java, F. Jacques 03 (P), KY365664, KY365728, KY365681, KY365696, KY365712, KY365628. *Tinospora macrocarpa* Diels, Malaysia, AS213, -, KU853223, KU853097, -, KU853168, -. *Tinospora malabarica* (Lam.) Hook.f. & Thomson, India, Ahmad & al. (2009), AY626991, -, -, -, DQ414465, DQ353859. *Tinospora neocaledonica* Forman, New Caledonia, H.S. McKee 41473 (P), MK670928*, -, -, -, -. *Tinospora oblongifolia* (Engl.) Troupin, Kenya, J.B. Gillett & S.P. Kibuwa 19891 (P), MK670929*, MK670932*, -, -, MK670942*, -. *Tinospora siamensis* Forman, Thailand, Wang HC 111 (PE), KY365674, KY365738, KY365691, KY365706, KY365722, KY365638. *Tinospora sinensis* (Lour.) Merr., Thailand, Wang HC 109 (PE), AY017386, EF143886, EF143855, KX384105, FJ626602, KY365637. *Tinospora smilacina* Benth., Australia, Gray 8798 (MO), KY365675, JN051800, JN051865, EF624343, HQ260809, HQ260865. *Tinospora* sp., Indonesia, Chen ZD&Lu LM227 (PE), MK670930*, MK670933*, MK670935*, MK670937*, MK670943*, MK670946*. *Tinospora tenera* Miers, South Africa, OM1369, -, -, JX517669, -, JX573051, -. *Tinospora tinosporoides* (F.Muell.) Forman, Australia, 129307961, -, -, KM894867, -, KM896038, -.

OUTGROUPS: *Anamirta cocculus* (L.) Wight & Arn., Thailand, Wang HC 103 (HIB), FN870379, EF143887, EF143856, EF624262, FJ626591, HQ260815. *Arcangelisia flava* (L.) Merr., cult. Malaysia, F. Jacques 26 (P), FJ603109, JN051744, JN051810, EF624269, HQ260763, EU526980. *Coscinium fenestratum* Colebr., Sri Lanka, Chase 17404 (K), FJ603111, JN051757, JN051823, JN051706, FJ026479, FJ026419.

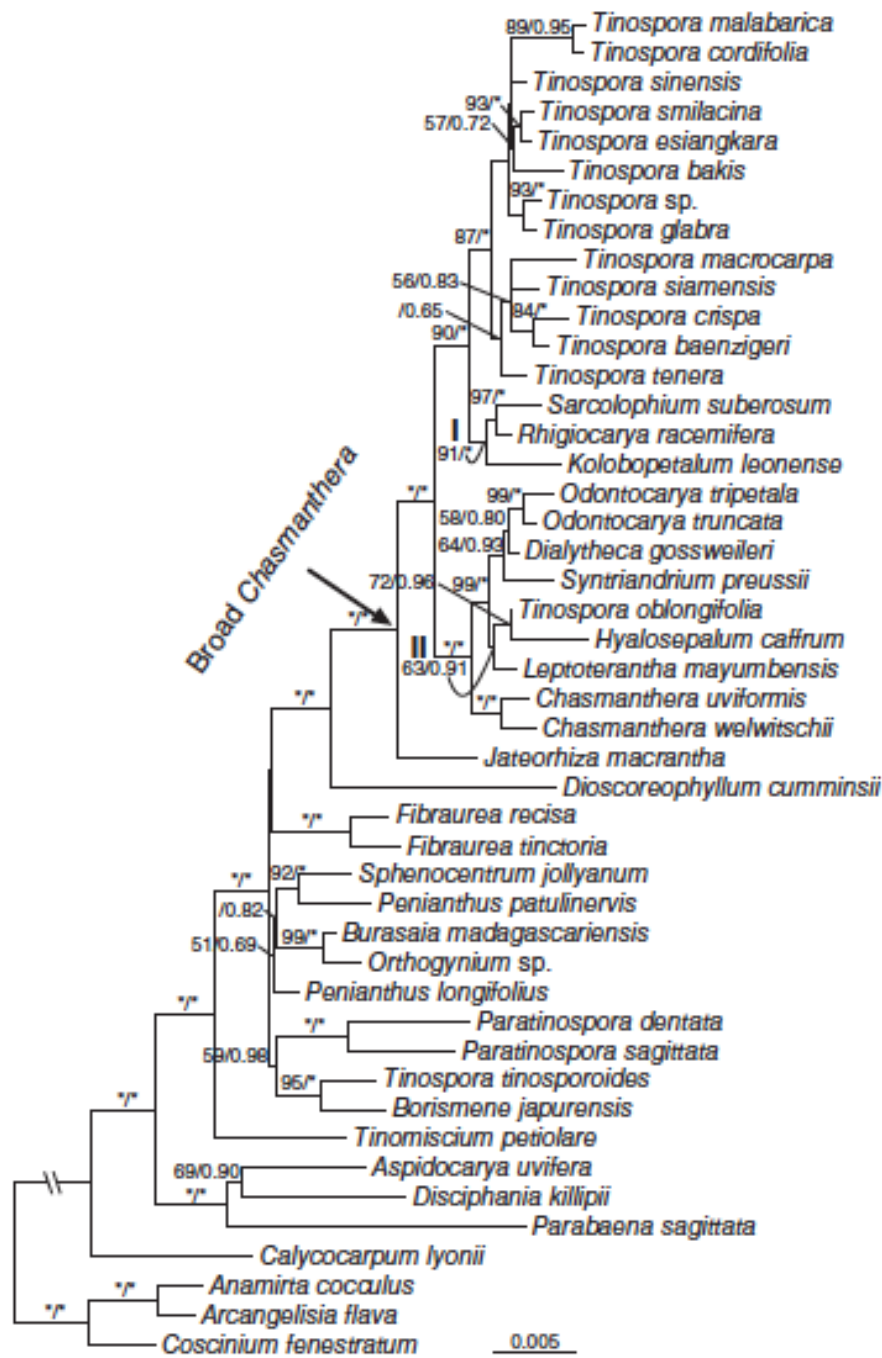


Fig. 1. ML tree inferred from the cpDNA dataset. Numbers above branches are bootstrap values (BS \geq 50%) and posterior probabilities (PP \geq 0.60). An asterisk (*) indicates BS = 100 or PP = 1.0.

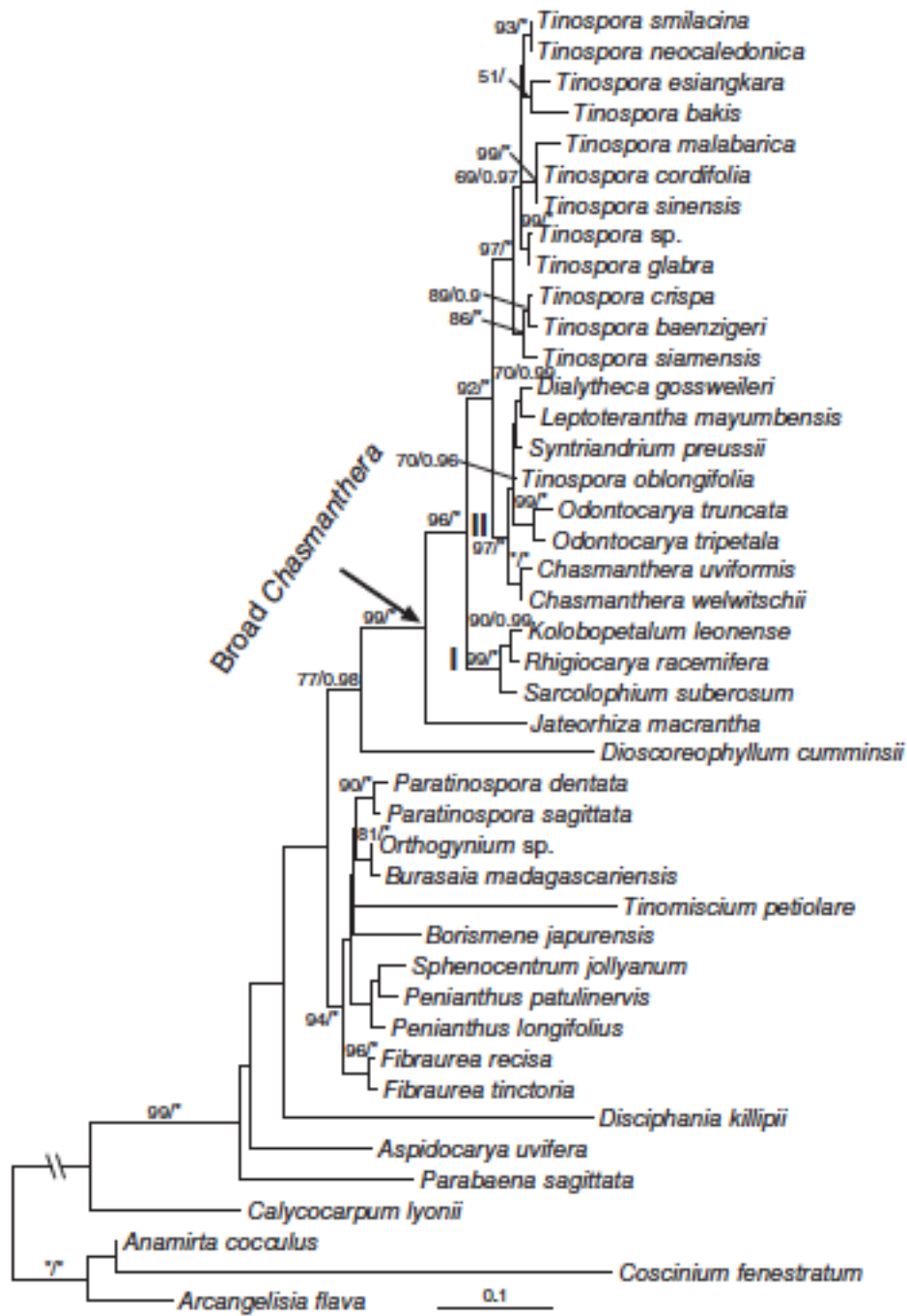


Fig. 2. ML tree inferred from the ITS dataset. Numbers above branches are bootstrap values (BS \geq 50%) and posterior probabilities (PP \geq 0.60). An asterisk (*) indicates BS = 100% or PP = 1.0.

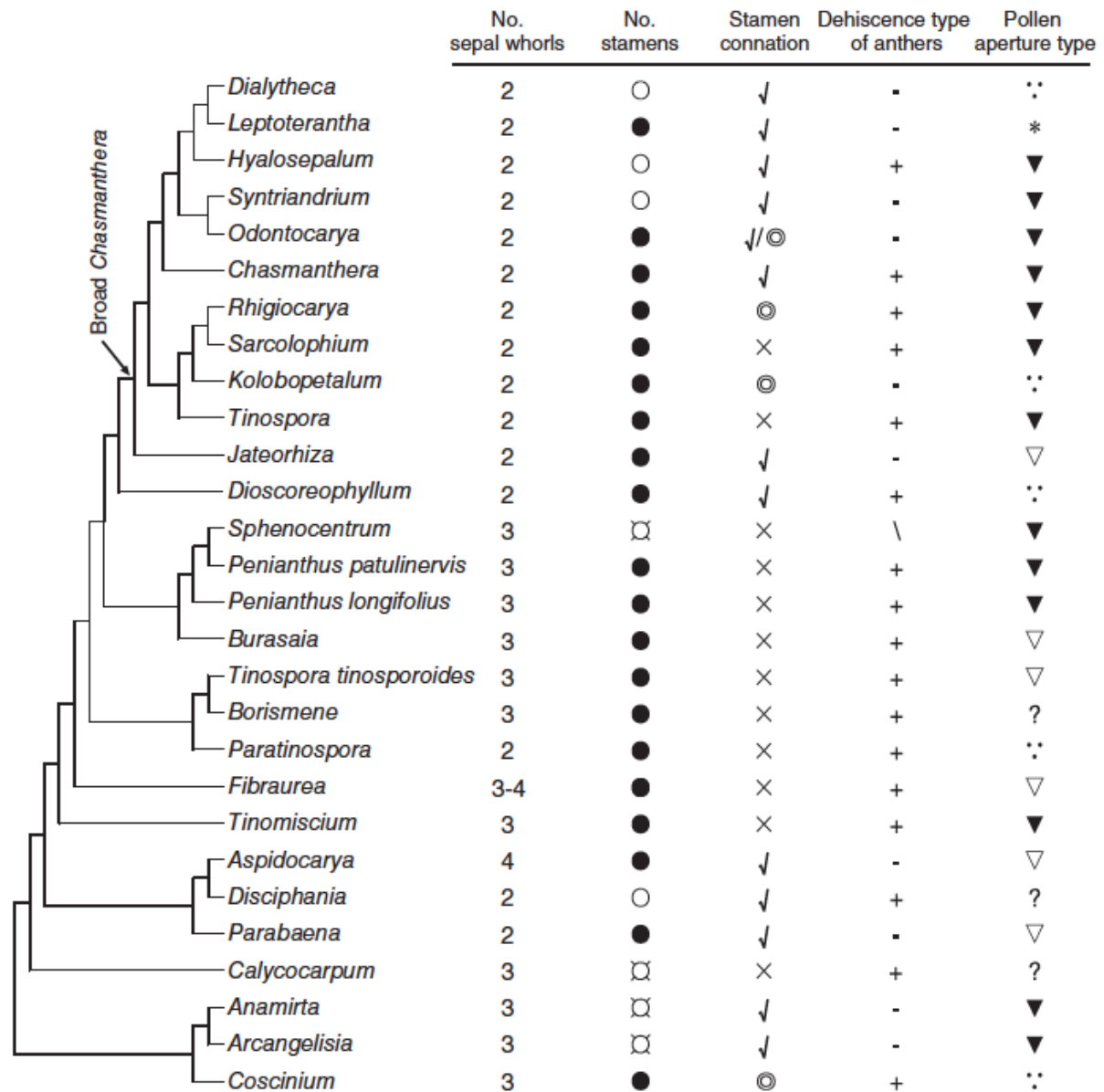


Fig. 3. Simplified ML tree generated from the combined cpDNA and ITS data showing the distribution of selected character states. Branches in bold indicate BS \geq 70% and PP \geq 0.95. Characters are: number of sepal whorls (2, 3, 4), number of stamens (○, 3; ●, 6; ⊘, \geq 9), stamen connation (⊘, no; √, yes; concentric circles, outer free and inner connate), dehiscence type of anthers (+, longitudinal; -, transversal; \, lateral), and pollen aperture type (∴, triporate; ▽, tricolpate; ▼, tricolporate; *, 6-cryptoporate; ?, missing data).

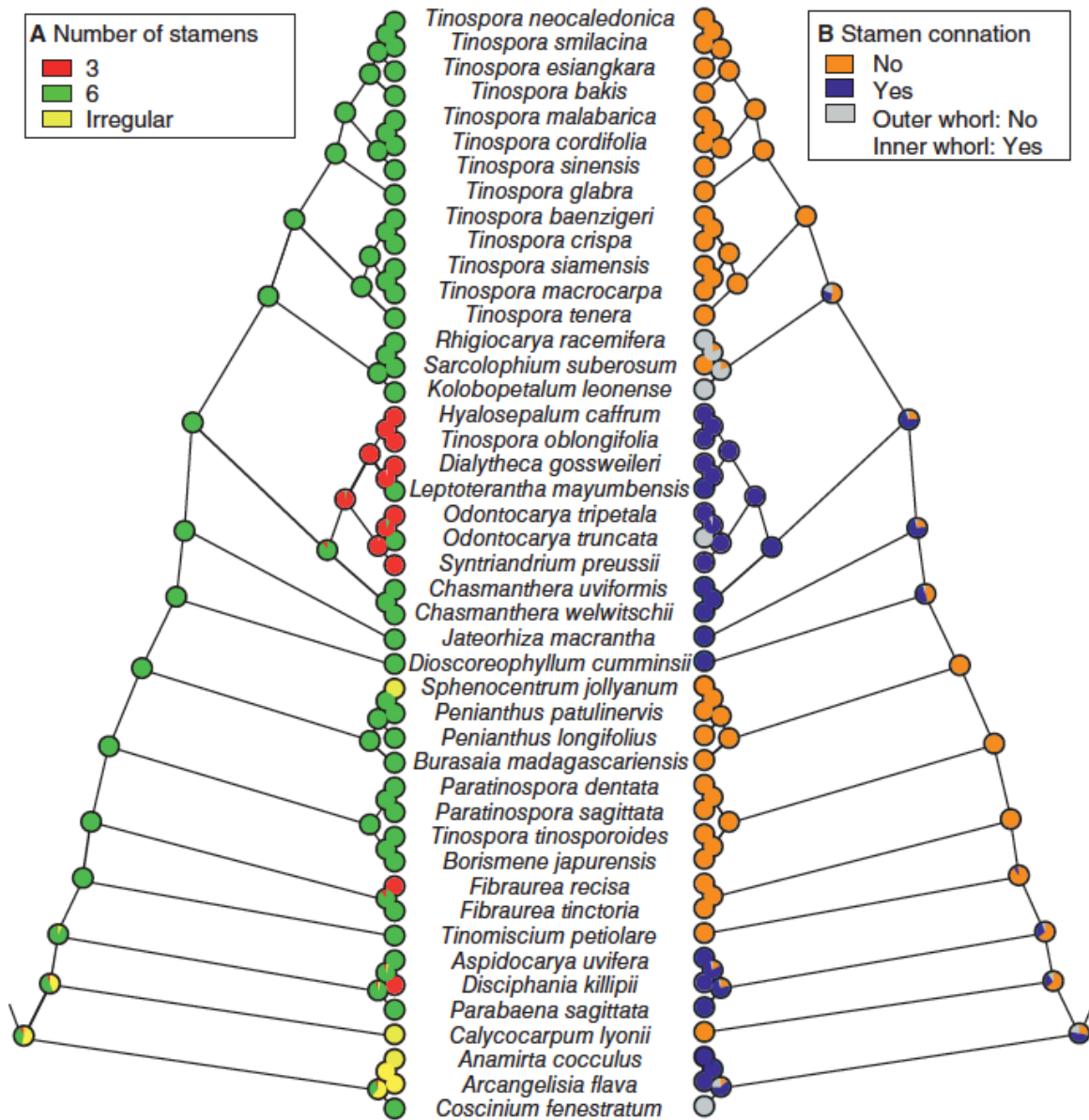


Fig. 4. Likelihood inference of character evolution in Burasaieae using Mesquite v.2.75 (Maddison & Maddison, 2011). A, Number of stamens; B, Stamen connation.

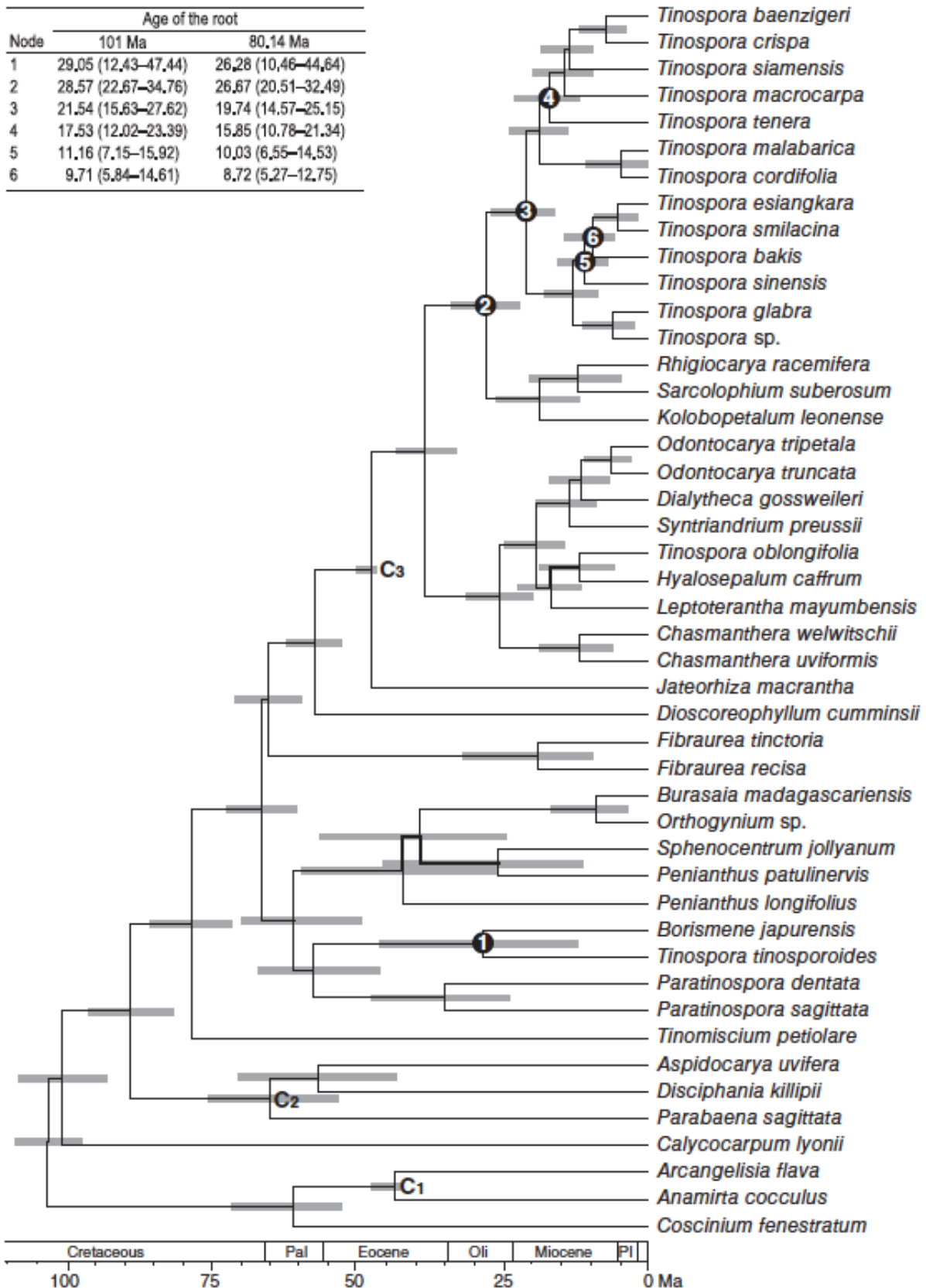


Fig. 5. Chronogram of Burasaieae based on the cpDNA data using BEAST with a 101 Ma maximum age for the root. Gray bars represent 95% highest posterior density intervals. The C1–3 indicate the locations of fossil calibration points. Nodes of interest were marked as 1–6. A comparison of estimated times for the nodes of interest is inserted in the upper left. Pal = Paleocene; Oli = Oligocene; Pl = Pliocene.

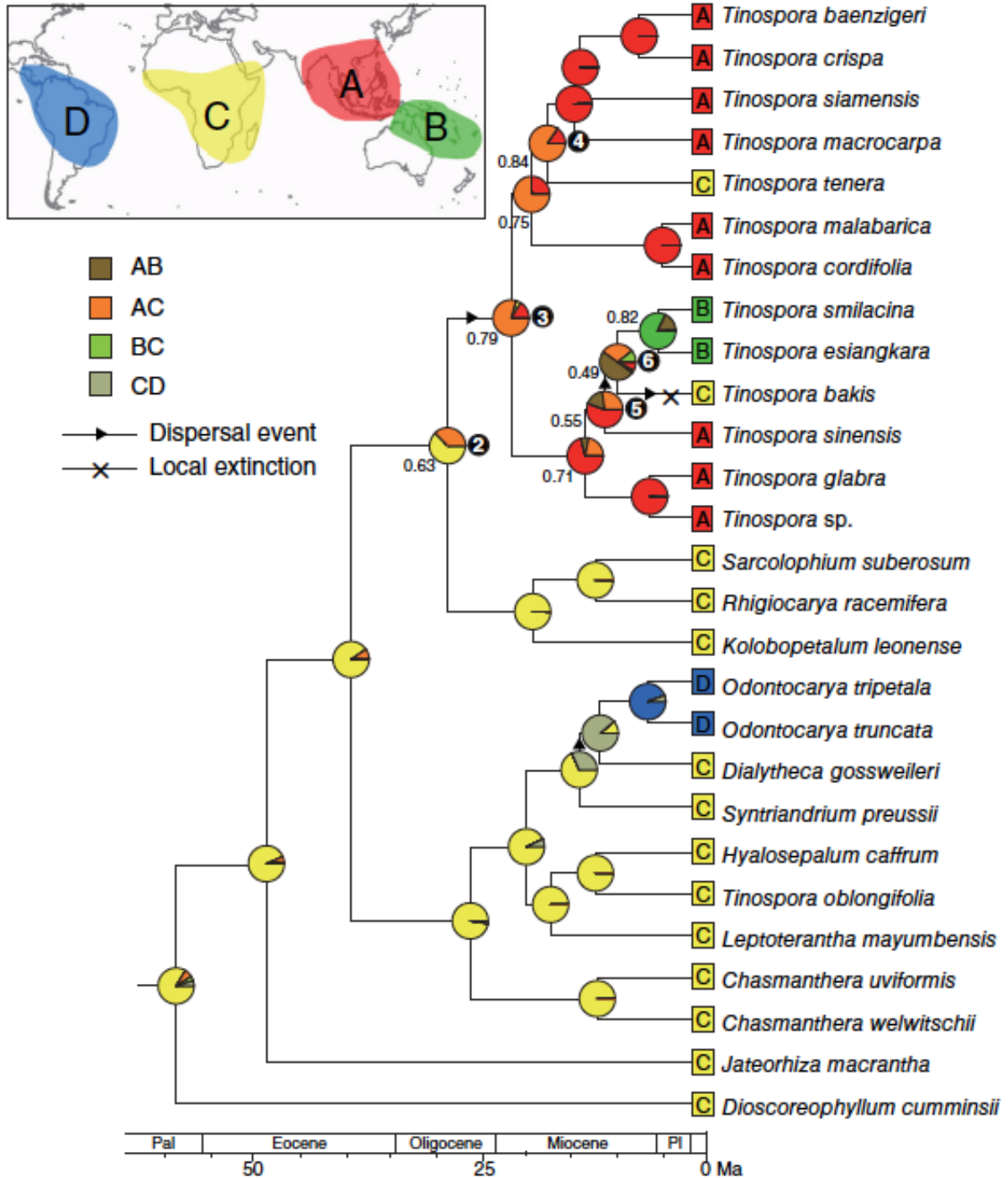


Fig. 6. Ancestral range reconstructions of the re-delimited *Tinospora* using BioGeoBEARS under the DEC model. Pie charts show the relative probabilities of alternative ancestral distributions, and numbers near the nodes indicate the highest ML probabilities. The node numbers correspond to those in Fig. 5. Pal = Paleocene; Pl = Pliocene.