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Phylogeny of the non-monophyletic *Cayratia* Juss. (Vitaceae) and implications for character evolution and biogeography

Limin Lu [a,b], Wei Wang [a], Zhiduan Chen [a,*], Jun Wen [c,*]

[a] *State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China*
[b] *Graduate School of Chinese Academy of Sciences, Beijing 100049, China*
[c] *Department of Botany, National Museum of Natural History, MRC166, Smithsonian Institution, Washington, DC 20013-7012, USA*

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ABSTRACT

Cayratia consists of ca. 60 species primarily distributed in the tropical and subtropical regions of Asia, Australia, and Africa. It is an excellent candidate for exploring the evolution of intercontinental disjunct distributions in the Old World. Previous phylogenetic work of Vitaceae with a few species of *Cayratia* sampled showed that *Cayratia* was not monophyletic and was closely related to *Cyphostemma* and *Tetrastigma*. We herein expanded taxon sampling of *Cayratia* (25/60 species) with its allied genera *Cyphostemma* (39/150 species), *Tetrastigma* (27/95 species), and other related genera from Vitaceae represented, employing five plastid markers (*atpB-rbcL*, *rps16*, *trnC-petN*, *trnH-psbA*, and *trnL-F*), to investigate the phylogeny, character evolution and biogeography of *Cayratia*. The phylogenetic analyses have confirmed the monophyly of the *Cayratia-Cyphostemma-Tetrastigma* (CCT) clade and resolved *Cayratia* into three lineages: the African *Cayratia* clade, subg. *Cayratia*, and subg. *Discypharia*. The African *Cayratia* was supported as the first diverging lineage within the CCT clade and *Tetrastigma* is resolved as sister to subg. *Discypharia*. Character optimizations suggest that the presence/absence of a membrane enclosing the ventral infolds in seeds is an important character for the taxonomy of *Cayratia*. The presence of bracts on the lower part of the inflorescence axis is inferred to have arisen only once in *Cayratia*, but this character evolved several times in *Tetrastigma*. Both the branching pattern of tendrils and the leaf architecture are suggested as important infrageneric characters, but should be used cautiously because some states evolved multiple times. Ancestral area reconstruction and molecular dating suggest that the CCT clade originated from continental Africa in the late Cretaceous, and it then reached Asia twice independently in the late Cretaceous and late Oligocene, respectively. Several dispersals are inferred from Asia to Australia since the Eocene.

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1. Introduction

Vitaceae (the grape family) represents the earliest diverging lineage within the rosids (Jansen et al., 2006; Wang et al., 2009). The family consists of 14 genera and approximately 900 species primarily distributed in tropical regions (Wen, 2007; Wen et al., 2007). The family is economically important as the source for grapes, wine, and raisins (species of *Vitis* L.), as well as some ornamentals (e.g., *Parthenocissus quinquefolia* (L.) Planch., *P. tricuspidata* Planch., and *Tetrastigma planicaule* Gagnep.), and local medicines (e.g., *Ampelopsis japonica* Makino, *Cissus quadrangularis* L., and *Tetrastigma hemsleyanum* Diels & Gilg) (Wen, 2007). Species of Vitaceae can be divided into two major groups: the 5-merous group and the 4-merous group, based on perianth merosity (Ren et al., 2011; Wen et al., 2007). Recent phylogenetic analyses have greatly

contributed to our understanding of the relationships within Vitaceae at various taxonomic levels. Studies by Soejima and Wen (2006), Rossetto et al. (2007), Wen et al. (2007), Ren et al. (2011) and Trias-Blasi et al. (2012) have provided insights into the phylogenetic relationships at the family level. Excellent progresses have been made concerning the phylogeny, biogeography and genome evolution of the economically important genus *Vitis* (De Andres et al., 2012; Goremykin et al., 2009; Lin et al., 2011; Péros et al., 2011; Schaal et al., 2010; Tröndle et al., 2010; Wu et al., 2010). Furthermore, Nie et al. (2010), Chen et al. (2011a, 2011b), Lu et al. (2012), Nie et al. (2012), and Liu et al. (2013) have reconstructed the phylogeny and biogeography of *Parthenocissus*, *Tetrastigma*, *Ampelopsis* and *Cissus*, respectively. Some of the studies with a limited sampling scheme suggested that the 4-merous genus *Cayratia* Juss. was non-monophyletic and had a close but unresolved relationship with *Cyphostemma* (Planch.) Alston and *Tetrastigma* (Miq.) Planch. (Chen et al., 2011a; Ren et al., 2011; Rossetto et al., 2007, 2002; Soejima and Wen, 2006; Wen et al., 2007).

Cayratia (ca. 60 species) and its closely allied genera *Cyphostemma* (ca. 150 species) and *Tetrastigma* (ca. 95 species) include approximately 34% of the species diversity of the grape family. It is important to clarify the phylogenetic relationships among the three genera to better understand the evolution of Vitaceae.

Cayratia is widely distributed in the Old World tropics (Galet, 1967; Wen, 2007). Species of the genus are usually hermaphroditic herbaceous or woody climbers, sometimes with tuberous underground systems, and possess 4-merous flowers, and axillary, pseudo-axillary or leaf-opposed inflorescence. Different from *Cayratia*, *Cyphostemma* usually bears floral buds with a constriction near the middle (vs. straight in *Cayratia*) and *Tetrastigma* has its characteristic 4-lobed stigmas (vs. unlobed in *Cayratia*) (Chen et al., 2007; Li, 1998; Verdcourt, 1993; Wen, 2007). Süessenguth (1953) classified *Cayratia* into two sections: sect. *Koilosperma* Suess. and sect. *Discypharia* Suess., which was followed by Latiff (1981). Li (1998) divided the Chinese *Cayratia* into two subgenera: subg. *Cayratia* and subg. *Discypharia* C.L. Li based on seed morphology and inflorescence structure. In addition, the branching pattern of tendrils and the leaf architecture were usually recognized as important infrageneric taxonomic characters for Vitaceae (Li, 1998; Süessenguth, 1953). Nevertheless, these characters have never been evaluated using a phylogenetic framework.

Several phylogenetic analyses of the grape family have been conducted, but all had only a few species of *Cayratia* sampled (Ren et al., 2011; Rossetto et al., 2007; Soejima and Wen, 2006; Wen et al., 2007). A *Cayratia-Cyphostemma-Tetrastigma* or CCT clade was supported by these analyses and the monophyly of *Cyphostemma* and *Tetrastigma* was also well supported. *Cayratia* was initially supported as paraphyletic with *Cayratia japonica* (Thunb.) Gagnep. and its close relatives forming a clade with *Tetrastigma* (Rossetto et al., 2007, 2002; Soejima and Wen, 2006; Wen et al., 2007). With only several species from Africa and Asia sampled, Ren et al. (2011) resolved *Cayratia* into two lineages that seemed to correlate with their distribution in Africa and Asia. Phylogenetic analysis of *Tetrastigma* (Chen et al., 2011a) sampled eight species of *Cayratia* and showed that *Cayratia* formed three clades corresponding to their distributions. The phylogenetic relationships within *Cayratia* remain poorly understood due to the limited sampling in previous studies.

Understanding the origin, spread, and diversification of biotas has been an important common goal for many evolutionary biologists for centuries (Lomolino et al., 2006). Previous biogeographic analyses have emphasized temperate taxa in the Northern Hemisphere (Li, 1952; Wen, 1999; Xiang et al., 2000). With the availability of more global collections and the recently improved methods for dating and biogeographic analyses (Ronquist and Sanmartín, 2011), it has become possible to investigate biogeographic diversifications of tropical floras involving both Northern and Southern Hemispheres (Clayton et al., 2009; Nie et al., 2012; Wang et al., 2012; Zhou et al., 2012). *Cayratia* exhibits a broad Old World tropical distribution in Asia, Africa, Australia, and the Pacific Islands (Fig. 1A) and share some overlapping distribution with its close relatives *Cyphostemma* and *Tetrastigma* (Figs. 1B and C). *Cyphostemma* is mainly distributed in Africa and Madagascar, with only two species in India and Sri Lanka, extending into Thailand (J. Wen, pers. observ.), and *Tetrastigma* is primarily in the tropical and subtropical Asia with five species in Australia (Wen, 2007). The CCT clade thus represents an excellent candidate to explore the evolution of tropical intercontinental disjunctions concerning both Northern and Southern Hemispheres in the Old World.

The objectives in this study are primarily to: (1) reconstruct the phylogenetic relationships of *Cayratia* within the CCT clade using five plastid loci; (2) interpret evolution of key morphological characters; and (3) explore the historical biogeography of *Cayratia* and its close relatives.

2. Materials and methods

2.1. Taxon sampling, DNA extraction, amplification, and sequencing

The study sampled 171 individuals representing 25 species of *Cayratia*, 39 species of *Cyphostemma*, 27 species of *Tetrastigma*, and 29 species of other genera of Vitaceae and Leeaceae. Five plastid markers including *atpB-rbcL*, *rps16*, *trnC-petN*, *trnH-psbA*, and *trnL-F* were sequenced. Our sampling of *Cayratia* represented its biogeographic distribution in Africa, Asia, Australia and Madagascar (Fig. 1A) and included a wide range of morphological variation. Two to three representatives from the eight major lineages of *Tetrastigma* were sampled based on Chen et al. (2011a). Sampling of *Cyphostemma* also represented its distribution in Africa, Asia, and Madagascar. We also included 27 taxa from other genera of Vitaceae to place our analyses in a broad phylogenetic framework. Two species of *Leea* (*L. guineensis* G. Don and *L. indica* (Burm. f.) Merr.) (Leeaceae, the sister family of Vitaceae) were selected as outgroups based on Soejima and Wen (2006). Voucher information and GenBank accession numbers are listed in Appendix A.

Total genomic DNAs were extracted from silica gel-dried leaves or herbarium material using a DNeasy Plant Mini Kit (Qiagen, Crawley, UK). Amplification protocol and primers for amplifying *atpB-rbcL*, *rps16*, *trnC-petN*, *trnH-psbA*, and *trnL-F* followed Soejima and Wen (2006), Chen et al. (2011a) and Ren et al. (2011). The amplified products were purified using the polyethylene glycol (PEG) precipitation (Wen et al., 2007). Cycle sequencing was conducted using the BigDye 3.1 reagents with an ABI 3730 automated sequencer (Applied Biosystems, Foster City, CA, USA). The program Sequencher 5.0 (Gene Codes Co., Ann Arbor, Michigan, USA) was used to evaluate chromatograms for base confirmation and to edit contiguous sequences. Sequence alignment was initially aligned using MUSCLE 3.8.31 (Edgar, 2004), followed by manual adjustments in Geneious 5.5.6 (Drummond et al., 2011).

2.2. Phylogenetic analyses

Phylogenetic analyses were initially conducted for individual DNA regions/markers using the maximum parsimony (MP) method with bootstrap analyses (BS). Results of the individual analyses revealed no well-supported topological conflicts (i.e., incongruences with BS >70%; Hillis and Bull, 1993) among individual markers. We thus conducted further analyses using the combined 5-locus data set with MP, Bayesian inference (BI), and maximum likelihood (ML) methods on a matrix including 171 taxa.

MP analysis was conducted in PAUP* 4.0 b10 (Swofford, 2003) with a heuristic search strategy followed by random addition starting trees with tree-bisection-reconnection (TBR) branch swapping and MulTrees selected. Gaps were treated either as missing data or coded as simple indels (Simmons and Ochoterena, 2000) using the program SeqState (Müller, 2005). Bootstrap values (BS) were obtained from 1000 replicates of heuristic searches as described above (TBR branch swapping, and MulTrees selected), but with branch swapping limited to 10,000,000 rearrangements per replicate due to memory constraints (Felsenstein, 1985).

The model-based analyses (BI and ML) were conducted in MrBayes 3.2.1 (Ronquist and Huelsenbeck, 2003) and RAxML 7.2.6 (Stamatakis, 2006), respectively. Prior to analysis, the best-fitting models for each of the five plastid data partitions, as well as for the combined dataset, were determined under the Akaike Information Criterion (AIC) as implemented in MrModeltest 2.3 (Nylander, 2004). The generalized time reversible model (GTR) (Tavaré, 1986) with a gamma-distributed rate variation (G) (Yang, 1993) was suggested as the most appropriate nucleotide substitution model for each of the five plastid regions and the combined
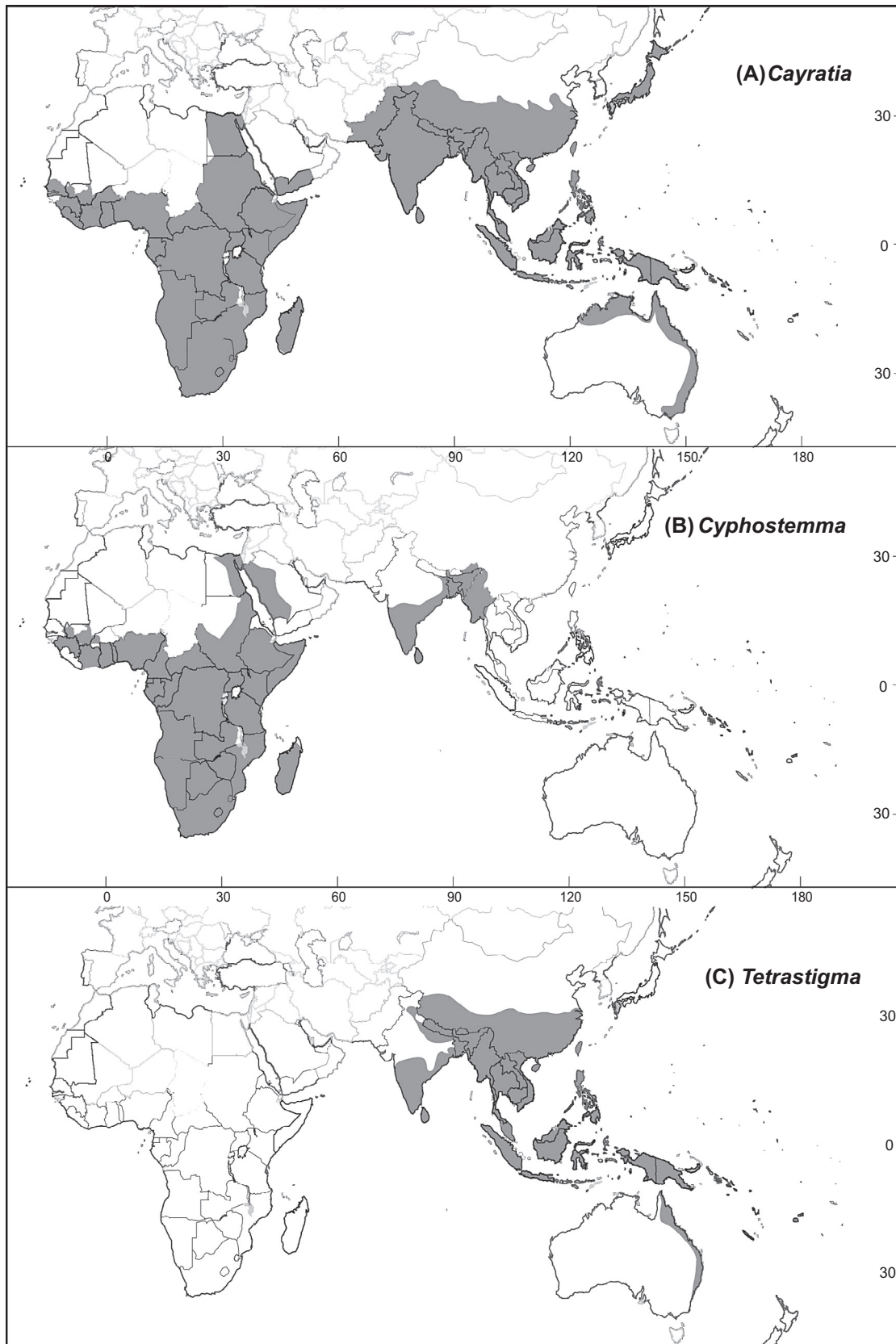
Fig. 1. Geographic distribution of *Cayratia* (A), *Cyphostemma* (B), and *Tetrastigma* (C).

dataset. A partitioned Bayesian analysis of the five datasets was then implemented by applying the GTR + G model as determined above. Analyses were run until the average standard deviation of the split frequencies approached 0.01, indicating that two runs converged onto a stationary distribution. Bayesian inference for the combined dataset was run with two replicates for 20,000,000

generations, sampling one tree every 2000 generations. With the first 2,500,000 generations (2500 trees) discarded as burn-in, a 50% majority-rule consensus tree and posterior probabilities (PP) were obtained using the remaining trees. A partitioned ML analysis was carried out using RAxML, with 1000 bootstrap replicates. The best-fitting models for each of the data partitions and the combined data in the ML analysis were the same as those used in the BI analysis.

2.3. Character evolution

Four characters concerning inflorescence structure, seed morphology, leaf architecture, and tendril morphology were selected for ancestral character optimization. *Cayratia* was divided into two subgenera (Li, 1998) or sections (Süessenguth, 1953) largely based on whether a membrane is present to enclose the ventral infolds of seeds and/or whether bracts are present on the lower part of inflorescence axis (also see Chen et al., 2007; Latiff, 1981). Branching pattern of tendrils and leaf architecture are quite polymorphic within Vitaceae and they have usually been highlighted in infrageneric classifications in the family (Jackes, 1987; Latiff, 1981; Li, 1998; Süessenguth, 1953). To evaluate their taxonomic significance, we traced these two characters on a data set with all major lineages of Vitaceae represented. Five character states were defined for the tendril branching pattern: (1) 2–3 branched; (2) simple; (3) absent; (4) digitately branched; and (5) 3–5-racemosely branched. Five states of leaf architecture were recognized: (1) simple; (2) trifoliate; (3) digitate; (4) pedate; and (5) pinnate.

The evolutionary history of each of the four characters was traced over the Bayesian 50% majority-rule tree with 127 taxa sampled, using both MP and ML approaches available in Mesquite 2.75 (Maddison and Maddison, 2011). In the MP reconstruction, the character states were treated as unordered. The ML reconstructions relied on the Markov k-state one-parameter model. Only MP reconstruction was conducted for leaf architecture because the polymorphism in some taxa was not allowed for the ML analyses (Xiang and Thomas, 2008). We used the "Trace Character History" option to reconstruct each character.

2.4. Molecular dating

We estimated the divergence time of clades on a combined plastid (*atpB-rbcL*, *rps16*, *trnC-petN*, *trnH-psbA*, and *trnL-F*) matrix including 127 representatives from the entire grape family. Duplicated sampling from *Cayratia* was reduced with only one accession retained per species, except that the widespread species and morphologically variable *Cayratia japonica* (Ren et al., 2011) was represented by three accessions to cover its geographic range. The strict molecular clock model was rejected from our dataset based on a likelihood ratio test. We thus estimated divergence time using a Bayesian relaxed clock model with rate variation across branches uncorrelated and lognormally distributed as accomplished in BEAST 1.7.0 (Drummond and Rambaut, 2007). The data set was partitioned into five subsets corresponding to five plastid regions with unlinked substitution models as in the Bayesian analysis. To satisfy the temporal and topological constraints, we specified a starting tree derived from the majority-rule consensus tree of the BI analyses. All dating runs relied on the GTR + G model (with four rate categories) and a Yule process tree prior. Two separate Markov chain Monte Carlo (MCMC) analyses were run, each with 100,000,000 generations and sampling every 10,000 generations. The program Tracer 1.5 (Rambaut and Drummond, 2007) was used to check that effective sample size (ESS) for all relevant parameters were well above 200 and that stationarity probably had been reached. Maximum clade credibility tree was then built using TreeAnnotator 1.7.0 (beast.bio.ed.ac.uk/TreeAnnotator) with the ini-

tial 25% of trees discarded as burn-in. Final tree was edited in FigTree 1.3.1 (Rambaut, 2009) to view dates of all nodes and variation of rate of substitutions on branches.

The family Vitaceae has abundant fossil records including leaves, pollen, stems, and seeds. However, many fossils of leaves and pollen grains assigned to this family have been questioned because it was difficult to distinguish from other angiosperm families with similar characters (Chen and Manchester, 2007). Seeds of Vitaceae can be recognized by series of unique characters such as a dorsal chalaza and a pair of ventral infolds, and fossil seeds of Vitaceae frequently have been identified to extant genera (Chen and Manchester, 2007; Chen, 2009). Vitaceae has a rich record of fossil seeds in the Tertiary. *Ampelocissus parvisemina* Chen & Manchester from the Beicegala Creek locality in North Dakota (56.8–62.0 Ma) was known as the oldest Vitaceae fossil (Chen and Manchester, 2007), and was either constrained at the crown or stem of the *Ampelocissus-Vitis* clade because previous poorly resolved relationship between *Ampelocissus* and its relatives (Chen et al., 2011b; Liu et al., 2013; Nie et al., 2010, 2012). *Ampelocissus parvisemina* was inferred as an early member of the *Ampelocissus* clade, which can be distinguished from *Vitis* by its wider ventral infolds (Chen and Manchester, 2007). In the current study, *Ampelocissus* was resolved as non-monophyletic with *Nothocissus*, *Pterisanthes*, and *Vitis* nested in. We thus fixed *Ampelocissus parvisemina* to the crown of the *Ampelocissus-Vitis* clade with a lognormal distribution (mean: 58.5 Ma; log (stdev): 0.03; offset: 0 Ma; mean in real space) to include the 95% HPD interval of the fossil date (56.8 –62 Ma). We did not use any fossils from the CCT clade, because no reliable fossils have been confirmed to *Cayratia*, *Cyphostemma* or *Tetrastigma* (Chen, 2009; Chen and Manchester, 2007; Tiffney and Barghoorn, 1976). Following Nie et al. (2012) and Liu et al. (2013), we constrained the stem age of Vitaceae as 90.7 ± 1.0 with a normal prior distribution based on the estimated age of 90.65–90.82 Ma by Magallón and Castillo (2009).

2.5. Ancestral area reconstruction

Ancestral areas at internal nodes within the phylogenetic tree were inferred using two methods: (1) a Bayesian approach to dispersal-vicariance analysis (Bayes-DIVA) (Nylander et al., 2008) implemented in the software package RASP (Yu et al., 2011); (2) a likelihood approach using the dispersal-extinction-cladogenesis (DEC) model implemented in Lagrange 20120508 (Ree and Smith, 2008). Five areas of endemism were defined to cover the distributional range of *Cayratia* and its relatives: A, Asia (including the Sino-Himalayan, Indochina, and Malesian regions); B, Australia (including continental Australia and New Guinea); C, continental Africa; D, Madagascar; and E, the New World. The New World is defined broadly, as none of the species in the CCT clade is distributed in the area. The current species distribution was mainly based on herbarium and literature studies. For the Bayes-DIVA, we sampled 10,000 trees from the BEAST analysis and computed a condense tree as the final representative tree with the first 2500 trees discarded as burn-in to account for the phylogenetic uncertainty in the biogeographic analysis. Relative frequencies of ancestral areas reconstructed for each node were recorded and plotted onto the maximum clade credibility tree of the BEAST analysis. For the likelihood ancestral area analysis, python scripts were generated using the online Lagrange configurator (http://www.reelab.net/lagrange/configurator). The MCC tree of the BEAST analysis was used as the input tree. The probability of dispersal between areas was modelled as equal, and all values in the dispersal constraint matrix were set to 1. In both analyses, the maximum number of areas in ancestral ranges was constrained to two, as no species of the CCT clade is distributed in more than two areas of endemism (Chen et al., 2011b).

3. Results

3.1. Phylogenetic relationships

The aligned positions of atpB-rbcL, rps16, trnC-petN, trnH-psbA, and trnL-F datasets were 981, 1103, 1168, 741 and 1097 base pairs, respectively. The combined matrix of the five markers consisted of 5151 characters with 1833 variable characters and 1221 parsimony-informative characters. Parsimony analysis retrieved more than 100,000 most parsimonious trees (MPTs) (length = 3470 steps; CI = 0.661; RI = 0.915) with gaps treated as missing data. MP and BI analyses with gaps treated as new characters generated a similar topology as well as support values with those when gaps were treated as missing data. Thus only the strict consensus tree of the combined data set, treating gaps as missing data, with PP values, and BS values from both MP and ML analyses was presented in Fig. 2.

Cayratia, Cyphostemma, and Tetrastigma formed a strongly supported monophyletic group (PP = 1.0 and BS = 100%). Five major clades were detected within the CCT clade: Cyphostemma, Tetrastigma, and three lineages from Cayratia (Fig. 2). Cayratia species from Africa were supported as monophyletic (PP = 1.0 and BS = 100%) with the current sampling. This African Cayratia clade was sister to the clade of all remaining species from the CCT clade. Cayratia species from Asia and Australia were resolved as two distinct and strongly supported clades corresponding to the two subgenera (subg. Cayratia and subg. Discypharia) (e.g., Li, 1998), or sections (sect. Koilosperma and sect. Discypharia) (Latiff, 1981; Süessenguth, 1953). Furthermore, Tetrastigma was strongly supported (PP = 1.0 and BS = 98%) as sister to the clade including species from subg. Discypharia.

3.2. Character evolution

Ancestral character state optimization (characters 1, 2, and 3) based on ML and MP methods yielded similar results and only reconstructions with ML were shown in Figs. 3 and 4. For characters 1 and 2, "absent" was inferred to be the ancestral state in the CCT clade. Reconstructions of character 1 indicated that presence of membrane over ventral infolds was derived only once in the CCT clade. Whereas reconstruction for character 2 suggested that bracts present on the lower part of inflorescence axis was not unique in Cayratia and evolved multiple times in Tetrastigma. Optimization for branching pattern of tendrils suggested that the 2–3 branched tendrils was the ancestral state in the CCT clade (Fig. 4). Simple tendril was detected in Cyphostemma and Tetrastigma, which was also quite common in the 5-merous taxa of Vitaceae. Absence of tendrils seems to be unique in Cyphostemma but has evolved multiple times. The parsimony reconstruction of leaf architecture suggests the pedate leaves as ancestral, which has evolved multiple times within the CCT clade. Nevertheless, the pedate leaves are only rarely observed in the extant taxa of Cissus and the 5-merous taxa of Vitaceae. Simple leaves rarely occur within the CCT clade (once in Cyphostemma), but are very common in the 5-merous group. Both the digitate and trifoliate leaves have evolved multiple times in the CCT clade. The pinnate leaves may have evolved at least three times in Vitaceae (in Ampelopsis, Cayratia, and Cyphostemma).

3.3. Biogeography and divergence times

Divergence time estimates for the CCT clade and other representative groups from Vitaceae are presented in Fig. 5. Ancestral area reconstruction using ML in Lagrange and Bayes-DIVA in RASP yielded similar results (see Table 1). Results with highest relative probability from Lagrange are shown in Fig. 6. The CCT clade was estimated to have diverged from its closest relatives at 79.88 Ma (95% HPD: 72.11 –86.88 Ma; node 0, Fig. 5), and diverged initially at 68.49 Ma (95%HPD: 58.61–77.45 Ma; node 1, Fig. 5) in continental Africa during the late Cretaceous (node 1, Fig. 6). The most recent common ancestor of the CCT clade was in continental Africa, followed by two dispersals to Asia. The first dispersal (node 3, Fig. 6) gave rise to Tetrastigma and two subgenera of Cayratia and the second dispersal (node 12, Fig. 6) with Cyphostemma colonized Asia. Several independent migrations from Asia to Australia were detected within Cayratia (Fig. 6). The crown ages of the monophyletic genera Tetrastigma and Cyphostemma were estimated to be 47.59 Ma (95% HPD: 36.36–59.42 Ma) and 34.27 Ma (95% HPD: 22.32–46.96 Ma), respectively. African Cayratia was the first diverging lineage, but the crown of African Cayratia clade was dated to 23.19 Ma (95% HPD: 11.44 –37.98 Ma; node 2). Subgenus Cayratia began its diversification around 34.52 Ma (95% HPD: 21.80–48.67 Ma; node 5), and the crown of subgenus Discypharia was estimated as 47.04 Ma (95% HPD: 36.02 –58.31 Ma; node 9).

4. Discussion

4.1. Phylogenetic relationships

The close relationship among Cayratia, Cyphostemma, and Tetrastigma has been suggested by previous phylogenetic analyses (Chen et al., 2011a; Ren et al., 2011; Rossetto et al., 2007, 2002; Soejima and Wen, 2006; Wen et al., 2007). In particular, Chen et al. (2011a) reported that Cayratia had three subclades corresponding to their distributions with Tetrastigma nested within it. However, their study mainly focused on Tetrastigma and sampled only eight species of Cayratia. Our results support that Cayratia, Cyphostemma, and Tetrastigma form a robust clade (BS = 100%, PP = 1.00). With the current sampling, Cyphostemma and Tetrastigma are both resolved as monophyletic. While Cayratia is not monophyletic, three lineages within the genus are detected (Fig. 2). Different from Chen et al. (2011a), the three lineages supported by our study are not completely corresponding to their distributions. The African Cayratia forms a distinct clade with our current sampling, and species from Asia and Australia form two strongly supported clades. Instead of corresponding to their distribution in Asia and Australia, these two clades are supported to be correlated with the two subgenera: Cayratia and Discypharia, based on seed and inflorescence morphology of the Chinese species (Li, 1998). Subgenus Cayratia is defined as having a membrane enclosing ventral infolds in seeds, and bracts subtending the lower part of inflorescence axis, whereas subgenus Discypharia does not possess these two character states. The Australian endemic species Cayratia clematidea (F. Muell.) Domin is resolved as sister to the clade of all other species from subgenus Discypharia. The other five Australian (including New Guinea) endemic species (Cayratia acris (F. Muell.) Domin, C. cardiophylla Jackes, C. grandifolia (Warb.) Merr. & L.M. Perry, C. saponaria (Benth.) Domin, and C. schumanniana (Gilg) Suess.) are inferred as the second diverged lineage in subgenus Cayratia (Fig. 2). Our phylogenetic results suggest the need to redefine Cayratia more narrowly, and raise subg. Discypharia to the generic rank, and describe the African Cayratia clade as a new genus. The taxonomic treatment will be provided in a separate paper (J. Wen, L.M. Lu, and Z.D. Chen, in prep.).

4.2. Morphological character evolution

Our character optimizations suggest that the membrane enclosing the ventral infolds in seeds (character 1) evolved only once in Cayratia, but the bracts on the lower part of inflorescence axis
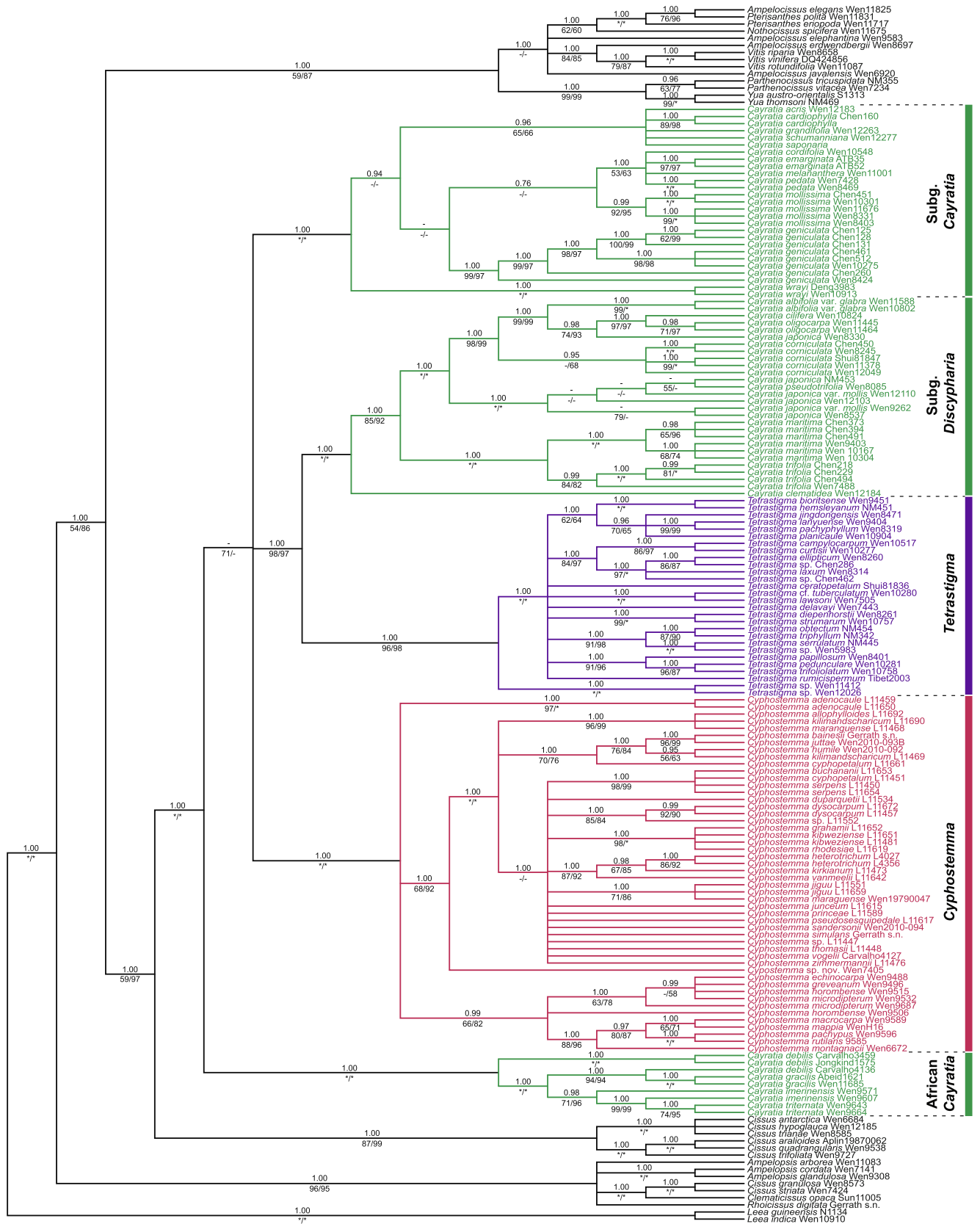
Fig. 2. Strict consensus tree of *Cayratia* and its close relatives obtained from maximum parsimony analysis of the combined plastid data set. Posterior probabilities displayed above branches and parsimony and likelihood bootstrap values displayed below branches ("*" represents BS = 100%; "−" indicates BS < 50%). Specimen details are listed in Appendix A.
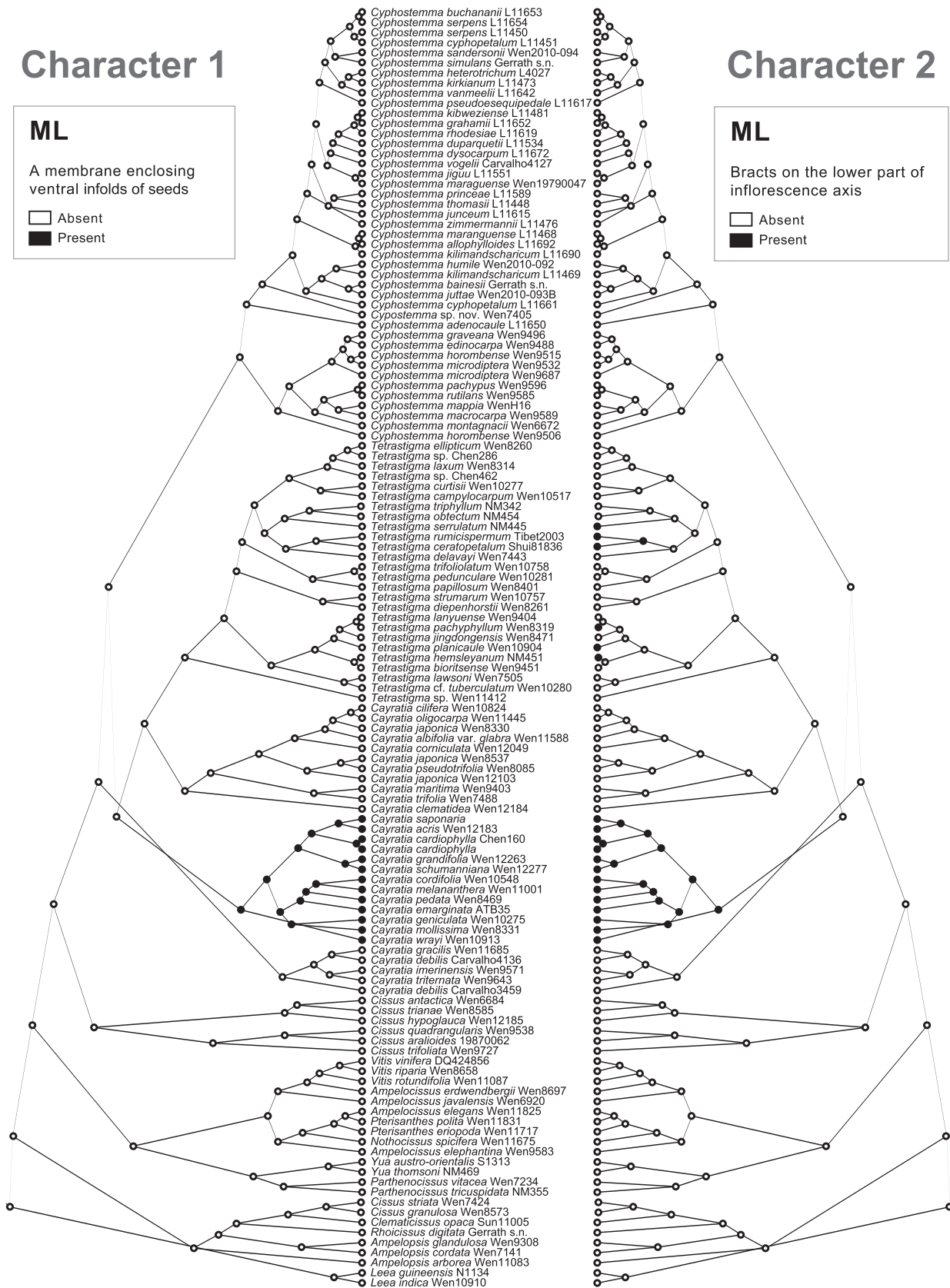
Fig. 3. Character optimization for the membrane enclosing ventral infolds of seeds (character 1) and bracts on the lower part of inflorescence axis (character 2) inferred on a Bayesian majority-rule tree for 127 taxa, using the maximum likelihood method.
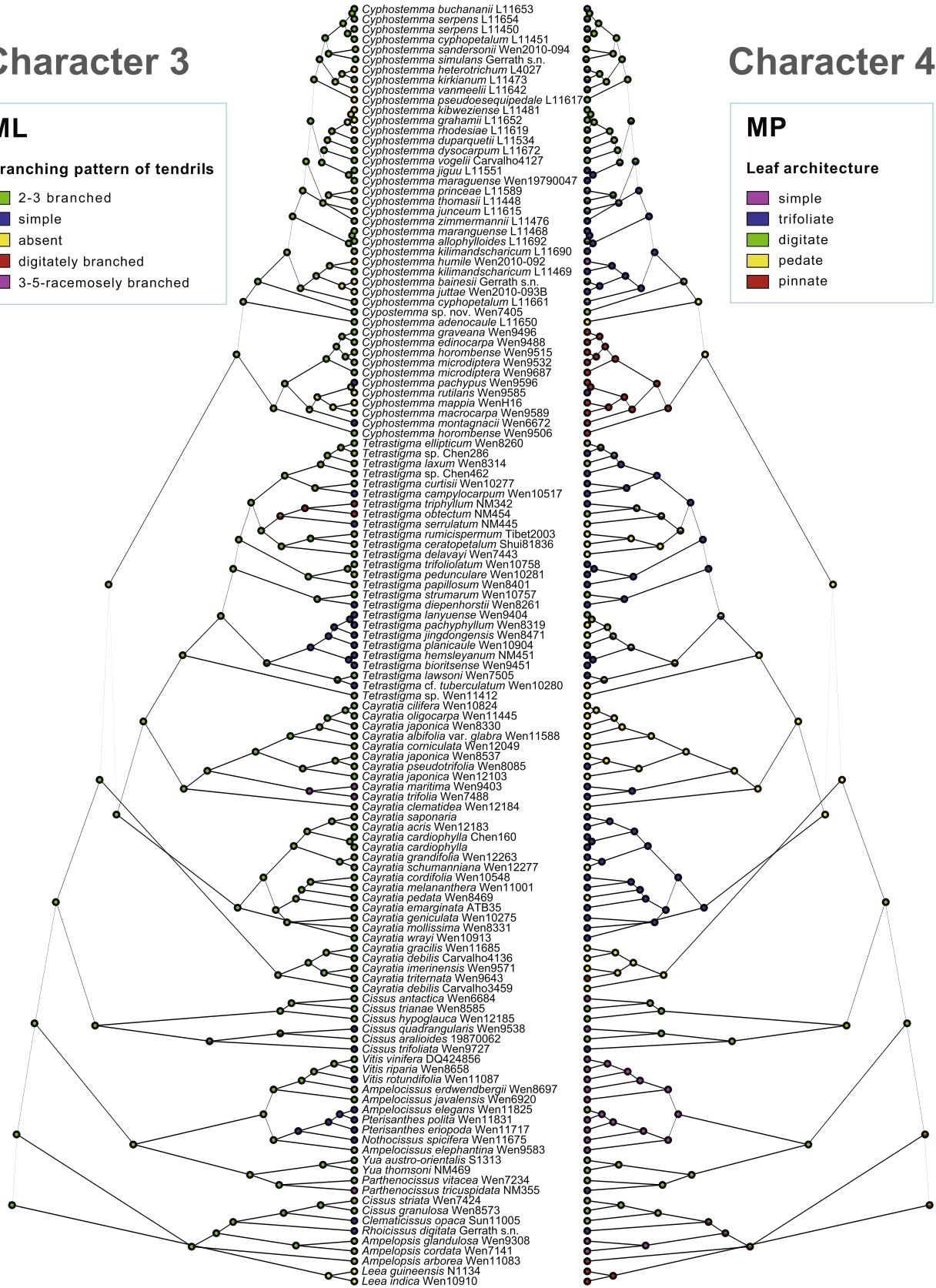
Fig. 4. Character optimization for branching pattern of tendrils (character 3) and leaf architecture (character 4) inferred on a Bayesian majority-rule tree for 127 taxa, based on the maximum likelihood and the maximum parsimony method, respectively.
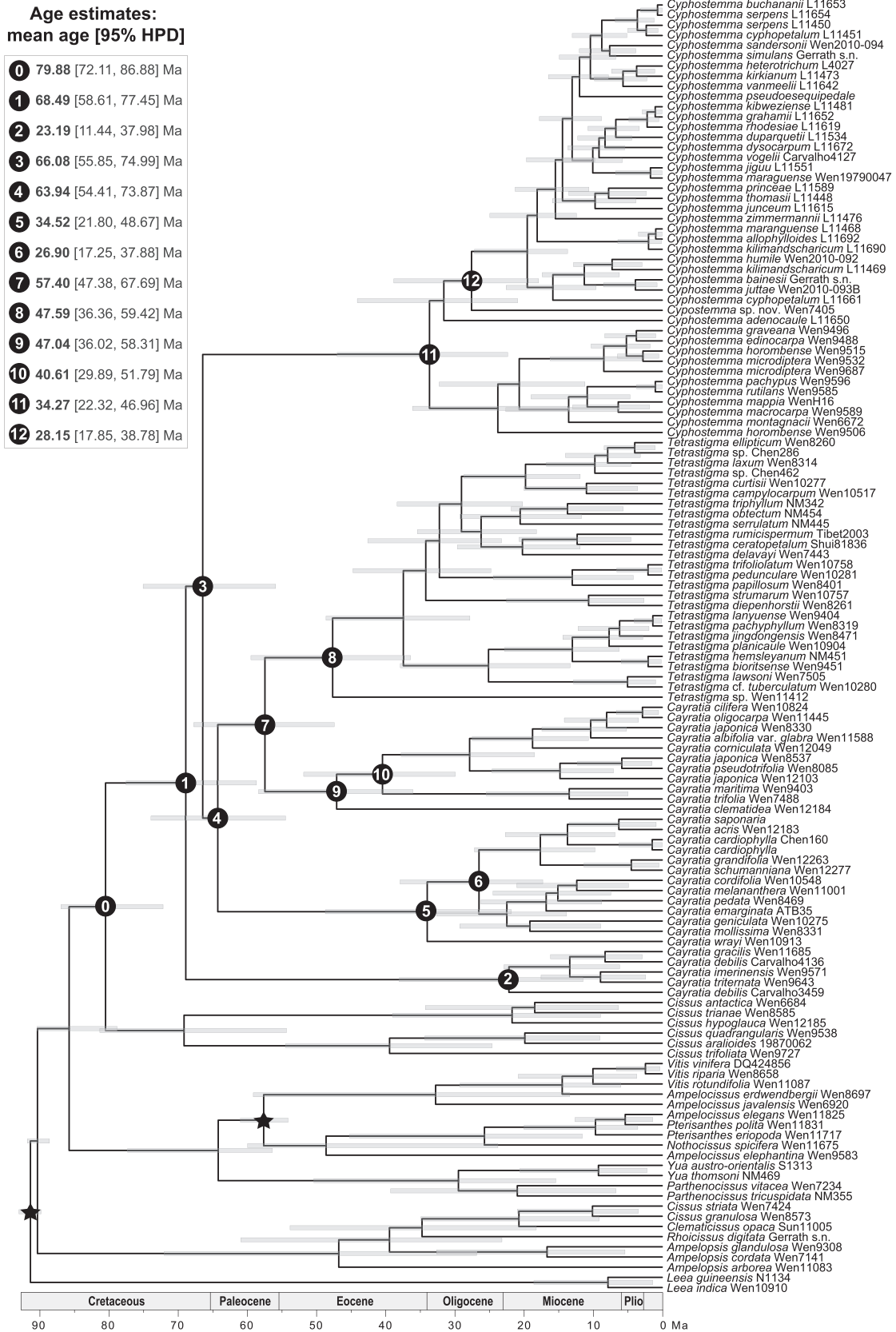
Age estimates:
mean age [95% HPD]

0	**79.88**	[72.11, 86.88] Ma
1	**68.49**	[58.61, 77.45] Ma
2	**23.19**	[11.44, 37.98] Ma
3	**66.08**	[55.85, 74.99] Ma
4	**63.94**	[54.41, 73.87] Ma
5	**34.52**	[21.80, 48.67] Ma
6	**26.90**	[17.25, 37.88] Ma
7	**57.40**	[47.38, 67.69] Ma
8	**47.59**	[36.36, 59.42] Ma
9	**47.04**	[36.02, 58.31] Ma
10	**40.61**	[29.89, 51.79] Ma
11	**34.27**	[22.32, 46.96] Ma
12	**28.15**	[17.85, 38.78] Ma

Fig. 5. Maximum clade credibility tree inferred from combined *atpB-rbcL*, *rps16*, *trnC-petN*, *trnH-psbA*, and *trnL-F* data using BEAST. Gray bars indicate 95% highest posterior density intervals. Clade constraints are indicated with black asterisks. Nodes of interests were marked as 0–12.

Table 1

Clade support, divergence age estimates (Ma) and ancestral area reconstructions with ML and Bayes-DIVA. Node numbers refer to Figs. 5 and 6. Area abbreviations are as follows: A, Asia; B, Australia (including New Guinea); C, continental Africa; D, Madagascar; and E, the New World. The vertical bar indicates the split of areas into two daughter lineages, i.e., upper branch | lower branch and only relative probability >0.1 are given.

Node	Bayesian PP	Age estimates mean (95% HPD) [Ma]	Likelihood-DEC (relative probability)	Bayes-DIVA (marginal probability)
0	1.00	79.88 (72.11, 86.88)	C|CE (0.26) A|E (0.25) AC|C (0.19) C|E (0.11)	C (41.6) A (25.3) E (16.6)
1	1.00	68.49 (58.61, 77.45)	AC|C (0.37) C|C (0.19) A|C (0.17) AD|D (0.15)	C (84.0)
2	1.00	23.19 (11.44, 37.98)	CD|C (0.63) C|C (0.36)	C (98.3)
3	<0.90	66.08 (55.85, 74.99)	C|A (0.53) A|A (0.20) AD|A (0.11) D|A (0.10)	C (55.1) A (28.4)
4	<0.90	63.94 (54.41, 73.87)	A|A (0.94)	A (96.8)
5	1.00	34.52 (21.80, 48.67)	A|A (0.51) AB|A (0.48)	A (98.4)
6	0.94	26.90 (17.25, 37.88)	B|A (0.99)	A (95.3)
7	1.00	57.40 (47.38, 67.69)	A|A (0.85) A|AB (0.13)	A (90.6)
8	1.00	47.59 (36.36, 59.42)	A|A (1.00)	A (99.7)
9	1.00	47.04 (36.02, 58.31)	AB|B (0.69) A|B (0.26)	AB (58.3) A (31.0) B (10.5)
10	1.00	40.61 (29.89, 51.79)	A|AB (0.49) A|A (0.28)	AB (83.7) A (15.6)
11	1.00	34.27 (22.32, 46.96)	C|D (0.66) AC|C (0.38)	C (69.4) D (17.7)
12	0.99	28.15 (17.85, 38.78)	C|A (0.92)	C (87.0)

(character 2) seem to have appeared in both *Cayratia* and *Tetrastigma* (Fig. 3). Character 1 is thus a good character to distinguish the two subgenera of *Cayratia*, whereas character 2 seems not appropriate for the infrageneric classification of *Cayratia*.

The occurrence of leaf-opposed tendrils is a distinctive character for Vitaceae (Gerrath et al., 2001; Wen, 2007). The branching pattern of tendrils has been used in both intergeneric and infrageneric classifications of Vitaceae (Chen et al., 2007; Jackes, 1987; Li, 1998; Shetty and Singh, 2000; Verdcourt, 1993; Wen, 2007). To evaluate its taxonomic significance within the CCT clade, we optimized the branching pattern of tendrils with five character states onto a Bayesian majority-rule tree (Fig. 4). Our reconstruction suggests that the state of 2–3 branched tendrils is ancestral in the CCT clade. Consistent with Chen et al. (2011a), the digitately branched tendrils are unique in *Tetrastigma*. The 3–5-racemosely branched tendrils are not unique in *Cayratia*, and also appear in taxa of *Parthenocissus* (Fig. 4). Although both the digitately branched tendrils and the 3–5-racemosely branched tendrils possess multiple branches, they share different evolutionary history based on our character reconstruction. Simple tendril was detected in *Cyphostemma* and *Tetrastigma*, which also evolved multiple times in the 5-merous taxa. Given parallel and convergent evolution in the branching pattern of tendrils, this character needs to be used cautiously in classifications within the family. Most species of Vitaceae are lianas with leaf-opposed tendrils, whereas a few taxa are shrubs or small trees that often lack tendrils (Gerrath and Posluszny, 2007; Wen, 2007; Wilson et al., 2006). Our reconstruction infers that the absence of tendrils is unique in some *Cyphostemma* species and has evolved multiple times. This character state appears to be an adaptation to the dryer habitat in various parts of Africa, which are usually covered with grasses, herbs and shrubs but have few trees for vines to climb.

Vitaceae exhibits extraordinary leaf polymorphism. Reconstructions of leaf architecture by Nie et al. (2010) and Chen et al. (2011a) showed that this character was highly labile in *Parthenocissus* and *Tetrastigma*, respectively. Ingrouille et al. (2002) proposed that pinnate leaves might be a plesiomorphic character shared by several species of *Ampelopsis* with the outgroup *Leea*. To investigate the taxonomic significance of leaf architecture in Vitaceae, especially in *Cayratia*, we herein traced this character onto a data set representing all major lineages of Vitaceae. Optimization of leaf architecture suggests that pedate leaves are ancestral in the CCT clade and each of the five states of leaf architecture evolved multiple times within Vitaceae. Our reconstruction also confirms that the trends in leaf evolution are reversible as described in Takhtajan (1991). For instance, the pedate leaves may have initially originated from digitate leaves, but may have then reversed to digitate leaves several times in both *Cyphostemma* and *Tetrastigma* (Fig. 4). Furthermore, it is very common to observe both trifoliate leaves and digitate leaves in *Cyphostemma*. Leaf architecture seems to have a complex history in the CCT clade and it should be used cautiously in the infrageneric classification for *Cayratia*. Furthermore, the pinnate leaves are not unique in *Ampelopsis* and probably have evolved at least three times in Vitaceae (*Ampelopsis*, *Cayratia*, and *Cyphostemma*).

4.3. Historical biogeography

The biogeographic analyses and divergence time estimates suggest that the CCT clade originated in continental Africa, then
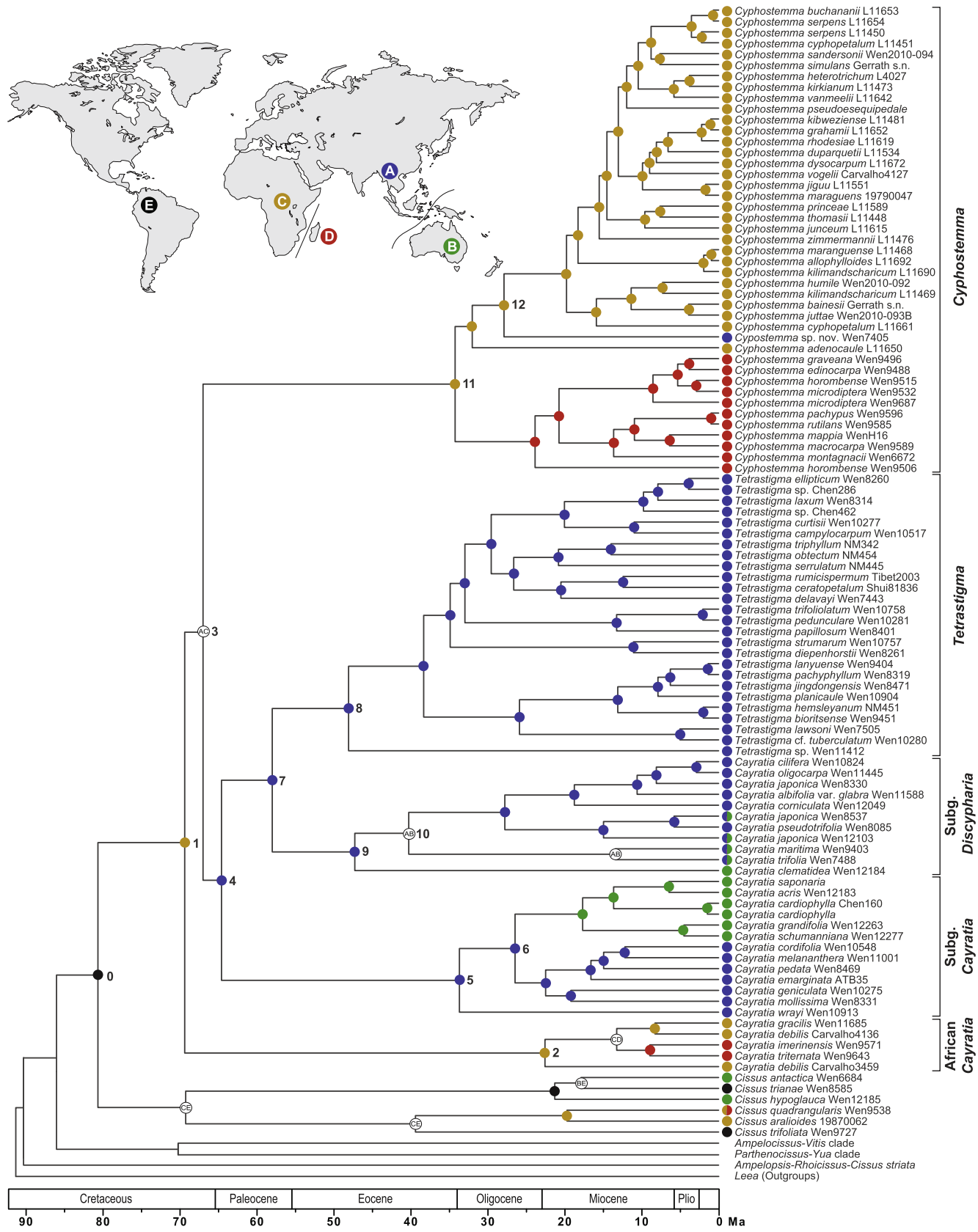
Fig. 6. Likelihood ancestral area reconstructions under the dispersal-extinction-cladogenesis (DEC) model with options of the highest relative probability indicated. Pie charts at nodes represent relative frequencies of ancestral area reconstruction. Geologic time scale is shown at the bottom, and major clades of the CCT clades are indicated on the right-hand side. Numbers in italics outside nodes correspond to the node numbers of Fig. 5. Area abbreviations are as follows: A, Asia; B, Australia (including New Guinea); C, continental Africa; D, Madagascar; and E, the New World.

migrated/dispersed into Asia twice independently at 66.08 Ma (95% HPD: 55.85–74.99 Ma; node 3, Fig. 6) and 28.15 Ma (95% HPD: 17.85–38.78 Ma; node 12, Fig. 6), respectively. Biogeographic disjunctions between Africa and Asia are common in plants with the palaeotropical distributions and have attracted much attention in recent years (Clayton et al., 2009; Conti et al., 2002; Couvreur et al., 2011; Renner, 2004a, 2004b; Yuan et al., 2005; Zhou et al., 2012). The African–Asian disjunctions have been explained by four hypotheses: (1) rafting on the Indian plate (Conti et al., 2002; Dayanandan et al., 1999); (2) migration via the Eocene boreotropical forests (Davis et al., 2002; Muellner et al., 2006; Weeks et al., 2005); (3) transoceanic long-distance dispersal (Clayton et al., 2009; Renner, 2004a; Yuan et al., 2005); and (4) overland migration via land bridges (Zhou et al., 2012). The first hypothesis holds that some Asian elements have an ancient Gondwanan origin and arrived in Asia by rafting on the Indian plate (McKenna, 1973). It is generally accepted that the Indian plate split from eastern Gondwana in the early Cretaceous, migrated rapidly northwards in the late Cretaceous and Paleocene, and eventually collided with the Asian plate in the Paleocene, at 50–55 Ma (Ali and Aitchison, 2008). Although the Indian plate became isolated from Gondwana at least 20 Ma before the first African–Asian disjunction in *Cayratia* (66.08 Ma, 95% HPD: 55.85–74.99 Ma, Fig. 6), there was once a time that the Indian plate drifted very close to the African plate during its northbound journey (Morley, 2000). Therefore, it is possible that the common ancestor of the Asian CCT clade rafted from Africa via the Indian plate during the late Cretaceous-early Paleocene and reached Asia after the collision of the Indian and Asian plates. The second hypothesis relies on the existence of extensive boreotropical forests from Europe across southern Asia associated with the late Paleocene-early Eocene thermal maximum (Zachos et al., 2001). During the climatic optimum, most regions of northern Africa, including areas now occupied by the Sahara Desert, were dominated by rainforest (Axelrod and Raven, 1978; Raven and Axelrod, 1974). These tropical forests would have extended much further north than equivalent extant forests, enabling floristic exchanges between Africa and Asia in both directions (Wolfe, 1975). This hypothesis has been used to explain the African–Asian disjunctions in several angiosperm families (Davis et al., 2002; Weeks et al., 2005). The timing of this expansion of boreotropical forests did not coincide with the late Cretaceous–early Paleocene African–Asian disjunction within the CCT clade between the African *Cayratia* and its sister containing the remaining species of the CCT clade. Besides the diversity of Vitaceae is very low in northern Africa and Europe. There is also no fossil record supporting such a diversity there in the late Cretaceous to the Tertiary. The long-distance dispersal hypothesis has been shown to be important in explaining plant intercontinental disjunctions (Clayton et al., 2009; Nie et al., 2012; De Queiroz, 2005; Thiv et al., 2011; Warren et al., 2010; Yuan et al., 2005). Vitaceae are generally good dispersers, which can be dispersed by animals (especially birds) that eat their berries (McAtee, 1906; Ridley, 1930; Tiffney and Barghoorn, 1976; Wen, 2007). The repeated appearance of sizeable islands across the western Indian Ocean may have served as "stepping stones", greatly reducing the isolation of continental Africa and Asia (Miller et al., 2005; Schatz, 1996; Warren et al., 2010). The overland migration hypothesis suggests that floristic elements may have migrated between Africa and Asia around 20 Ma, when the closure of the Tethys Sea established direct land connection between Africa and western Asia (Raven and Axelrod, 1974; Zohary, 1973). But the first African–Asian disjunction occurred much earlier than the closure of the Tethys Sea. Nevertheless, the second African–Asian disjunction within *Cyphostemma* seems to fit the time frame of the overland migration hypothesis. But in Asia the *Cyphostemma* taxa are in southern India and northern Thailand, not in route of the overland migration hypothesis. Long-distance

dispersal may be the most plausible hypothesis to explain the disjunction between Africa and Asia in *Cyphostemma*. For the earlier disjunction between African *Cayratia* and *Cyphostemma* and its close Asian relatives, the evidence available is consistent with the hypothesis that the Indian plate carried the common ancestor of the Asian CCT members and rafted north and reached Asia. The long-distance dispersals may have facilitated the diversification of the CCT clade within Asia.

Dispersal from continental Africa to Madagascar is inferred to have occurred twice in the Oligocene and Miocene, respectively. The disjunctions between continental Africa and Madagascar can be explained by either vicariance in the form of fragmentation of Gondwanan landmasses or later oceanic dispersal events. It is now generally accepted that Madagascar separated from continental Africa in the Middle Jurassic and has attained its present position relative to Africa in the Early Cretaceous (Rabinowitz et al., 1982; Rabinowitz and Woods, 2006; Segoufin, 1981). Since the isolation of Madagascar from continental Africa has occurred much earlier than the two dispersal events, the disjunctions are unlikely explained by the breakup of Gondwanna landmasses. Long-distance dispersal to Madagascar has been suggested for many taxa, both animals (Fuller et al., 2005; Poux et al., 2005) and plants (Baum et al., 1998; Clayton et al., 2009; Meimberg et al., 2001; Renner, 2004b; Yuan et al., 2005). We herein hypothesize that both migrations from continental Africa to Madagascar were achieved by long-distance dispersal.

Our ancestral area reconstruction infers that *Cayratia* dispersed from Asia to Australia multiple times since the Eocene (Fig. 6). Disjunctions between Asia and Australia have been suggested as closely related to plate tectonics and climate (Morley, 1998). With its predominantly Gondwanan substrate, Australia began to split from Antarctica perhaps 80 Ma in the late Cretaceous and formed its current distribution in the Miocene (Morley, 2003). Island-hoping dispersal has commonly been used to explain the very recent disjunctions between Asia and Australia (Morley, 1998, 2003). The first dispersal from Asia to Australia was estimated to have occurred around 47.04 Ma (95% HPD: 36.02–58.31 Ma; node 9, Fig. 6) in the middle Eocene, which gave rise to the Australian endemic *Cayratia clematidea* (Fig. 6). This disjunction is unlikely to have evolved via island-hoping mechanism because there were no available islands between Asia and Australia during the Eocene (Morley, 1998). Furthermore, there were wide oceanic barriers between Asia and Australia based on the plate tectonic reconstruction of that time (Morley, 2003). Long distance dispersal seems to be the most plausible explanation for this first disjunction between Asia and Australia. A recent disjunction occurred around 18.02 Ma (95% HPD: 9.71–27.13 Ma) in the early Miocene have involved five Australian (including New Guinea) endemic species (*Cayratia acris*, *C. cardiophylla*, *C. grandifolia*, *C. saponaria*, and *C. schumanniana*). Island–hoping dispersal may explain this disjunction since many island chains between mainland Asia and Australia have appeared during the Neogene (Clayton et al., 2009; Meimberg et al., 2001; Morley, 2003). In addition, after a period of much drier and cooler climates during the Oligocene and earliest Miocene, a period with markedly warm and moist climatic conditions occurred in the large part of southeastern Asia in the early Miocene (Zachos et al., 2001). The warm climate may have facilitated the migration of *Cayratia* from Asia, through southeastern Asia islands, to Australia. Relatively recent dispersals from Asia to Australia may have occurred at least three times, such as in *Cayratia japonica*, *C. trifolia* (L.) Domin, *and C. maritima* Jackes, all with a broad distribution in Asia and Australia (Fig. 6). These species may also have achieved their broad distribution by island-hoping dispersals with islands of the Malesian region as stepping-stones.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.04.023.

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