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Origins and evolution of cinnamon and camphor: A phylogenetic and historical biogeographical analysis of the *Cinnamomum* group (Lauraceae) ☆

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ABSTRACT

Tropical and subtropical amphi-Pacific disjunction is among the most fascinating distribution patterns, but received little attention. Here we use the fossil-rich *Cinnamomum* group, a primarily tropical and subtropical Asian lineage with some species distributed in Neotropics, Australasia and Africa to shed light upon this disjunction pattern. Phylogenetic and biogeographic analyses were carried out using sequences of three nuclear loci from 94 *Cinnamomum* group and 13 outgroup samples. Results show that although there are three clades within a monophyletic *Cinnamomum* group, *Cinnamomum* and previously recognized subdivisions within this genus were all rejected as natural groups. The *Cinnamomum* group appears to have originated in the widespread boreotropical paleoflora of Laurasia during the early Eocene (ca. 55 Ma). The formation and breakup of the boreotropics seems to have then played a key role in the formation of intercontinental disjunctions within the *Cinnamomum* group. The first cooling interval (50–48 Ma) in the late early Eocene resulted in a floristic discontinuity between Eurasia and North America causing the tropical and subtropical amphi-Pacific disjunction. The second cooling interval in the mid-Eocene (42–38 Ma) resulted in the fragmentation of the boreotropics within Eurasia, leading to an African–Asian disjunction. Multiple dispersal events from North into South America occurred from the early Eocene to late Miocene and a single migration event from Asia into Australia appears to have occurred in the early Miocene.

1. Introduction

The occurrence of intercontinental disjunctions in the natural geographic ranges of many seed-plant groups has long fascinated biologists (Raven, 1972; Thorne, 1972), with 16 categories of intercontinental disjunction recognized by Thorne (1972). Among them, the amphi-Pacific tropical disjunction is applied to plants that are distributed in tropical regions on both sides of the Pacific Basin with the highest plant diversity on Earth (Thorne, 1972; Raven, 1988). However, this disjunction pattern has received relatively little attention, compared to the more extensively studied eastern Asian–North American disjunction (Li et al., 2011; Li and Wen, 2013).

In order to explain the amphi-Pacific tropical disjunction, multiple hypotheses and plausible migration pathways have been postulated. Among them, that there was a continuous boreotropical paleoflora during the climatically warm periods of the Paleogene in the Northern Hemisphere (Wolfe, 1975; Tiffney, 1985). Evidence for this biome has been supported by molecular analysis for a number of plant groups, including Amaryllidaceae (Meerow

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et al., 1999), Annonaceae (Couvreur et al., 2011; Erkens et al., 2009, 2012), Fabaceae (Lavin and Luckow, 1993; Lavin et al., 2005), Lauraceae (Chanderbali et al., 2001; Li et al., 2011), Magnoliaceae (Azuma et al., 2001) and Malpighiaceae (Davis et al., 2002b, 2005), as well as animal groups like Cladocera (Van Damme and Sinev, 2013).

The Bering and North Atlantic land bridges have been used to explain the migration of subtropical and tropical lineages in the context of the boreotropics hypothesis (e.g. Tiffney, 1985; Davis et al., 2002a; Li et al., 2011) and van Steenis (1962) postulated various transoceanic land bridges to account for the amphi-Pacific disjunctions of many plant genera. Long-distance dispersal may also play a significant role in disjunct tropical genera with fleshy fruits, or fruits that can float and remain viable for a longer time in salt water (Thorne, 1972; Raven and Axelrod, 1974; Givnish and Renner, 2004). Testing these competing hypotheses and dispersal pathways is important for understanding the origins of these intercontinental disjunction patterns.

The *Cinnamomum* group, as proposed by Chanderbali et al. (2001), is a subset of the tribe Cinnamomeae (Lauraceae) ranging from tropical and subtropical Asia, Australia and Pacific Islands, to tropical America and Africa. As defined currently, it contains more than 350 species represented by the genera *Aiouea* Aubl., *Cinnamomum* Schaeff., *Mocinnodaphne* Lorea-Hern. and the species of *Ocotea ikonyokpe* van der Werff. Phylogenetic analysis of ITS sequence data unexpectedly placed the African *O. ikonyokpe* within the *Cinnamomum* group, rather than the remainder of the genus *Ocotea* Aubl. (Chanderbali et al., 2001). Described by van der Werff (1996) from Cameroon, *O. ikonyokpe* is the only African element within the *Cinnamomum* group, which otherwise has a tropical and subtropical amphi-Pacific disjunct distribution.

Cinnamomum with ca. 350 spp. (Rohwer, 1993), comprises the bulk of the *Cinnamomum* group and occurs in subtropical and tropical regions on both sides of the Pacific Basin. Its members have long been recognized for their economic importance as the sources of camphor, spices, phytomedicines and high quality wood (Wijesekera et al., 1975; Farrell, 1985; Loi, 1996; Ravindran et al., 2003). In addition, as conspicuous elements of tropical and subtropical evergreen broad-leaved forests, *Cinnamomum* species are also ecologically important (Lin, 1965; Kira, 1991; Wang et al., 2007). Tropical Asia is the most significant center of *Cinnamomum* species diversity, followed by the Neotropics with a further ca. 47 species (Lorea-Hernández, 1996). The Asian *Cinnamomum* species are divided traditionally into two sections based on morphological traits such as leaf arrangement, leaf venation pattern, presence or absence of perulate buds or domatia: sect. *Camphora* Meissn. and sect. *Cinnamomum*. Based on similar grounds, all the five Australian native *Cinnamomum* species have been placed in sect. *Cinnamomum* (Hyland, 1989). However, unlike the Asian and Australian species, Neotropical *Cinnamomum* species present a mixture of the characters found in the two Asian sections (Lorea-Hernández, 1996). Most of the Neotropical species currently included in *Cinnamomum* had originally been described in *Phoebe* Nees, but were transferred to *Cinnamomum* by Kostermans (1961). The affinity between Neotropical *Phoebe* and Asian *Cinnamomum* species has been noted previously by Nees von Esenbeck (1836) and Meissner (1864), who created *Phoebe* subgenus *Persoideae* Meisn. for the Asian species and subgenus *Cinnamoideae* Meisn. for the American ones.

The question of whether *Cinnamomum* is monophyletic has been ongoing and 35 years after Kostermans (1961), the Neotropical species of *Cinnamomum* were revised by Lorea-Hernández (1996), with 47 species accepted. Based on a cladistic analysis of 36 morphological features for Lauraceae genera, Neotropical *Cinnamomum* species are more closely related to Asian *Cinnamomum* species than to *Phoebe* (Lorea-Hernández, 1996). In contrast, a molecular phylogenetic study of the family by Chanderbali et al. (2001) showed that the Neotropical *Cinnamomum* species included in their analysis formed a clade with *Aiouea dubia* Mez, *A. guianensis* Aubl. and *Mocinnodaphne cinnamomoidea* Lorea-Hern., rather than forming a monophyletic group with the Asian *Cinnamomum* species. However, forcing monophyly of *Cinnamomum* and its allies added just one extra step in the maximum parsimony analysis (see Figs. 3 and 4 in Chanderbali et al., 2001), suggesting that branch support was potentially weak or strongly character dependent.

The monotypic Mexican genus *Mocinnodaphne* was described by Lorea-Hernández (1995) and separated from genera such as *Cinnamomum*, *Ocotea*, *Nectandra* Rolander ex Rottb. based on the reduction in number of fertile staminal whorls. *Aiouea*, with ca. 20 species (Renner, 1982), was not supported as monophyletic by either morphological (Penagos, 2010) or molecular data (Chanderbali et al., 2001) and of the three *Aiouea* species sequenced by Chanderbali et al. (2001), two were nested within the Neotropical *Cinnamomum* clade and one in the genus *Ocotea*.

Cinnamomum has an abundant and widespread fossil record and has been reported from the Upper Cretaceous of Asia (Guo, 1979), Europe (Coiffard et al., 2008), North America (e.g. Berry, 1929; Bell, 1957, 1963; Lozinsky et al., 1984; Crabtree, 1987; van Boskirk, 1998; Johnson, 2002) and Australasia (von Ettingshausen, 1883, 1887a,b, 1891; Pole, 1992; Cantrill et al., 2011), making the geographical origin of the genus uncertain. Its Cenozoic diversity reached the climax in the Eocene, gradually decreasing from the Oligocene to Miocene (Berry, 1916). Though numerous fossil records should make the *Cinnamomum* group a desired target to explore the origins of its amphi-Pacific disjunction pattern, the majority of the fossils attributed to *Cinnamomum*, especially the 19th and early 20th Century determinations, is based purely on superficial similarities of venation features and are not conclusive.

Previous studies have revealed that cpDNA makers are of limited use for reconstructing phylogenetic relationships in Lauraceae, particularly for the Perseeae–Laureae clades (Rohwer, 2000; Chanderbali et al., 2001; Rohwer and Rudolph, 2005; Fijridiyanto and Murakami, 2009; Rohwer et al., 2009; Li et al., 2011). Therefore for this study, we selected three nuclear markers, ITS and two low-copy nuclear genes (*LEAFY* and *RPB2*), based on results of the above-mentioned studies to resolve phylogenetic relationships within the *Cinnamomum* group along with a significant increase in taxon sampling. Accordingly, the main objectives of this study were to

(1) reconstruct phylogenetic relationships within the *Cinnamomum* group and elucidate if the group, the genus *Cinnamomum* and previously recognized subdivisions within it are monophyletic;
(2) explore the biogeographic history of the *Cinnamomum* group and elucidate the origin and nature of its amphi-Pacific and other disjunctions, including the tropical North and South American disjunction, the African–Asian disjunction and the disjunction between Asia and Australia.

2. Materials and methods

2.1. Taxon sampling

A total of 94 accessions for 76 species in the *Cinnamomum* group were included (Supplementary Table S1), covering nearly the entire distribution range of the group. ITS sequences deposited in Genbank were downloaded for four Neotropical *Cinnamomum* group species and the African *O. ikonyokpe*. Five *Persea* group and eight core Laureae species were selected as outgroups based on previous studies (Chanderbali et al., 2001; Li et al., 2011) which

showed they are closely related to the study group. Within the *Persea* group, we selected species from *Phoebe* and *Alseodaphne* Nees, allowing the use of *Alseodaphne changchangensis* Jin et Li (Li et al., 2009) as an external fossil calibration point, based on the work of Li et al. (2011).

2.2. DNA extraction, PCR and sequencing

Total genomic DNA was extracted from silica-gel dried material or herbarium leaf specimens using the Plant Genomic DNAKit (Tiangen Biotech, Beijing, China). The primers of White et al. (1990) and Chanderbali et al. (2001), with minor modifications published in Li et al. (2004), were used for ITS amplification following the procedure of Li et al. (2011). The second intron of *LEAFY* gene was amplified using the primers and protocols reported in Li et al. (2011). For *RPB2*, forward and reverse primers were designed at the 19th (*RPB2*-19F: 5′-GWT CAT TAT TTT TCC GCT CAT ACA-3′) and 23rd exon (*RPB2*-23R: 5′-ATC TCA TTC TTA CTT TCA CAA ATC TCA AC-3′) respectively (Li et al., unpublished data). However, in order to improve the amplification of the herbarium leaf samples, we designed another reverse primer (*RPB2*-22R: 5′-AAC TAG AAT TAA TAA CCC CTT AC-3′) at the 22nd exon of *RPB2* to match with the *RPB2*-19F and to shorten the length of the targeted fragment. The primer pair of *RPB2*-19F and *RPB2*-22R was used when amplification with *RPB2*-19F and *RPB2*-23R failed. The PCR protocol for the two primer pairs of *RPB2* were identical, as follows: 94 °C for 2 min; 35 cycles of 94 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min; with a final 10 min extension at 72 °C.

The amplified products of *LEAFY* and *RPB2* were purified using the EZNA Cycle-Pure Kit (Omega Bio-Tek, Georgia, USA) and cloned using the pEASY-T3 Cloning Kit (TransGen Biotech, Beijing, China). At least five positive clones from each individual sample were sequenced and up to 14 positive *LEAFY* clones were sequenced for some samples. Each fragment was sequenced in both directions using BigDye 3.1 reagents with an ABI 3770 automated sequencer (Applied Biosystems, Carlsbad, California, USA). The sequencing results were assembled and edited using the program Sequencher 4.5 (GeneCodes, Ann Arbor, Michigan, USA) and deposited in GenBank (see Supplementary Table S1 for accession numbers).

2.3. Sequence alignment and phylogenetic analyses

Sequences were aligned with MUSCLE 3.8.31 (Edgar, 2004) and then adjusted manually using BioEdit 7.0.9.0 (Hall, 1999). Maximum parsimony (MP) and Bayesian inference phylogenetic analyses were conducted initially on the *LEAFY* and *RPB2* datasets separately. These results indicated the presence of two *LEAFY* copies, named "long sequence" and "short sequence", in nearly all the sect. *Cinnamomum* samples (Huang et al., 2015). The "long sequence" copy (a ca. 47 bp insertion compared to the "short sequence" copy) sequences were selected for phylogenetic analysis. For *LEAFY* "long sequence" copy and *RPB2*, one of several different sequences obtained from an individual sample was selected randomly to be combined with the corresponding ITS sequence obtained from the same sample, because different sequences of *LEAFY* "long sequence" and *RPB2* from the same individual sample almost invariably formed a clade. Finally, individual and combined datasets for the three markers were assembled as follows: ITS, *LEAFY*, *RPB2*, ITS + *LEAFY*, ITS + *RPB2*, *LEAFY* + *RPB2*, and ITS + *LEAFY* + *RPB2*. Gaps were coded as simple indels using the program Gapcoder (Young and Healy, 2003). Maximum parsimony analyses were conducted using the program PAUP*4.0b10 (Swofford, 2003) and Bayesian inference analyses were conducted using the program MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003).

MP analysis was implemented using the following heuristic search options: tree-bisection-reconnection (TBR) branch swapping, collapse of zero length branches and MulTrees on, with 1000 random taxon additions, saving 100 trees from each random sequence addition. All character states were treated as unordered and equally weighted. Bootstrap support values (BS) for internal nodes were estimated with 100 heuristic bootstrap replicates, using the same options described above, except that a maximum of 10 trees were saved per round.

For the Bayesian analyses, the dataset was partitioned by locus. Modeltest 3.7 (Posada and Crandall, 1998; Posada and Buckley, 2004) was used to select the best-fit evolutionary model and gamma rate heterogeneity using Akaike Information Criterion (AIC) for each partition. The Markov chain Monte Carlo (MCMC) algorithm was run for 5,000,000 generations with one cold and three heated chains, starting from random trees and sampling one out of every 500 generations. Examination of the log likelihood values suggested that stationarity was reached in about 500,000 generations. Thus, the first 1000 trees (10%) were discarded as burn-in and the remaining 9000 trees were used to construct the consensus tree with the proportion of bifurcations found in this consensus tree given as posterior probabilities (PP).

2.4. Molecular dating and estimation of divergence times

There are numerous fossil records attributed to *Cinnamomum*; however, almost none of them can be assigned unambiguously to an extant group within the genus. Therefore, it is difficult to choose a reliable fossil calibration point within *Cinnamomum*. Here we applied the strategy of secondary calibration, a useful alternative approach when direct calibration (e.g. fossil or geological) is unavailable (Berry et al., 2004; Hedges and Kumar, 2004; Renner, 2005; Zhou et al., 2006). Firstly, stem and crown ages of the *Cinnamomum* group were estimated using the ITS + *psb*A-*trn*H dataset which included 52 species representing four Lauraceae groups (*Chlorocardium* Rohwer, H.G. Richt. & van der Werff–*Mezilaurus* Kuntze ex Taub. clade, *Persea* group, core Laureae, the *Cinnamomum* group) (Supplementary Table S2). Only 18 species representing the major clades of the *Cinnamomum* group were included to even the tree, as Yule processes were assumed (Velasco, 2008). Two calibrations points were used in primary calibration. The Upper mid-Cretaceous separation of South America from Africa ca. 90 Ma was used to date the divergence of the *Chlorocardium*–*Mezilaurus* clade from the *Persea* group–core Laureae–*Cinnamomum* group (90 ± 1.0 Ma, node C1 in Table 1 and Supplementary Fig. S4), as this divergence point has been considered to represent a realistic age for the radiation of Lauraceae in previous studies (Chanderbali et al., 2001; Nie et al., 2007). In addition, *Alseodaphne changchangensis* Jin et Li, a perfectly preserved fossil leaf described from the late early Eocene to early late Eocene coal-bearing series of the Changchang Formation in the Changchang Basin of Hainan Island, China (Li et al., 2009) was selected as a fossil calibration point as it has been used successfully for estimating divergence times of the major clades within the *Persea* group (Li et al., 2011). Based on the work of Li et al. (2011), the stem age of *Alseodaphne* lineages was constrained to 43 ± 3.5 Ma in our study (node C2 in Table 1, Fig. 2 and Supplementary Fig. S4). The GTR + I + G model for ITS and K81uf + I + G for *psb*A-*trn*H were suggested by Modeltest. Secondly, the stem and crown age of the *Cinnamomum* group obtained from the first analysis were used as secondary calibration points for the ITS + *LEAFY* + *RPB2* dataset. The stem age of *Alseodaphne* was used again as a fossil calibration point.

Molecular dating analyses for the two datasets, ITS + *psb*A-*trn*H and ITS + *LEAFY* + *RPB2*, were implemented in program BEAST v1.7.5 (Drummond et al., 2012). Input files were created using the program BEAUti v1.7.5 (distributed with BEAST). The dataset

Table 1
Divergence time estimates of BEAST analysis for major nodes of the *Cinnamomum* group and its closely related outgroups.

Node	Primary calibration		Secondary calibration	
	Mean	95% HPD	Mean	95% HPD
C1: Chlorocardium–Mezilaurus clade stem	90.02	91.96–88.05	–	–
C2: Alseodaphne stem	41.06	47.43–34.58	41.11	47.61–34.87
a: Split between *Cinnamomum* group–core Laureae and *Persea* group	59.10	73.14–45.59	57.97	69.08–47.47
b: *Persea* group crown	51.87	64.90–40.95	–	–
c: *Cinnamomum* group stem	55.97	69.26–43.23	54.66	64.56–45.09
d: *Cinnamomum* group crown	46.51	60.07–34.25	51.13	60.47–41.89
e: Split between Clade 2 and Clade 3	–	–	48.37	57.47–38.99
f: Clade 2 lineage crown	–	–	39.28	48.30–30.07
g: Clade 3 lineage crown	–	–	29.09	37.98–20.69
h: Clade 1 lineage crown	–	–	22.69	30.08–15.51
i: Australian–Asian *Cinnamomum* sister clade stem	–	–	21.62	27.37–15.59
j: Split between Australian and Asian *Cinnamomum*	–	–	20.43	26.46–14.06
k: Australian lineage crown	–	–	15.68	9.93–21.75
l: Split between neotropical *C. triplinerve* and neotropical *C. cinnamomifolium*–N American *C. chavarrinum*	–	–	12.05	16.69–7.50
m: Split between N American *C. chavarrinum* and neotropical *C. cinnamomifolium*	–	–	8.09	13.58–2.81

Notes: HPD, high posterior density; "–" indicates no data available, all time estimated with a unit of Ma, *C.* = *Cinnamomum*.

was partitioned by locus and the appropriate nucleotide substitution model for each partition was determined by Modeltest. Model parameters were unlinked across partitions. The Yule process for the tree prior model was employed and lognormal relaxed clock model of rate change were conducted. A normal distribution was specified for the priors as it is thought to better reflect uncertainty related to secondary calibration points (Ho, 2007; Bergh and Linder, 2009; Ho and Phillips, 2009). Posterior distributions of parameters were approximated using two independent MCMC analyses of 50 million generations sampled every 5000 generations. Tree Annotator v1.7.5 (distributed with BEAST) was used to summarize the set of post burn-in (10%) trees and their parameters. The log files was checked using the program Tracer v1.5 (Rambaut and Drummond, 2007) to ensure that plots of the two analyses were converging on the same area and that the value of the effective sample size (ESS) for each statistic was above 200.

2.5. Ancestral area reconstructions

Five biogeographic regions were delimited for the *Cinnamomum* group, based on the species endemic distributions (A) tropical and subtropical Asia; (B) tropical North America; (C) tropical South America; (D) Australia; (E) tropical Africa. A Dispersal–Extinction–Cladogenesis (DEC) model (Ree et al., 2005; Ree and Smith, 2008) was conducted using the program RASP v3.0 (Yu et al., 2014) for ancestral area reconstructions of the *Cinnamomum* group, based on the ITS + *LEAFY* + *RPB2* dataset. *Lindera erythrocarpa* Makino and *Neolitsea sericea* (Blume) Koidz. were selected as outgroups. The maximum area number at each node was set as 2, since no species included in this study occurred in more than two of the defined biogeographic regions.

3. Results

3.1. Phylogenetic analyses

The three DNA loci, ITS, *LEAFY* and *RPB2* included 661, 895 and 1061 aligned positions, yielded 169, 214, 147 informative sites and were best explained by the GTR + I + G, HKY + G and TVM + I + G substitution models respectively. The topologies of the consensus trees obtained from the MP and Bayesian analysis were mostly congruent or at least compatible for each of the individual datasets (Fig. 1 and Supplementary Figs. S1–S3). The major clades were retrieved consistently, and only minor variation in the composition and relationships of a few terminal nodes was observed, possibly caused by insufficient phylogenetic signal in the data and unequal sample size. Moreover, these inconsistencies received only very weak support. For the *LEAFY* (Supplementary Fig. S2) and *RPB2* (Supplementary Fig. S3) datasets, the relationships between the *Cinnamomum* group and core Laureae could not be resolved, but the ITS analysis (Supplementary Fig. S1) showed well-resolved topological structure among the *Cinnamomum* group, core Laureae and the *Persea* group. The ITS + *LEAFY* and ITS + *RPB2* tree topologies were nearly identical to the ITS dataset, but received better support for the clades. In the *LEAFY* + *RPB2* analysis, the relationships of core Laureae and the *Cinnamomum* group were not resolved.

The phylogenetic analysis of the ITS + *LEAFY* + *RPB2* dataset was the most successful in reconstructing the evolutionary relationships within the *Cinnamomum* group, as well as its relationships with closely related outgroups. Three well-supported monophyletic groups were recovered within the equally strongly supported monophyletic *Cinnamomum* group (BS = 94%, PP = 1.00; Fig. 1). Clade 1 (BS = 100%, PP = 1.00; Fig. 1) included almost all the sampled Asian sect. *Camphora* samples, whereas the American *Cinnamomum* species, along with *M. cinnamomoidea* and the three *Aiouea* samples formed Clade 3 (BS = 99%, PP = 1.00; Fig. 1). All the remaining ingroup samples, including three sect. *Camphora* samples, all the Asian sect. *Cinnamomum* species, six Australian samples and African *O. ikonyokpe*, formed Clade 2 (BS = 92%, PP = 1.00; Fig. 1).

These three clades also received moderate to strong support in the analyses of the single marker datasets (Supplementary Figs. S1–S3), with the only exception that Clade 1 was paraphyletic in the *RPB2* dataset (Supplementary Fig. S3). Within Clade 2, *O. ikonyokpe* was placed sister to the remainder (BS = 92%, PP = 1.00; Fig. 1) and the Australian samples formed a clade (BS = 59; PP = 1.00; Fig. 1) nested within the Asian sect. *Cinnamomum* taxa. In contrast, neither the samples from Japan nor Taiwan formed monophyletic groups. In Clade 3, the species endemic to South America were monophyletic (BS = 81%, PP = 1.00; Fig. 1) and sister to a clade (BS = 64%, PP = 1.00; Fig. 1) comprised of species ranging from North to South America, as well as those endemic to North America. Within the outgroups, the samples from core Laureae and *Persea* group taxa each formed monophyletic lineages. Nevertheless, whereas the *Persea* group showed strong support (BS = 93%, PP = 1.00; Fig. 1), the core Laureae were only very weakly supported (BS < 50%, PP < 0.90; Fig. 1).

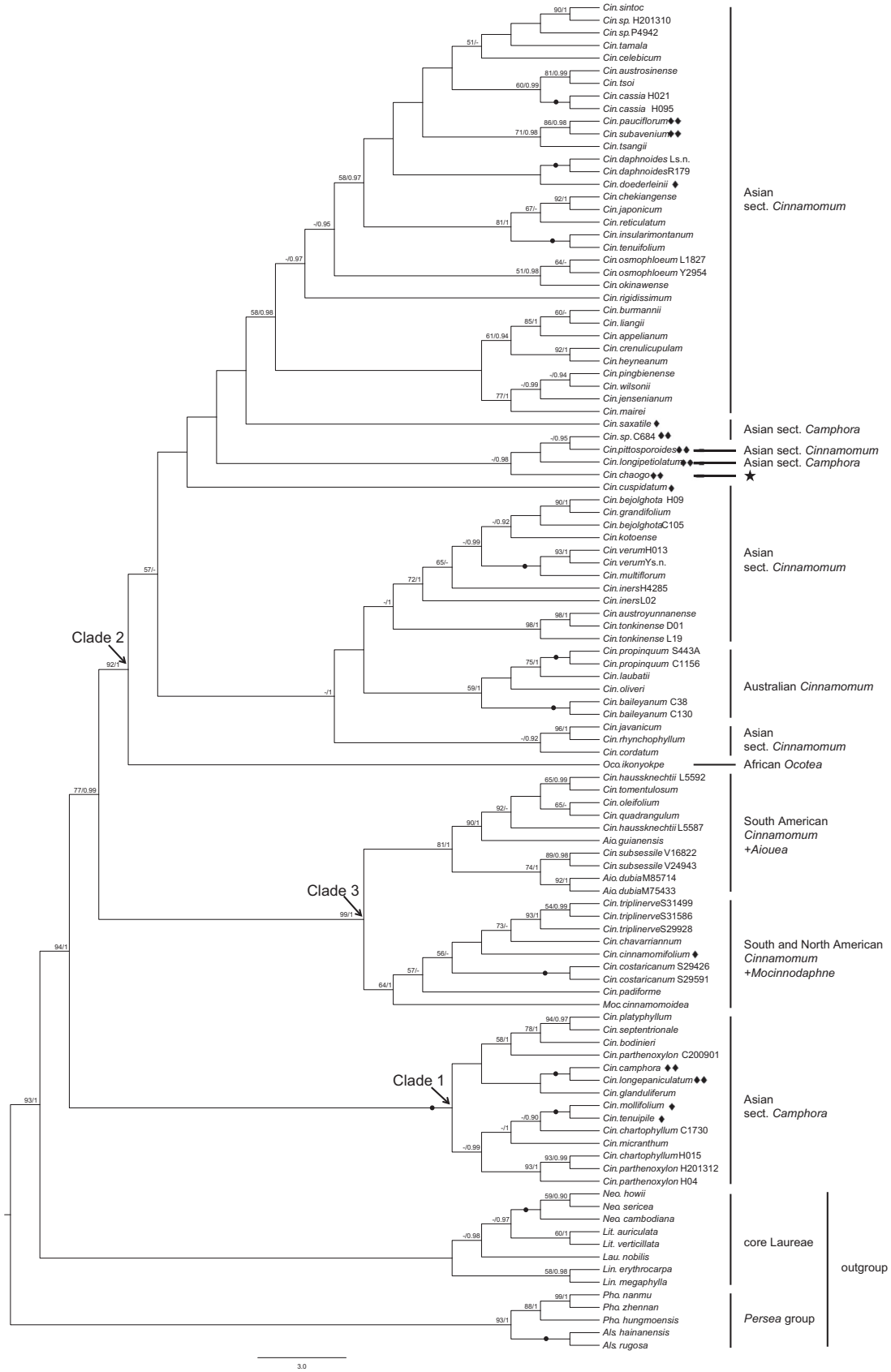

Fig. 1. Bayesian consensus tree based on ITS + *LEAFY* + *RPB2*. Bootstrap support values (⩾50%)/Bayesian posterior probabilities (⩾0.9) are shown above the branches. ● = bootstrap support value 100% and Bayesian posterior probabilities 1.00. Species with ◆/◆◆ indicate conflicts of these major clades between consensus trees from Bayesian inference and MP/BEAST. Vertical bars to the right circumscribe main clades. Abbreviations: *Aio.* = *Aiouea*, *Als.* = *Alseodaphne*, *Cin.* = *Cinnamomum*, *Lau.* = *Laurus*, *Lin.* = *Lindera*, *Lit.* = *Litsea*, *Moc.* = *Mocinnodaphne*, *Neo.* = *Neolitsea*, *Oco.* = *Ocotea*, *Pho.* = *Phoebe*.

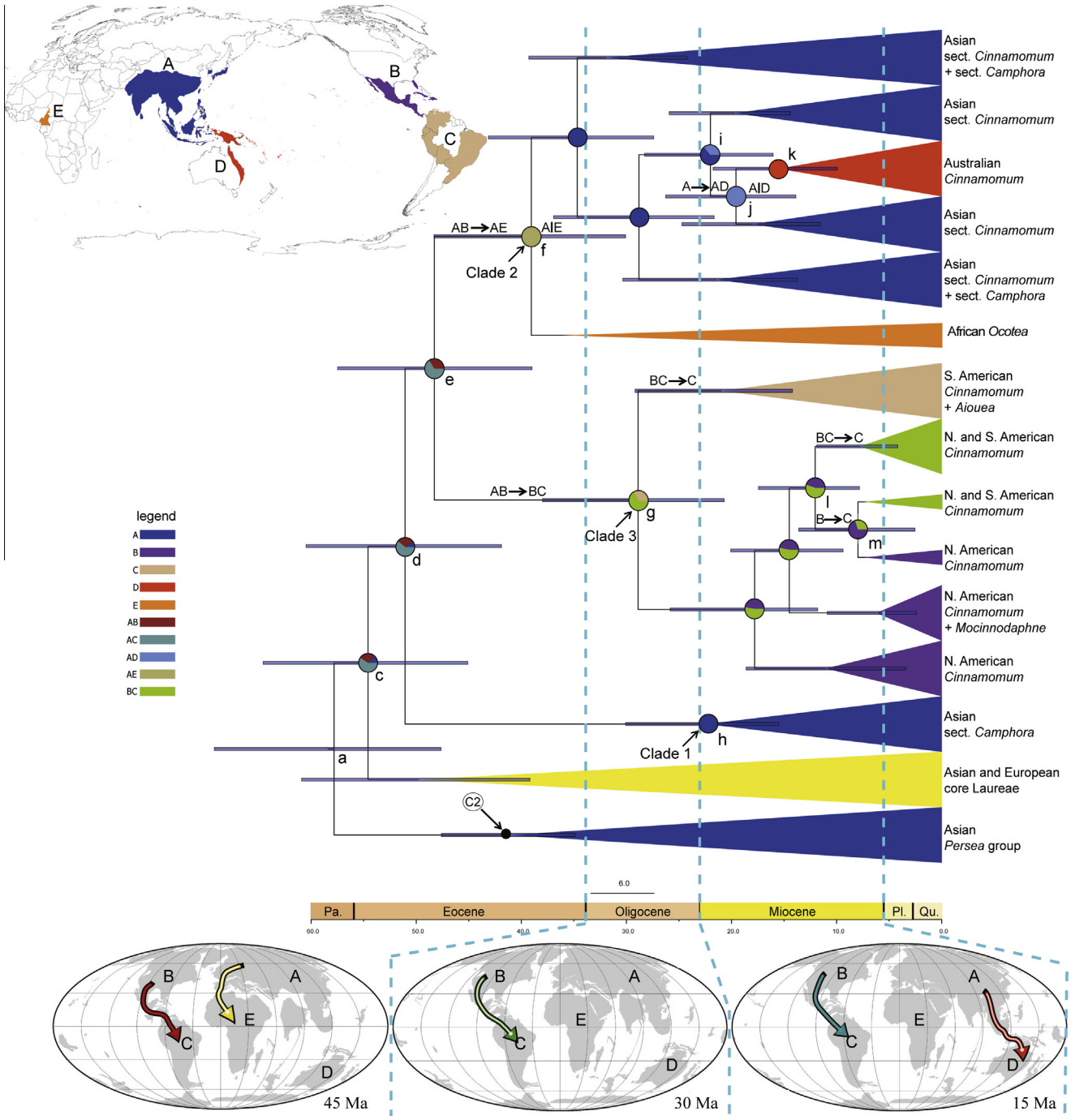

Fig. 2. Chronogram of the *Cinnamomum* group and closely-related outgroups obtained by a BEAST analysis of the ITS + *LEAFY* + *RPB2* dataset, with biogeographical inferences based on a DEC analysis. The chronogram is simplified to show relationships between major clades only. The pie charts at nodes represent the relative frequencies of possible ancestral areas for the clade optimized by the DEC analysis, the horizontal arrows on the branches indicate the inferred dispersal event, the vertical lines next to the nodes indicate the vicariance, and blue bars represent 95% high posterior density credibility intervals for node ages. The maps at the bottom show hypothesized routes of major dispersal events within the Eocene, Oligocene and Miocene epochs, respectively. The top left map shows the color-coded biogeographical areas containing extant species of the *Cinnamomum* group defined prior to analysis: clades, pie charts, and dispersal routes are colored according to this scheme. The yellow indicated the Asian and European core Laureae is not shown in the color legend, because we did not code the Europe as no extant *Cinnamomum* group species distributed in Europe.

3.2. Divergence time estimates

Results from the BEAST analysis of the ITS + *psb*A-*trn*H dataset indicate that the *Cinnamomum* group split from core Laureae at ca. 55.97 Ma (95% HPD = 69.26–43.23 Ma; node c in Table 1 and Supplementary Fig. S4) and began to diversify at ca. 46.51 Ma (95% HPD = 60.07–34.25 Ma; node d in Table 1 and Supplementary Fig. S4).

Topologies obtained for the Bayesian consensus tree (Fig. 1) and BEAST analysis (Fig. 2) based on the ITS + *LEAFY* + *RPB2* dataset were almost identical and only conflicted in few weakly-supported terminal branches (Fig. 1). Results from the BEAST analysis under secondary calibration indicate that the *Cinnamomum* group originated at ca. 54.66 Ma (95% HPD = 64.56–45.09 Ma; node c in Table 1 and Fig. 2), which is largely consistent with the results from BEAST analysis of the ITS + *psb*A-*trn*H dataset. Nevertheless, this analysis

produced a slightly older estimate of the crown age at ca. 51.13 Ma (95% HPD = 60.47–41.89 Ma; node d in Table 1 and Fig. 2) compared with the primary calibration result. The split between Clade 2 and Clade 3 was ca. 48.37 Ma (95% HPD = 57.47–38.99 Ma; node e in Table 1 and Fig. 2). Within Clade 2, the African *O. ikonyokpe* diverged at ca. 39.28 Ma (95% HPD = 48.30–30.07 Ma; node f in Table 1 and Fig. 2) and the Australian lineage diverged at ca. 20.43 Ma (95% HPD = 26.46–14.06 Ma; node j in Table 1 and Fig. 2). Within Clade 3, the species endemic to South America split from their South and North American relatives at ca. 29.09 Ma (95% HPD = 37.98–20.69 Ma; node g in Table 1 and Fig. 2).

3.3. Ancestral area reconstructions

The ancestral area reconstructions based on the DEC model inferred Asia and South America as the most likely ancestral areas of the *Cinnamomum* group, followed by Asia and North America (node c in Fig. 2). *O. ikonyokpe* was estimated to have dispersed from Laurasia into Africa during the mid-Eocene (ca. 48–39 Ma; between node e and f in Table 1 and Fig. 2). Multiple dispersals were also suggested from North into South America lasting from the Paleogene (ca. 48–29 Ma; between node e and g in Table 1 and Fig. 2) to the Neogene (ca. 12–8 Ma; between node l and m in Table 1 and Fig. 2). The extant Australian *Cinnamomum* lineage was estimated to have arrived from Asia in the early Miocene (ca. 22–20 Ma; between node i and j in Table 1 and Fig. 2).

4. Discussion

4.1. Phylogenetic relationships of the Cinnamomum group

Based on increased taxon sampling and additional DNA markers, we were able to obtain well-resolved phylogenetic relationships for major clades within the *Cinnamomum* group. This group had been recognized by Chanderbali et al. (2001), but it was poorly supported in their study. Although our analyses strongly supported the *Cinnamomum* group as monophyletic based on the present taxon samples, more other Neotropical genera samples of tribe Cinnamomeae are needed to inspect this tentative conclusion. However, our analyses rejected *Cinnamomum* and the previously recognized subdivisions within it as phylogenetic lineages. Despite the presence of several anomalous species (like *C. longipetiolatum*, *C. saxatile* and *C.* sp. C684), this study suggests strongly that the *Cinnamomum* group consists of three clades; sect. *Camphora*, sect. *Cinnamomum* and the Neotropical species respectively correspond to our Clades 1, 2 and 3.

Cinnamomum as defined currently is polyphyletic with species of *Aiouea*, *Ocotea* and *Mocinnodaphne* nested within it. The close relationship between Neotropical and Asian *Cinnamomum* species based on the present and previous molecular phylogenetic studies (Chanderbali et al., 2001), indicate that the transfer of all Neotropical *Phoebe* species into *Cinnamomum* by Kostermans (1961) was partly justified, and not all the Neotropical *Phoebe* species belong in *Cinnamomum*, as previous revisionary work has claimed (Lorea-Hernández, 1996, 1997).

Neotropical *Cinnamomum* possesses a mixture of the traits found in both the two traditional Asian sections (Lorea-Hernández, 1996), but these mixed features are not restricted to Neotropical *Cinnamomum*, also occurring in their close relatives in Asia. For example, *C. camphora*, a widely cultivated sect. *Camphora* species (Li et al., 1982, 2008), characterized by having triplinerved (sometimes inconspicuously 5-nerved) leaves with conspicuously domatia, and *C. chaogo* (indicated by a star in Fig. 1 and Supplementary Figs. S1–S3), described by Sun and Zhao (1991) as having naked buds, (sub)-opposite and penninerved leaves and lacking domatia; a mixture of the characters found in both Asian sections. These species with mixed characters further support the close relationship between the *Cinnamomum* species of both sides of Pacific Basin.

Three samples from sect. *Camphora*, *C. longipetiolatum*, *C. saxatile* and *C.* sp. C684, were nested unexpectedly in sect. *Cinnamomum* and the phylogenetic analysis of ITS + *LEAFY* + *RPB2* indicated a close relationship between two of these three samples with *C. chaogo* and *C. pittosporoides* (Fig. 1). The close molecular relationship of these four species is supported by their shared possession of alternate leaves. Although the presence of domatia in lateral vein axils is deemed a synapomorphy for sect. *Camphora* (Li et al., 1982), it was found to be absent in several sect. *Camphora* samples. Moreover, the precise description of this character is unclear (Li et al., 1982, 2008). The specimens of *C. longipetiolatum*, *C. saxatile* and *C.* sp. C684 used in our study all lacked domatia, as does *C. chaogo*.

The analysis of Chanderbali et al. (2001) indicated that *Mocinnodaphne* and some species of *Aiouea*, and *Ocotea* were nested in *Cinnamomum*, noting that *O. ikonyokpe* shared (sub)-opposite leaves with the East African *O. michelsonii* Robyns & Wilczek and *O. usambarensis* Engl.; a feature different from most African *Ocotea* species which bear spirally arranged leaves. In the current analysis *O. ikonyokpe* was also related more closely to the mostly (sub)-opposite leaved members of sect. *Cinnamomum* than the alternate-leaved sect. *Camphora* and Neotropical species. Given the phylogenies of the present and previous (Chanderbali et al., 2001) studies, we would accept that the *O. ikonyopke* was mistakenly placed in *Ocotea* and that it really belongs in *Cinnamomum*. Furthermore, *O. ikonyopke* has staminodia with a swollen tip, as in *Cinnamomum*, but not in *Ocotea*, supporting its transfer to *Cinnamomum*.

Aiouea has been regarded as polyphyletic by many authors (Burger, 1988; van der Werff, 1987, 1988; Rohwer et al., 1991; van der Werff and Richter, 1996; Chanderbali et al., 2001), with both Rohwer et al. (1991) and van der Werff and Richter (1996) noting the striking morphological similarity between South American *Aiouea* and Neotropical *Cinnamomum* species. In the present study, all three South American *Aiouea* samples were nested in the Neotropical *Cinnamomum* clade.

The placement of *Mocinnodaphne* within *Cinnamomum* supports previous studies on other Lauraceae genera that indicate that the number of fertile staminal whorls as a criterion to distinguish genera is probably artificial. The number of fertile staminal whorls is known to be variable in many genera of Lauraceae, e.g. *Aiouea*, *Aniba* Aubl., *Aspidostemon* Rohwer & H. G. Richt., *Beilschmiedia* Nees, *Dehaasia* Blume, *Litsea* Lam., *Persea* Mill. and *Phoebe* (Rohwer, 1993; Li et al., 2008) and can even vary within some species, such as *Litsea elongata* (Nees) J. D. Hooker (Li et al., 2008).

Lauraceae genera are generally circumscribed by a combination of characters, rather than by single unique characteristics (Rohwer et al., 1991), but despite being strongly supported as a monophyletic group based on molecular evidence, there are no obvious potential morphological synapomorphies for the *Cinnamomum* group. As for the molecular subdivisions of the *Cinnamomum* group seen in the present study, there were no obvious potential synapomorphies for Clades 2 or 3, whereas the diagnostic characteristics of sect. *Camphora*, including the alternate, penninerved leaves, perulate buds and domatia, could be regarded as synapomorphies for Clade 1.

4.2. Biogeographic history of the Cinnamomum group

4.2.1. Fossil record, secondary calibration and origin of the Cinnamomum group

There are plentiful fossils attributed to *Cinnamomum*, including leaves (e.g. von Ettingshausen, 1883, 1887a,b; Shi et al., 2014), fruits (Reid and Chandler, 1933), flowers (Conwentz, 1886) and

wood (Watari, 1950). Numerous compression or impression leaf fossils have been described from Upper Cretaceous to late Cenozoic deposits from many localities of both hemispheres. However, for many of these fossils, especially those reported from the 19th and early 20th Centuries, assignment to *Cinnamomum* was based on similarities of leaf morphology and venation, without supporting cuticular or other evidence. More recent studies on Lauraceae have shown that leaf morphology and venation patterns alone are frequently too variable to reliably identify leaves to genus (Christophel and Rowett, 1996; Li and Christophel, 2000; Guo et al., 2010). For example, the various trinerved, triplinerved and pinnate venation patterns seen in *Cinnamomum* occur in other Lauraceae genera such as *Cryptocarya* R. Br. (Holden, 1982; Conran and Christophel, 1998).

Seward (1927) suggested the use of a form genus *Cinnamomoides* Seward for fossil Lauraceae-like leaves characterized by the type of venation represented by *Cinnamomum camphora* (L.) J. Presl. The fossil *Cinnamomum* fruit described from the London Clay by Reid and Chandler (1933) also is regarded as questionable (Little et al., 2009). Kvaček (1971) and Bannister et al. (2012) noted that fossil generic determinations are difficult and even in extant Lauraceae it is usually impossible to determine genera based on isolated leaves or fruits only, unless the species is clearly recognizable (Rohwer, 1993). Thus, many of the fossils attributed to *Cinnamomum* need to be re-investigated.

Because there is no undisputed fossil calibration point within the *Cinnamomum* group, we applied the strategy of secondary calibration. However, this approach has been criticized for generating large confidence intervals (Graur and Martin, 2004) or leading to unreliable dates (Shaul and Graur, 2002; Sauquet et al., 2012) and therefore particular care should be taken. As suggested by previous studies (Ho, 2007; Bergh and Linder, 2009; Ho and Phillips, 2009; Sauquet et al., 2012), we specified a normal prior distribution in the BEAST analyses and included an external fossil age constraints in secondary calibration. In addition, our inferences from divergence time and biogeographical analyses are consistent with early predictions about the formation of the tropical and subtropical amphi-Pacific distribution of the *Cinnamomum* group (Chanderbali et al., 2001).

The molecular dating analyses suggested an early Eocene origin for the *Cinnamomum* group (node c in Table 1 and Fig. 2), with a first appearance in Australia during the early Miocene (between node i and j in Table 1 and Fig. 2). This estimate conflicts with the occurrence of Upper Cretaceous *Cinnamomum* fossils and especially has a huge time gap with the Southern Hemisphere Upper Cretaceous fossils (e.g. von Ettingshausen, 1883, 1887a,b). A BEAST analysis of ITS + *psb*A-*trn*H sequences from 81 Lauraceae species (results not shown) in which the *Cinnamomum* stem age was fixed at Upper Cretaceous (83 ± 8.0 Ma), placed the root age of Lauraceae (298 ± 67 Ma) in the Permian, which far precedes the earliest undisputed angiosperms fossils (Sun et al., 1998). Therefore, the Upper Cretaceous *Cinnamomum* fossils should be regarded as unreliable and in need of re-examination. While the fossil description work by von Ettingshausen (e.g. 1883, 1887a,b, 1891) has made significant contributions to the understanding of Australian and New Zealand paleobotany, there are still major problems with many of his identifications, including some *Cinnamomum*-like fossils (Hill, 1988a,b). For example, the fossil species *Cinnamomum nuytsii* Ett. preserved as leaf impressions and described by von Ettingshausen (1887a) was transferred to the organ genus *Laurophyllum* Goeppert by Hill (1988b) based on the cuticular morphology.

Despite the problem of many unreliably identified fossils, the fact that numerous fossils with *Cinnamomum*-like Lauraceae leaves reached a peak of diversity in the Eocene paleoforests of Eurasia and North America (Berry, 1916) cannot be neglected. Similarly, the hemispherical cupules seen in the London Clay Flora (Reid and Chandler, 1933) are restricted to Laureae and Cinnamomeae and well-preserved flowers described from Eocene deposits in North America (Taylor, 1988) and late Eocene Baltic amber (Conwentz, 1886) display features now confined to genera of the Cinnamomeae and *Persea* group. These fossils therefore suggest that our dating of the onset of diversification of the *Cinnamomum* group, core Laureae and *Persea* group (Table 1) around the early Eocene is realistic, but still tempered by the need for better-identified fossils.

Combined analysis of ancestral area reconstructions and fossil records implied a Laurasian origin for the *Cinnamomum* group and coeval fossils attributed to *Cinnamomum* occurring in Eurasia and North America tend to support this. Although South America was also inferred as part of the ancestral area, this seems less likely; due to few fossils reported in the Eocene of South America. Furthermore, both fossil records and ancestral area reconstructions indicated that Asia is part of the ancestral area. It would be conflicting that two widely separated continents, Asia and South America, were the common original regions of the *Cinnamomum* group. Besides, we cannot exclude Europe from ancestral area due to the plentiful European *Cinnamomum* fossil records (e.g. Bandulska, 1926; Reid and Chandler, 1933). Therefore, we consider that North America + Eurasia is the more likely ancestral area.

Paleobotanical and geological evidence indicate that the early Eocene (54–50 Ma) was the warmest period of the Cenozoic and the boreotropical paleoflora which was composed mainly of megatherms and mesotherms spread circumboreally to high latitudes in the Northern Hemisphere (Reid and Chandler, 1933; Chandler, 1964; Collinson et al., 1981; Miller et al., 1987; Wolfe, 1975, 1978, 1997). During this thermal maximum, elements of the paleoflora could have spread easily between Eurasia and North America through high-latitude land bridges such as Beringia or the North Atlantic land bridge (Wolfe, 1972, 1975). Analysis of fossil records, molecular dating and ancestral area reconstructions, indicate that the *Cinnamomum* group probably originated in early Eocene Laurasia, ca. 54.66 Ma (95% HPD = 64.56–45.09 Ma; node c in Table 1 and Fig. 2) when the ancestral lineages of modern *Cinnamomum* group species could disperse between Eurasia and North America.

4.2.2. The tropical and subtropical amphi-Pacific disjunction

According to the paleobotanical evidence, global temperatures during the Cenozoic reached a peak in the early Eocene (54–50 Ma), then underwent significant cooling in late early Eocene (50–48 Ma), followed by two steady intervals (46–43 Ma and 37–34 Ma) separated by a second cooling interval (42–38 Ma) in the middle Eocene (Reid and Chandler, 1933; Chandler, 1964; Wolfe, 1978, 1997). Sedimentary climate signal data also show matching climatic fluctuations (Miller et al., 1987; Zachos et al., 2001). Thermophilic elements of the boreotropical paleoflora may have moved to lower latitudes as the climate cooled, which could have resulted in a discontinuous boreotropical paleoflora at high latitudes, leading to the disjunction seen between thermophilic elements in Eurasia and North America. The divergence time between Old World and New World *Cinnamomum* taxa is estimated at ca. 48.37 Ma (95% HPD = 57.47–38.99 Ma; node e in Table 1 and Fig. 2) and corresponds to the first cooling period of the Cenozoic. As thermophilic plants, extant *Cinnamomum* species are found in subtropical and tropical regions and are generally very sensitive to cooling. As a consequence, the likely movement of *Cinnamomum* lineages away from high latitudes during the Eocene cooling intervals appears to have resulted in their disjunct distribution between Eurasia and North America. There is also evidence from the analyses of multiple later dispersals from North into South America from the early Eocene to late Miocene (between node e and g, l and m in

Table 1 and Fig. 2) and a single migration event from Asia into Australia in the early Miocene (between node i and j in Table 1 and Fig. 2), all of which shaped the present tropical and subtropical amphi-Pacific disjunction pattern seen in the *Cinnamomum* group.

4.2.3. The disjunction between Asia and Africa

Laurasia was inferred to be the ancestral area for the lineage represented by the African *O. ikonyokpe*. Multiple hypotheses might account for the spread of ancestral *Cinnamomum* group lineages into Africa from Laurasia: transoceanic long-distance dispersal between Africa and America (Givnish et al., 2004), or Africa and Asia (Yuan et al., 2005); Eocene–Oligocene "Lemurian stepping-stones" between Africa and Asia (Schatz, 1996; Yuan et al., 2005); dispersal of the high-latitude boreotropical paleoflora (Davis et al., 2002a); and Miocene overland migration via the Arabian Peninsula (Kosuch et al., 2001; Zhou et al., 2011). However, of these hypotheses, Miocene overland migration via the Arabian Peninsula is too recent to the produce an Eocene African *Cinnamomum* lineage. The other pathways are reasonable within the temporal framework; however, considering that African *O. ikonyokpe* is more closely related to extant Asian, rather than American *Cinnamomum* species and abundant *Cinnamomum*-like fossils have been found in the Eocene of Europe (e.g. Bandulska, 1926; Reid and Chandler, 1933), the hypothesis of southwards dispersal of the boreotropical paleoflora is more likely. The areas of northern and central Africa that would have been close to Europe 75–30 Ma were covered by lowland rainforest (Axelrod and Raven, 1978), so a pathway into Africa from Europe in the middle Eocene (ca. 48–39 Ma; between node e and f in Table 1 and Fig. 2), is both plausible and parsimonious. This migration route would have been further facilitated by land connections to North Africa via the Iberian Peninsula (Smith et al., 1994; Morley, 2000).

The disjunction between *O. ikonyokpe* and Asian *Cinnamomum* species was estimated at ca. 39.28 Ma (95% HPD = 48.30–30.07 Ma; node f in Table 1 and Fig. 2), coinciding with the second Eocene cooling period between 42 and 38 Ma (Wolfe, 1978, 1997; Zachos et al., 2001). This stage is prior to the significant global cooling during the Eocene–Oligocene transition (ca. 33 Ma; Zachos et al., 2001) and *Cinnamomum* species did not disappear from Europe until much later, based on Oligocene fossil records (e.g. Mai and Walther, 1978; Hably, 1994) so the migration route between Africa and Europe would have been open. Paleobotanical evidence indicates that the geographical extent of the boreotropical paleoflora fluctuated with the climate, expanding during warm intervals and shrinking during cooling intervals (Wolfe, 1975). The disjunction between African *O. ikonyokpe* and extant Asian *Cinnamomum* species may therefore have resulted from the fragmentation of the boreotropical paleoforest in Eurasia during the second Eocene cooling interval.

4.2.4. The disjunction between Asia and Australia

Our results suggest that *Cinnamomum* arrived in Australia from Asia in the early Miocene (ca. 22–20 Ma, between node i and j in Table 1 and Fig. 2). Although this is prior to the Sahul and Sunda shelves merging around 12 Ma (Crayn et al., 2015), biotic interchange between Australia and Asia had become possible (Morley, 2003; Crayn et al., 2015), as dispersal from Asia into Australia may have been assisted by seasonally migratory frugivorous birds that disperse the fleshy fruits of *Cinnamomum*, such as some pigeons (Snow, 1981; Gosper and Gosper, 2008). The numerous islands between the Asian and Australian plates in this period (Morley, 2003) should have served as stepping stones to aid this dispersal. Several other lineages are inferred to have migrated between Sahul (e.g. Australia) and Sundaland (e.g. southeast Asia) during this time, including *Planchonella* (Sapotaceae) and *Tapeinochilus* (Costaceae) which migrated from Sundaland, and *Livistona* palms which migrated in the opposite direction (Crayn et al., 2015).

4.2.5. The tropical North and South American disjunction

A Laurasian origin of the *Cinnamomum* group, as argued above, implies that the South American lineages were derived from North America. Indeed, the ancestral area reconstructions indicate that the dispersal direction was from North to South America (between node l and m in Fig. 2). The original disjunction between endemic species in South America and their relatives distributed in North and South America was estimated to be in the late early Oligocene (29.09 Ma, 95% HPD = 37.98–20.69 Ma; node g in Table 1 and Fig. 2). Scattered continental and/or volcanic islands that connected North and South America in the Cenozoic (Raven and Axelrod, 1974; Iturralde-Vinent and MacPhee, 1999; Morley, 2003) may have served as the stepping-stones for the migration of North American lineages into South America. Migratory birds feeding on *Cinnamomum* group fruits could have played an important role along this long distance migration route. Long after this initial dispersal event, the gradual closing of the Isthmus of Panama from 13 to 1.9 Ma (Keller et al., 1989; Duque-Caro, 1990; Collins et al., 1996), sharply accelerated biotic exchange between North and South America (Marshall et al., 1979, 1982), which may have facilitated the dispersal of *Cinnamomum* lineages. During this scenario, at least two dispersal events from North America into South America have been detected within the *Cinnamomum* group between 12 Ma (node l in Table 1 and Fig. 2) and 8 Ma (node m in Table 1 and Fig. 2). The long-term dispersal interruption prior to the closing of Panama Isthmus after the initial long-distance dispersal event before the late early Oligocene further suggest that the long-distance dispersal is "chance dispersal" (Carlquist, 1981).

5. Conclusions

Phylogenetic analyses recovered strongly supported monophyletic *Cinnamomum* group containing three well-supported subclades. However, as currently defined, neither the genus *Cinnamomum* nor sections *Camphora* and *Cinnamomum* were supported as monophyletic. Assemblages of morphological characters which were used previously to define lineages within *Cinnamomum* such as leaf arrangement, venation pattern, perulate buds and domatia were found not to be very reliable for this purpose. Similarly, based on both the present and some previous studies, the *O. ikonyopke* is suggested to be transferred into *Cinnamomum*. The *Aiouea* and *Ocotea* are unlikely to be monophyletic, but more work is needed to resolve the relationships within these two genera. The monotypic genus *Mocinnodaphne* was also nested within an American *Cinnamomum* lineage, suggesting that the number of fertile staminal whorls which is often used as a criterion to distinguish genera in Lauraceae is homoplasious.

Molecular dating and biogeographic reconstructions suggested that the *Cinnamomum* group arose in the early Eocene of Laurasia, radiating during the warmest period of the Cenozoic accompanied by the expansion of a boreotropical paleoflora in high latitudes of the Northern Hemisphere. After that, the contraction and southward retreats to lower latitudes during the cooling intervals of the later Eocene and onwards caused the intercontinental disjunctions seen in extant *Cinnamomum* group species. The first cooling interval (50–48 Ma) resulted in the split between North American and Eurasian taxa and shaped the subtropical and tropical amphi-Pacific disjunction patterns. The second cooling interval (42–38 Ma) contributed to the breakup of boreotropical continuity within Eurasia and apparently created the Asian–African disjunction. Multiple dispersal events from North into South America lasted from the early Eocene to late Miocene, whereas only a single

dispersal event in the early Miocene was suggested from Asia to Australia. Birds feeding on fleshy *Cinnamomum* group fruits could have played an important role in the dispersals from North into South America before the establishment of direct land connections, as well from Asia into Australia.

However, the accuracy of the estimates of the timing of these events may be affected by potential problems with fossils identity. Many of the fossils currently placed in *Cinnamomum* or related morphotaxa are based on incomplete evidence, so that the identity of a large number of these and especially of Cretaceous *Cinnamomum* fossils is doubtful. However, the presence of plentiful and widespread Northern Hemisphere *Cinnamomum*-like Lauraceae fossils during the Eocene and their steady decline in abundance after that epoch indicates that significant cooling at the Eocene–Oligocene transition and then during the Ice Ages resulted in the extinction of diverse *Cinnamomum* group lineages from the high latitude forests of the Northern Hemisphere. The current distribution of the group in Asia and America therefore represents a relic of a once widespread Northern Hemisphere distribution (Wolfe, 1975). The formation and eventual breakup of this now extinct boreotropical paleoflora during the Cenozoic thus helped to shape the biogeographic history of the *Cinnamomum* group.

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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.2015.12.007.

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