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ORIGINAL ARTICLE

Island hopping, long-distance dispersal and species radiation in the Western Indian Ocean: historical biogeography of the Coffeeae alliance (Rubiaceae)

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ABSTRACT

Aim The Western Indian Ocean region (WIOR) is home to a very diverse and largely unique flora that has mainly originated via long-distance dispersals. The aim of this study is to gain insight into the origins of the WIOR biodiversity and to understand the dynamics of colonization events between the islands. We investigate spatial and temporal hypotheses of the routes of dispersal, and compare the dispersal patterns of plants of the Coffeeae alliance (Rubiaceae) and their dispersers. Rubiaceae is the second most species-rich plant family in Madagascar, and includes many endemic genera. The neighbouring archipelagos of the Comoros, Mascarenes and Seychelles also harbour several endemic Rubiaceae.

Location The islands of the Western Indian Ocean.

Methods Phylogenetic relationships and divergence times were reconstructed from plastid DNA data of an ingroup sample of 340 species, using Bayesian inference. Ancestral areas and range evolution history were inferred by a maximum likelihood method that takes topological uncertainty into account.

Results At least 15 arrivals to Madagascar were inferred, the majority of which have taken place within the last 10 Myr. Most dispersal events were supported as being from mainland Africa, but *Catunaregam* may have dispersed from Asia. Although most Coffeeae alliance lineages are zoochorous, the general pattern of dispersals from Africa is incongruent with the biogeographic origins of the extant Malagasy volant frugivores. Several out-of-Madagascar dispersals were inferred to the neighbouring islands, as well as back-colonizations of Africa.

Main conclusions The African flora has been of foremost importance as source of dispersal to the islands of the Western Indian Ocean. Following the colonization of Madagascar, rapid radiations appear to have taken place in some clades, and Madagascar has also been an important source area for subsequent dispersal to the Comoros, Mascarenes and Seychelles.

Keywords

angiosperm, Comoros, dispersal–extinction–cladogenesis, divergence times, island biogeography, long-distance dispersal, Madagascar, Mascarenes, molecular dating, Seychelles

INTRODUCTION

The Western Indian Ocean region (WIOR) comprises Madagascar, the Comoros, Mascarenes and Seychelles and has been recognized as a hotspot of global biodiversity (Myers *et al.*, 2000). As such, it has become a hotspot for biogeographical studies detailing the origins of this diversity (e.g. Yoder & Nowak, 2006; Agnarsson & Kuntner, 2012; Samonds *et al.*, 2013). Madagascar in particular has long been considered to have an extraordinary biodiversity –

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while some otherwise widely distributed taxa are notably absent, other groups are very species rich (Simpson, 1940). Overall, the flora of Madagascar comprises more than 11,000 species of vascular plants, 82% of which are endemic (Callmander *et al.*, 2011).

The WIOR harbours both old continental islands and young volcanic islands with a wide variety of habitats, offering an ideal system for studies of biodiversity formation (Losos & Ricklefs, 2009; Vences *et al.*, 2009). The continental islands were formed following the break-up of East Gondwana: Madagascar was isolated from the Indian subcontinent about 88 Ma, and drifted towards the equator alongside Africa (Storey, 1995; Storey *et al.*, 1995; Wells, 2003), and the granitic Seychelles were subsequently separated from India about 64 Ma (Plummer & Belle, 1995; Collier *et al.*, 2008). Volcanic activity in the region gave rise to the Mascarene islands, comprising Mauritius, Réunion and Rodrigues (8, 2 and 1.5 Ma respectively; McDougall *et al.*, 1965; McDougall, 1971; Duncan, 1990). Older islands may have existed in the trail of the Réunion hotspot in the past, but have since been eroded and submerged (Gardner, 1986; Warren *et al.*, 2010). The Comoros archipelago is also the result of recent volcanism, of which the oldest island is Mayotte, about 8 Ma (Nougier *et al.*, 1986). In addition to the continental and volcanic islands, there are also small coralline islands, such as the Aldabra atoll (Seychelles).

Although it has long been recognized that the flora of Madagascar is affiliated with the African flora, biogeographic theories on the origin of the island's biodiversity have emphasized its Gondwanan heritage, as "a centre of survival for archaic autochthonous plants" (Koechlin, 1972; Leroy, 1978; p. 583). The historical proximity to the Indian subcontinent as well as extant phylogenetic connections between Madagascar and Asia has also prompted theories of biotic exchange between these regions by an isthmian land connection ("Lemurian land bridge"; Van Steenis, 1962; p. 343; Rage, 2003), or by island stepping stones (Schatz, 1996; Warren *et al.*, 2010). However, recent studies have highlighted the importance of long-distance dispersal, and indicated that the majority of the extant biota in Madagascar descended from African ancestors that arrived during the Cenozoic (e.g. Yoder & Nowak, 2006; Buerki *et al.*, 2013; Samonds *et al.*, 2013). Madagascar has in turn been an important source of dispersal to the neighbouring archipelagos of the Comoros, Mascarenes and Seychelles (e.g. Micheneau *et al.*, 2008; Le Péchon *et al.*, 2010; Wikström *et al.*, 2010). Despite much recent interest in the biogeography of Madagascar, there are few in-depth studies of the spatio-temporal history of its flora (Vences *et al.*, 2009).

Next to Orchidaceae, Rubiaceae is the most species-rich family in Madagascar, also in terms of number of endemic species (Callmander *et al.*, 2011). In this study, we focus on the Coffeeae alliance of subfamily Ixoroideae (Razafimandimbison *et al.*, 2011; Kainulainen *et al.*, 2013). In the WIOR, this clade is represented by the tribes Alberteae, Bertiereae, Coffeeae, Gardenieae, Octotropideae and Pavetteae. Many genera are endemic to Madagascar, i.e. *Canephora*, *Chapelieria*, *Flagenium*, *Jovetia*, *Homollea*, *Lemyrea*, *Mantalania*, *Melanoxerus*, *Nematostylis*, *Pseudomantalania*, *Razafimandimbisonia*, *Robbrechtia* and *Schizenterospermum*, but endemic genera are also found in the Mascarenes (*Fernelia* and *Ramosmania*) and the Seychelles (*Paragenipa*). Other genera are widespread in the region – *Coffea* and *Coptosperma*, for example, occur in all the archipelagos except the Seychelles, and *Paracephaelis* and *Tarenna* are only absent from the Mascarenes.

Dispersal by birds is a commonly invoked explanation for the colonization of Madagascar by fleshy-fruited plants (e.g. Renner, 2004), and the fruits of the Coffeeae alliance are with few exceptions fleshy. However, according to Hawkins & Goodman (2003); and references therein, few species of birds in Madagascar are frugivores, and none of them is migrational. Only seven species of forest-dwelling birds are listed as essential frugivores: a bulbul and two species each of parrot, pigeon and asitie. Notably, it has been suggested that these birds have an Asian or Australasian origin (Shapiro *et al.*, 2002; Warren *et al.*, 2005; Moyle *et al.*, 2006; Schweizer *et al.*, 2010; although the ancestral area of the Madagascar green pigeon is unknown).

Here, we use an extensive sample of species from the WIOR and sequence data of multiple molecular markers in order to reconstruct the biogeographic histories of the tribes of the Coffeeae alliance in the WIOR and understand how, when and from where they have colonized this region. Specifically, we investigate (1) predominance of African or Asian dispersal events to the WIOR; (2) incidence and direction of stepping-stone dispersal; (3) evidence of back-colonization from islands to continents; and (4) if the biogeographic patterns of plants and their presumed seed dispersers are congruent.

MATERIALS AND METHODS

Taxon sampling

Efforts were made to sample all 27 species of the Coffeeae alliance present on the Comoros, Mascarenes and Seychelles, and at least one representative of the 26 genera known from Madagascar. However, attempts to sequence DNA from the Malagasy endemic *Pseudomantalania* were unsuccessful. Also missing are *Polysphaeria lanceolata* subsp. *comorensis* from Anjouan, *P. multiflora* from Aldabra and *Coptosperma mitochondrioides* from Mayotte. Sampling density was increased in species-rich and widespread genera such as *Coffea*, *Gardenia*, *Rothmannia* and *Tarenna*. Of the 55 genera of the Coffeeae alliance occurring in Africa, 49 where sampled, as were 32 of the 52 genera found in Asia, Australasia or the Pacific. In contrast, the sampling of Neotropical taxa was limited (*Bertiera* is the only genus of the Coffeeae alliance present both in the Indian Ocean and the Neotropics). The Malagasy sampling included nine as of yet undescribed species of *Hyperacanthus*, and at least 10 undescribed taxa of Pavetteae.

The sole species of the Coffeeae alliance found on Socotra (*Kraussia socotrana*) was also included. All 12 extant species from the Mascarenes were sampled along with nine out of 11 species from Comoros and four out of five species from the Seychelles. Eighty-five out of 159 currently recognized Malagasy species were included (although the estimated number of species on Madagascar is at least 240). In total, the taxon sampling comprised 387 specimens from 364 species. An overview of species names, voucher information and GenBank accession numbers are given in Appendix S1 in the Supporting Information. The nomenclature follows that of Govaerts *et al.* (2013), with a few exceptions (i.e. *Empogona ruandensis*, *Pelagodendron vitiense*, *Sukunia pentagonioides* and *Tarenna malacophylla*), and the tribal classification follows that of Mouly *et al.* (2014).

DNA extraction, amplification and sequencing

DNA was extracted following the protocol of Doyle & Dickson (1987), and purified using the QIAquick® PCR purification kit (Qiagen, Hilden, Germany). Four plastid DNA regions were chosen for this study: the *rps16* intron, *ndh*F–*trn*L (UAG), *trn*K intron (including *mat*K) and *trn*T–*trn*F; all amplified using the primers and PCR protocol detailed by Kainulainen & Bremer (2014). PCR products were cleaned using Multiscreen Filter plates (Millipore, Billerica, MA, USA), sequenced using the amplification primers and the BigDye® terminator cycle sequencing kit, and subsequently analysed on a ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). Alternatively, sequencing was done using the EZ-seq v.2.0 sequencing service provided by Macrogen Europe (Amsterdam, the Netherlands). Sequence reads were assembled using the STADEN PACKAGE v1.5.3 (Staden, 1996; Staden *et al.*, 2000), and sequences new to this study (1172) were deposited in GenBank (Appendix S1 in the Supporting Information). Additional sequences (286) were obtained from GenBank (for references, see Appendix S1). *Acc*D-*psa*I, *pet*B-*pet*D and *rpl16* data for Bertiereae and Coffeeae (166 sequences in total; Appendix S1) were also added to the data set from Davis *et al.* (2007, 2011), Maurin *et al.* (2007) and Tosh *et al.* (2009).

Phylogenetic analyses

Sequence data were aligned using MUSCLE 3.8.31 (default settings; Edgar, 2004), after having been sorted by size using BIOEDIT (Hall, 1999). The latter program was also used to edit the alignments; alternative sequence versions of suspected sequence inversions were separated from each other in the alignments (but not excluded from the analyses; i.e. corresponding to positions 114471–114508 (KJ816005–6, KJ816018), 114501–114524 (KJ816122), 114899–114990 (KJ136920), 114585–114592 (KJ816044, KJ816046–7) and 115063–115083 (KJ136903) of the *Coffea arabica* L. plastid genome (GenBank accession number, EF044213; Samson *et al.*, 2007; all within the *ndh*F–*trn*L region). Homoplastic sequence inversions in *mat*K, *rps16*, *acc*D-*psa*I and *pet*B-*pet*D, corresponding to positions 2022–2023, 5412–5430, 60199–60216 and 77852–77866 of EF044213, respectively, were treated in the same manner.

Phylogenetic reconstructions were done using Markov chain Monte Carlo (MCMC) methods (Yang & Rannala, 1997). Bayesian analyses were conducted using MRBAYES 3.2.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) and BEAST 1.8 (Drummond & Rambaut, 2007; Drummond *et al.*, 2012). Data were treated as a single partition, and the GTR + I + G nucleotide substitution model was chosen based on the corrected Akaike information criterion (AICc) as calculated using the program jMODELTEST 2.1.6 (Darriba *et al.*, 2012). The MRBAYES analysis comprised four runs of four chains each that were run for 5×10^6 generations, the first 25% of which were excluded as burn-in.

Divergence times were estimated using BEAST 1.8, implementing the uncorrelated lognormal clock model and the birth-death tree prior (Gernhard, 2008). The root node was assigned a normally distributed age prior with a mean of 96 Ma and a standard deviation of 4.6 Myr; secondary calibration priors were similarly applied to the nodes representing the most recent common ancestor (mrca) of Rubiaceae (87 ± 4.6 Ma), Ixoroideae (59 ± 7.2 Ma) and the core Ixoroideae (36 ± 4.6 Ma); all strongly supported nodes. These age priors conform to the 95% highest posterior density (HPD) interval of corresponding nodes inferred in a study of Rubiaceae divergence times by Wikström *et al.* (2015). The BEAST analysis comprised eight runs of 50×10^6 generations. The individuals runs were combined and resampled (every 20000th generation) after removal of the burn-in (25%) to produce a sample of 15000 trees. Effective samples sizes of the parameters were evaluated using the program TRACER 1.6 (Rambaut & Drummond, 2013). Mean node ages and age density intervals were summarized on the sampled topology of the maximum product of clade credibilities. All analyses were performed on the Cipres science gateway portal v3.3 (Miller *et al.*, 2010).

Biogeographic analyses

Seven geographic areas were recognized in the biogeographic analyses: mainland Africa (1), Americas (2), Asia (3); including Australasia and the Pacific, Comoros (4), Madagascar (5), Mascarenes (6) and the Seychelles (7). Distribution data were obtained from the World checklist of Rubiaceae (Govaerts *et al.*, 2013). Undescribed or undetermined taxa were coded according to where they were collected, as were samples of species occurring in more than one geographic area (i.e. typically the species of interest and therefore more extensively sampled across their distribution). The geographic range evolution of the group was reconstructed using the dispersal–extinction–cladogenesis (DEC) model of Ree & Smith (2008) implemented in the program LAGRANGE 20130526. The DEC model was unconstrained (transitions between all areas equally likely) with a maximum of two areas per node. In order to account for topological uncertainty, we compiled the likelihood reconstructions for each node across a subsample of 100 trees randomly selected from the posterior distribution of BEAST trees.

RESULTS

Clade posterior probabilities inferred by the two Bayesian MCMC methods (MrBayes and BEAST) did not differ greatly; both are reported in Appendix S2 in the Supporting Information, along with mean divergence times, 95% HPD intervals and the results of the biogeographic analyses. The maximum clade credibility (MCC) tree from the BEAST analyses is shown in Figs 1–5. The inferred phylogenetic hypothesis was overall congruent with that of previous molecular studies (e.g. Kainulainen *et al.*, 2013; Mouly *et al.*, 2014). The results of the biogeographic analyses using the DEC model are summarized in Appendix S2 in the Supporting Information.

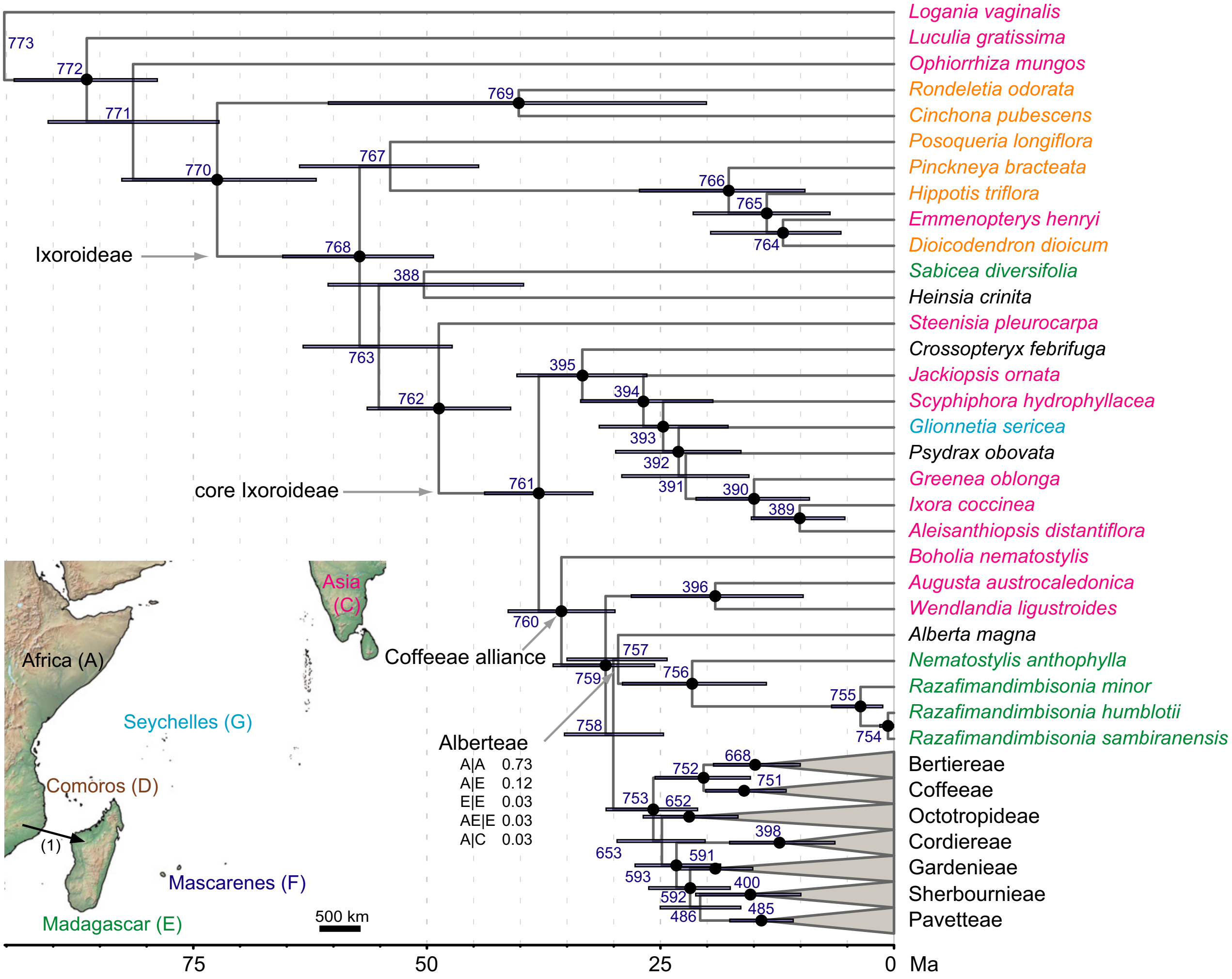
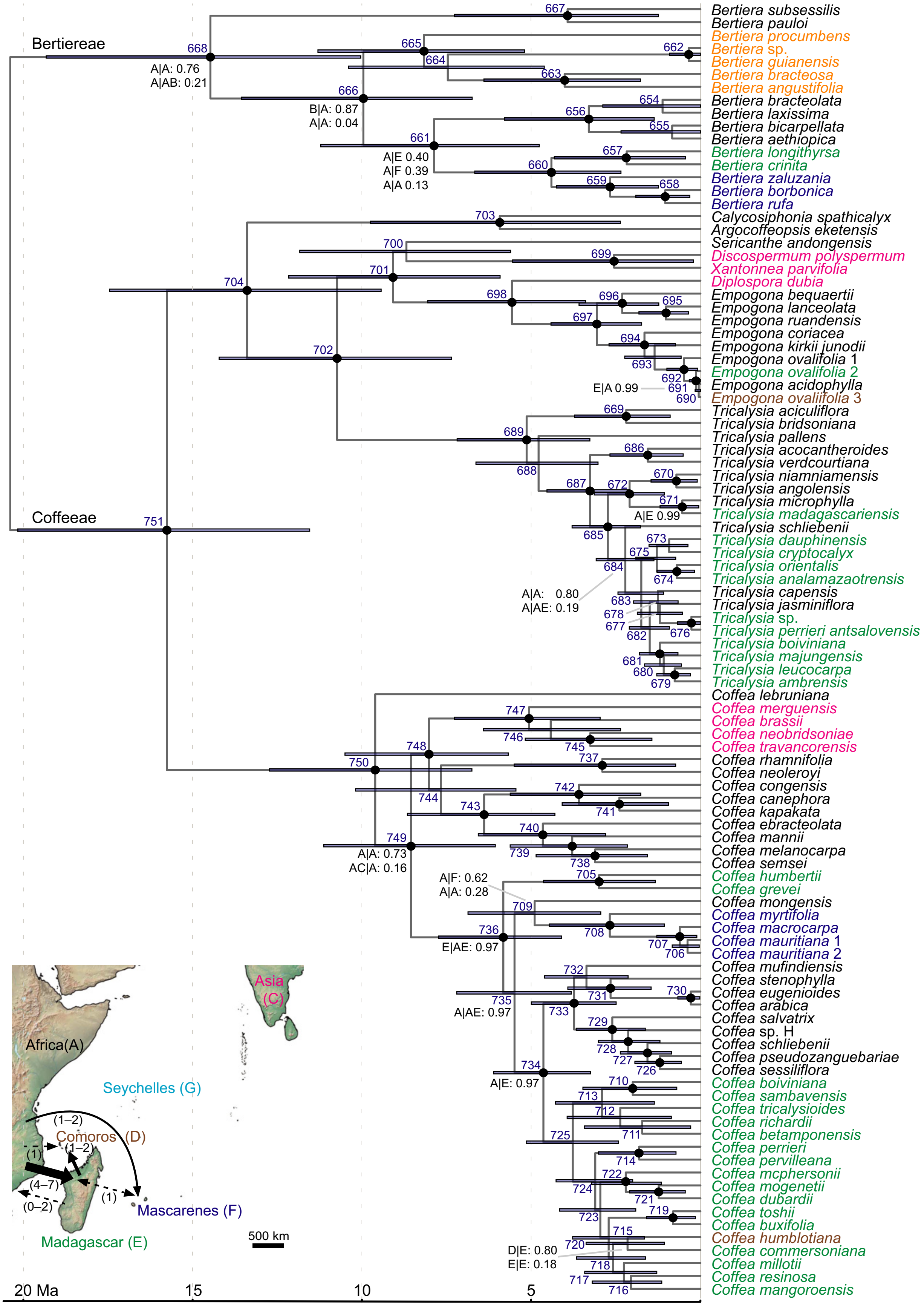


Figure 1 The Maximum clade credibility (MCC) tree from the BEAST analyses of the combined Coffeeae alliance data set. The tree is drawn as a chronogram with node heights representing the mean of the posterior sample of trees. Age estimates are summarized for each node (95% highest posterior density intervals). Well-supported nodes (posterior probability ≥ 0.95) are shown as black bullets. Node numbers correspond to those listed for the biogeographic results (Appendix S2). Relationships within the collapsed clades are detailed in Figs 2–5. Results from the LAGRANGE analyses are shown for nodes of interest. The inferred dispersal events are summarized on the map of the Western Indian Ocean region (WIOR; Lambert projection). The colours of the taxon names represent geographic origin: Africa = black, Americas = orange, Asia-Pacific = magenta, Madagascar = green and Seychelles = cyan.

Figure 2 Part of the Maximum clade credibility (MCC) tree from the BEAST analyses of the combined Coffeeae alliance data set, showing tribes Bertiereae and Coffeeae. Age estimates are summarized for each node (95% highest posterior density intervals). Well-supported nodes (posterior probability ≥ 0.95) are shown as black bullets. Results from the LAGRANGE analyses are shown for nodes of interest. The inferred dispersal events are summarized on the map of the Western Indian Ocean region (WIOR; Lambert projection; dashed arrows represent uncertain routes). The colours of the taxon names: Africa = black, Americas = orange, Asia-Pacific = magenta, Comoros = brown, Madagascar = green, Mascarenes = blue and Seychelles = cyan.


Bertiereae
668
A|A: 0.76
A|AB: 0.21
667
665
664
662
663
666
B|A: 0.87
A|A: 0.04
654
656
655
661
A|E 0.40
A|F 0.39
A|A 0.13
657
660
659
658
Bertiera subsessilis
Bertiera pauloi
Bertiera procumbens
Bertiera sp.
Bertiera guianensis
Bertiera bracteosa
Bertiera angustifolia
Bertiera bracteolata
Bertiera laxissima
Bertiera bicarpellata
Bertiera aethiopica
Bertiera longithyrsa
Bertiera crinita
Bertiera zaluzania
Bertiera borbonica
Bertiera rufa
703
704
700
699
701
698
696
695
697
694
693
692
E|A 0.99
691
690
702
Calycosiphonia spathicalyx
Argocoffeopsis eketensis
Sericanthe andongensis
Discospermum polyspermum
Xantonnea parvifolia
Diplospora dubia
Empogona bequaertii
Empogona lanceolata
Empogona ruandensis
Empogona coriacea
Empogona kirkii junodii
Empogona ovalifolia 1
Empogona ovalifolia 2
Empogona acidophylla
Empogona ovaliifolia 3
669
689
688
686
687
672
670
671
A|E 0.99
685
673
675
684
674
A|A: 0.80
A|AE: 0.19
683
678
677
682
676
681
680
679
Tricalysia aciculiflora
Tricalysia bridsoniana
Tricalysia pallens
Tricalysia acocantheroides
Tricalysia verdcourtiana
Tricalysia niamniamensis
Tricalysia angolensis
Tricalysia microphylla
Tricalysia madagascariensis
Tricalysia schliebenii
Tricalysia dauphinensis
Tricalysia cryptocalyx
Tricalysia orientalis
Tricalysia analamazaotrensis
Tricalysia capensis
Tricalysia jasminiflora
Tricalysia sp.
Tricalysia perrieri antsalovensis
Tricalysia boiviniana
Tricalysia majungensis
Tricalysia leucocarpa
Tricalysia ambrensis
Coffeeae
751
747
746
745
748
750
737
742
744
743
741
740
749
A|A: 0.73
AC|A: 0.16
739
738
A|F: 0.62
A|A: 0.28
705
709
736
E|AE: 0.97
708
707
706
732
735
A|AE: 0.97
731
730
733
729
728
727
726
734
A|E: 0.97
710
713
712
725
711
714
722
724
721
723
719
715
D|E: 0.80
E|E: 0.18
720
718
717
716
Coffea lebruniana
Coffea merguensis
Coffea brassii
Coffea neobridsoniae
Coffea travancorensis
Coffea rhamnifolia
Coffea neoleroyi
Coffea congensis
Coffea canephora
Coffea kapakata
Coffea ebracteolata
Coffea mannii
Coffea melanocarpa
Coffea semsei
Coffea humbertii
Coffea grevei
Coffea mongensis
Coffea myrtifolia
Coffea macrocarpa
Coffea mauritiana 1
Coffea mauritiana 2
Coffea mufindiensis
Coffea stenophylla
Coffea eugenioides
Coffea arabica
Coffea salvatrix
Coffea sp. H
Coffea schliebenii
Coffea pseudozanguebariae
Coffea sessiliflora
Coffea boiviniana
Coffea sambavensis
Coffea tricalysioides
Coffea richardii
Coffea betamponensis
Coffea perrieri
Coffea pervilleana
Coffea mcphersonii
Coffea mogenetii
Coffea dubardii
Coffea toshii
Coffea buxifolia
Coffea humblotiana
Coffea commersoniana
Coffea millotii
Coffea resinosa
Coffea mangoroensis
Africa(A)
Asia (C)
Seychelles (G)
Comoros (D)
Madagascar (E)
Mascarenes (F)
(1–2)
(1–2)
(1)
(4–7)
(0–2)
(1)
500 km
20 Ma
15
10
5

Asia was inferred as the most likely ancestral area for the Coffeeae alliance clade, but Africa was supported as the ancestral area for the tribes Alberteae, Bertiereae, Coffeeae, Gardenieae, Octotropideae and Pavetteae, that are present in the WIOR. Multiple independent dispersal events were found between mainland Africa and Asia, represented by the *Discospermum-Xantonnea* clade, *Diplospora* and a clade in *Coffea* (Coffeeae, Fig. 2); the *Hyptianthera-Morindopsis* clade (Octotropideae, Fig. 3); *Benkara*, the *Brachytome-Catunaregam* clade and clades in both *Aidia* and *Rothmannia* (Gardenieae, Fig. 4); and clades in both *Pavetta* and *Tarenna* (Pavetteae, Fig. 5). Dispersal events from mainland Africa to the Americas were also inferred, represented by Cordiereae, a clade in *Bertiera* and the *Randia-Tocoyena* clade (Gardenieae). Early range evolution within the *Genipa-Gardenia* clade could not be unequivocally resolved.

In the WIOR, the ancestral area reconstructions indicated at least 15 dispersals to Madagascar, 8–11 dispersals out of

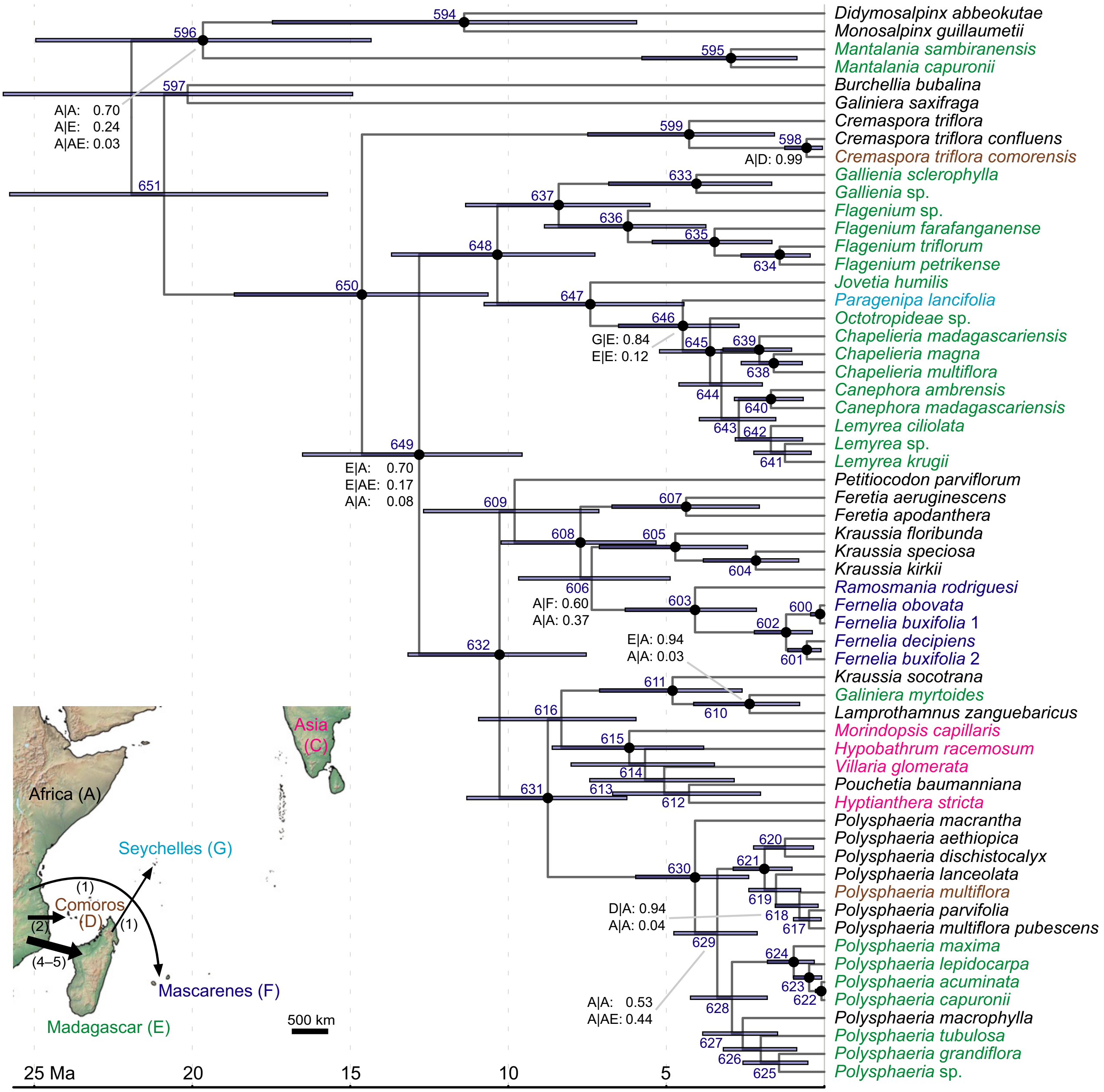


Figure 3 Part of the Maximum clade credibility (MCC) tree from the BEAST analyses of the combined Coffeeae alliance data set, showing Octotropideae. Age estimates are summarized for each node (95% highest posterior density intervals). Well-supported nodes (posterior probability ≥ 0.95) are shown as black bullets. Results from the LAGRANGE analyses are shown for nodes of interest. The inferred dispersal events are summarized on the map of the Western Indian Ocean region (WIOR; Lambert projection). The colours of the taxon names represent geographic origin: Africa = black, Asia-Pacific = magenta, Comoros = brown, Madagascar = green, Mascarenes = blue and Seychelles = cyan.

Madagascar, four dispersals to the Mascarenes, four dispersals to the Seychelles and 8–9 dispersals to the Comoros. Most dispersals have occurred within the last 10 Myr, but at least the colonization of Madagascar by the *Razafimandimbisonia-Nematostylis* clade is older (crown age 21.6 Ma; HPD, 13.7–29.1 Ma). Support for a monophyletic Alberteae was low (Fig. 1), but the biogeographic analyses favoured a single dispersal event from Africa to Madagascar. Africa was also indicated as the ancestral area of the Indian Ocean radiation of *Bertiera* (Fig. 2). A single dispersal event into the WIOR was supported, but whether Madagascar or the Mascarenes were colonized first was equivocal.

At least four dispersals to Madagascar were inferred in Coffeeae. However, patterns of range evolution in *Coffea* were inconclusive, mainly due to topological uncertainty. The species from Madagascar were not supported as monophyletic; the majority of the sampled species formed a clade together with mainly East African species, whereas a *Coffea grevei-C. humbertii* clade was resolved as more early divergent. The biogeographical interpretation largely depended on the relationships among these clades and that of a clade comprising the Mascarene species (*Coffea macrocarpa*, *C. mauritiana* and *C. myrtifolia*) together with *C. mongensis*. The DEC analyses based on the MCC topology favoured a vicariance scenario in which the ancestor of the East African-Malagasy clade was distributed in both these areas (A|AE: 0.97). The Mascarene *Coffea* clade was supported as being the result of an independent dispersal event from Africa.

Empogona ovalifolia dispersed from Africa to the Comoros and to Madagascar. The biogeographic analyses favoured two independent dispersal events, although support within the *Empogona ovalifolia* clade was low. Phylogenetic support within *Tricalysia* was poor and consequently the biogeographic results were uncertain for this clade. At least two independent arrivals to Madagascar were indicated: (1) *T. madagascariensis* and (2) a weakly supported clade comprising the remaining sampled Malagasy species as well as the two African species *T. capensis* and *T. jasminiflora*. The former represent a well-supported out-of-Africa dispersal event, but biogeographic reconstructions of the latter clade were inconclusive because of phylogenetic uncertainty.

At least four dispersals to Madagascar were reconstructed in Octotropideae (Fig. 3). An out-of-Africa dispersal event was supported for *Mantalania*. The Malagasy Octotropideae *Canephora*, *Chapelieria*, *Flagenium*, *Gallienia*, *Jovetia* and *Lemyrea* formed a clade together with *Paragenipa* from the Seychelles. The ancestral area of this clade is Africa. Dispersal from Madagascar to the Seychelles was inferred for *Paragenipa*. The genus *Galiniera* was not resolved as monophyletic. The Malagasy *Galiniera myrtoides* formed a clade with East African *Lamprothamnus zanguebaricus*, whereas *G. saxifraga* from Tropical Africa is grouped with the South African *Burchellia bubalina*. Dispersal from Africa to Madagascar was supported for the ancestor of *Galiniera myrtoides*. The Malagasy species of *Polysphaeria* were not resolved as monophyletic. However, clade support within the genus was low. The ancestral area of *Polysphaeria* was inferred as Africa. The DEC model favoured a vicariance scenario for the MCC topology. Out-of-Africa dispersal was supported for the ancestor of the Comoran *Polysphaeria multiflora*, as well as for *Cremaspora triflora* subsp. *comorensis*. *Fernelia* and *Ramosmania* from the Mascarenes formed a well-supported clade nested within a clade of African taxa, and Africa was the ancestral area of the *Fernelia-Ramosmania* clade.

Gardenieae included at least four dispersals to Madagascar (Fig. 4). The Malagasy *Gardenia* species are monophyletic, nested within a clade of African species. Dispersal from Africa to Madagascar was also inferred for *Melanoxerus*. In contrast, *Catunaregam* is nested within a clade of Asian taxa. The genus is not supported as monophyletic, because the Indian *Deccania pubescens* is nested within the clade as a poorly supported sister group to *Catunaregam* sp. 2 from Madagascar. Out-of-Asia dispersal was supported for the latter species. Phylogenetic relationships within *Hyperacanthus* were poorly supported, although a clade comprising all sampled Malagasy species but one (*Hyperacanthus* sp. 7) was resolved with strong support. The biogeographic analyses supported an African origin of the genus. The DEC model favoured a vicariance scenario for the MCC topology. A single long-distance dispersal from Africa to the Seychelles was inferred for *Rothmannia annae*.

The Indian Ocean Pavetteae are strongly supported as being monophyletic (Fig. 5), and are nested within an African clade. The biogeographic analyses supported a single dispersal to Madagascar, followed by many out-of-Madagascar dispersal events, including: (1) dispersal to the Mascarenes in the *Coptosperma borbonicum-cymosum* clade; dispersals to the Comoros in (2) *C. nigrescens*, (3) *C. supra-axillare*, (4) *Paracephaelis cinerea*, (5) *Tarenna grevei* and (6) *T. spiranthera*; dispersals to the Seychelles in (7) *P. trichanta* and (8) *T. sechellensis*; and dispersal back to Africa in the *C. littorale-rhodesiacum* clade. *Coptosperma nigrescens* and *C. supra-axillare* have also dispersed to Africa, either via the Comoros or independently from Madagascar.

DISCUSSION

The Lemurian land-bridge or stepping-stone hypothesis of dispersal postulates that biotic exchange has occurred from Asia to Madagascar across the Indian Ocean by island hopping, and via the Seychelles in particular (Van Steenis, 1962; Schatz, 1996; Warren *et al.*, 2010). Quaternary scenarios of the Indian Ocean geography at lower sea levels estimated by Warren *et al.* (2010), indicated that several submerged banks as well as the area that is now the Seychelles archipelago, were large islands and subaerial during long time intervals (see also Weigelt *et al.*, 2016). These islands should be considered in the study of the biogeographic history of the Indian Ocean and may at least for birds have facilitated dispersal from Asia and subsequent colonization of Madagascar (cf. Samonds *et al.*, 2013). However, our analyses indicate that the "Lemurian" route of dispersal has been of less importance to the Coffeeae alliance, and that the predominant pattern of plant colonization in the WIOR is from mainland Africa.

Although no stepping-stone dispersal was inferred via the Seychelles to Madagascar or the rest of the WIOR, this study shows that, conversely, Madagascar has been important as a stepping-stone for dispersal to the Seychelles (*Paracephaelis*, *Paragenipa* and *Tarenna*), as well as to the Comoros (*Coffea*, *Coptosperma*, *Paracephaelis* and *Tarenna*) and the Mascarenes (*Coptosperma* and probably *Bertiera*). That the Malagasy flora has been an important source for colonizing the surrounding archipelagos has previously been shown in several groups (e.g. Micheneau *et al.*, 2008; Le Péchon *et al.*, 2010; Strijk *et al.*, 2012; Stride *et al.*, 2014). We also find evidence for back-colonization from Madagascar to mainland Africa, a biogeographical pattern previously reported in plant families such as Gentianaceae (Yuan *et al.*, 2005) and Celastraceae (Bacon *et al.*, 2016). Specifically, at least three independent dispersal events to eastern Africa was inferred in *Coptosperma* (possibly also in *Coffea* and *Tricalysia*).

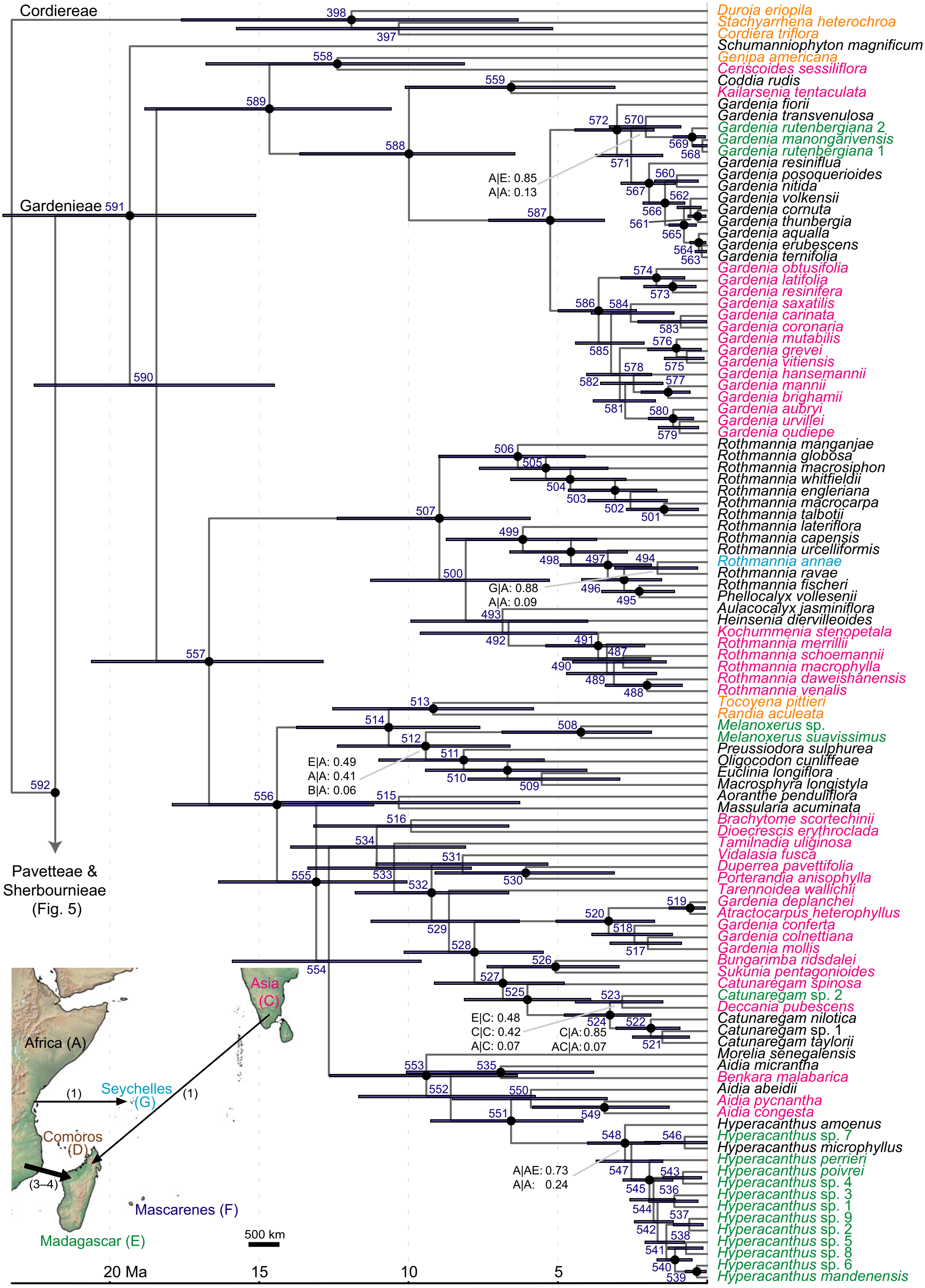
Except Alberteae, which have wind-dispersed pterocarps, the fruits of the Coffeeae alliance are typically fleshy, and presumably zoochorous. In contrast to the Asian or Australasian origins of the majority of Cenozoic bird introductions to Madagascar (Samonds *et al.*, 2013; Table S1, and references therein), we find that Africa has been the foremost source of plants of the Coffeeae alliance in the region, a pattern that has been suggested as being the predominant of most Malagasy plant groups (Yoder & Nowak, 2006). The discrepant patterns in the origins of the extant frugivore birds and plants could indicate that the African frugivorous birds have not been very successful in colonizing Madagascar, and that the colonization opportunities for the African zoochorous plants may have been very sporadic. Alternatively, the frugivorous bird species in question may have gone extinct. The dispersal of seeds by fruit bats should also be considered in relation to long-distance dispersal of fleshy fruits (e.g. Shilton *et al.*, 1999). However, as with the Malagasy frugivorous birds, the fruit bat fauna is not very diverse: "rather limited in comparison with other Old World tropical regions" (Hutcheon, 2003; p;. 1205; in reference to the three species present in Madagascar), and at least in the case of the flying foxes (*Pteropus*), they are recent arrivals from Asia (O'Brien *et al.*, 2009). It is possible that rafting by washed-off mats of vegetation has been the dominant means of seed dispersal in the region as has been suggested for non-volant animals (Simpson, 1940; Ali & Huber, 2010).

All dispersals to Madagascar within the Coffeeae alliance are from Africa, with the exception of *Catunaregam* (Asia; Fig. 4) and possibly *Bertiera* (Mascarenes?; Fig. 2). The first to disperse to Madagascar was likely the African ancestor of the *Nematostylis-Razafimandimbisonia* clade (crown age 21.6 Ma; HPD, 13.7–29.1 Ma), followed by the *Gallienia-Lemyrea* clade (crown age 10.4 Ma; HPD, 7.3–13.7 Ma) and the WIOR Pavetteae (crown age 8.5 Ma; HPD, 6.5–10.7 Ma). The *Melanoxerus* clade has been present in Madagascar since 4.2 Ma (HPD, 1.9–6.9 Ma). The estimated crown age of *Mantalania* is only 3.0 Ma (HPD, 0.9–5.8 Ma), but the minimum age of colonization by this lineage would likely have been older had *Pseudomantalania* also been included in the analyses. It is not clear if Malagasy *Coffea* originate from one or two colonization events. The minimum age of colonization in the former scenario is 5.8 Ma (HPD, 4.1–7.7 Ma; Fig. 2, node 736), whereas two independent arrivals would likely have been more recent. Although the inferred pattern of range expansion in *Bertiera* is not conclusive, it is likely that this genus has been present in the WIOR since 4.4 Ma (HPD, 2.4–6.7 Ma; Fig. 2, node 660). We hypothesize that Madagascar was colonized before the Mascarenes. *Gardenia*, *Hyperacanthus*, *Polysphaeria*, *Tricalysia* and the ancestor of *Galiniera myrtoides* likely colonized Madagascar from Africa within the last 5 Myr. *Catunaregam* is a similarly recent arrival, but according to the Lagrange analysis from Asia. Although Asia is the ancestral area of this genus, it should be noted that the phylogenetic relationships between its Asian, African and Malagasy species are not resolved with strong support in this study.

The extant Coffeeae alliance native to the Seychelles have reached the archipelago either via long-distance dispersal events from the East African mainland (*Rothmannia annae*; and most likely the Aldabran *Polysphaeria multiflora* and *Empogona ovalifolia*, not included in the analysis), or from Madagascar (*Paragenipa lancifolia*, *Paracephaelis trichantha* and *Tarenna sechellensis*). However, it should be noted that *Glionnetia*, one of the outgroup taxa of our analyses (belonging to the Vanguerieae alliance; Ixoroideae; Razafimandimbison *et al.*, 2011), represents a clade that is inferred as having dispersed from Asia to the Seychelles (Fig. 1). The divergence ages indicate that the colonization events of *Paragenipa* (4.5 Ma, HPD: 2.7–6.5), *Rothmannia* (1.7 Ma, HPD: 0.3–3.1), *Tarenna* (1.2 Ma, HPD: 0.4–2.1) and *Paracephaelis* (0.7 Ma, HPD: 0.2–1.3) all occurred within the last 6.5 Ma.

The Comoran *Coffea humblotiana*, *Coptosperma nigrescens*, *C. supra-axillare*, *Paracephaelis cinerea*, *Tarenna grevei* and *T. spiranthera* all appear to have dispersed from Madagascar,

Figure 4 Part of the Maximum clade credibility (MCC) tree from the BEAST analyses of the combined Coffeeae alliance data set, showing tribes Cordiereae and Gardenieae. Age estimates are summarized for each node (95% highest posterior density intervals). Well-supported nodes (posterior probability ≥ 0.95) are shown as black bullets. Results from the LAGRANGE analyses are shown for nodes of interest. The inferred dispersal events are summarized on the map of the Western Indian Ocean region (WIOR; Lambert projection). The colours of the taxon names represent geographic origin: Africa = black, Americas = orange, Asia-Pacific = magenta, Madagascar = green and Seychelles = cyan.


Cordiereae
398
397
Duroia eriopila
Stachyarrhena heterochroa
Cordiera triflora
Schumanniophyton magnificum
558
Genipa americana
Ceriscoides sessiliflora
559
Coddia rudis
Kailarsenia tentaculata
589
Gardenia fiorii
Gardenia transvenulosa
572
570
Gardenia rutenbergiana 2
Gardenia manongarivensis
569
568
Gardenia rutenbergiana 1
588
571
Gardenia resiniflua
A|E: 0.85
A|A: 0.13
560
Gardenia posoquerioides
Gardenia nitida
567
562
Gardenia volkensii
Gardeniеae 591
566
Gardenia cornuta
587
561
Gardenia thunbergia
565
Gardenia aqualla
564
Gardenia erubescens
563
Gardenia ternifolia
574
Gardenia obtusifolia
Gardenia latifolia
573
Gardenia resinifera
586
584
Gardenia saxatilis
Gardenia carinata
583
Gardenia coronaria
576
Gardenia mutabilis
585
Gardenia grevei
575
Gardenia vitiensis
578
Gardenia hansemannii
582
577
Gardenia mannii
Gardenia brighamii
581
Gardenia aubryi
580
Gardenia urvillei
579
Gardenia oudiepe
590
506
Rothmannia manganjae
Rothmannia globosa
505
Rothmannia macrosiphon
504
Rothmannia whitfieldii
503
Rothmannia engleriana
502
Rothmannia macrocarpa
501
Rothmannia talbotii
507
499
Rothmannia lateriflora
Rothmannia capensis
498
497
494
Rothmannia urcelliformis
Rothmannia annae
500
Rothmannia ravae
G|A: 0.88
A|A: 0.09
496
Rothmannia fischeri
495
Phellocalyx vollesenii
493
Aulacocalyx jasminiflora
Heinsenia diervilleoides
492
491
Kochummenia stenopetala
Rothmannia merrillii
487
557
Rothmannia schoemannii
490
Rothmannia macrophylla
489
Rothmannia daweishanensis
488
Rothmannia venalis
513
Tocoyena pittieri
514
Randia aculeata
508
Melanoxerus sp.
Melanoxerus suavissimus
512
Preussiodora sulphurea
511
Oligocodon cunliffeae
E|A: 0.49
A|A: 0.41
B|A: 0.06
510
Euclinia longiflora
509
Macrosphyra longistyla
592
Aoranthe penduliflora
556
515
Massularia acuminata
Brachytome scortechinii
516
Dioecrescis erythroclada
534
Tamilnadia uliginosa
531
Vidalasia fusca
Duperrea pavettifolia
533
555
530
Porterandia anisophylla
532
Tarennoidea wallichii
519
Gardenia deplanchei
520
Atractocarpus heterophyllus
529
518
Gardenia conferta
Gardenia colnettiana
517
528
Gardenia mollis
526
Bungarimba ridsdalei
554
527
Sukunia pentagonioides
525
Catunaregam spinosa
523
Catunaregam sp. 2
Deccania pubescens
E|C: 0.48
C|C: 0.42
A|C: 0.07
524
C|A: 0.85
AC|A: 0.07
522
Catunaregam nilotica
Catunaregam sp. 1
521
Catunaregam taylorii
Morelia senegalensis
553
535
Aidia micrantha
Benkara malabarica
552
550
Aidia abeidii
Aidia pycnantha
549
Aidia congesta
551
Hyperacanthus amoenus
548
546
Hyperacanthus sp. 7
Hyperacanthus microphyllus
A|AE: 0.73
A|A: 0.24
547
543
Hyperacanthus perrieri
Hyperacanthus poivrei
545
536
Hyperacanthus sp. 4
Hyperacanthus sp. 3
544
537
Hyperacanthus sp. 1
542
538
Hyperacanthus sp. 9
Hyperacanthus sp. 2
541
Hyperacanthus sp. 5
Hyperacanthus sp. 8
540
Hyperacanthus sp. 6
539
Hyperacanthus mandenensis
Pavetteae & Sherbournieae (Fig. 5)
Africa (A)
Asia (C)
Seychelles (G)
(1)
(1)
Comoros (D)
(3–4)
Mascarenes (F)
Madagascar (E)
500 km
20 Ma
15
10
5

whereas *Cremaspora triflora*, *Polysphaeria lanceolata* and *P. multiflora* have reached the Comoros from eastern Africa. Unfortunately, no samples of *Coptosperma mitochondrioides* or *Polysphaeria lanceolata* from the Comoros were included in our analyses. However, considering the phylogenetic positions of these species (Figs 3 & 5), it can be inferred that the former species dispersed from Madagascar and the latter from Africa. Regarding *Empogona ovalifolia*, it is unclear if its distribution in the Comoros and Madagascar is the result of independent dispersal events from East Africa, or stepping-stone dispersal via either the Comoros or Madagascar. The divergence time analysis indicates that all dispersals to the Comoros from Madagascar have occurred within the last 3.4 Ma, and those from Africa within the last 1.6 Ma. *Coptosperma nigrescens* and *C. supra-axillare* have also colonized eastern Africa, possibly by stepping-stone dispersal via the Comoros; at least those scenarios are not contradicted by or results. Out-of-Madagascar dispersal to Africa is also found in the *Coptosperma littorale-C. rhodesiacum* clade, and probably in *Paracephaelis* (no African material sampled).

The Mascarenes are home to *Bertiera*, *Coffea*, *Coptosperma*, *Fernelia* and *Ramosmania*, and the latter two are endemic to this archipelago. *Fernelia* and *Ramosmania* are nested within a clade of East African taxa, and Africa is supported as the ancestral area. The divergence time of the *Fernelia-Ramosmania* clade is estimated to 7.4 Ma (HPD: 4.9–9.7), an age comparable to that of the formation of Mauritius (8 Ma; Duncan, 1990). The crown group, however, is considerably younger (4.1 Ma, HPD: 2.1–6.3 Ma). Notably, the stem age of *Ramosmania* is older than the island of Rodrigues (1.5 Ma; McDougall *et al.*, 1965; but see Strijk *et al.*, 2012), to which *Ramosmania* is currently restricted. However, these age estimates are not necessarily conflicting, because we have no estimate of the crown age of *Ramosmania*, and cannot preclude that, until recently, *Ramosmania* was native to Mauritius as well. In contrast, Strijk *et al.* (2012) conjectured an older origin of Rodrigues, and suggested that the island has served as a stepping stone for regional colonization of *Psiadia* (Asteraceae; although their analyses showed a HPD for the crown age of the Rodriguesian taxa that fits well with the young age of the island).

Bertiera and *Coffea* may have arrived in the Mascarenes in close concert; at least they have a similar estimated crown age of 2.7 Ma (HPD: 1.2–4.2 Ma for *Bertiera* and 1.1–4.5 Ma for *Coffea*). A somewhat younger minimum age estimate of 1.8 Ma (HPD: 0.8–2.8 Ma) for the Mascarene *Coffea* arrival was reported by Nowak *et al.* (2014). Like the *Fernelia-Ramosmania* ancestor, *Coffea* is supported as having dispersed from Africa, whereas the ancestral area of *Bertiera* is equivocal, either Africa or Madagascar. *Coptosperma* dispersed out-of-Madagascar, and probably represents the most recent arrival to the Mascarene islands, with a crown age of 0.5 Ma (HPD, 0.1–1.1 Ma). All four groups have dispersed between Mauritius and Réunion, and with the possible exception of the *Bertiera borbonica-B. rufa* clade (crown age: 1.0, HPD, 0.3–1.9), within the last 1 Ma. Compared with the Coffeeae alliance colonization events of the Comoros and Seychelles, the Mascarene radiations appear more diverse in terms of the number of species, although taxonomic inflation may also be part of the explanation. The biogeography of the Coffeeae alliance in the WIOR is discussed in more detail in Appendix S3 in the Supporting Information.

In summary, we find that Madagascar has predominantly been colonized by dispersal from (eastern) Africa. Colonizations of the neighbouring archipelagos of the Comoros, Mascarenes and Seychelles, have partly also been from Africa but have mainly been the result of subsequent stepping-stone dispersals from Madagascar, whereas floristic exchange between the WIOR and India or Southeast Asia has not been prominent in the Coffeeae alliance. Most dispersals have occurred in the last 10 Myr, and dispersal opportunities appear to have been sporadic, presumably in part due to a paucity of frugivorous migratory birds. This is also reflected in the high levels of endemism in the region. Following successful colonization, radiation appears to have taken place in some groups and on Madagascar in particular. Most notable both in terms of species number and range of habitats occupied are the radiations of *Coffea* (60 sp.; Davis *et al.*, 2010), *Hyperacanthus* (50 sp.; Rakotonasolo & Davis, 2006) and Pavetteae (70 sp.; De Block, 2003), which are present in most vegetation types of Madagascar.

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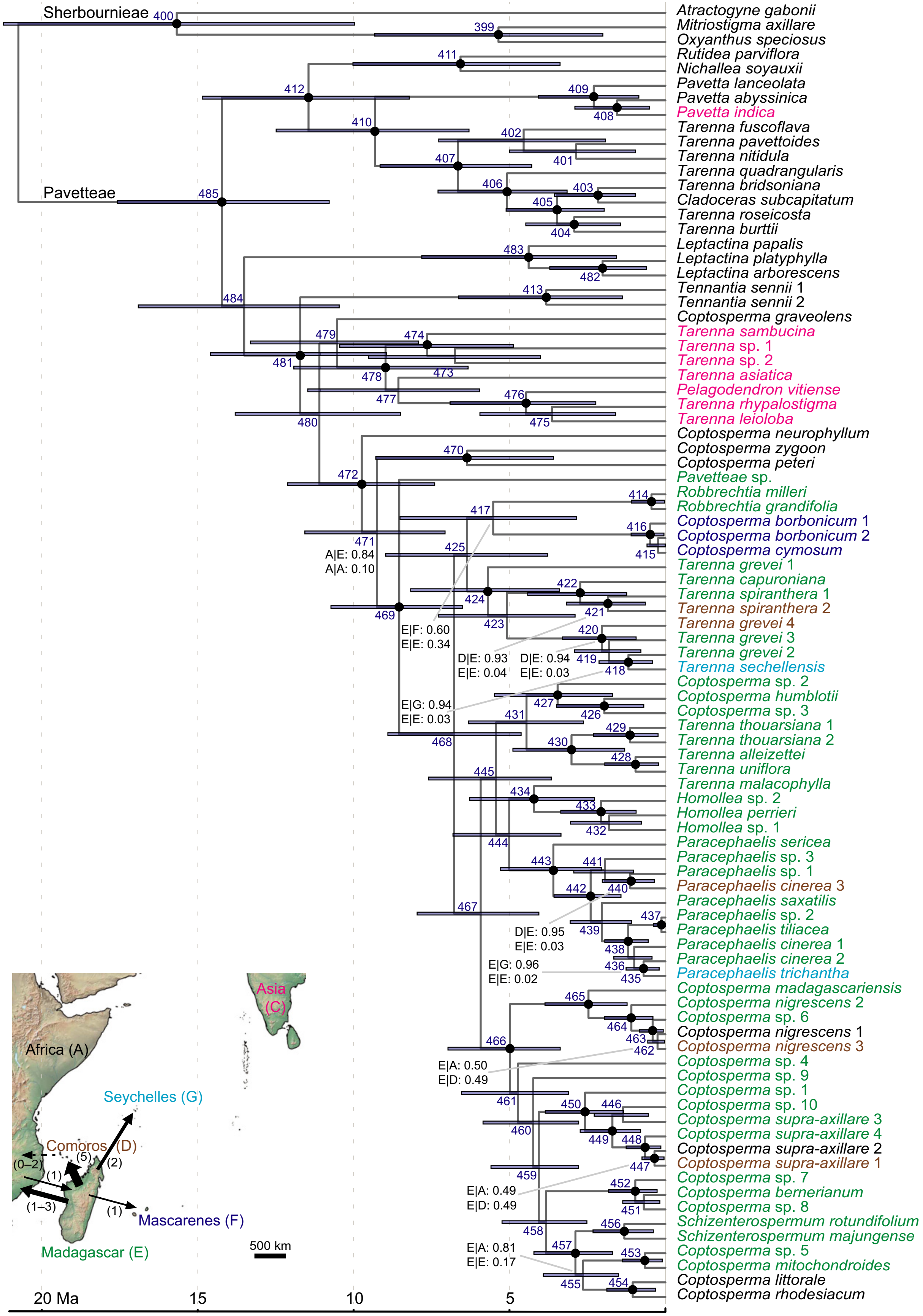
Figure 5 Part of the maximum clade credibility (MCC) tree from the BEAST analyses of the combined Coffeeae alliance data set, showing tribes Sherbournieae and Pavetteae. Age estimates are summarized for each node (95% highest posterior density intervals). Well-supported nodes (posterior probability ≥ 0.95) are shown as black bullets. Results from the LAGRANGE analyses are shown for nodes of interest. The inferred dispersal events are summarized on the map of the Western Indian Ocean region (WIOR; Lambert projection; dashed arrow represent uncertain route). The colours of the taxon names represent geographic origin: Africa = black, Asia-Pacific = magenta, Comoros = brown, Madagascar = green, Mascarenes = blue and Seychelles = cyan.


Sherbournieae
400
399
411
412
409
408
410
402
401
407
406
403
405
404
Pavetteae
485
483
482
484
413
479
474
481
478
473
477
476
475
480
470
472
471
A|E: 0.84
A|A: 0.10
414
417
416
415
425
422
424
421
469
423
E|F: 0.60
E|E: 0.34
420
D|E: 0.93
E|E: 0.04
D|E: 0.94
E|E: 0.03
419
418
427
E|G: 0.94
E|E: 0.03
426
431
429
468
430
428
445
434
433
432
444
443
441
442
440
467
437
D|E: 0.95
E|E: 0.03
439
438
E|G: 0.96
E|E: 0.02
436
435
465
464
463
466
462
E|A: 0.50
E|D: 0.49
461
450
446
460
449
448
447
459
E|A: 0.49
E|D: 0.49
452
451
458
456
E|A: 0.81
E|E: 0.17
457
453
455
454
20 Ma
15
10
5
Atractogyne gabonii
Mitriostigma axillare
Oxyanthus speciosus
Rutidea parviflora
Nichallea soyauxii
Pavetta lanceolata
Pavetta abyssinica
Pavetta indica
Tarenna fuscoflava
Tarenna pavettoides
Tarenna nitidula
Tarenna quadrangularis
Tarenna bridsoniana
Cladoceras subcapitatum
Tarenna roseicosta
Tarenna burttii
Leptactina papalis
Leptactina platyphylla
Leptactina arborescens
Tennantia sennii 1
Tennantia sennii 2
Coptosperma graveolens
Tarenna sambucina
Tarenna sp. 1
Tarenna sp. 2
Tarenna asiatica
Pelagodendron vitiense
Tarenna rhypalostigma
Tarenna leioloba
Coptosperma neurophyllum
Coptosperma zygoon
Coptosperma peteri
Pavetteae sp.
Robbrechtia milleri
Robbrechtia grandifolia
Coptosperma borbonicum 1
Coptosperma borbonicum 2
Coptosperma cymosum
Tarenna grevei 1
Tarenna capuroniana
Tarenna spiranthera 1
Tarenna spiranthera 2
Tarenna grevei 4
Tarenna grevei 3
Tarenna grevei 2
Tarenna sechellensis
Coptosperma sp. 2
Coptosperma humblotii
Coptosperma sp. 3
Tarenna thouarsiana 1
Tarenna thouarsiana 2
Tarenna alleizettei
Tarenna uniflora
Tarenna malacophylla
Homollea sp. 2
Homollea perrieri
Homollea sp. 1
Paracephaelis sericea
Paracephaelis sp. 3
Paracephaelis sp. 1
Paracephaelis cinerea 3
Paracephaelis saxatilis
Paracephaelis sp. 2
Paracephaelis tiliacea
Paracephaelis cinerea 1
Paracephaelis cinerea 2
Paracephaelis trichantha
Coptosperma madagascariensis
Coptosperma nigrescens 2
Coptosperma sp. 6
Coptosperma nigrescens 1
Coptosperma nigrescens 3
Coptosperma sp. 4
Coptosperma sp. 9
Coptosperma sp. 1
Coptosperma sp. 10
Coptosperma supra-axillare 3
Coptosperma supra-axillare 4
Coptosperma supra-axillare 2
Coptosperma supra-axillare 1
Coptosperma sp. 7
Coptosperma bernerianum
Coptosperma sp. 8
Schizenterospermum rotundifolium
Schizenterospermum majungense
Coptosperma sp. 5
Coptosperma mitochondroides
Coptosperma littorale
Coptosperma rhodesiacum
Asia (C)
Africa (A)
Seychelles (G)
Comoros (D)
(0–2)
(5)
(2)
(1)
(1–3)
(1)
Mascarenes (F)
Madagascar (E)
500 km

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary table.
Appendix S2 Supporting data.
Appendix S3 Supplementary discussion.

BIOSKETCH

This research group focuses on phylogenetic and biodiversity studies of the large tropical plant family Rubiaceae.

Author contributions: B.B. conceived the ideas; B.B., K.K. and S.G.R. collected the data; K.K. and N.W. analysed the data, and K.K. led the writing.

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