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Biogeography of the Malagasy Celastraceae: Multiple independent origins followed by widespread dispersal of genera from Madagascar ☆

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ABSTRACT

Of the 97 currently recognized genera of Celastraceae, 19 are native to Madagascar, including six endemics. In this study we conducted the most thorough phylogenetic analysis of Celastraceae yet completed with respect to both character and taxon sampling, and include representatives of five new endemic genera. Fifty-one new accessions, together with 328 previously used accessions of Celastrales, were sampled for morphological characters, two rDNA gene regions, and two plastid gene regions. The endemic Malagasy genera are resolved in two separate lineages—*Xenodrys* by itself and all other endemic genera in a clade that also includes four lineages inferred to have dispersed from Madagascar: *Brexia madagascariensis* (Mascarene Islands, coastal Africa), *Elaeodendron* (West Indies, Africa to New Caledonia), and *Pleurostylia* (Africa to New Caledonia). Of the 12 extant Malagasy Celastraceae lineages identified, eight are clearly of African origin. The origins of the remaining four lineages are less clear, but reasonable possibilities include America, Eurasia, Africa, southern India, Malesia, and Australia. Based on 95% credible age intervals from fossil-calibrated molecular dating, all 12 extant Malagasy Celastraceae lineages appear to have arisen following dispersal after the separation of Madagascar from other landmasses within the last 70 million years.

1. Introduction

Madagascar is one of the five leading biodiversity hotspots, and is ranked third in terms of endemic plants (Myers et al., 2000). This island nation is home to at least 11,220 described species of vascular plants, of which 82% are endemic, including five entire families (Callmander et al., 2011). Many biogeographic studies have been conducted on the Malagasy flora, with the large majority indicating dispersal to Madagascar from Africa and Asia (e.g., Bartish et al., 2011; Zhou et al., 2012; Ali et al., 2013), followed by, in some cases, dispersal from Madagascar to the nearby volcanic Comoro and Mascarene islands (e.g., Janssen et al., 2008; Wikstrom et al., 2010; Buerki et al., 2013). But few Malagasy lineages have been documented as dispersing broadly across the Indian Ocean, to the Arabian Peninsula and Asia (Yuan et al., 2005; Bukontaite et al., 2015).

The plant family Celastraceae is unusually diverse in Madagascar (Raven and Axelrod, 1974). Of the 97 currently recognized genera, 19 are native to Madagascar and these include at least 57 currently recognized species (Perrier de la Bâthie, 1946a, 1946b; Hallé, 1978; Schatz, 2001; Schatz and Lowry, 2004). Three genera cited by Perrier de la Bâthie (1946a) are not included in these figures. *Brexiopsis* H. Perrier is a synonym of *Drypetes* Vahl (Leandri, 1958), no known specimens of *Pleurostylia* Wight and Arn. have been collected from Madagascar, and the report of the New World *Rhacoma* L. (since synonymized with *Crossopetalum* P. Browne) was probably based on a mis-recorded herbarium specimen. Six of these 19 genera are endemic to Madagascar (*Brexiella* H. Perrier, *Evonymopsis* H. Perrier, *Hartogiopsis* H. Perrier, *Polycardia* Juss., *Ptelidium* Thouars, and *Salvadoropsis* H. Perrier). Two additional as yet unpublished endemic genera are *Astrocassine* ined. and *Pseudocatha* ined. (see Simmons et al., 2008, 2012b).

René P.R. Capuron made extensive annotations on Malagasy Celastraceae herbarium specimens, including draft descriptions of four new genera and ~30 new species, but these were not published before his untimely death at age 50 in 1971 (Schatz,

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2001). In large part because Capuron's work was never published, Schatz (2001, p. 98) stated that, "The Celastraceae are probably the least well known of all woody families in Madagascar at both the generic and specific levels. . .. A thorough revision of the Malagasy Celastraceae in the context of the family globally is required before generic concepts can be resolved." In this study we attempt to help redress this shortcoming by sampling all but one of the Celastraceae genera that are native to Madagascar, including five additional undescribed genera (*Astrocassine* ined., *Erythrostelegia* ined., *Halleriopsis* ined., *Macrynodrys* ined., and *Xenodrys* ined.) in the context of the most thorough phylogenetic analysis of Celastraceae yet conducted (with respect to both character and taxon sampling).

To place the Malagasy Celastraceae into biogeographical context we need to take into account its geological history. When part of Gondwana, Madagascar was adjacent to Africa, Antarctica, and India (Du Toit, 1937; Dietz and Holden, 1970; Smith and Hallam, 1970). Beginning ca. 165 million years ago, Madagascar, then attached to India, drifted southeast from its original position off the coast of present-day Somalia, Kenya, and Tanzania, arriving at its current position off the coast of Mozambique ca. 121 million years ago (Rabinowitz et al., 1983; Coffin and Rabinowitz, 1987). There have been no direct land connections between Africa and Madagascar for at least 140 million years (Krause et al., 1997; Reeves and de Wit, 2000). India was sheared from Antarctica ca. 130 million years ago (Chand et al., 2001). Through sea-floor spreading, India then separated from Madagascar, perhaps over the course of 30 million years, from ca. 118 to 88 million years ago, as a result of the Marion hotspot (Storey et al., 1995; Seward et al., 2004). India and the granitic Seychelles then moved rapidly northward and separated from one another ca. 65 million years ago (Gnos et al., 1997; Reeves and de Wit, 2000).

The context for this study of Malagasy Celastraceae is provided by sampling 31 of the 34 genera of Celastraceae that are native to Africa (Robson et al., 1994; Palgrave, 2002) and 17 of the 18 genera that are native to Australia (Barker, 1984; Jessup, 1984a, 1984b). Unfortunately, we have limited sampling of Indian species, though we do include nine of the 14 native genera (Lawson, 1875; Raju, 1965; Pullaiah and Chennaiah, 1997; Pullaiah and Rao, 2002). All three species from Mauritius and Réunion Islands (*Elaeodendron orientale*, *Gymnosporia pyria*, and *Pleurostylia leucocarpa*) are sampled (Baker, 1877), as are both species from the Seychelles (*Gymnosporia senegalensis* and *Mystroxylon aethiopicum*; Friedmann, 1994).

There are two primary objectives of this study. The first is to infer the minimum number of independent successful colonization events of Celastraceae to Madagascar. Because Madagascar has been isolated for so long, many of its native plant and animal lineages are inferred to have arisen by dispersal from Africa across the Mozambique Channel rather than by vicariance (Darlington, 1957; LeRoy, 1978; Raven and Axelrod, 1974; Schatz, 1996; McLoughlin, 2001; Yoder and Nowak, 2006). In addition to bird-mediated dispersal, another possibility is by ocean currents during the Paleogene (Ali and Huber, 2010). Our second primary objective is to identify the closest non-Malagasy relatives and infer where the dispersal events were from. Although most dispersal events to Madagascar are inferred to have been from Africa, other colonizations may have occurred from Australia (Raven, 1979) and still other lineages may be shared with India because of vicariance (Schatz, 1996). To address these objectives we used parsimony- and likelihood-based phylogenetic analyses of morphological and molecular data to infer the relationships of the Malagasy Celastraceae. We then used fossil-calibrated molecular dating together with both parametric and non-parametric biogeographic methods to infer the biogeographic history of the Malagasy lineages.

2. Methods

2.1. Taxon sampling

A total of 328 accessions of Celastrales (Celastraceae, Lepidobotryaceae, and Parnassiaceae) that were previously sampled by Coughenour et al. (2011), Simmons et al. (2012a, 2012b) and Simmons and Cappa (2013) were used to provide the systematic context for 51 new Malagasy accessions (Appendix A). Most of these new accessions were obtained through fieldwork by R.H.A., J.A., M.P.S., and Helene Razamatsoa in 2006–2007. The new accessions represent 13 genera and 29 species, including seven genera (*Brexiella*, *Erythrostelegia*, *Evonymopsis*, *Macrynodrys*, *Halleriopsis*, *Salvadoropsis*, and *Xenodrys*) that, to our knowledge, have never been previously included in a published phylogenetic analysis. These new accessions, together with others from Madagascar previously sampled by Simmons et al. (2008, 2012a, 2012b) and Coughenour et al. (2010, 2011), include representatives from all published Malagasy Celastraceae genera except for *Ptelidium*, as well as five new undescribed genera. We attempted numerous DNA isolations of *Ptelidium* from herbarium specimens at the Missouri Botanical Garden but were unable to successfully amplify any gene regions from them. Lepidobotryaceae and Parnassiaceae were used as outgroups based on the results from Zhang and Simmons (2006).

2.2. Morphological characters

Morphological characters were derived from matrices originally published by Simmons and Hedin (1999) and later refined and added to by Simmons et al. (2001a, 2001b, 2008, 2012a, 2012b), Islam et al. (2006), Coughenour et al. (2010, 2011) and McKenna et al. (2011). For the 318 taxa sampled in this study, 71 characters are parsimony informative, representing variation in vegetative, floral, and pollen morphology; leaf, seed, and stem anatomy; and chromosome numbers. To the degree possible, characters were scored using reductive rather than composite coding (Wilkinson, 1995; Simmons and Freudenstein, 2002). The characters and character states are listed in Appendix 2 of Simmons et al. (2012a), and the bases for most characters are described in detail by Simmons and Hedin (1999, pp. 746–751).

2.3. Molecular methods

Total genomic DNA was extracted from herbarium specimens and silica gel-preserved (Chase and Hills, 1991) leaves using the protocol described by Alexander et al. (2006). New sequences for two loci from the plastid genome (*matK* and *trnL-F*) and two gene regions from the nuclear genome (ITS and 26S rDNA) were generated for this project. Primers, PCR, and sequencing protocols all followed those described by Simmons et al. (2012a, 2012b). All new sequences generated in this study have been deposited in GenBank under accession numbers JX203389 to JX203629 (Appendix A).

2.4. Alignment and gap coding

Individual sequences that had previously been identified as problematic because of their extreme sequence divergence and potential for long-branch attraction (Felsenstein, 1978; ITS from the former Stackhousiaceae; Simmons et al., 2008) or strong topological incongruence with multiple other gene regions (26S rDNA for *Lepidobotrys* Engl.; ITS for *Wilczekra*, Simmons and Cappa, 2013; *phyB* for 12 taxa, perhaps caused by inadvertently sampling

paralogous copies, Simmons et al., 2008, 2012a, 2012b; Coughenour et al., 2011) were excluded prior to alignment.

Because of alignment ambiguity in the ITS 1 and ITS 2 regions when attempting to align them across Celastraceae and Parnassiaceae, an unconventional alignment approach was implemented whereby the 18S, 5.8S, and 26S rDNA regions (together with three adjacent positions from ITS 1 and nine adjacent positions from ITS 2) were globally aligned across these two families whereas the remaining positions of ITS 1 and ITS 2 were only locally aligned within each of seven monophyletic or paraphyletic groups consisting of 26–88 terminals that were well supported in previous analyses and/or trees generated by preliminary analyses of four plastid loci (*atpB*, *matK*, *rbcL*, and *trnL-F*). The seven compartmentalized groups are as follows: (1) Parnassiaceae + early derived Celastraceae (26 terminals; paraphyletic), (2) Austral-Pacific clade + relatives (43 terminals; monophyletic), (3) *Elaeodendron* Jacq. + *Kokoona* Thwaites + primarily Malagasy relatives (67 terminals; monophyletic), (4) *Euonymus* L. + New World *Maytenus* Molina + relatives (88 terminals; paraphyletic), (5) *Gymnosporia* (Wight and Arn.) Hook.f. + relatives + *Salaciopsis* Baker f. (49 terminals; paraphyletic), (6) Hippocrateoideae (48 terminals; monophyletic), and (7) Salacioideae (26 terminals; monophyletic). The seven blocks of locally aligned characters (from 477 to 544 characters per block after exclusion of ambiguously aligned regions) were then concatenated, one after the other, to the block of 260 globally aligned characters to create the complete ITS matrix. This alignment approach was derived from a presentation by K.S. MacDonald and M.E. Siddall at the Hennig XXVI meeting in 2007, which was based on Barta's (1997) proposal on a way to integrate hypervariable regions into molecular phylogenetic analyses.

Preliminary nucleotide alignments were obtained independently for each gene region using MAFFT ver. 6.5 (Katoh and Toh, 2008a). Q-INS-i, which considers inferred secondary structure of rDNA (Katoh and Toh, 2008b), was used for alignments of 18S and 26S rDNA. G-INS-i, the most accurate MAFFT algorithm for aligning loci other than rDNA, was used for all but one other locus. The exception was ITS, for which Q-INS-i was used for the seven local alignments and the less computationally intensive G-INS-I was used for the global alignment of the conserved regions. The 20PAM nucleotide scoring matrix was used for the more divergent ITS and *trnL-F* loci, whereas the 1PAM matrix was used for all other loci because of their lower divergence. The default gap opening penalty was applied (1.53) and the gap offset value was set to 0.1.

Manual adjustments to the MAFFT alignments were performed in MacClade ver. 4.08 (Maddison and Maddison, 2001) using the procedure outlined by Simmons (2004a), following Zurawski and Clegg (1987). We observed some ambiguously aligned regions where one or more sequences had a duplicate insertion (or the others had a deletion of one of two repeats) and the character-state distribution among the characters in the ambiguously-aligned region was identical for those sequences that have both repeats such that the character-state distribution among the positions in question would be identical for either of the alternative alignments. In these cases the ambiguously-aligned regions were kept in the analysis following the method used by Davis et al. (1998). A total of 693 ambiguously-aligned positions were excluded from the analyses (26S rDNA: 26 positions from two regions; ITS: 357 positions from 21 regions [36 positions from two regions in the Austral-Pacific clade; 50 positions from four regions in the *Elaeodendron* clade; 109 positions from five regions in the *Euonymus* + *Maytenus* group; 110 positions from six regions in the Hippocrateoideae clade; and 52 positions from four regions in the Salacioideae clade]; *trnL-F*: 310 positions from six regions). Ambiguously-aligned nucleotides of individual sequences in regions that could not be unambiguously aligned with the remaining sequences were scored as ambiguous ("?").

Gap characters, whose inclusion often affects the inferred tree topology and increase branch-support values (Simmons et al., 2001c), were manually scored using modified complex indel coding (Simmons and Ochoterena, 2000; Müller, 2006). One qualification is that, when applicable, step matrices (Sankoff and Rousseau, 1975) were not used given that up to 379 terminals were sampled (Table 1) and the step matrices would have substantially slowed the tree searches. In cases where exclusion of the step matrix would have dramatically decreased the potential phylogenetic signal, simple indel coding, which performs nearly as well as complex indel coding (Simmons et al., 2007), was applied instead. A total of 322 parsimony-informative gap characters were scored from unambiguously aligned regions (18S rDNA: five; 26S rDNA: 13; ITS: six from the global alignment, 206 from the seven local alignments; *matK*: 13; *trnL-F*: 79) for inclusion in the parsimony analyses.

2.5. Phylogenetic analyses

As a means of data exploration, several alternative potential process partitions (Bull et al., 1993) of the characters were analyzed. Each of the eight gene regions was analyzed independently of one another to resolve their respective gene trees. Putative coalescent genes (Hudson, 1990; Doyle, 1995) were then analyzed and their trees compared to check for well-supported, contradictory signal. As such, gene trees for the three adjacent rDNA gene regions and the four plastid loci were analyzed independently of each other to check for potential introgression of the plastid genome or rDNA (Doyle, 1992; Wendel et al., 1995) or unrecognized paralogy problems with rDNA (Álvarez and Wendel, 2003; Bailey et al., 2003). An analysis of all molecular characters was then performed, followed by a simultaneous analysis of all morphological and molecular characters (using parsimony only), which was conducted as the primary basis for phylogenetic inference (Kluge, 1989; Nixon and Carpenter, 1996). The simultaneous-analysis data matrix is posted as supplemental online data.

Equally weighted parsimony tree searches were conducted on each data matrix by using a two-part search. Branches with a minimum possible optimized length of zero were collapsed to improve efficiency of tree searches and help minimize artifacts caused by missing data (Kitching et al., 1998; Davis et al., 2005). In the first part up to 50 trees were held (Davis et al., 2005) within each of 5000 random-addition-sequence (RAS) tree-bisection-reconnection (TBR) searches that also implemented 100 ratchet iterations, which alternated between equal character weighting and each character having a 10% chance of being upweighted and a 5% chance of being downweighted. The second part of the search consisted of TBR swapping on all trees obtained from the first part of the search with up to 500,000 trees retained, after which the strict consensus was calculated. Parsimony jackknife (JK; Farris et al., 1996) analyses were conducted using TNT (Goloboff et al., 2008) with the removal probability set to approximately e^{-1} (0.37). One-thousand JK replicates were performed with 100 RAS TBR searches (each with a maximum of 50 trees held) per replicate.

jModeltest ver. 0.1.1 (Posada, 2008) was used to select the best-fit likelihood model for each data matrix using the Akaike Information Criterion (Akaike, 1974) without considering invariant-site models following Yang's (2006) reasoning. The models selected all incorporated gamma distributed rate heterogeneity (Yang, 1993). The Q-matrices selected are all variants of TIM, TPM, TVM, or GTR.

Maximum likelihood analyses (Felsenstein, 1973) were performed with GARLI ver. 2.0.1019 (Zwickl, 2006). Because the TIM, TPM, and TVM *Q*-matrices are not implemented in GARLI, the GTR + Γ model with four rate categories was applied to all matrices. Following the recommended setting in GARLI, branches with

Table 1
Data-matrix and tree statistics for each of the phylogenetic analyses. "CI" = ensemble consistency index (Kluge and Farris, 1969) on the most parsimonious tree(s) for the parsimony-informative characters. "RI" = ensemble retention index (Farris, 1989).

Matrix	# terminals	# characters analyzed	# of parsimony informative characters	% missing/ inapplicable	Most parsimonious tree length	# of most parsimonious trees	# of jackknife/bootstrap clades ⩾50%	Average jackknife/bootstrap support (%)	CI	RI
18S rDNA	31	1802	140	5.9	293	24	8/13	75/78.1	0.61	0.83
26S rDNA	364	967	282	9.0	1972	500,000	140/157	81.4/79.2	0.22	0.84
ITS rDNA	347	4026	2008	83.7	6993	500,000	29/190	82.9/80.8	0.50	0.80
rDNA (18S, ITS, 26S)	378	6795	4080	76.6	9378	500,000	226/262	87.2/87.0	0.44	0.81
phyB	28	1123	225	9.4	544	5	19/19	86.5/87.3	0.58	0.64
atpB	32	1506	210	4.9	440	1	21/23	82.1/83.3	0.64	0.84
matK	346	1453	696	16.8	2329	500,000	104/165	79.8/80.4	0.48	0.86
rbcL	33	1428	171	4.4	407	1	15/13	79.8/80.5	0.54	0.72
trnL-F	352	1863	617	49.0	2070	500,000	147/171	78.7/80.0	0.53	0.90
Plastid (*atpB* – > *trnL-F*)	365	6250	1685	63.2	5284	500,000	153/217	81.5/83.5	0.51	0.87
Morphology only	318	76	71	42.8	379	500,000	19	67.6	0.29	0.86
All molecular	379	14,168	4340	72.6	15,415	500,000	279/296	87.9/89.1	0.46	0.83
Simultaneous complete	379	14,244	4411	72.5	15,995	500,000	288	90.1	0.45	0.83
Simult./molec. reduced	357	14,244	4368	71.8	15,628	7168	284/299	91.0/89.7	0.46	0.83

a length of 1×10^{-8} (i.e., effectively zero; Zwickl, 2012) were collapsed. The GARLI analyses were performed by using the least rigorous settings for an intensive search recommended by Zwickl (2009; streefname = stepwise; attachmentspertaxon = 50, genthreshfortopoterm = 20,000, numberofprecreductions = 20, treerejectionthreshold = 100) for both optimal-tree searches (1000 search replicates) and the bootstrap (BS; Felsenstein, 1985; 1000 pseudoreplicates, each with one search).

In an attempt to obtain increased resolution and support within clades that included large polytomies and/or weak jackknife support in the complete-taxon-sampling parsimony-based simultaneous-analysis strict consensus, a reduced-taxon-sampling simultaneous analysis was performed after removing 19 terminals. These 19 terminals were selected from nine separate clades of the strict consensus tree and were generally sampled for only one or two gene regions. In two cases (*Platypterocarpus* Dunkley and Brenan and *Torralbasia* Krug and Urb.) the single representative of a genus was removed.

2.6. Reevaluation of the fossil record of Celastraceae

Fossils that have been assigned to Celastraceae include wood, leaves, flowers, pollen, fruits, and seeds; most are leaf fossils. Several form genera have been reported from the Late Cretaceous through the Early Tertiary. These include: *Celastrinoxylon celastroides* (Schenk) Kräusel, petrified wood fossils from the Farafra Oasis (Egypt) of the Campanian Age in the Late Cretaceous (Kamal El-Din, 2003); *Lophopetalumoxylon indicum* Mehrotra, Prakash and Bande, a petrified wood fossil from the Deccan Intertrappean Beds (India) of the Late Cretaceous that was hypothesized to be closely related to *Kokoona littoralis* Laws. (Mehrotra et al., 1984); and *Wuyunanthus hexapetalus* Y.F. Wang, C.S. Li, Z.Y. Li, and D.Z. Fu, a flower impression from the Wuyun Formation (China) of the Paleocene that was hypothesized to be closely related to *Celastrus* and *Euonymus* (Wang et al., 2001). Despite the comparisons with extant genera made by the original authors, we remain doubtful as to whether these fossils are in fact members of Celastraceae (see also Matthews and Endress (2005) for *Wuyunanthus*).

Salard-Cheboldaeff (1974, 1979) proposed that the tetrad pollen grains of *Triporotetradites campylostemonoides* Salard-Cheboldaeff from the Miocene and Oligocene of Cameroon may be assigned to the extant genus *Campylostemon*. Muller (1981) supported this generic assignment, but tetrad grains are also present in the other African genera of tribe Campylostemoneae, *Bequaertia* and *Tristemonanthus* (and New World *Hylenaea* and south Asian *Lophopetalum*; Lobreau-Callen, 1977). *Campylostemon* and *Tristemonanthus* were highly supported (100% parsimony JK; 91% likelihood BS) as a monophyletic group, though *Bequaertia* was not sampled (Coughenour et al., 2011).

Reid and Chandler (1933) assigned two fruit and seed fossils from the London Clay Formation (United Kingdom) of the Early Eocene (52–49 Ma; Poole and Wilkinson, 1999) to Celastraceae. Their description of *Cathispermum pulchrum* Reid and Chandler is of particular interest because its seeds have a small, thin, aril-derived wing, which led them to suggest that *C. pulchrum* is most closely related to the extant African species *Catha edulis* (Vahl) Forssk. ex Endl., albeit not a member of the same genus. A similar seed wing, which is non-arillate, occurs in *Canotia holacantha* Torr. (Johnston, 1975; Tobe and Raven, 1993) from the southwest U.S.A. Poole and Wilkinson (1999) described a single pyritized twig from the London Clay Formation and placed it in the form genus *Celastrinoxylon* as *C. ramunculiformis* Poole and Wilkinson. They recognized affinities of the specimen to both Apocynaceae and Celastraceae, but focused on the fossil's similarities to *Catha edulis*.

Two other fossil fruits that may be assigned to extant lineages of Celastraceae both date to the Pliocene and consequently are not particularly informative for inferring family-wide ages because they are too young (see Section 2.7 below). Ozaki (1991) assigned both leaf and fruit fossils from the Kabutoiwa Formation of the Japanese island of Hunshu to *Tripterygium kabutoiwanum* Ozaki and noted strong similarities to the extant species *T. regelii* Sprague and Takeda. The Kabutoiwa fossil flora has been dated using potassium–argon to over 3.4 ± 0.2 Ma (Kohei, 2007). Wijninga and Kuhry (1993) assigned a Celastraceae subfamily Hippocrateoideae mericarp from fluvial-lacustrine sediment of the Late Pliocene (3.6–2.6 Ma) in Colombia to either *Hippocratea* or *Pristimera*. But *Hippocratea* and *Pristimera* are not sister genera. Rather they are a polyphyletic group (Coughenour et al., 2011) and this mericarp is also consistent with other New World genera of Hippocrateoideae such as *Elachyptera* and *Hylenaea*. Neither of these fossils were applied as calibration points because they are much younger than the calibrations provided by leaf fossils of *Celastrus gaudini* Lesquereux (see below) and pollen fossils of *Triporotetradites campylostemonoides* (see above).

Most fossil leaves that have been assigned to extant Celastraceae genera were described in the late 1800s and early 1900s; these have generally not been re-assessed since the original publications. Many were poorly preserved and the published descriptions do not detail diagnostic genus-specific traits. One of us (L.-C. Zhao) evaluated these publications for the reliability of their generic assignments by examining the following four factors: the key preserved traits that place the fossil in the genus; the full taxonomic description and diagnosis of the fossil; the photographs, drawings, and/or reconstructions of the fossil; and the thoroughness of voucher information provided. Rather than applying the sediment age estimates from the original papers, we used recently accepted estimates from the literature. To assign numerical dates to time periods we used the older bound of each period from the 2009 Geologic Time Scale (Walker and Geissman, 2009). We suggest that the leaf fossils discussed in the following paragraphs are confidently assigned to their respective genera of *Celastrus*, *Euonymus*, and *Paxistima*. Within each genus we report the oldest fossils first, and these are the ones used for our fossil calibrations, although we also present younger fossils for all three genera as additional corroborative evidence following Sauquet et al. (2012). Note that all of these generic assignments are based on the intuitive rather than the apomorphy-based method, and consequently are based partially on plesiomorphies and cannot distinguish between stem lineages and crown groups (Sauquet et al., 2012).

Leaves of extant *Celastrus* species vary from elliptic to oblong, or from broadly ovate to orbicular. The apices range from acute to obtuse or rotund, and the bases may be rotund to cuneate, but not cordate. Leaf margins are usually serrate, serrulate or subentire. The leaves of all species have pinnate and netted veins. Both surfaces of the midrib are usually elevated. There are 4–9 secondary veins on each side of the midrib, which are arcuate toward the apex. Leaves of some *Celastrus* species are similar to those of *Populus* (Salicaceae), but the latter are characterized by the presence of salicoid teeth (Hickey and Wolfe, 1975) and a pair of distinct, opposite, basal secondary veins.

Leaf fossils of *Celastrus gaudini* were collected from the Denver Formation of the Denver Basin in Colorado (Knowlton, 1930), which dates to the very end of the Late Cretaceous to the Paleocene (e.g., Higley and Cox, 2007). The fossil leaves are similar to those of extant *Celastrus* species, in particular those from East Asia such as *C. glaucophyllus* Rehder and E.H. Wilson, *C. orbiculatus* Thunb., and *C. paniculatus* Willd. We assigned this species a minimum age of 55.8 Ma, at the end of the Paleocene.

Leaf fossils of *Celastrus typica* (Lesquereux) MacGinitie were collected from the Florissant Formation in Colorado, U.S.A. (MacGinitie, 1953), which dates to ~34.07 ± 0.10 Ma (Evanoff et al., 2001). The fossil leaves are very similar to those of the extant *C. scandens* L. (MacGinitie, 1953; Becker, 1969) with respect to their shape, base, apex, margin, and venation, but they have more secondary veins.

Leaf fossils of *Celastrus mioangulata* Hu and Chaney were collected from the Shanwang Formation in Shandong Province, China (Hu and Chaney, 1940), which dates to 17–15 Ma in the Middle Miocene (e.g., Li et al., 2010). The fossil leaves resemble those of the extant species *C. angulatus* Maxim, which is widely distributed in China (Hu and Chaney, 1940).

Leaves of some extant *Euonymus* species are similar to those of *Prunus* (Rosaceae), but the latter are serrate or biserrate and often have gland-tipped teeth and two nectaries at the apex of the petiole or base of the blade. Leaf fossils of *E. splendens* Berry were collected from the Wilcox Formation in Louisiana, Mississippi, Tennessee, and Texas, U.S.A. (Berry, 1916), which dates to 59–54 Ma in the Late Paleocene to the Early Eocene (e.g., Pitman and Rowan, 2012). The shape, base, apex, margin, and venation of the fossil leaves are very similar to those of the extant North American species *E. atropurpureus* Jacq.

Leaf fossils of *Euonymus pacificus* Brown were collected from the Latah Formation in Washington, U.S.A. (Brown, 1937), which has been potassium–argon dated to 21.3–12.1 Ma in the Miocene (Gray and Kittleman, 1967). Although *Euonymus pacificus* Brown is a nomen nudum, as the author did not supply a detailed description or specify the holotype, the short petiole, crenulate leaf margin, and venation are very similar to the extant North American species *E. americanus* L. (Brown, 1937).

Leaf fossils of *Euonymus protobungeana* Hu and Chaney were described by Hu and Chaney (1940) in the same formation (dated to 17–15 Ma) as *Celastrus mioangulata*, which is described above. The fossil species was named based on its resemblance to the extant Chinese species *E. bungeanus* Maxim.; both species are variable with respect to their shape, venation, and margin (Hu and Chaney, 1940).

Leaf fossils of *Paxistima deweyensis* Axelrod were collected from the Thunder Mountain caldera in Idaho, U.S.A. (Axelrod, 1998a). The Thunder Mountain ash flows have been dated to 50–43 Ma (Leonard and Marvin, 1982). The leaves of this fossil species are nearly identical to *P. myrsinites* (Pursh) Raf. from western North America (Axelrod, 1998a). Leaf fossils of *Paxistima lemhiensis* Axelrod were collected from the Haynes Creek assemblage of the Salmon City Formation in Idaho (Axelrod, 1998b). The Haynes Creek assemblage has been radioisotopically dated to at least 30.7 Ma in the Early Oligocene (Axelrod, 1998b; Erwin and Schorn, 2006).

2.7. Fossil-calibrated molecular dating

Given that most of the fossils cited above were identified using the intuitive method rather than on the basis of synapomorphies, we conservatively applied the minimum age calibrations to the stem node rather than the crown node (Magallón and Sanderson, 2001). Instead of relying strictly upon the most reliable fossil calibration point(s) and implicitly assuming a molecular clock, we integrated plausible fossil calibration points from as many divergent lineages as possible (Ho and Phillips, 2009). Exponential priors were applied to the six fossil calibrations and a normal prior was applied to the secondary calibration. Exponential priors were defined with the mean age of the fossil as the offset value and the mean value of the prior was chosen so that 95% of the probability is contained between the rigid minimum bound and a soft maximum bound, sensu Yang and Rannala (2006). The normal prior was defined by the mean fossil age as the mean age of the prior distribution and the standard deviation was set to capture the variation recognized in the fossil age.

The minimum age of 23 Ma (the end of the Oligocene) for *Triporotetradites campylostemonoides* was used as the hard lower bound for the stem node of tribe Campylostemoneae (in this case the stem node for the clade of *Campylostemon* + *Tristemonanthus*), which is unambiguously supported (100% JK/100% BS). The soft lower bound extended to the start of the Oligocene (33.9 Ma). The minimum age of 49 Ma for *Cathispermum pulchrum* and *Celastrinoxylon ramunculiformis* from the London Clay were used for the stem node of the monotypic *Catha*, with a soft lower bound at 52 Ma. The clade of *Catha* + *Allocassine*, *Cassine*, *Lauridia*, and *Maurocenia* is highly supported (96% JK/99% BS). Following Ho and Phillips (2009), the minimum age of 55.8 Ma (and a soft lower bound of 70.6 Ma at the start of the Maastrichtian Age) for *Celastrus gaudini* was used for the stem node for the unambiguously supported clade of *Celastrus* + *Tripterygium* (100% JK/100% BS) because the clade of *Celastrus* is only weakly supported (<50% JK/53% BS). The minimum age of 54 Ma (and a soft lower bound of 59 Ma) for *Euonymus splendens* was used for the stem node of the clade of *Euonymus* + *Glyptopetalum* because the clade of *Euonymus* is only weakly supported (<50% JK and BS). The minimum age of 43 Ma (and a soft lower bound of 50 Ma) for *Paxistima deweyensis* was used for the stem node for the unambiguously supported (100% JK/100% BS) clade of *Paxistima*.

Celastrales are most closely related to Malpighiales and Oxalidales (Soltis et al., 2000; Zhang and Simmons, 2006; Wurdack and Davis, 2009). Based on minimum-age node mapping (Crepet et al., 2004), the clade of Celastrales, Malpighiales, and Oxalidales is at least 90 Ma based on the fossils of *Paleoclusia* (Clusiaceae; Crepet and Nixon, 1998) and *Platydiscus* (Cunoniaceae; Schönenberger et al., 2001). Wang et al. (2009) estimated the Celastrales crown clade to be (100–) 91–56 (–50) Ma after constraining the root of their rosid tree to be no more than 125 million years old. Xi et al. (2012) estimated the Celastrales crown clade to be (103.9–) 90.6 (–78.4) Ma. Given the need for a maximum age constraint (or point calibration) to provide older bounds on the age estimates (Ho and Phillips, 2009) and that we do not have any justifiable older bounds for members of Celastrales, we imported the secondary age estimate from Xi et al. (2012) and set the crown clade of Celastrales as a normal distribution centered on 90.6 Ma and ranging from 103.9 to 78.4 Ma.

Molecular-dating analyses were conducted in an Amazon Elastic Compute Cloud (aws.amazon.com/ec2/) using BEAST ver. 1.7.4 (Drummond et al., 2012) with the GTR + gamma (four rates) model applied to each of the eight molecular-data partitions. Nucleotide-substitution and clock parameter values were allowed to vary among data partitions. Eight data partitions were originally used (18S rDNA, 26S rDNA, ITS, *phyB*, *atpB*, *matK*, *rbcL*, and *trnL-F*), but because of failure to obtain convergence by BEAST in preliminary analyses, we reduced the number to five partitions by combining the two rDNA subunits into one partition and the three plastid exons into another partition. The same time and topology constraints, tree prior (speciation prior that accommodates the birth–death for incomplete sampling; Stadler, 2009), and mutation-rate prior (gamma UCLD mean prior; Ferreira and Suchard, 2008) were applied to all partitions.

We reduced the number of terminals and amount of missing data in the matrix by merging multiple accessions of individual species into a single terminal by using the "merge" command in MacClade, thereby representing the observed variation within these species by nucleotide ambiguity codes. Specimen-level phylogenies can introduce artificial speciation events into divergence time estimation, which increases estimates of speciation rate and other parameters (Van Dam and Matzke, unpublished data). The one exception to merging accessions of individual species is *Maytenus undata*, for which the two accessions are divergent and paraphyletic, and therefore kept separate.

Rather than allowing BEAST to estimate the tree topology while employing a relaxed molecular clock, we constrained the topology of our analysis using the first most parsimonious tree found for the reduced simultaneous analysis data matrix of 357 terminals and 14,244 characters as a topological constraint. This topological constraint is based on extensive taxon and character sampling, including gap and morphology characters, and represents the best estimate to date of phylogenetic relationships between families, genera, and species of Celastrales. We implemented this approach because the parsimony analysis incorporated morphological and gap characters that cannot be imported into BEAST and because application of a relaxed molecular clock in BEAST cannot be expected to improve quality of phylogenetic inference (Wertheim et al., 2010). The constraint tree was made ultrametric and consistent with our time calibrations using penalized likelihood in the R package APE (Paradis et al., 2004). The BEAST XML file was manually adjusted by replacing the function that generates a random starting tree with the constraint tree and by removing the four operators that search tree space following Couvreur et al.'s (2011) approach.

2.8. Biogeography

The same tree topology used for molecular dating was also used for both parametric and non-parametric biogeographic analyses. Parametric analyses were performed using the diversification–extinction–cladogenesis model (DEC; Ree and Smith, 2008) with an additional jump parameter "*J*" that corresponds to cladogenic speciation mediated by founder events (Matzke, 2014) in the BioGeoBEARS ver. 0.2.1 (Matzke, 2013) R package (R Development Core Team, 2013). The *J* parameter allows daughter species to "jump" outside the geographical range of parental species, which is highly appropriate for the lineages considered in this study that colonized Madagascar, and represents the process of founder-event speciation. Our DEC + *J* analyses were unconstrained, allowing for equal dispersal among areas through time. Non-parametric analyses were performed using dispersal–vicariance analysis (DIVA; Ronquist, 1997) as implemented in RASP ver. 3.0 (Yu et al., 2015). All other options in RASP, except maximum areas, used default settings. The results of both our DEC- and DIVA-based biogeographic analyses are dependent upon our inferred phylogeny and taxon sampling. Consequently, if relevant taxa from different areas are unsampled in our study then our biogeographic inferences are subject to later correction.

Following Buerki et al. (2011), the following seven biogeographical regions were applied: (A) Eurasia; (B) Africa; (C) Madagascar, Comoro and Mascarene Islands; (D) southern India, Malesia, Pacific Islands; (E) Australia, New Guinea, New Caledonia, New Zealand; (F) North America; and (G) Caribbean, Central and South America. The biogeographical regions are broadly defined and the extant members of Celastraceae that we sampled are distributed in a maximum of two separate regions (with the exception of *Pleurostylia opposita* from three regions, though this taxon likely includes two cryptic species; M.P. Simmons, unpublished data). Therefore, we restricted the maximum areas occupied by hypothetical ancestors as well as the maximum areas set to two (Ronquist, 1996; Nylander et al., 2008).

3. Results

A simplified version (wherein selected genera that do not have any species native to Madagascar are each represented by a single terminal) of the reduced-taxon-sampling simultaneous-analysis parsimony strict consensus of all eight gene regions and morphological characters is presented in Figs. 1 and 2. Parsimony JK values

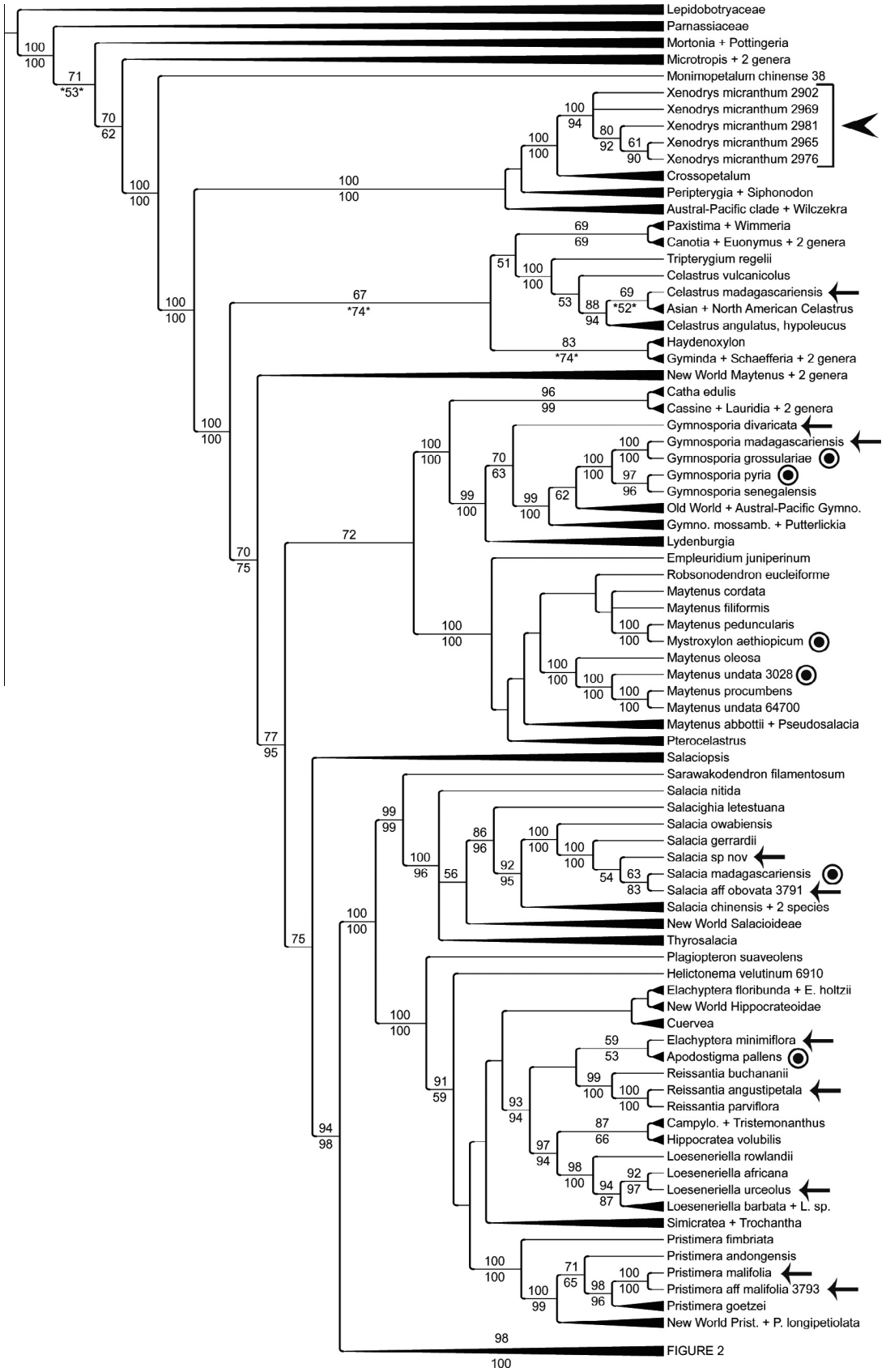

Fig. 1. Basal portion of the reduced-taxon-sampling simultaneous-analysis parsimony strict consensus that is simplified to focus on Malagasy lineages. Genera that are endemic to Madagascar are indicated using the "◄" arrows, individual species (but not their entire genus) endemic to Madagascar are indicated using the "←" arrows, and species that are native but not endemic to Madagascar are indicated using circles. Parsimony jacknife (JK) values ⩾50% are shown above each branch and likelihood BS values ⩾50% for all nucleotide characters are shown below each branch. Clades that were contradicted by ⩾50% BS support are indicated by *XX* with BS support for the contradictory clade with the highest support listed.

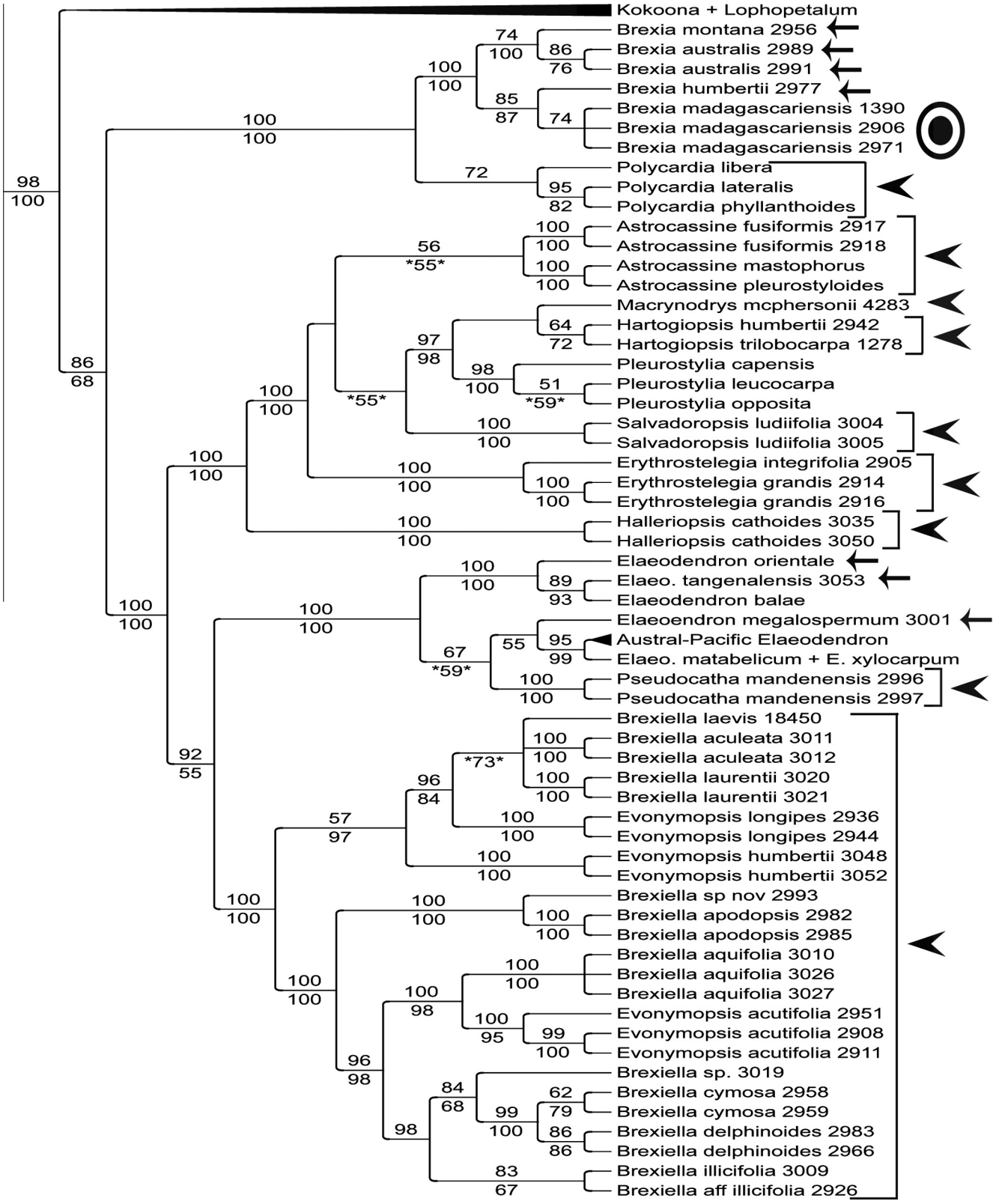

Fig. 2. Distal portion of the reduced-taxon-sampling simultaneous-analysis parsimony strict consensus that is simplified to focus on Malagasy lineages. Genera that are endemic to Madagascar are indicated using the "◄" arrows, individual species (but not their entire genus) endemic to Madagascar are indicated using the "←" arrows, and species that are native but not endemic to Madagascar are indicated using circles. Parsimony jacknife (JK) values ⩾50% are shown above each branch and likelihood BS values ⩾50% for all nucleotide characters are shown below each branch. Clades that were contradicted by ⩾50% BS support are indicated by *XX* with BS support for the contradictory clade with the highest support listed.

⩾50% are shown above each branch and BS values ⩾50% are shown below each branch for the likelihood analysis of nucleotide characters from all eight gene regions. The complete tree is presented in Fig. S1 as supplemental online data. The complete-taxon-sampling simultaneous-analysis parsimony strict consensus is presented as Fig. S2. Equivalent trees for each of the 12 partitioned analyses listed in Table 1 are presented in Figs. S3–S14. All of these trees were created using TreeGraph ver. 2.0.45 (Stöver and Müller, 2010). Support values were mapped onto the parsimony strict consensus tree so as to help minimize undersampling-within-replicates BS and JK artifacts (Goloboff and Farris, 2001; Simmons and Freudenstein, 2011). The data-matrix and tree statistics for all 14 analyses are presented in Table 1. In addition to being incorporated into the parsimony-based tree searches, the gap and morphological characters were mapped onto the strict consensus of the most parsimonious trees from the simultaneous analyses using unambiguous optimization in MacClade to infer synapomorphies for selected clades as described below.

3.1. Incongruence

One case of mutually well supported (⩾70% JK and BS support) topological incongruence was identified on the individual gene trees: *Brexiella delphinoides* accession 2966 was resolved as sister to the clade of all other *Brexiella* (including *B. delphinoides* accession *Archer et al. 2983*) and *Evonymopsis* species sampled on the 26S rDNA gene tree (73% JK/75% BS; Fig. S4) whereas that accession was sister to *B. delphinoides* accession 2983 on the *trnL-F* and plastid trees (Figs. S11 and S12) and part of a polytomy with *B. delphinoides* accession *Archer et al. 2983* and *B. cymosa* on the rDNA tree (Fig. S6). Based on the incongruence of 26S rDNA with the ITS and plastid characters, we excluded the 26S rDNA sequence of *B. delphinoides* accession *Archer et al. 2966* from the simultaneous analyses to represent a single hierarchy and exclude misleading data (Lecointre and Deleporte, 2005).

Seven notable cases of incongruence were identified between the rDNA and plastid coalescent trees (Figs. S6 and S12). First, *Canotia holacantha* Torr. was resolved as sister to *C. wendtii* M.C. Johnst. on the rDNA tree (100% JK/99% BS) but sister to *Acanthothamnus* Brandegee on the plastid tree (98% JK/94% BS). Based on the morphological synapomorphy of leaves reduced to scales for *Canotia*, we follow Simmons et al. (2012a) by favoring the rDNA tree and eliminated the *C. holacantha matK* and *trnL-F* sequences from the simultaneous analyses.

Pottingeria Prain was resolved as sister to Parnassiaceae on the rDNA tree (66% JK/60% BS) but sister to *Mortonia* A. Gray on the plastid tree (94% JK/92% BS). As discussed by Simmons et al. (2012a, pp. 460–461), we consider the phylogenetic placement of *Pottingeria* to be ambiguous, but for the purpose of the simultaneous analyses we eliminated the *Pottingeria* 18S rDNA sequence given that this taxon is better sampled for the plastid genome (*atpB*, *rbcL*, and *trnL-F*).

Crossopetalum managuatillo (Loes.) Lundell was resolved as sister to *C. decussatum* (Baill.) Lourteig on the rDNA tree (61% JK/64% BS) whereas it was resolved by itself as sister to all other members of *Crossopetalum* on the plastid tree (67% JK/82% BS). As discussed by Simmons et al. (2012a, p. 460), the phylogenetic relationship between these two species is ambiguous. For the simultaneous analyses we eliminated the *C. decussatum* 26S rDNA sequence because this accession is better sampled for the plastid genome (*matK* and *trnL-F*).

Astrocassine mastophorus was resolved as sister to *A. pleurostyloides* ined. on the rDNA tree (71% JK/100% BS) whereas it was resolved as sister to *A. fusiformis* ined. on the plastid tree and separated from *A. pleurostyloides* by two successive clades on the plastid tree (57% JK/88% BS, 64% JK/85% BS). For the simultaneous analyses we arbitrarily deleted *A. mastophorus* from the plastid partition because the plastid partition was sampled for fewer terminals than the rDNA partition (365 vs. 378; Table 1).

Mortonia scabrella A. Gray was resolved as sister to the other three species of *Mortonia* sampled on the rDNA tree (82% JK/contradicted by 53% BS), whereas it was resolved as sister to *M. greggii* A. Gray on the plastid tree (99% JK/100% BS). We were unable to identify any morphological synapomorphies to select between these alternative resolutions of *M. scabrella*. Based on this conflict and the desire not to add additional missing data to terminals that are near the base of Celastraceae, we excluded *M. scabrella* from the simultaneous analyses.

Pristimera tenuiflora (Mart. ex Peyr.) A.C. Sm. was resolved as sister to *P. verrucosa* Miers on the rDNA tree (74% JK/88% BS), whereas it was resolved as sister to *P. andina* Miers on the plastid tree (96% JK/100% BS). We were unable to identify any morphological synapomorphies to select between these alternative resolutions of *P. tenuiflora*. We consider the sister-group relationship of *P. tenuiflora* to be ambiguous, but for the purpose of the simultaneous analyses we arbitrarily eliminated its 26S rDNA and ITS sequences because the plastid-based resolution was better supported.

Finally, Groppo et al. (2014) identified conflict between the plastid and rDNA trees for *Plenckia* Reissek. Although *Plenckia* and its closely related genera (*Fraunhofera* Mart. and New World members of *Maytenus*) are part of a large polytomy in our plastid tree (Fig. S12), in Groppo et al.'s (2014) analyses the resolution of *Plenckia* was better supported in the reduced-taxon-sampling plastid tree (100% parsimony JK) than in the rDNA tree (77% parsimony JK). Therefore, for the purpose of our simultaneous analyses, we arbitrarily eliminated the 26S rDNA and ITS sequences for *Plenckia populnea* Reissek accession *Schinini & Bordas 21279*. In an attempt to increase resolution and support we also deleted the other two accessions of *P. populnea* (*Anderson 8611* and *Irwin et al. 12780*), which were only sampled for *matK*.

One case of mutually well supported incongruence was resolved on the parsimony vs. likelihood reduced-taxon-sampling simultaneous-analysis/all-molecular trees: *Haydenoxylon* M.P. Simmons was resolved as sister to the clade of (*Gyminda* Sarg., *Orthosphenia* Standl., *Rzedowskia* Medrano, *Schaefferia* Jacq.) on the parsimony tree with 83% JK, whereas *Haydenoxylon* was resolved outside the clade that includes the most recent common ancestor of *Gyminda* and *Celastrus* L. on the likelihood tree; the latter clade was supported by 74% BS. The only morphological synapomorphy for the parsimony-based resolution of *Haydenoxylon* is carpel number = two, but this character is highly homoplasious and *Haydenoxylon urbanianum* (Loes.) M.P. Simmons can have three carpels. We were unable to identify any indel synapomorphies for the parsimony-based resolution. Unlike some other lineages (Lepidobotryaceae, Parnassiaceae, and members of the formerly recognized Stackhousiaceae), neither *Haydenoxylon* nor other closely related taxa (in either the parsimony or likelihood trees) were resolved on unusually long branches in the GARLI all-molecular tree (data not shown), so we have no reason to suspect long-branch attraction. Nonetheless, to test for stability of the parsimony-based resolution we re-ran the parsimony reduced-taxon-sampling simultaneous analysis after excluding the clade of (*Gyminda*, *Orthosphenia*, *Rzedowskia*, *Schaefferia*) following Siddall and Whiting's (1999) alternative-taxon-exclusion approach, and obtained the likelihood-based resolution of *Haydenoxylon*, albeit with <50% JK support (Fig. S15). Based on these results we tentatively favor the likelihood-based resolution of *Haydenoxylon* as a separate lineage from the clade that includes the most recent common ancestor of *Gyminda* and *Celastrus*.

3.2. Phylogenetic inference of Malagasy lineages

All of the following systematic inferences are based on the simultaneous-analysis parsimony tree (Figs. 1 and 2), with the qualifications noted above for the two cases of incongruence that involve Malagasy taxa. The endemic Malagasy genera are resolved in two separate lineages—*Xenodrys* by itself (Fig. 1) and all other genera in a monophyletic group that also includes *Pleurostylia*, for which no species are native to Madagascar; *Brexia madagascariensis*, which is also native to the Comoro Islands, Seychelles, Mozambique, and Tanzania (Verdcourt, 1968; Schatz and Lowry, 2004); and several non-native species of *Elaeodendron* (Fig. 2).

Xenodrys is unambiguously supported (100% JK/100% BS) as sister to *Crossopetalum* (Fig. 1), which is endemic to the New World. Synapomorphies for the clade of (*Crossopetalum*, *Xenodrys*) include a 6-bp deletion at positions 591–599 of 26S rDNA, a 6-bp deletion at positions 509–515 of ITS, a 3-bp deletion at positions 521–523 of ITS, a 1-bp insertion at position 528 of ITS (although this character is homoplasious within the Austral-Pacific clade), and a reduction from a 5-merous to a 4-merous perianth (although this character is homoplasious across the tree).

The smallest clade that includes all other endemic Malagasy genera is highly supported (98% JK/100% BS) as most closely related to the unambiguously supported (100% JK/100% BS) clade of (*Kokoona*, *Lophopetalum*) (Fig. 2, S1), whose members are native to India, Sri Lanka, southeast Asia, Macronesia, and Australia (Loesener, 1942; Simmons, 2004b). Within the smallest clade that includes the endemic Malagasy genera, the clade of (*Brexia*, *Polycardia*) is unambiguously supported (100% JK/100% BS) and is sister to the unambiguously supported clade (100% JK/100% BS) of the remaining genera. Synapomorphies for the clade of (*Brexia*, *Polycardia*) include a 1-bp deletion at position 122 of ITS, a 9-bp deletion at positions 868–876 of the *trnL* intron, and an 8-bp deletion at positions 361–368 of the *trnL-F* spacer.

Within the unambiguously supported clade of the remaining genera (Fig. 2), the clade of (*Elaeodendron*, *Pseudocatha*, *Brexiella*, *Evonymopsis*) is highly supported, but only in the parsimony analysis (92% JK/55% BS). Synapomorphies for this clade include a 1-bp insertion at position 654 of ITS and a 7-bp insertion at positions 342–348 of the *trnL-F* spacer. Within this larger clade, the clade of (*Brexiella*, *Evonymopsis*) was unambiguously supported (100% JK/100% BS) and synapomorphies include a 1-bp insertion at position 269 of ITS and 1 1-bp insertion at position 69 of the *trnL-F* spacer. Within this clade, the three sampled species of *Evonymopsis* are resolved as a polyphyletic group.

The clade of (*Astrocassine*, *Erythrostelegia*, *Halleriopsis*, *Hartogiopsis*, *Macrynodrys*, *Pleurostylia*, *Salvadoropsis*) is unambiguously supported (100% JK/100% BS) (Fig. 2). Synapomorphies for this clade include a 2-bp deletion at positions 222–223 of ITS. Within this clade, all genera other than *Halleriopsis* are unambiguously supported (100% JK/100% BS) as a subclade. Synapomorphies for this clade of (*Astrocassine*, *Erythrostelegia*, *Hartogiopsis*, *Macrynodrys*, *Pleurostylia*, *Salvadoropsis*) include a 4-bp insertion at positions 45–48 of ITS. Synapomorphies for the clade of *Erythrostelegia* include three separate 1-bp insertions in ITS—at positions 331, 338, and 508. The insertion at position 331 was also found in *Brexiella laurentii*, and the insertion at position 508 was also found within *Elaeodendron*.

3.3. Molecular dating and biogeography of Malagasy lineages

We tested for and rejected a strict molecular clock for these data using two metrics following Bacon et al. (2013). First, the covariance statistic was examined in Tracer ver. 1.5, which provides an approximation of phylogenetic autocorrelation for molecular rates. The distribution for this analysis centered on zero, indicating no support for molecular rates to be inherited from parent to daughter nodes. Second, the coefficient of variation, which measures the proportion of the variation in molecular rates around the mean, was also examined in Tracer. The distribution of possible coefficients of variation among the data partitions ranged from 0.48 to 1.36, all far from zero, indicative of the rate variation that was specifically accounted for in the relaxed-clock model.

Following Brown et al.'s (2010) and Marshall's (2010) suggestions, we examined the individual partition rate estimates, but did not identify any unexpected outliers relative to the expected relative rates (Wolfe et al., 1987).

The extant Malagasy Celastraceae comprise at least 12 distinct lineages (Figs. 3 and 4, S16, S17; Table 2). Most are endemic to Madagascar (area C), but some are also represented in Africa (distribution coded as BC). Eight of these 12 lineages are clearly of African origin, all of which have a mean stem-node age estimate of <35 Ma. Of the remaining four lineages, that leading to *Celastrus madagascariensis* appears to be of Eurasian origin based on our current species sampling of *Celastrus*. The last relatively recent Malagasy lineage, that leading to *Loeseneriella urceolus*, with a mean stem-node age estimate of 8 Ma, appears to be of African or southern Indian origin based on our current species sampling of *Loeseneriella*.

Whereas eight of the 10 Malagasy lineages with mean stem-node age estimates of <35 Ma are clearly of African origin, the two Malagasy lineages with the oldest mean stem-node age estimates might not have African origins (Figs. 3 and 4, S16, S17; Table 2). *Xenodrys micranthum* ined., with a mean stem-node estimate of 43.4 Ma, appears to have an American origin (or, in examining still earlier stem nodes, an Australian origin). Finally, the main Malagasy lineage, with the oldest mean stem-node estimate (61.7 Ma) of the 12 Malagasy lineages, appears to have been derived from the eastern Indian Ocean region, although the node ancestral to the stem node of the main Malagasy lineage is weakly assigned by DEC as either African (0.52) or Australian (0.33; 68 Ma; Fig. 3).

4. Discussion

4.1. Phylogenetic inference of Malagasy lineages

Our inferred phylogeny of the Malagasy Celastraceae is consistent with previously generated phylogenies that sampled a more limited set of these taxa (i.e., that did not include the 51 new Malagasy accessions used in this study, with representatives of seven previously unsampled endemic genera). Simmons et al. (2008) identified the clade of (*Brexia*, *Polycardia*), which is still supported after an increase of nine additional genera in its sister group (Fig. 2). Likewise, Simmons et al. (2008) identified the clade of (*Elaeodendron*, *Pseudocatha*), and it is unambiguously supported in our inferred phylogeny. On the other hand, Simmons et al. (2012a) identified the clade of (*Astrocassine*, *Hartogiopsis*, *Pleurostylia*), but with our expanded sampling that includes *Macrynodrys* and *Salvadoropsis*, we identified these two genera as additional members of that clade.

The nearly complete generic-level sampling of Malagasy Celastraceae enabled us to test the following six published systematic hypotheses. First, Perrier de la Bâthie's (1933) hypothesis that *Brexia*, *Brexiella*, and *Polycardia* are closely related to each other is supported (Fig. 2), *contra* Loesener's (1942) and Perrier de la Bâthie's (1942b, 1946a) assertions that *Brexia* is not a member of Celastraceae. Second, Perrier de la Bâthie (1944) asserted that *Salvadoropsis* is closely related to *Evonymopsis*, but we found that it is more closely related to six other Malagasy genera than it is to *Evonymopsis*. Third, Perrier de la Bâthie (1942a, 1946a) considered

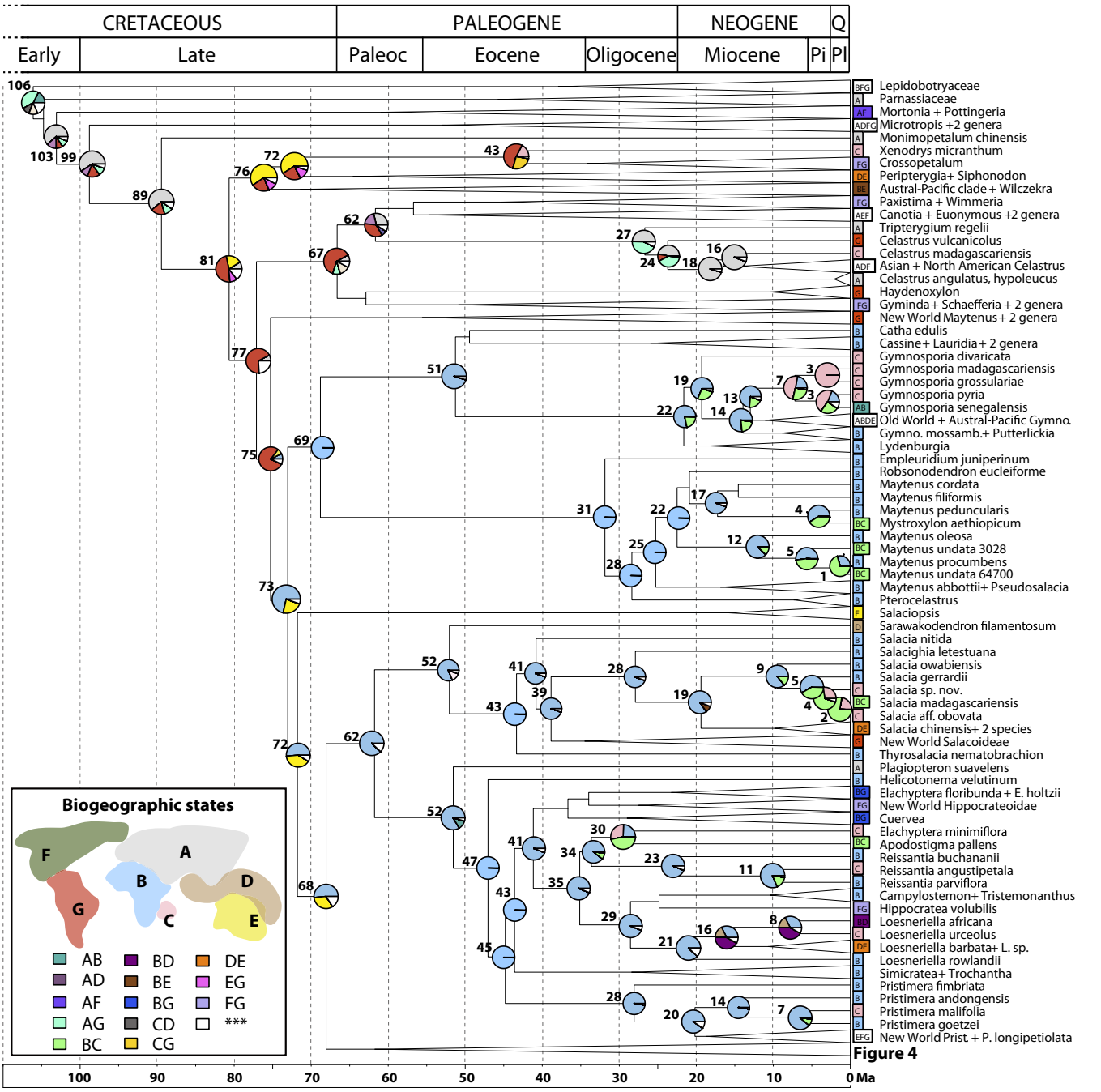

Figure 4

Fig. 3. Basal portion of the reduced-taxon-sampling simultaneous-analysis parsimony strict consensus from Fig. 1 that shows mean age estimates in millions of years (rounded to the nearest Ma) and DEC-based biogeographic reconstructions. White sections of the pie charts at ancestral nodes represent all distributions with a probability of less than 0.07 inferred for that node and may represent more than one area. The Quaternary is abbreviated as Q, the Pleistocene as Pl, the Pliocene as Pi, and the Paleocene as Paleoc.

the assignment of *Elaeodendron humberti* H. Perrier. to that genus as questionable, and in our inferred phylogeny it is resolved as sister to *Hartogiopsis trilobocarpa* (Baker) H. Perrier (Fig. 2). Fourth, Schatz and Lowry (2004) recognized 11 species of *Brexia* while Verdcourt (1968) considered the genus to be monotypic and limited to *B. madagascariensis* (Lam.) Ker Gawl. In our phylogeny the three accessions of *B. madagascariensis* sampled are an exclusive lineage that is distinct from *B. australis*, *B. humbertii*, and *B. montana*, which is consistent with Schatz and Lowry's (2004) more narrow delimitation of *B. madagascariensis*.

Fifth, Perrier de la Bâthie (1942a, 1946a) considered the generic placement of *Elaeodendron micranthum* Tul. as questionable. Indeed, in our phylogeny this species, which we refer to as *Xenodrys micranthum*, is only distantly related to *Elaeodendron* (Figs. 1 and 2). *Xenodrys* has a shrubby habit with small, delicate, puberulous inflorescences and flowers. By contrast, *Elaeodendron* primarily consists of trees with stout, prominent, glabrous inflorescences and flowers.

Xenodrys, like its close relative *Crossopetalum* (Fig. 1), has small, slightly asymmetrical, obovoid drupes, whereas most species of *Elaeodendron* have large drupes with prominent hard and/or woody stones. *Xenodrys* and *Crossopetalum* also both have seeds with postchalazal bundles (a.k.a., branched raphes), but this convergent synapomorphy is shared with the distantly related genera

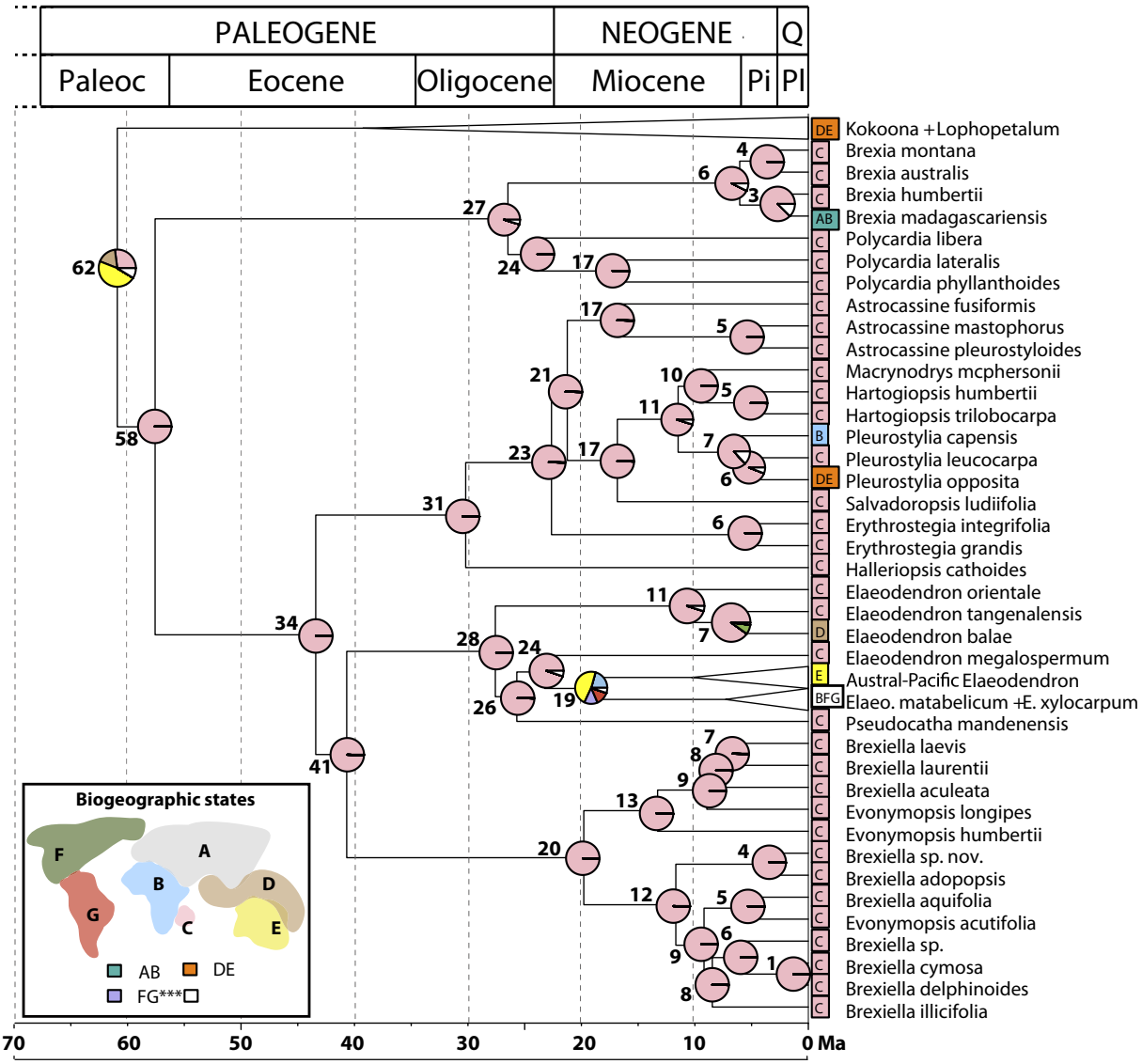

Fig. 4. Distal portion of the reduced-taxon-sampling simultaneous-analysis parsimony strict consensus from Fig. 2 that shows mean age estimates in millions of years (rounded to the nearest Ma) and DEC-based biogeographic reconstructions. White sections of the pie charts at ancestral nodes represent all distributions with a probability of less than 0.07 inferred for that node and may represent more than one area. The Quaternary is abbreviated as Q, the Pleistocene as Pl, the Pliocene as Pi, and the Paleocene as Paleoc.

Brexiella and *Glyptopetalum* (Ding Hou, 1962; Corner, 1976; Simmons and Hedin, 1999) as well as *Elaeodendron* and *Mystroxylon* (R.H.A., pers. obs.). There are few important morphological characters that can be used to separate *Xenodrys* from *Crossopetalum*. But *Xenodrys* often has unisexual 4- or 5-merous flowers versus bisexual 4-merous flowers in *Crossopetalum*. Furthermore, *Xenodrys* ovaries have two locules with two ovules per locule whereas *Crossopetalum* has ovaries with two or four locules (Edwin and Ding Hou, 1975) with one ovule per locule.

Sixth, Perrier de la Bâthie (1942a) segregated *Evonymopsis* from *Brexiella*, but this distinction is not supported in our inferred phylogeny in which *Brexiella* is a paraphyletic group that includes a polyphyletic *Evonymopsis* (Fig. 2). The morphological distinction between *Brexiella* and *Evonymopsis* is not as clear as the distinctions made in Perrier de la Bâthie's (1942a, 1946a) and Schatz's (2001) generic keys. For example, *Brexiella cymosa* is very similar to *Evonymopsis* in having petals spread flat at anthesis (as shown in Schatz's (2001) figure 85). Because these genera have fleshy discs the position of the stamens is variable. Likewise, the numbers of carpels and ovules per carpel are also variable within species. Furthermore, we lack data on most species for the putatively diagnostic fruit and seed differences between the genera.

Pseudocatha has been consistently resolved as an early derived lineage with *Elaeodendron* in earlier studies (Simmons et al., 2008, 2012b) and again here. The unpublished genus name is René Capuron's. The main morphological distinction for *Pseudocatha* is its dry, woody, loculicidally dehiscent capsule that is up to 25 mm long and contains six ± free seeds. In *Elaeodendron* the fruit is a drupe with a typical woody stone (hence the genus name), ovules from one to three locules usually aborted, and the seed embedded in a narrow cavity within the stone. But the general floral morphology of *Pseudocatha* (5-merous flowers with three carpels, two erect ovules per carpel) is consistent with *Elaeodendron* (3-, 4- or 5-merous flowers with 2, 3, or 4 carpels; two erect ovules per carpel). Based on the phylogenetic position of *Pseudocatha* as well as its shared floral morphology, we believe that *Pseudocatha mandenensis* should be recognized as a member of *Elaeodendron*.

Table 2
Origin of the 12 Malagasy Celastraceae lineages inferred by DIVA and DEC. Lineages are ordered based on the reduced-taxon-sampling simultaneous-analysis parsimony strict consensus presented in Figs. 1–4. The seven biogeographical regions are: (A) Eurasia; (B) Africa; (C) Madagascar, Comoro and Mascarene Islands; (D) southern India, Malesia, Pacific Islands; (E) Australia, New Guinea, New Caledonia, New Zealand; (F) North America; and (G) Caribbean, Central and South America.

#	Malagasy lineage	Distribution	Stem node			Crown node		
			Age[a]	DEC distribution[b]	RASP distribution	Age[a]	DEC distribution[b]	RASP distribution
1	*Xenodrys micranthum*	C	43.4 (55.3–33.0)	G (0.47), CG (0.25), C (0.25)	CG	N/A	C	C
2	*Celastrus madagascariensis*	C	16.5 (21.7–11.7)	A (0.94)	AC	N/A	C	C
3	*Gymnosporia divaricata*	C	19.3 (25.0–14.2)	B (0.69), BC (0.27)	BC	N/A	C	C
4	*Gymnosporia mad.*, *G. gross.*, *G. pyria*, *G. senegal.*[c]	C and BC	13.0 (16.5–9.9)	B (0.74), BC (0.21)	B, BC	7.2 (9.9–4.6)	C (0.49), BC (0.26), B (0.22)	BC, C
5	*Mystroxylon aethiopicum*	BC	4.1 (6.7–1.7)	B (0.59), BC (0.41)	B	N/A	BC	BC
6	*Maytenus undata*, *M. procumbens*[c,d]	BC	12.2 (17.4–7.1)	B (0.88)	B	5.6 (8.7–2.7)	B (0.52), BC (0.47)	B
7	*Salacia* sp. nov., *mad.*, *S. obovata*	C and BC	4.7 (7.1–2.8)	B (0.58), BC (0.41)	BC	3.7 (5.7–1.9)	BC (0.67), C (0.28)	C
8	*Elachyptera minimiflora*, *Apodostigma pallens*	C and BC	33.6 (39.2–28.1)	B (0.89)	B, BC	29.9 (36.7–22.8)	BC (0.47), C (0.29), B (0.24)	BC, C
9	*Reissantia angustipetala*	C	10.6 (15.8–5.8)	B (0.81)	BC	N/A	C	C
10	*Loeseneriella urceolus*	C	8.0 (13.3–3.7)	BD (0.42), B (0.32)	BC, CD	N/A	C	C
11	*Pristimera malifolia*	C	6.8 (10.6–3.2)	B (0.89)	BC	N/A	C	C
12	Main Malagasy clade	C	61.7 (69.6–53.8)	E (0.47), C (0.27)	CD, CE	58.4 (66.1–50.3)	C (0.99)	C

[a] Mean age estimate in millions of years with 95% credible interval indicated in parentheses.
[b] Probabilities (expressed as percentages) ⩾ 0.2 are shown in parentheses.
[c] Although treated as part of broader Malagasy lineages, neither *Gymnosporia senegalensis* nor *Maytenus procumbens* are native to Madagascar.
[d] The "*Maytenus undata* 64700" specimen, from Fairchild Tropical Garden, might be mis-identified and actually *M. procumbens*, in which case the dispersal of *M. undata* to Madagascar would be inferred as more recent.

4.2. Molecular dating and biogeography of Malagasy lineages

Our molecular-dating estimates are potentially subject to many sources of error, as reviewed by Gandolfo et al. (2008), Parham et al. (2012) and Sauquet et al. (2012). Age estimates can span an order of magnitude (Sauquet et al., 2012), independently of potential for fossil misidentifications, which is a serious concern for this study given that most of the fossils we used were identified using the intuitive method rather than based on one or more synapomorphies. Furthermore, there is particular reason to be concerned with dating estimates for lineages of intermediate age (Soubrier et al., 2012). With these qualifications in mind, our age estimates for the lineages of Malagasy Celastraceae (69.6–1.7 Ma; Table 2) are consistent with Yoder and Nowak's (2006) inference that most Malagasy lineages dispersed to the island within the last 65 million years during the Cenozoic, and Buerki et al.'s (2013) inference that many of the Malagasy angiosperm lineages arrived during the Miocene.

It is widely recognized that the large majority of the Malagasy lineages, including most or all of the angiosperms, arrived via dispersal after the breakup of Gondwana, with most of them having dispersed from Africa (Schatz, 1996; McLoughlin, 2001; Yoder and Nowak, 2006; Buerki et al., 2013). Indeed, 81% of the non-endemic native angiosperms in Madagascar are also native to Africa (Callmander et al., 2011), and more Malagasy endemic angiosperm genera have biogeographical affinities to African genera than to those from any other region aside from Madagascar itself (Buerki et al., 2013).

Of the 12 extant Malagasy Celastraceae lineages that we identified, we infer that eight of them are clearly of African origin (Table 2), which is fully consistent with the studies cited above. Of the remaining four lineages, our analyses indicate that *Celastrus madagascariensis* is of Eurasian origin. No species of *Celastrus* are native to Africa (Ding Hou, 1955). *Celastrus* is, however, native to Australia (Jessup, 1984a) and Malesia (Ding Hou, 1962), and we only sampled one of the seven species (*C. hindsii* Benth., in Malesia) from those areas. Hence our inference that *C. madagascariensis* is of Eurasian rather than Australian or Malesian origin may be an artifact of taxon undersampling. Similarly, we only sampled four of the 16 currently recognized species of *Loeseneriella*, which includes species from Africa, Madagascar, southeast Asia, Malesia, and Australia (Simmons, 2004b). We sampled the single Australian species (*L. barbata* (F. Muell.) C. T. White) as well as a single cultivated specimen from Indonesia (*L.* sp.), but there are also four species in Malesia (Ding Hou, 1964). Based on our biogeographic results (Table 2) and our limited taxon sampling within *Loeseneriella*, we cannot confidently identify a unique origin for the Malagasy *Loeseneriella urceolus* lineage.

The two Malagasy lineages with the oldest mean stem-node age estimates likewise might not have African origins (Table 2). The sister-group relationship between *Xenodrys micranthum* ined. from Madagascar and *Crossopetalum* from the West Indies and tropical Americas was unexpected, but this type of disjunct distribution has previously been documented in *Dichrostachys* Wight & Arn. (Fabaceae; Lavin and Luckow, 1993) and the clade of *Arcoa* Urb. + *Tetrapterocarpon* Humbert (Fabaceae; Herendeen et al., 2003). Buerki et al. (2013) noted that 7.7% of the Malagasy angiosperm genera have affinities with South American taxa. Yet the *Crossopetalum* lineage does include undescribed African species (F. Breteler, S. Buerki, I. Darbyshire, M.P. Simmons, J.J. Cappa, unpublished data), and the clade of (*Crossopetalum*, *Xenodrys*) is nested within a primarily Australian lineage (Figs. S3 and S16), which also includes the endemic African genus *Wilczekra* (Simmons and Cappa, 2013). Hence the current sister-group relationship between *Xenodrys* and *Crossopetalum* does not necessarily indicate that taxa from the West Indies and Madagascar are each other's closest extant relatives.

Finally, the main Malagasy lineage, with the oldest mean stem-node estimate (61.7 Ma) of the 12 Malagasy lineages, appears to have been derived from the eastern Indian Ocean region, based in large part on its sister-group relationship with the clade of (*Kokoona*, *Lophopetalum*) (Figs. 2 and 4, S16; Table 2). This sister-group relationship is consistent with the closer position of Madagascar to India at the mean stem-node estimate of their most recent common ancestor (61.7 Ma). But even in this case an eastern-Indian-Ocean origin is uncertain as an African origin cannot be ruled out based on biogeographic reconstructions for the next stem nodes down the tree (Figs. S3 and S16).

4.3. Out-of-Madagascar dispersal

Numerous Malagasy lineages have been documented as having dispersed to the nearby volcanic archipelagos of the Comoros (e.g., Wikstrom et al., 2010; Kruger et al., 2012) and Mascarenes (e.g., Janssen et al., 2008; Micheneau et al., 2008; Le Péchon et al., 2010; Strijk et al., 2012). Malagasy lineages have also dispersed to the Gondwanan landmasses of Africa (e.g., Yuan et al., 2005) and the Seychelles (e.g., Wikstrom et al., 2010). But few Malagasy lineages have been documented as dispersing broadly across the Indian Ocean, to the Arabian Peninsula and Asia (Yuan et al., 2005; Bukontaite et al., 2015).

Our study provides unambiguous evidence for at least four out-of-Madagascar dispersal events, all of which are within the main Malagasy clade (Figs. 2 and 4). First, *Brexia* consists of 12 species, including 10 that are endemic to Madagascar (Schatz and Lowry, 2004). *Brexia madagascariensis*, is native to Madagascar, the Comoros, and coastal Africa. *Brexia microcarpa* Tul., which we did not sample, but which has been treated as a variety of *B. madagascariensis*, is endemic to the Seychelles.

Second, *Pleurostylia*, which currently consists of seven species that are distributed from Africa to India, Sri Lanka, southeast Asia, Macronesia, Australia, and New Caledonia (Loesener, 1942; Simmons, 2004b), is unambiguously nested within the main Malagasy clade. *Pleurostylia pachyphloea* Tul. is endemic to Mauritius and Reunion Island (Baker, 1877) and *P. putamen* Marais is endemic to Rodrigues Island (Marais, 1981), but to our knowledge no confirmed specimens of *Pleurostylia* have been collected from Madagascar. The dispersal of the lineage leading to *Pleurostylia* from Madagascar might even represent two independent dispersals—one to Africa and the other to the east, followed by extinction of the Malagasy ancestor(s).

Third, *Elaeodendron*, which comprises about 40 species, includes some that are endemic to Madagascar, which form a basal grade, as well as others that are variously native to the West Indies, Africa, India, Sri Lanka, Macronesia, Australia, and New Caledonia (Kostermans, 1986; Müller, 1996; Archer and van Wyk, 1998). Members of the genus from Australia and New Caledonia form a clade and a single clear biogeographic lineage (Figs. 2 and 4), whereas the biogeographic history of the African and New World species we sampled is less clear.

Fourth, we infer an independent dispersal of the *Elaeodendron balae* Kosterm. ined. (Kostermans, 1986) lineage from Madagascar to Sri Lanka, albeit with the qualifications that the species identification for this specimen is tentative. Additional future sampling of other species of *Elaeodendron* from the Indian Ocean region is necessary to test whether this dispersal was direct or indirect via intermediary regions.

Schatz (1996, p. 80) noted the "far eastern character" of many elements of the Malagasy flora and partially attributed this to long distance dispersal across the Indian Ocean to Madagascar. Schatz (1996) also noted that dispersal may have been bi-directional, with Malagasy flora dispersing eastward, across the Indian Ocean. Indeed, in *Elaeodendron* and *Pleurostylia*, we infer that this far eastern character of the Malagasy flora is the result of dispersal across the Indian Ocean from Madagascar. Following Schatz (1996), we assert that Madagascar should be considered more broadly as a potential source for dispersal to other regions (beyond the Comoro and Mascarene Islands) rather than being viewed primarily as a region to which dispersal took place.

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Appendix A

List of taxa sampled with taxonomic authorities, voucher information, and GenBank accession numbers (26S rDNA, ITS rDNA, *matK*, *trnL* intron, *trnL-F* spacer, respectively, unless otherwise noted) for new sequences generated for this study. Unless otherwise noted, all specimens were collected from Madagascar and are vouchered at CS and PRE. "—" in the GenBank accession list indicates that no sequence of the given gene region was generated for that accession.

Brexia australis G.E. Schatz & Lowry—*R.H. Archer* et al., *2989*; JX203549, JX203488, JX203585, JX203399, JX203444. ***Brexia australis*** G.E. Schatz & Lowry—*R.H. Archer* et al., *2991*; JX203552, JX203489, JX203595, JX203404, JX203449. ***Brexia humbertii*** H. Perrier—*R.H. Archer* et al., *2977*; JX203553, JX203485, JX203594, JX203400, JX203445. ***Brexia madagascariensis*** (Lam.) Ker Gwal.—*R.H. Archer* et al., *2906*; JX203551, JX203486, JX203591, JX203401, JX203446. ***Brexia madagascariensis*** (Lam.) Ker Gwal.—*R.H. Archer* et al., *2971*; JX203550, JX203487, JX203592, JX203402, JX203447. ***Brexia montana*** H. Perrier—*R.H. Archer* et al., *2956*; JX203548, JX203484, JX203593, JX203403, JX203448. ***Brexiella aculeata*** ined.—*R.H. Archer* et al., *3011*; JX203567, JX203509, JX203603, JX203417, JX203463. ***Brexiella aculeata*** ined.—*R.H. Archer* et al., *3012*; JX203568, JX203510, JX203604, JX203414, JX203459. ***Brexiella apodopsis*** ined.—*R.H. Archer* et al., *2982*; JX203572, JX203499, JX203618, —, JX203460. ***Brexiella apodopsis*** ined.—*R.H. Archer* et al., *2985*; JX203570, JX203500, JX203620, JX203422, JX203468. ***Brexiella aquifolia*** ined.—*R.H. Archer* et al., *3010*; JX203563, JX203492, JX203607, JX203432, JX203478. ***Brexiella aquifolia*** ined.—*R.H. Archer* et al., *3026*; JX203564, JX203493, JX203606, JX203433, JX203479. ***Brexiella aquifolia*** ined.—*R.H. Archer* et al., *3027*; JX203565, JX203494, JX203610, JX203430, JX203476. ***Brexiella cymosa*** H. Perrier—*R.H. Archer* et al., *2958*; JX203577, JX203505, —, JX203425, JX203471. ***Brexiella cymosa*** H. Perrier—*R.H. Archer* et al., *2959*; JX203578, JX203506, JX203611, JX203424, JX203470. ***Brexiella delphinoides*** ined.—*R.H. Archer* et al., *2966*; JX203571, JX203503, JX203619, JX203416, JX203462. ***Brexiella delphinoides*** ined.—*R.H. Archer* et al., *2983*; JX203576, JX203504, JX203614, JX203418, JX203464. ***Brexiella* aff. *ilicifolia*** H. Perrier—*R.H. Archer* et al., *2926*; JX203579, JX203490, JX203617, JX203426, JX203472. ***Brexiella ilicifolia*** H. Perrier—*R.H. Archer* et al., *3009*; JX203580, JX203501, JX203613, JX203428, JX203474. ***Brexiella laurentii*** ined.—*R.H. Archer* et al., *3020*; JX203561, JX203513, JX203601, JX203419, JX203465. ***Brexiella laurentii*** ined.—*R.H. Archer* et al., *3021*; JX203562, JX203514, JX203602, JX203420, JX203466. ***Brexiella laevis*** ined.—*G. McPherson & J. Rabenantoandro 18450* (MO); JX203569, JX203512, JX203599, JX203392, JX203437. ***Brexiella longipes*** H. Perrier—*R.H. Archer* et al., *2936*; JX203581, JX203491, JX203605, JX203415, JX203461. ***Brexiella longipes*** H. Perrier—*R. H. Archer* et al., *2944*; JX203582, JX203511, JX203598, JX203421, JX203467. ***Brexiella* sp.**—*R.H. Archer* et al., *3019*; JX203566, JX203502, JX203612, JX203427, JX203473. ***Brexiella* sp. nov.**—*R.*

H. Archer et al., *2993*; JX203573, JX203498, JX203615, JX203423, JX203469. ***Celastrus madagascariensis*** Loes.—*R.H. Archer 3795*; JX203532, JX203481, JX203583, JX203389, JX203435. ***Elaeodendron megalospermum*** ined.—*R.H. Archer* et al., *3001*; JX203556, JX203522, JX203596, JX203393, JX203438. ***Elaeodendron tangenalensis*** ined.—*R.H. Archer* et al., *3053*; JX203557, JX203521, JX203597, JX203413, JX203458. ***Erythrostelegia integrifolia*** ined.—*R.H. Archer* et al., *2905*; JX203536, JX203529, JX203625, JX203406, JX203451. ***Erythrostelegia grandis*** ined.—*R.H. Archer* et al., *2914*; JX203538, JX203530, JX203626, JX203407, JX203452. ***Erythrostelegia grandis*** ined.—*R.H. Archer* et al., *2916*; JX203537, JX203531, JX203627, JX203408, JX203453. ***Evonymopsis acutifolia*** (H. Perrier) H. Perrier—*R.H. Archer* et al., *2908*; JX203559, JX203496, JX203608, JX203431, JX203477. ***Evonymopsis acutifolia*** (H. Perrier) H. Perrier—*R.H. Archer* et al., *2911*; JX203560, JX203497, JX203609, JX203434, JX203480. ***Evonymopsis acutifolia*** (H. Perrier) H. Perrier—*R.H. Archer* et al., *2951*; JX203558, JX203495, JX203616, JX203429, JX203475. ***Evonymopsis humbertii*** H. Perrier—*R.H. Archer* et al., *3048*; JX203575, JX203507, JX203600, —, —. ***Evonymopsis humbertii*** H. Perrier—*R.H. Archer* et al., *3052*; JX203574, JX203508, —, —. ***Hartogiopsis humbertii*** (H. Perrier) ined.—*R.H. Archer* et al., *2942*; JX203540, JX203525, JX203621, JX203409, JX203454. ***Macrynodrys mcphersonii*** ined.—*R. Rabevohitra 4283* (MO); JX203539, JX203526, JX203624, JX203410, JX203455. ***Halleriopsis cathoides*** ined.—*R.H. Archer* et al., *3035*; JX203554, JX203523, JX203622, JX203411, JX203456. ***Halleriopsis cathoides*** ined.—*R.H. Archer* et al., *3050*; JX203555, JX203524, JX203623, JX203412, JX203457. ***Pristimera* aff. *malifolia*** (Baker) N. Hallé—*R.H. Archer* et al., *3793*; JX203533, JX203482, JX203584, JX203390, JX203436. ***Salacia* aff. *obovata*** Boiv. ex Tul.—*R.H. Archer* et al., *3791*; JX203534, JX203483, —, JX203391, —. ***Salavadoropsis ludiifolia*** ined.—*R.H. Archer* et al., *3004*; JX203541, JX203527, JX203628, JX203394, JX203439. ***Salavadoropsis ludiifolia*** ined.—*R.H. Archer* et al., *3005*; JX203542, JX203528, JX203629, JX203405, JX203450. ***Xenodrys micranthum*** ined.—*R.H. Archer* et al., *2902*; JX203546, JX203516, JX203586, JX203397, JX203442. ***Xenodrys micranthum*** ined.—*R.H. Archer* et al., *2965*; JX203535, JX203517, JX203588, —, —. ***Xenodrys micranthum*** ined.—*R.H. Archer* et al., *2969*; JX203543, JX203518, JX203589, JX203395, JX203440. ***Xenodrys micranthum*** ined.—*R.H. Archer* et al., *2976*; JX203544, JX203519, JX203590, —, —. ***Xenodrys micranthum*** ined.—*R.H. Archer* et al., *2981*; JX203545, JX203515, JX203587, JX203398, JX203443. ***Xenodrys micranthum*** ined.—*R.H. Archer* et al., *2990*; JX203547, JX203520, —, JX203396, JX203441.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2015.09.013.

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