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A SMALLER *MACADAMIA* FROM A MORE VAGILE TRIBE: INFERENCE OF PHYLOGENETIC RELATIONSHIPS, DIVERGENCE TIMES, AND DIASPORE EVOLUTION IN *MACADAMIA* AND RELATIVES (TRIBE MACADAMIEAE; PROTEACEAE)[1]

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Tribe Macadamieae (91 spp., 16 genera; Proteaceae) is widespread across the southern hemisphere on all major fragments of Gondwana except New Zealand and India. *Macadamia* is cultivated outside its natural range as a "nut" crop (notably in Hawaii, where it is the principal orchard crop). We sampled seven DNA regions and 53 morphological characters from the tribe to infer its phylogeny and address the common assumption that the distribution of the extant diversity of the tribe arose by the rafting of ancestors on Gondwanan fragments. *Macadamia* proves to be paraphyletic with respect to the African genus *Brabejum,* the South American genus *Panopsis*, and the Australian species *Orites megacarpus.* We erect two new generic names, *Nothorites* and *Lasjia,* to produce monophyly at that rank. The earliest disjunctions in the tribe are inferred to be the result of long-distance dispersal out of Australia (with one possible exception), rather than vicariance. Evolution of tardy fruit dehiscence is correlated with these dispersals, and the onset of the Antarctic Circumpolar Current (ACC) precedes them. We suggest that the ancestors of extant diversity arrived on their respective continents via the ACC, and we recognize that this is a mechanism precluded, rather than facilitated, by Gondwana's terrestrial continuity.

Key words: biogeography; fruit evolution; Gondwana; hydrochory; long-distance dispersal; *Macadamia*; relaxed-clock molecular dating; phylogenetics; Proteaceae; vicariance.

"I have reason to suppose that no well informed naturalist will claim that the dispersal of the Proteaceae [and other groups] is in any way recent." —Léon Croizat (1962, p. 173)

Macadamia F.Muell. and relatives in tribe Macadamieae (91 spp. in 16 genera; Fig. 1) are the most widespread group recognized at tribal rank in the Proteaceae (Macadamia nut family; ca. 1800 spp. in 80 genera). Today, the tribe naturally occurs on all the major landmasses thought to have once been part of the southern supercontinent Gondwana (Fig. 2), with the exception of India and New Zealand (though it can be found in the fossil record of New Zealand; Carpenter, 1994; Pole, 1998). The tribe also can be found on landmasses that are not derived from Gondwana, such as Central America and parts of the Southeast Asian mainland. *Macadamia* (*M. integrifolia* Maiden & Betche, *M. tetraphylla* L.A.S.Johnson, and their hybrids; Fig. 1A) and other members of the tribe [*Athertonia diversifolia* (C.T.White) L.A.S.Johnson & B.G.Briggs, *Gevuina avellana* Molina, *Hicksbeachia pinnatifolia* F.Muell.; Fig. 1B] are cultivated outside of their native range for their edible, fleshy embryos. At the generic rank, the tribe is most diverse in Australia, where six small (1–9 spp. each), narrowly distributed genera occur in the eastern rainforests and adjacent regions. At the specific rank, the tribe is more diverse in South America, where two larger genera (*Panopsis* Salisb. and *Euplassa* Salisb.; 25 and 20 spp., respectively) and one small genus (*Gevuina* Molina; 1 sp.) naturally occur. Fossils attributed to the family extend back to the late Cenomanian (ca. 93 million years before present [Ma BP]; Dettmann and Jarzen, 1998), prior to most fragmentation events in the southern supercontinent Gondwana. The family's far-flung distribution in the southern hemisphere is generally explained by the rafting of ancestors on those fragments (e.g., Venkata Rao, 1971; Johnson and Briggs, 1975; Weston and Crisp, 1994, 1996; Prance and Plana, 1998; Prance et al., 2007; cf. Barker et al., 2007), as is the distribution of many other organisms (reviewed in Sanmartín and Ronquist, 2004). Here, we infer a phylogeny for the tribe, the areas occupied by ancestors, the dates of biogeographic disjunctions among the ancestors, and the significance of correlations between disjunctions and the evolution of the tribe's fruits to address the veracity of this explanation for the tribe's widespread distribution.

The current classification for tribe Macadamieae is that of Weston and Barker (2006), in which the tribe and four subtribes are circumscribed based on clades resolved in a supertree summary of phylogenies produced for the family to date. This supertree does not resolve the relationships among the subtribes and resolves just two relationships among genera within subtribes: *Brabejum* L. as sister to *Panopsis* and *Cardwellia* F.Muell. as sister to a clade composed of the remaining genera in subtribe Gevuininae. Three of the phylogenies that they used for the supertree were published (Hoot and Douglas, 1998; Mast and Givnish, 2002; Barker et al., 2002), and two were

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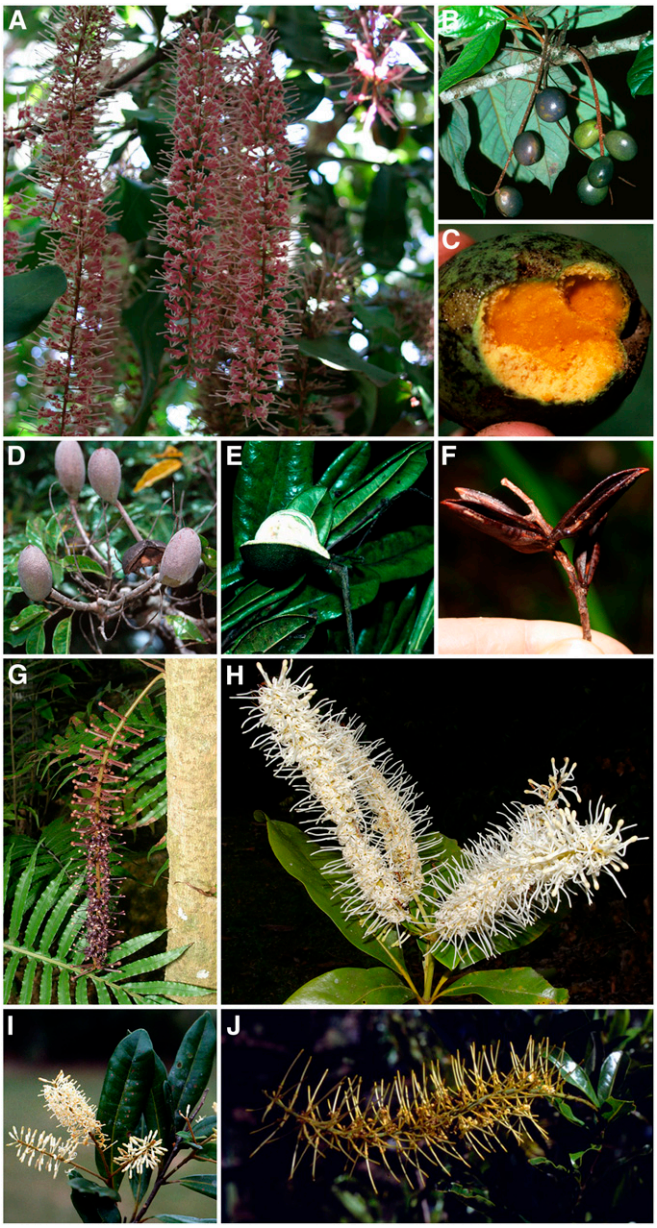


Fig. 1. Diversity in tribe Macadamieae and relatives. (A) A hybrid of *Macadamia integrifolia* and *M. tetraphylla*, the sources of edible macadamia nuts; (B) *Athertonia diversifolia*, an Australian species with a purple exocarp that dehisces late (at germination); (C) *Virotia neurophylla*, a New Caledonian species with a succulent outer mesocarp that dehisces late; (D) *Cardwellia sublimis*, an Australian species with early fruit dehiscence; (E) *Orites megacarpus*, an Australian species that has fruits that are unusual for the genus; (F) *O. excelsus*, an Australian species with a fruit typical of the genus; (G) *Hicksbeachia pilosa*, an Australian species that is cauliflorous; (H) *M. claudiensis*, an Australian species that is the type of the new genus *Lasjia*; (I) *O. megacarpus*, the type of the new genus *Nothorites*; (J) *V. leptophylla*, a New Caledonian species that is the type of genus *Virotia*. *Photo credits:* Austin Mast (A, F), Gary Sankowsky (B, D, E, G–I) and Peter Weston (C, J).

unpublished (one data set from the internal transcribed spacers of the nuclear ribosomal DNA (ITS) and another from the *rbcL* gene). These previously unpublished ITS data are, in part, published here. In Weston and Barker's (2006) supertree, clades corresponding to the four subtribes of tribe Macadamieae are part of a polytomy with a 17th genus, *Carnarvonia* F.Muell., but they consider *Carnarvonia* to be incorrectly placed based on its morphology. Orthotropous ovules, tardily dehiscent fruits, unwinged seeds, and fleshy cotyledons are usually present in members of tribe Macadamieae, but all are missing from *Carnarvonia* (and *Cardwellia*, but molecular results strongly support the position of *Cardwellia* in the tribe; Fig. 1D). Some or all of these features are also seen in *Floydia* L.A.S.Johnson & B.G.Briggs, *Roupala* Aubl., and *Lambertia* Sm.—three genera that Johnson and Briggs (1975) included in tribe Macadamieae but Weston and Barker (2006) moved to tribe Roupaleae. This character state distribution makes tribes Macadamieae and Roupaleae difficult to diagnose from each other morphologically. Previously published phylogenetic work on the family sampled the *atpB* gene and *atpB-rbcL* spacer (Hoot and Douglas, 1998) or these two regions in combination with the *rbcL* gene (Barker et al., 2007) from one species each of *Macadamia*, *Brabejum*, *Panopsis*, *Cardwellia*, *Euplassa* (not in Barker et al., 2007), and *Gevuina* and resolved these as a monophyletic group. This prior sampling represents two of four subtribes in tribe Macadamieae.

Synapomorphies have been recognized for Weston and Barker's (2006) subtribes Gevuininae (8 genera), Macadamiinae (3 genera) and Virotiinae (3 genera), but not for subtribe Malagasiinae (2 genera). Subtribe Gevuininae is composed of genera from South America (*Euplassa,* 20 spp.; *Gevuina*, 1 sp.), Australia-New Guinea (*Hicksbeachia* F.Muell., 2 spp.; *Bleasdalea* F.Muell. ex Domin, 2 spp.; *Cardwellia,* 1 sp.), New Caledonia (*Kermadecia* Brongn. & Gris, 4 spp.; *Sleumerodendron* Virot, 1 sp.), and Fiji and Vanuatu (*Turrillia* A.C.Sm., 3 spp.; Fig. 2). The orientation of the carpel and the production of floral zygomorphy through curvature of the style and curvature of three of four tepals are synapomorphies for subtribe Gevuininae (Douglas and Tucker, 1996a; Weston and Barker, 2006), though the last two character states have undergone reversals in some members. Subtribe Macadamiinae is composed of *Macadamia* (9 spp.) from Australia and Sulawesi, *Brabejum* (1 sp.) from southern Africa, and *Panopsis* (25 spp.) from South and Central America. A cuplike nectary surrounding the ovary (thought to have arisen independently in *Virotia* L.A.S.Johnson & B.G.Briggs) and frequent opposite or whorled phyllotaxy are synapomorphies for subtribe Macadamiinae (Johnson and Briggs, 1975; Weston and Barker, 2006). Subtribe Malagasiinae is composed of *Malagasia* L.A.S.Johnson & B.G.Briggs (1 sp.) from Madagascar and *Catalepidia* P.H.Weston (1 sp.) from Australia. A morphological synapomorphy for subtribe Malagasiinae has yet to be identified. Subtribe Virotiinae is composed of *Heliciopsis* Sleumer (14 spp.) from Burma and southeast China to Malesia (northwest of Wallace's Line), *Virotia* (6 spp.) from New Caledonia, and *Athertonia* (1 sp.) from Australia. Distinctive surface sculpturing of the woody inner mesocarp is a synapomorphy for subtribe Virotiinae (Weston and Barker, 2006). Five of the six New Caledonian species that Johnson and Briggs (1975) assigned to *Virotia* were placed there informally; all six had been previously treated as members of *Macadamia* (e.g., Virot, 1968). Although they have mostly been treated since 1975 as members of *Virotia* (e.g., Weston and Crisp, 1996; Weston, 2006; Weston and Barker, 2006), the new combinations for them in that genus have never been validly published. We find that group to be monophyletic (though with poor statistical support), and thus we treat those five New

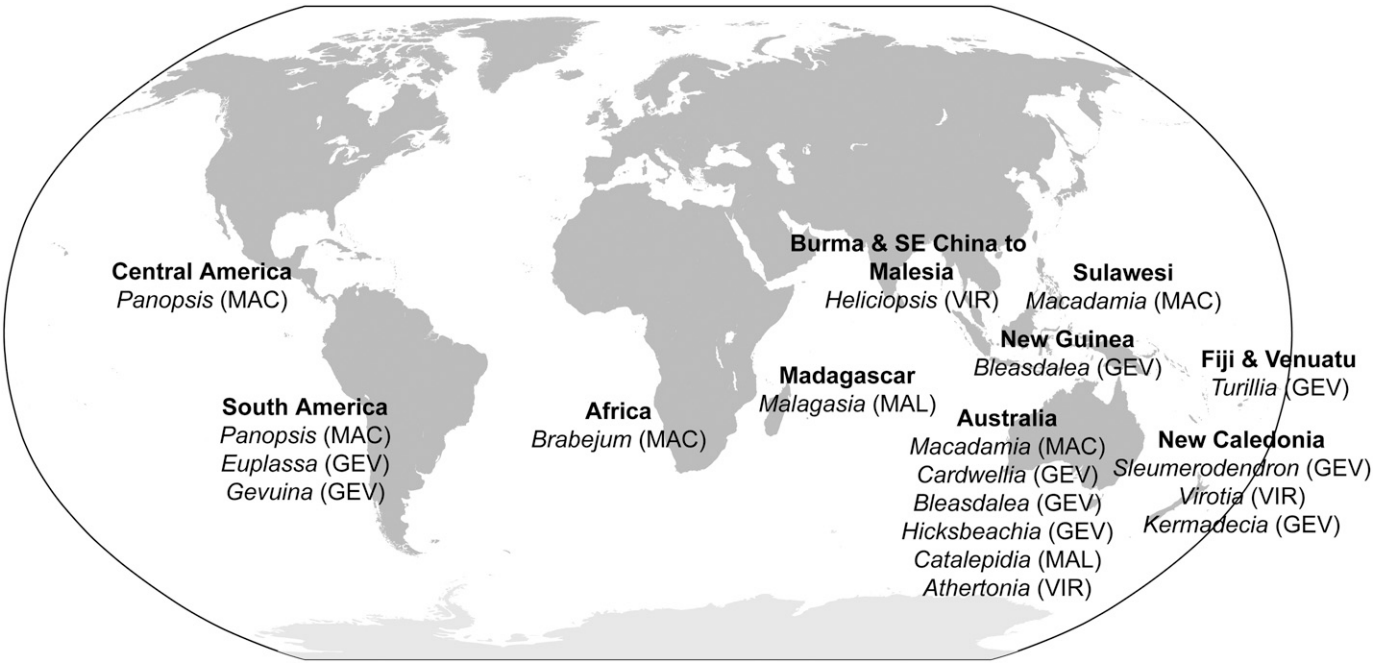


Fig. 2. Distribution of genera and their subtribal affiliation. Subtribes: Macadamiinae (MAC), Malagasiinae (MAL), Virotiinae (VIR), Gevuininae (GEV).

Caledonian species as members of *Virotia* and make the necessary combinations.

Fossil evidence from the large and widespread subtribe Gevuininae provides a minimum age for the basal split in that subtribe that predates the last continental connections between some, but not all, of the landmasses that it occupies. Fossil cuticle that has been attributed to subtribe Gevuininae appears in the Early Miocene deposits of the Manuherikia Group of Central Otago, New Zealand (Carpenter, 1994; Pole, 1998), and in the Eocene deposits of the Pidinga Formation in the Lefroy paleodrainage of southern Western Australia (Carpenter and Pole, 1995). The fossil cuticle shares derived features of the trichome base ("a thickened, round platform-like base with a crimped margin"; Carpenter and Pole, 1995, p. 1113) with genera other than *Cardwellia* in the subtribe. However, both fossils occur in locations not occupied by extant Gevuininae. Macphail (personal communication in Carpenter and Pole 1995, p. 1108) considered the samples taken from the Pidinga Formation to have a maximum age of Middle Eocene (lower boundary of 48.6 Ma BP) and a minimum age of Late Eocene (upper boundary of 33.9 Ma BP; we take all absolute geological ages from Gradstein et al., 2004). This time is prior to the end of continental connections between Australia and Antarctica (via Tasmania and the South Tasman Rise) at ca. 33 Ma BP (Veevers, 2000, 2001; J. J. Veevers, Macquarie University, personal communication) and between Antarctica and South America between 33 and 29 Ma BP (Florindo et al., 2003). Fossils attributable to a second subtribe (Virotiinae) are known from this period of Antarctic isolation. Fossil fruits that share the synapomorphy of an ornamented inner mesocarp with extant members of subtribe Virotiinae are known from the Oligocene deposits of the Glencoe locality in central eastern Queensland (Rozefelds, 1992) and the Miocene deposits of the Gulgong locality in New South Wales (Von Mueller, 1879, 1883; Rozefelds, 1992).

While these fossils predate or co-occur with the period of Antarctic isolation, most of the other fragmentation events involving Gondwana predate the fossils by substantial time spans. Continental connections between a combined Madagascar/India and the rest of Gondwana, in this case via eastern Antarctica, ended by ca. 132 Ma BP (Lawver et al., 1992; McLoughlin, 2001), and continental connections between Africa and the remaining contiguous part of Gondwana, in this case via South America, ended by ca. 105 Ma BP (McLoughlin, 2001). Continental connections between Zealandia (New Caledonia, New Zealand, and a number of now submerged of ridges and plateaus) and the remaining contiguous part of Gondwana, in this case via western Antarctica, began separating 84 Ma BP (McLoughlin, 2001) but might have remained contiguous in places until the Early Paleocene (62–66 Ma BP; Ladiges and Cantrill, 2007). Barker et al. (2007) found in their molecular dating study of the family (the study in which they sampled just five of the 16 genera in tribe Macadamieae) that inferred ages for the older disjunctions involving New Zealand or Africa were inconsistent with a vicariance hypothesis, whereas those for younger disjunctions (e.g., between Australia and South America) were consistent with it.

If the tribe and the landmasses that it occupies did indeed "co-speciate" (as in the vicariance framework commonly accepted for the family) and the habitats and suite of available dispersers on the daughter landmasses are analogous, then we would expect that evolution in the tribe's diaspores will be uncorrelated with the disjunctions. The genera of tribe Macadamieae produce early or tardily dehiscent fruits (dehiscing at fruit maturity or seed germination, respectively) that are mostly >1 cm in size (Filla, 1926; Sleumer, 1955a; Virot, 1968; Venkata Rao, 1971; Johnson and Briggs, 1975; Weston, 1995a–d; Weston and Crisp, 1996; Prance and Plana, 1998; Qiu and Weston, 2003; Prance et al., 2007; Fig. 1). With the exception of *Cardwellia*, these fruits contain 1–2 wingless seeds.

Cardwellia produces follicles that each open to release many thin, winged seeds (Hyland, 1995). The fruits are typically inconspicuous—most species have dull fruits that are black, brown, bronze, green, or gray at maturity. However, more apparent red fruits occur in subtribes Malagasiinae (the Australian genus *Catalepidia*) and Gevuininae (the Australian genus *Hicksbeachia*). The mesocarp in subtribes Gevuininae (with a few exceptions), Malagasiinae, and Virotiinae is succulent (Fig. 1C), and it is leathery to woody in subtribe Macadamiinae. There is a strongly lignified and bony inner mesocarp in subtribes Gevuininae, Malagasiinae, and Virotiinae, but not in subtribe Macadamiinae. Instead, in some members of *Macadamia* there is a bony testa—one of the hardest in the angiosperms (Venkata Rao, 1971). Johnson and Briggs (1975) considered the production of indehiscent fruits and large wingless seeds to have arisen independently at least four times in subfamily Grevilleoideae, each time in lineages inhabiting moist closed forests. They contend that in those habitats wind dispersal was lost in favor of dispersal by fruit-eating mammals (including fruit bats) and birds (cf., Venkata Rao, 1971). Weston and Crisp (1996) consider the fruits of *Virotia*, *Kermadecia*, *Turrillia*, and *Sleumerodendron* to be typical bat fruits, with their dull color, sour or mildly sweet odor, lack of a protective rind, and possession of large hard parts.

In this study, we infer a phylogeny for *Macadamia* and relatives in the widespread tribe Macadamieae using molecular and morphological data. Then, we infer the geographic distributions of ancestors, the age of biogeographic disjunctions, and the significance of correlations between disjunctions and features of the diaspores. We use the results to test the hypotheses that (1) *Macadamia* and other genera, including *Virotia*, are monophyletic; (2) tribe Macadamieae and the component subtribes of Weston and Barker (2006) are monophyletic; (3) the most recent common ancestor of extant members of tribe Macadamieae occupied Australia, the area of greatest extant generic diversity; (4) biogeographic disjunctions involving Gondwanan fragments date back to the time of the last continental connection between the landmasses involved; and (5) evolution of the tribe's diaspores are uncorrelated with biogeographic disjunctions. We also use the results to make nomenclatural changes to maintain the monophyly of genera.

MATERIALS AND METHODS

Sampling—We sampled three chloroplast DNA (cpDNA: *matK*, *atpB*, and *ndhF* genes) and three nuclear DNA (nDNA; *waxy* loci *1* and *2* and *PHYA* genes) regions from 22 taxa of tribe Macadamieae and 10 taxa from outside the tribe (Appendix 1). The 22 taxa include 7 (of 9) species of *Macadamia* and 1 species from each of the remaining genera in the tribe (Appendix 1). The 10 extratribal taxa include 8 other representatives of subfamily Grevilleoideae: *Carnarvonia araliifolia* F.Muell., *Banksia serrata* L.f., *Floydia praealta* (F.Muell.) L.A.S.Johnson & B.G.Briggs, *Grevillea caleyi* R.Br., *Lambertia formosa* Sm., *Orites diversifolius* R.Br., *O. megacarpus* A.S.George & B. Hyland, and *Roupala montana.* Johnson and Briggs (1975) considered tribe Macadamieae to include *Floydia*, *Lambertia*, and *Roupala* Aubl., but the more recent classification of Weston and Barker (2006) excluded these genera from the tribe. *Orites diversifolius* is the type species of genus *Orites* R.Br., and it and *O. megacarpus* were included in this study because a parallel study (A. Mast and P. Weston, unpublished data) in which all species of *Orites* were sampled suggested that *O. megacarpus* (and only this species from that genus) might be nested in tribe Macadamieae. All four of the tribes of subfamily Grevilleoideae sensu Weston and Barker (2006) are represented in this sampling. The topology is shown with *Nelumbo lutea* Willd. (Nelumbonaceae) as sister to everything else, including the remaining taxon, *Platanus occidentalis* L. (Platanaceae). This topoglogy is based on previous molecular phylogenetic results (e.g., Angiosperm Phylogeny Group, 2003), which are supported by morphological synapomorphies for a clade composed of Proteaceae and Platanaceae (Hoot and Douglas, 1998).

We sampled the two internal transcribed spacers of the nuclear ribosomal DNA region and the 5.8S gene (ITS) from 31 taxa of tribe Macadamieae, two accessions of *O. megacarpus*, and *Carnarvonia* (Appendix 1). The 31 taxa included 8 (of 9) species of *Macadamia*, 4 (of 25) species of *Panopsis*, 3 (of 20) species of *Euplassa*, 3 (of 4) species of *Kermadecia*, 2 (of 6) species of *Virotia*, and 1 species from each of the remaining genera. All but one of the 22 species of tribe Macadamieae from which the non-ITS DNA regions were sampled are represented in the ITS data set. In the case of the remaining species, *Heliciopsis lanceolata* (Koord. & Valeton) Sleumer, it was replaced by its congener, *H. lobata* (Merr.) Sleumer, in the ITS data due to sequencing difficulties. Seven of 21 species represented in both the non-ITS and ITS data sets are represented by a different specimen (Appendix 1). This agglomeration of data from different specimens occurred because most of the ITS data set was generated several years before the non-ITS data sets were generated, and leaf tissue and DNA from some specimens had been used up. *Carnarvonia* is shown sister to the other taxa sampled in the ITS data set because this topology is consistent with the results from the other data sets. Specimen voucher information for the DNA samples is in Appendix 1.

We sampled morphological characters from 41 taxa of tribe Macadamieae and the same eight extratribal taxa sampled from subfamily Grevilleoideae for the non-ITS DNA data (Appendix 1). The 41 taxa included 9 (of 9) species of *Macadamia*, 5 (of 25) species of *Panopsis*, 2 (of 20) species of *Euplassa*, 4 (of 4) species of *Kermadecia*, 6 (of 6) species of *Virotia*, 3 (of 3) species of *Turrillia*, and 1 species from each of the remaining genera. All the taxa of tribe Macadamieae from which DNA data were sampled are represented in the morphological data set.

DNA extraction, amplification, cloning, and sequencing—We extracted the DNA used in the non-ITS DNA sequencing and in a small number of ITS sequencing reactions with a DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) following the manufacturer's instructions. We extracted DNA used in most of the ITS sequencing using the CTAB-diatomite protocol of Gilmore et al. (1993; a typographical error in Appendix 1B of that reference resulted in all "μL" abbreviations being replaced with "mL" at steps 4, 9, 11, and 12).

We amplified the target regions using the polymerase chain reaction (PCR; Mullis et al., 1986). To amplify the *matK*, *atpB*, and *waxy* genes, we used the primers provided in Mast et al. (2005). We amplified the *ndhF* gene in two reactions: the 5′ end with primer –52pro (a modified version of an unpublished primer of K.-J. Kim and R. K. Jansen; 5′ AGG TAA GAT CCG GTG AAT CGG AAA C 3′) and 972Rpro (a modified version of the 972R primer of Olmstead and Sweere, 1994; 5′ CAT AGT ATA ACC CAA TTG AGA C 3′) and the 3′ end with 803Fpro (a modified version of the 803F primer of Olmstead and Sweere, 1994; 5′ CTA TGG TAG CAG CGG GAA TTT TTC 3′) and 2100R (Olmstead and Sweere, 1994) or 972Fgre (a modified version of the 972F primer of Olmstead and Sweere, 1994; 5′ TAC AAT GTC TCA ATT GGG TTA TAT TAT G 3′) and 2100Rgre (a new primer; 5′ CTT GTA ACA CCA ATA CCA TTC GTA ATT C 3′). We amplified the *PHYA* gene with the new primers 34F (5′ CTC CAA TCA TAC AAA CTT GCT GCC AAG G 3′) and 1159R (5′ CCT TCC AAG GTA AAC TCC TTG TCT TAA C 3′). We amplified the ITS region using the PCR primers of Barker et al. (2002) or Leu 1 (sequence provided in Mast, 1998) and 4 (White et al., 1990). The cpDNA and ITS primers amplify the complete extent of their respective regions. The *waxy* primers amplify parts of exons 7 and 10 and the intervening introns and exons; the *PHYA* primers amplify part of exon 1.

We used Platinum PCR Supermix (Invitrogen, Carlsbad, California, USA) to amplify the cpDNA regions, the diagnostic region of *waxy* (described later), and ITS (from a few of the taxa). We used Platinum PCR Supermix High Fidelity (Invitrogen; a mix that includes a polymerase with proofreading 3′ to 5′ exonuclease activity) to amplify the nDNA regions that we cloned. We used nonproofreading *Taq* polymerase (Promega, Annandale, New South Wales, Australia and Boehringer Mannheim, Castle Hill, New South Wales, Australia) to amplify ITS from the majority of the taxa. We separated amplified PCR products on an agarose gel and imaged them using a Bio-Rad Transilluminator with Bio-Rad Quantity One version 4.1.1 Geldoc software (Bio-Rad, Hercules, California, USA) or a Vilber Lourmat TF-20M Transilluminator (Vilber Lourmat, Marne-la-Vallée, France) to determine their concentrations for cloning (in the case of the nDNA regions) and sequencing. We enzymatically cleaned the non-ITS and a few ITS PCR products produced for sequencing with the ExoSAP-IT protocol (Qiagen) following the manufacturer's instructions. We cleaned the majority of ITS PCR products using Wizard DNA Clean-up or PCR Preps Systems (Promega) using the manufacturer's instructions.

We cloned two PCR products that represented three nDNA regions. We amplified *waxy 1* and *2* in the same PCR, and then identified the locus inserted in each plasmid of screened colonies as locus *1* or *2* using the diagnostic PCR reaction described in Mast et al. (2005). We cloned PCR product for the *PHYA* and *waxy* regions with a TOPO TA cloning kit (Invitrogen), PCR 2.1 Topo vector, and One Shot TOP 10 chemically competent *E. coli* following manufacturer's instructions. We spread 38 μL of X-gal (20 ng/μL, 760 ng) on Luria–Bertani agar plates supplemented with ampicillin (100 μg/mL) prior to plating the cells on the agar. The culture plates incubated at 37°C overnight for 14–16 h. We picked cells from two colonies per plate for *PHYA* and five colonies per plate for *waxy* and transferred the cells to PCR reagents that included the m13F and m13R primers (Invitrogen; located on the plasmid adjacent to the point of insertion of the original PCR product). We enzymatically cleaned one *PHYA* insert, one *waxy 1* insert, and one *waxy 2* insert of the correct size for sequencing.

The Florida State University's Department of Biological Science DNA sequencing facility prepared the cycle-sequencing reactions for the non-ITS and a few of the ITS amplifications with the ABI PRISM Big Dye Terminators v3.1 Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, California, USA). The primers that the facility used to sequence *matK*, *atpB*, and the 2 *waxy* genes are the same as those used in Mast et al. (2005). The facility used the same primers that we used for the initial amplification of *ndhF* to sequence that product, and it used the m13F and m13R primers to sequence the cloned *PHYA* product. The facility precipitated each sequenced product in ethanol and EDTA to remove excess dye terminators before running each sequence on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems). We cycle sequenced the majority of the ITS amplifications using the ABI PrismTM DyeDeoxy Cycle Sequencing System (Applied Biosystems) using the same primers for sequencing as were used in Barker et al. (2002). We sent these reactions to the Sydney University and Prince Alfred Molecular Analysis Centre and Westmead Hospital for electrophoresis on an ABI 373 or 377 (Applied Biosystems). To detect mistakes and correct any uncertainties in the computer-generated sequence, we compared aligned trace-files in Sequencher versions 4.6 and earlier (Gene Codes, Ann Arbor, Michigan, USA).

Defining substitution characters—To determine the boundaries of each region, we compared the cpDNA sequences to the complete cpDNA sequence of *Nicotiana tabacum* L. (GenBank accession NC 001879), the *waxy* sequences to the complete *waxy* sequence of *Solanum tuberosum* L. (GenBank accession X58453), and the ITS sequences to the annotated sequences in Baldwin (1992). We aligned the coding regions to maintain the reading frame when the indels were in multiples of 3. We imported the aligned sequence data sets into the program PAUP* version 4.0b10 (Swofford, 2003) where they were formatted in the NEXUS format for phylogenetic inference in PAUP* and MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003).

Coding morphological characters—We coded the morphological characters using the literature and specimens. Important literature sources included Bosser and Rabevohitra (1991), Cooper and Cooper (2004), Douglas (1996), Douglas and Tucker (1996a, b), George (1981), Johnson and Briggs (1963, 1975), flora treatments in McCarthy (1995), McDonald and Ismail (1995), Makinson (2000), Prance et al. (2007), Sleumer (1955a,b), Smith and Haas (1975), Van Steenis (1952), Strohschen (1986a, b), Venkata Rao (1971), Virot (1968), De Vogel (1980), and Weston (2006). Specimens that served as sources for morphological data are given in Appendix 2. PAUP* calculated the consistency index (CI; the minimum number of state changes divided by the observed number of state changes on the tree; Kluge and Farris, 1969) for each character on the tree inferred with the combined molecular and morphological data. This tree does not include all of the taxa for which morphological data were coded because some of these are not represented in the molecular data sets.

Inference of phylogeny—We used the Akaike information criterion (AIC) in MrModelTest version 1.1b (available from J. A. A. Nylander, Uppsala University, Uppsala, Sweden) to select an adequately parameter-rich model of nucleotide substitution for each of the DNA regions. For the morphological data, we used the standard discrete model of MrBayes 3.1.2—a model based on the ideas of Lewis (2001). These models were then used for their respective partitions in the Bayesian analyses in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). We unlinked the sampling of state frequencies, substitution rates, the gamma shape parameter, and the proportion of invariant sites for each DNA partition; we linked branch lengths. MrBayes 3.1.2 spawns two Markov chain Monte Carlo (MCMC) runs, and we ran each for 5×10^6 generations (most runs) or 50×10^6 generations (only when all data were combined, sampling every 1000th generation. We determined that a burn-in of 1.25×10^6 generations was sufficient to get the average standard deviation of split frequencies below 0.01 (a threshold recommended by the authors of MrBayes) for the two runs of each analysis run to 5×10^6 generations. These numbers of MCMC generations also resulted in potential scale reduction factors (Gelman and Rubin, 1992) for all parameters within at least 2 units of 1 (typically within 0.1 of 1), as determined in MrBayes. We constructed a majority-rule consensus of the trees sampled after the burn-in period in PAUP* 4.0b10 (Swofford, 2003) to produce a tree where the posterior probabilities were ≥95% for internal nodes. When the majority rule consensus trees differed between the two runs in the number of branches resolved, the less resolved tree is presented and discussed. We inferred the phylogeny with each DNA region individually, with the three cpDNA regions combined, with the six non-ITS DNA regions combined, with the morphological data alone, and with the seven DNA regions and the morphological data combined.

We also used PAUP* 4.0b10 (Swofford, 2003) to do parsimony bootstrapping of each data set individually and in the combinations mentioned and to find the most parsimonious trees for the morphological data. PAUP* searched for the most parsimonious trees for the original morphological data and for the resampled data using a full heuristic search, tree-bisection-reconnection branch swapping, 10 random addition replicates, and, for the bootstrapping only, the maximum number of saved trees set at 10 000. The frequency that branches appeared in most parsimonious trees of resampled data were calculated from 100 replicates.

Inference of the origin of disjunctions—We used two optimization methods to determine where biogeographic disjunctions arose on the phylogeny. The first, Fitch parsimony (i.e., unordered parsimony), is a method that minimizes dispersal events among regions and does not reconstruct widespread ancestral lineages that would imply the maintenance of genetic interchange across multiple areas (and water barriers, if the interchange comes at a time when the areas are separated by these). We interpret the inferred dispersal events to cooccur with cladogenetic events, because inferring these to occur along the branches implies additional events (subsequent extinction of each source population's lineage on the original continent). The Ancestral State Reconstruction Packages version 1.06 (Maddison and Maddison, 2005) in Mesquite version 2.0 build i71 (Maddison and Maddison, 2007) inferred dispersal events on the tree. The second method that we used to determine where biogeographic disjunctions might have occurred is dispersal–vicariance analysis (DIVA; Ronquist, 1997). This method permits widespread ancestors and infers them prior to vicariance events to explain allopatric daughter lineages. The software DIVA version 1.1a (Ronquist, 1997) inferred dispersal and vicariance events using this method. We treated South and Central America as one area, given the young age of the Isthmus of Panama (ca. 3 Ma; Coates and Obando, 1996) and thus its inability to play a part in dispersal scenarios over most of the timeframe considered here. *Panopsis*, the genus found in Central America, is more diverse in South America and has only two (of 25) species endemic to Central America. We used the tree inferred with the seven DNA regions and the morphological data for the biogeographic reconstructions.

Inference of ancestral states and test of correlations between morphological change and the origin of disjunctions—We used two optimization methods to determine where morphological characters changed state on the phylogeny. The Ancestral State Reconstruction Packages for Mesquite (Maddison and Maddison, 2005) in Mesquite (Maddison and Maddison, 2007) inferred character state changes using Fitch parsimony on the tree topology inferred with the seven DNA regions and the morphological data. We explored the alternative resolutions of polytomies, when the alternative resolutions could affect the results. The Ancestral State Reconstruction Packages also calculated the proportional likelihood of the data with alternative states at each node on the chronogram inferred with the six non-ITS DNA regions. We had Mesquite use a one-parameter model of equal gain and loss (Lewis, 2001), unless the asymmetrical two-parameter model of gain and loss resulted in a significantly better likelihood, as determined using a likelihood ratio test (Goldman, 1993) with one degree of freedom. We compared the proportional likelihoods for the data with alternative states at each node using a threshold of significance set at 2, equivalent to the threshold of a log likelihood ratio of 7.4:1 advocated by Edwards (1972).

We determined the statistical significance of correlations between the origins of disjunctions and the following diaspore characters: lateral position of the conflorescence (cauliflorous or not; a modified version of character 16), exocarp color (red or not; a modified version of 41), fruit dehiscence (42), outer

mesocarp texture (43), inner mesocarp texture (45), testa thickness and texture (50), and seed wing (present or not; a modified version of 51). The Correl Package version 0.1 (Midford and Maddison, 2006) in Mesquite calculated the statistical significance of correlations between dispersal events and each of these characters, in turn, on the chronogram inferred with the six non-ITS DNA regions. The Correl Package is an implementation of the likelihood method proposed by Pagel (1994). Correl calculated each *p*-value using 1000 simulations and the likelihoods using 10 iterations. For the purpose of this analysis the distribution of the extant species were coded as in Australia or not. This modification and those noted for characters 41 and 51 make characters with >2 states binary, so that the analysis can be performed. The modification of character 16 reduces the number of uncertainties for that character.

Inference of ages—We used Thorne's Bayesian method (Thorne et al., 1998; Thorne and Kishino, 2002) to infer the age of divergence events using the six non-ITS DNA regions. Thorne's approach, like the nonparametric rate smoothing and penalized likelihood approaches of Sanderson (1997, 2002), relaxes the assumption of a constant rate of nucleotide substitution over time by modeling rate change with temporal autocorrelation (Gillespie, 1991). The rate in each branch is drawn from a lognormal distribution with a mean equal to the rate of its parent branch and a variance equal to the time between the midpoints of the two branches multiplied by a rate change parameter, ν (Thorne et al., 1998). Setting ν to 0 assumes constant rate change (i.e., a molecular clock). The method requires the user to specify a prior distribution for the rate at the root node, since this node does not have a parent branch. We explored the robustness of our results to alternative prior distributions for ν (described by brownmean and brownsd) and the rate at the root node (described by rtrate and rtratesd), as described later.

Yang's (1997) baseml program in PAML version 3.13 generated estimates of parameters for the F84 nucleotide substitution model (Felsenstein, 1984) with a discretized gamma approximation of rate variation among sites for each of the six regions, in turn, using the tree topology inferred for the respective region. Thorne's estbranches program estimated branch lengths and a variance-covariance matrix of branch lengths for each of the six regions, in turn, using the parameter values estimated in the previous step and the tree topology inferred in the combined analysis of all six regions. Thorne's multidivtime program used a MCMC to approximate the posterior distribution of substitution rates and divergence ages from the branch lengths and variance–covariance matrix generated for each region in the previous step and the tree topology inferred in the combined analysis of all six regions. We ran the MCMC 10^6 generations, sampling every 100th after a quarter (2.5×10^5) of the generations. We ran the MCMC twice for each analysis to determine whether the parameter values appeared to have reached stationarity after the burn-in.

We used a mean of 1.15 for the prior distribution of time separating the most recent common ancestor (MRCA) of the ingroup (for this purpose, the MRCA of Platanaceae and Proteaceae) from the present (rttm). This value is the mean of two age estimates for that node in a broad-scale dating study of the eudicots by Anderson et al. (2005). The standard deviation of this prior distribution (rttsd) was set to 0.15, a span that includes the earliest fossils that can be assigned to the stem of the Platanaceae (described later). We used a mean of 0.039 for the prior distribution of the rate of molecular evolution at the ingroup root node (rtrate). This value is one-half of the median distance between *Platanus* L. and each taxon in the sister group (0.0888), as determined using the uncorrected-*p* parameter in PAUP* 4.0b10 (Swofford, 2003), divided by our prior estimate of time between the root of the ingroup and today (1.15). The standard deviation of this prior distribution (rtratesd) was set to 0.039 (equal to the mean; see Wiegmann et al., 2003 for a justification to making the standard deviation of this prior large relative to the mean). The "bigtime" parameter, a parameter that specifies what we consider to be a maximum age for the ingroup, was set at 1.3. This value is equivalent to 130 Ma, which is older than the first appearance of the eudicots in the fossil record (Magallón et al., 1999). The mean (brownmean) and standard deviation (brownsd) for the Brownian motion constant "nu" were both set to 1.0, as was the prior for the times of the interior nodes given the time of the root, following recommendations made by Thorne in the multidivtime readme file. We left other parameters dealing with proposals in the MCMC at their default values (newk = 0.1, othk = 0.5, thek = 0.5).

We used three constraints in the analyses. The maximum age for the MRCA of Proteaceae and Platanaceae was set at 125 Ma. This age corresponds to the approximate time of appearance in the fossil record of the tricoplate pollen of the eudicots (Magallón et al., 1999), of which Proteales is an early-diverging branch. It has been used elsewhere as a calibration point for the MRCA of the eudicots (e.g., Bell et al., 2005), and we think that this is a conservative approach given the hypotheses to be tested (i.e., more recent divergences falsify them). The minimum age for the MRCA of Proteaceae and Platanaceae was set at 100 Ma. This value is the upper boundary of the Albian (rounded up from 99.6 Ma; Gradstein et al., 2004), the earliest period from which fossil inflorescences have been recovered that can be assigned to Platanaceae (e.g., Crane et al., 1993) using shared derived features (reviewed by Crepet et al., 2004; Anderson et al., 2005). For most analyses, the minimum age for the MRCA of subtribe Gevuininae was set to 34, rounded up from 33.9, the upper boundaries of the Eocene (Gradstein et al., 2004). This age corresponds to a period to which fossils from one of the two clades arising with the basal split in Gevuininae have been assigned using shared derived features (Carpenter and Pole, 1995). We used the occurrence of subtribe Virotiinae in the Oligocene (23–33.9 Ma BP), as determined using the derived surface sculpturing of the inner mesocarp (Rozefelds, 1992; Weston and Barker, 2006) as a means of assessing the veracity of the results.

We explored the sensitivity of the inference of ages to assumptions made in the dating analysis by systematically varying the assumptions in three ways. First, we varied the age constraints by setting the minimum age of the third constraint (for the crown age of subtribe Gevuininae) to the maximum age estimate for the formation in which the fossil was found (Middle Eocene according to Macphail personal communication in Carpenter and Pole, 1995, p. 1108; 49 Ma, rounded from 48.6, Gradstein et al., 2004) and by removing the third constraint altogether. Second, we performed analyses with eight other combinations of rtrate and brownmean values (and the original three age constraints). These were the combinations of the rtrate values of 0.0039, 0.039 (the original value), and 0.39 and the brownmean values of 0.1, 1 (the original value), and 10, with the standard deviation of each prior set equal to the mean. This set of sensitivity tests is modeled after those performed by Wiegmann et al. (2003) and Bell et al. (2005). Third, we incrementally increased the root age prior (rttm), the minimum and maximum age of the root, and the bigtime value by 10 Ma, and made appropriate changes to the mean rate at root node prior (rtrate) and the standard deviation of the rate at the root node prior (rtratesd) using the calculation given earlier. We did not use the Gevuininae constraint for this third sensitivity analysis; all other assumptions were identical to our preferred set of assumptions. This third sensitivity analysis is designed to determine the effect that new fossil discoveries pushing back the age of the eudicots would have on our conclusions. The incremental changes were made over a range of rttm values from 115 Ma (our preferred prior) to 225 Ma (100 Ma before the first appearance of eudicots in the fossil record).

RESULTS

Defining substitution characters—We generated >250 kilobases of aligned data for this study. We describe each DNA region in Table 1. We used 8248 aligned nucleotide positions in total: 7702 in the non-ITS data sets and 546 in the ITS data set. We were unable to locate a colony with a *waxy* locus *1* insert for *Orites megacarpus*, *Macadamia grandis* C.L.Gross & B.Hyland, and *M. ternifolia* F.Muell., and we were unable to amplify the 5′ end of *ndhF* from *O. megacarpus*. We were also unable to amplify any region other than ITS from the DNA of *M. hildebrandii* Steenis. We found the nDNA regions to have higher percentages of informative characters and greater maximum distances within the tribe than the cpDNA regions (Table 1).

Coding morphological characters—We coded 49 taxa for up to 53 morphological characters each. We provide the morphological characters and their character states in Table 2, and we provide the character state data for each of the 49 taxa in Table 3. The percentage of missing data for each taxon ranges from 2 to 55% (mean = 20%; Table 3). The percentage of missing data for each character ranges from 0 to 73% (mean = 20%; Table 3). Characters with >50% missing data either describe a feature that is not present in all taxa (characters 10, 23, 46–49), are impossible to score from herbarium specimens (53), or are difficult to score without special preparations (25; Tables 2, 3). The CI of the characters on the tree inferred with the combined molecular and morphological data ranges from 0.2–1 (Table 3).

TABLE 1. DNA character descriptions. The tribe is considered to include *Orites megacarpus* for these calculations. Distance is calculated using the HKY model of nucleotide substitution (Hasegawa et al., 1985). GTR = general time-reversible model (Tavaré, 1986), G = rate variation across sites modeled with a gamma distribution (Yang, 1994), I = proportion of sites modeled as invariant.

Gene region	Range of sequence lengths	Aligned length	Parsimony informative nt[a] positions (% of aligned positions) within tribe	Greatest sequence distance within tribe	Substitution model selected[b]
matK	1524–1545	1551	94 (6.1%)	0.04048	GTR+G
atpB	1496–1497	1497	24 (1.6%)	0.01409	GTR+I
ndhF	2193–2241	2256	158 (7.0%)	0.05812	GTR+I+G
waxy 1	613–616	616	72 (11.7%)	0.10297	GTR+G
waxy 2	616	616	78 (12.7%)	0.08651	GTR+I+G
PHYA	1124–1166	1166	107 (9.2%)	0.06858	HKY+I+G
ITS1	190–245	274	115 (42.0%)	0.44512	GTR+G
ITS2	233–254	272	115 (42.3%)	0.42442	GTR+G
Total		8248	763 (9.3%)		

[a] nt = nucleotide.
[b] Based on Akaike information criterion.

Some of the characters with >50% missing data have a CI of 1 (characters 10, 23, 25, 46, 53) or are not assigned a CI (48, 49) because they are invariant among the taxa included in both the molecular and morphological data sets. Other characters with less missing data have a CI of 1 and form a synapomorphy for a genus (character 7 for *Kermadecia*; character 38 for *Heliciopsis*) or for a subtribe (9 for *Gevuininae*; Tables 2, 3). Some of the characters with lower consistency indices will be discussed later in the context of the correlations between their evolution and dispersal of the lineage; others will be discussed in the context of congruence between molecular and morphological data.

Inference of phylogeny—We provide the models chosen as adequately parameter-rich for each data set in Table 1. The topologies of the 95% majority rule consensus trees generated for trees sampled after the burn-ins of each MCMC (two are spawned to run in parallel by MrBayes) were identical in the branches resolved, and the posterior probabilities of the internal nodes did not differ by >1% when rounded to the nearest percent. Figure 3 displays the 95% majority rule consensus of trees sampled after the burn-in (i.e., those branches with ≥95% posterior probability) for each cpDNA and nDNA region, the three cpDNA regions combined, and all six non-ITS regions combined. Figure 4 displays the 95% majority rule consensus of trees sampled after the burn-in for the ITS data alone, the morphological data alone, and the combined DNA and morphological data. Figure 4 also displays the strict consensus of the most parsimonious trees found for the morphological data.

With a few exceptions (indicated with less-than symbols), branches shown in Figs. 3 and 4 with ≥95% posterior probability (PP) had parsimony bootstrap frequencies ≥70% (a commonly used cut-off). Eight branches had parsimony bootstrap frequencies between 50 and 70% (denoted with "<"), and five had parsimony bootstrap frequencies <50% (denoted with "<<"). Conversely, four branches in the tribe had parsimony bootstrap frequencies ≥70%, but did not have PP ≥95%. A sister relationship between *Heliciopsis* and *Athertonia* is supported by bootstrap frequencies ≥ 70% (but PP ≤ 95%) in three analyses (*PHYA* alone, six non-ITS regions combined, and all data combined, in which the relationship had a PP of 90%, 89%, and 92%, respectively). A sister relationship between *Macadamia hildebrandii* and *M. claudiensis* C.L.Gross & B.Hyland is supported by a bootstrap frequency ≥70%, but a PP of only 85% in the analysis of all data in combination.

The tree inferred using the six non-ITS DNA regions in combination (Fig. 3) is well resolved, with just two points at which it is not bifurcating: a trichotomy in subtribe Virotiinae and a trichotomy in subtribe Gevuininae. Within the tribe, there is just one point of conflict between the branches resolved with ≥95% posterior probability in this tree and those resolved with ≥95% posterior probability with any DNA region individually (in the position of *M. whelanii* Bailey in the *matK* results; Fig. 3). A second point of conflict between the tree resolved with all six non-ITS DNA regions in combination and those generated with the data sets separately occurs among the extratribal taxa (in the position of *Lambertia* in the *PHYA* results). The tree inferred using the six non-ITS DNA regions in combination resolves a paraphyletic tribe Macadamieae and subtribe Macadamiinae with respect to *O. megacarpus*. Each of the other three subtribes is resolved as monophyletic. *Floydia*, *Lambertia*, and *Roupala*—the three genera that Johnson and Briggs (1975) considered to be included in tribe Macadamieae, but which Weston and Barker (2006) excluded from it—are more closely related to other extratribal taxa than to the taxa considered by Weston and Barker (2006) to be in the tribe. *Cardwellia*—the genus that Johnson and Briggs (1975) excluded from tribe Macadamieae, but which Weston and Barker (2006) included in it—is most closely related to other genera that Weston and Barker (2006) included in subtribe Gevuininae. The tree inferred using the six non-ITS DNA regions in combination also resolves a paraphyletic *Macadamia* with respect to *O. megacarpus*, *Brabejum*, and *Panopsis*. That result is seen in the separate analysis of half of the six DNA regions (all of the cpDNA regions); the results from the separate analysis of the nuclear DNA regions neither conflict with, nor support, the paraphyly of *Macadamia* with respect to those other taxa.

The tree inferred using the ITS data (Fig. 4) also resolves a paraphyletic tribe Macadamieae and subtribe Macadamiinae with respect to *O. megacarpus*. The two samples of that species are resolved as sisters in the ITS tree. Each of the other three subtribes are again resolved to be monophyletic. Four of the five genera from which multiple species were sampled (*Panopsis*, *Virotia*, *Kermadecia*, and *Euplassa*) are also resolved as monophyletic in the tree. The fifth genus, *Macadamia*, is resolved as two clades in a polytomy with *Brabejum* and a clade of *Panopsis* and *O. megacarpus*.

The tree inferred from the morphological data using the Bayesian approach contains just two branches with PP ≥95% (Fig. 4): one subtending a polytomy composed of *Macadamia*

TABLE 2. Characters and their corresponding states used in this study. F2 and F3 phases of leaf ontogeny (referenced in characters 8–12) are described by Johnson and Briggs (1975).

Number	Character	Character States
1	Hypocotyl	Extending at germination (0), vestigial (1)
2	Cotyledon indumentum	Absent (0), present (1)
3	Cotyledon coloration	Green (0), green with purple streaks (1), green above and purple below (2), purple on both surfaces (3)
4	First foliar organs following cotyledons	Foliage leaves (0), scale leaves (1)
5	Phyllotaxis of first foliar organs after cotyledons	Opposite (0), alternate (1)
6	Morphology of first foliage leaf	Unlobed (0), with three lobes (1), with > three lobes (2)
7	Peltate juvenile leaves	Absent (0), present (1)
8	F2 (dissected to compound) leaf phase	Present (0), absent (1)
9	Morphology of F2 leaf phase	Simple and lobed (0), simple and lobed then becoming compound (1), compound (2)
10	Rachis of compound F2 leaves	Not winged (0), winged (1)
11	Terminal lobe or leaflet of F2 leaves	Developed (leaves paripinnate) (0), suppressed (leaves paripinnate) (1)
12	F3 (adult simple, unlobed) leaf phase	Present (0), absent (1)
13	Phyllotaxis of adult foliage leaves	Alternate (0), opposite (1), whorled (2)
14	Marginal leaf teeth	Present throughout ontogeny (0), present then becoming absent (1), absent throughout ontogeny (2)
15	Conflorescence position	Lateral (0), terminal and lateral (1), terminal (2)
16	Lateral conflorescence position	Axillary to ramiflorous (0), cauliflorous (1)
17	Conflorescence form	Branched (0), simple and branched (1), simple (2)
18	Direction of anthesis in unit conflorescence	Acropetal (0), "telopetal" (from the middle towards the base and tip) (1), simultaneous/sporadic (2)
19	Shape of flower pair bracts	Narrowing from the base (triangular) or oblong (0), widening from the base (obovate to oblanceolate to ovate) (1), broadly two-lobed (2)
20	Common peduncle of flower pair	Present (0), absent (1)
21	Pedicels	Present (0), absent (1)
22	Floral bracts	Present (0), absent (1)
23	Floral bract position	Inserted at base of pedicels (0), decurrent on pedicels (1)
24	Receptacle form	Radially symmetrical (0), lower on anterior side of flower (1)
25	Gynoecial orientation	Adaxial (0); abaxial (1); mixed adaxial-lateral and lateri-axial in the same inflorescence (2); abaxial-lateral (3); adaxial-lateral (4); mixed lateri-axial, adaxial-lateral, and abaxial-lateral (5); distal abaxial-lateral (6)
26	Perianth symmetry	Radially symmetrical (0), curved towards anterior (1)
27	Posterior tepal curvature	Recurved like other tepals (0), erect (1)
28	Anthocyanin pigments in tepals	Absent (0), present (1)
29	Staminal filament adnation	Adnate to subtending tepal except at free distal tip (0), adnate to subtending tepal in basal half but otherwise free (1), free (2)
30	Hypogynous gland connation	Free (0), connate on anterior side of flower and absent on posterior side (1), connate and forming a ring (2)
31	Posterior hypogynous glands	Present (0), absent (1)
32	Ovary indumentum	Glabrous (0), hairy (1)
33	Style protrusion in bud	Not protruding from perianth in bud (0), hairpin bend of style protruding from between perianth segments in late bud (1), style protruding from perianth in bud in a broad arc (2)
34	Style curvature	Straight (0), curved to anterior (1), curved in abaxial-lateral direction (2)
35	Pollen presenter symmetry	Straight (0), oblique (1)
36	Ovule number	Numerous (0), two (1)
37	Ovule morphology	Hemitropous (0), orthotropous (1)
38	Sexuality	Bisexual (0), dioecious (1)
39	Fruit shape in lateral view	Elliptical (0), orbicular (1), obovate (2), beaked obovate (3), ovate (4), ±oblong with 90 degree bend at base (5), horned ovate (6)
40	Fruit shape in transverse section	Circular (0), elliptical (1)
41	Exocarp color at maturity	Grey (0), brown (1), black (2), red (3), purple (4), green (5), bronze (6)
42	Fruit dehiscence	Dehiscing at maturity (0), dehiscing on germination (1)
43	Outer mesocarp texture	Dry (leathery to woody) (0), succulent (1)
44	Outer mesocarp vasculature	With prominent radiating vascular bundles (0), lacking prominent radiating vascular bundles (1)
45	Inner mesocarp texture	Leathery (0), strongly lignified and bony (1)
46	Surface sculpture of bony inner mesocarp	Smooth (0), reticulate (1)
47	Bony inner mesocarp dorsiventral keels	Not keeled (0), keeled along dorsal and ventral sides (1)
48	Bony inner mesocarp lateral keels	Not keeled (0), keeled along lateral sides (1)
49	Bony inner mesocarp notch	Not notched (0), notched at distal end (1)
50	Testa thickness and texture	Chartaceous (0), bony (1)
51	Seed wing	Present and surrounding the embryo (0), present and terminal (1), absent (2)
52	Cotyledon shape in transverse section	Laminar (cotyledon flat and leaf-like) (0), semi-elliptical (cotyledon fleshy) (1), semi-circular (cotyledon fleshy) (2)
53	Chromosome number	14 (0), 13 (1)

tetraphylla, *M. ternifolia*, *M. integrifolia*, and *M. jansenii* C.L.Gross & P.H.Weston and one subtending a polytomy composed of *Kermadecia sinuata* Brongn. & Gris, *K. elliptica* Brongn. & Gris, and *K. rotundifolia* Brongn. & Gris. The tree inferred from the morphological data using a parsimony approach has three branches with ≥70% bootstrap frequencies (Fig. 4): the two branches with PP ≥95% and that resolving a sister relationship between *Euplassa inaequalis* Engl. and *E. duquei* Killip & Cuatrec. The genera *Heliciopsis* and *Virotia* are each resolved as monophyletic in the strict consensus of the most parsimonious trees, but with only 64% and <50% bootstrap support, respectively. *Floydia*—a genus that Johnson and Briggs (1975) considered to be included in tribe Macadamieae, but which Weston and Barker (2006) excluded from it—is resolved to be closely related to some members of the tribe in parsimony analysis, but with <50% bootstrap support.

The tree inferred using all seven of the DNA regions in combination with the morphological data (Fig. 4) is congruent with the trees resolved for the six non-ITS DNA regions in combination (Fig. 3) and the ITS data alone (Fig. 4). The two polytomies within the tribe in the combined non-ITS DNA result (noted above) remain unresolved when all data are combined. Three branches with PP ≥95% in the combined data tree have parsimony bootstrap frequencies <50%. Two of these, the sister relationship between *Bleasdalea* and *Hicksbeachia* and the sister relationship between *Banksia* L.f. and many of the other outgroup taxa, had bootstrap frequencies ≥70% in the analysis of the six non-ITS DNA data sets in combination. The third, the sister relationship between *Brabejum* and *O. megacarpus*/*Panopsis*, had a bootstrap frequency between 50 and 70% in that analysis.

Inference of the origin of disjunctions—For the purpose of inferring the origins of geographic disjunctions and state shifts in morphological characters, we resolved two of the three trichotomies in the tree inferred using the combined molecular and morphological data (Fig. 4) in just one way. We resolved *Heliciopsis* and *Athertonia* as sister to one another, as supported by a bootstrap frequency of 81% and PP of 92% in analyses of the combined molecular and morphological data, and *M. hildebrandii* and *M. claudiensis* as sister, as supported by a bootstrap frequency of 70% and a PP of 85% in those same analyses. The final trichotomy within the tribe (that in subtribe Gevuininae) is not resolved with a PP >50% or bootstrap support ≥70% in analyses of the combined molecular and morphological data. Its resolution is relevant to the reconstruction of ancestral geographic distributions but not relevant to the ancestral states that we discuss in the next section.

Fitch parsimony and DIVA resolve geographic disjunctions arising at identical nodes, and because our dating analysis infers all but one of these nodes to be younger than the last continental connections between the landmasses involved, we discuss the Fitch parsimony results (a dispersalist approach) at greater length here. Fitch parsimony reconstruction of ancestral geographic distributions infers a distribution in Australia for the MRCA of tribe Macadamieae and the MRCA of each subtribe, with subsequent dispersals from Australia (Fig. 5A). In subtribe Macadamiinae, dispersal events from Australia to Sulawesi, South America, and Africa led to the origins of *M. hildebrandii* (and presumably *M. erecta* J.A.McDonald & Ismail R.), *Panopsis*, and *Brabejum*, respectively. In subtribe Malagasiinae, a dispersal event from Australia to Madagascar led to *Malagasia*. In subtribe Virotiinae, dispersal events from Australia to New Caledonia and Southeast Asia led to *Virotia* and *Heliciopsis*, respectively. The trichotomy in subtribe Gevuininae complicates the interpretation of inferred ancestral distributions and dispersal events. The inference is unambiguous in resolving dispersal events from Australia to New Guinea in *Bleasdalea* and from New Caledonia to Fiji and Vanuatu in the ancestors of *Turrillia*. However, explanation of the remaining disjunctions in the subtribe depends on resolution of the trichotomy (Fig. 5B). If *Gevuina* is later resolved as sister to *Euplassa* and relatives, then dispersal from Australia to South America with a subsequent dispersal to New Caledonia is most parsimonious. However, if the trichotomy is resolved in one of the other two possible ways, then two scenarios are equally parsimonious. In the one, there is an early dispersal to South America (at node 9; Fig. 6), with a dispersal back to Australia leading to *Bleasdalea* and *Hicksbeachia*; in the other, there are two later dispersals to South America leading to *Gevuina* and *Euplassa* and relatives (Fig. 5B). With these exceptions in subtribe Gevuininae, Fitch parsimony infers that all of the expansions of the tribe's range occurred as a result of dispersal out of Australia. Nodes at which disjunctions are inferred to occur (or the earliest node at which they could occur, in the case of the polytomies) are labeled 1–9 in Fig. 6.

In the DIVA results, the MRCAs of tribe Macadamieae and subtribe Macadamiinae are inferred to have occupied Australia, as is the MRCA of subtribes Malagasiinae and Virotiinae. A vicariance event is inferred to have occurred at each of nodes 2–7 (actually, at each of the two nodes in the resolution of the trichotomy at node 5) and at none of the other nodes in subtribes Macadamiinae, Malagasiinae, and Virotiinae. The inference of vicariance events in subtribe Gevuininae, like the inference of dispersal events, depends upon the resolution of that subtribe's trichotomy. If *Hicksbeachia* and *Bleasdalea* are resolved as sister to a clade composed of the other two clades in the trichotomy (resolution 1 in Fig. 5B), then the MRCA of the subtribe is inferred to have occupied Australia with a later dispersal to South America followed by a vicariance event (i.e., a later arrival in South America). If one of the other two resolutions are instead made (resolutions 2 or 3), then this later arrival in South America scenario is equally parsimonious with one in which an early dispersal to South America is followed by a vicariance event at node 9. Thus, these two biogeographic inference methods resolve biogeographic disjunctions in the group to have arisen at the same nodes (1–9).

Inference of ancestral states and test of correlations between morphological change and the origin of disjunctions—Of the diaspore characters examined, three are significantly correlated with dispersals in the tribe at a threshold of $P = 0.05$, as determined using Midford and Maddison's (2006) implementation of Pagel's (1994) test of correlations between discrete characters. These three characters are fruit dehiscence at maturity vs. germination (character 42; $P = 0.002$), outer mesocarp texture dry vs. succulent (43; $P = 0.022$), and inner mesocarp texture leathery vs. strongly lignified and bony (45; $P = 0.027$; Fig. 5A). In the case of the first character, Fitch parsimony infers 4–5 state changes to later dehiscence (at germination) immediately preceding, or potentially co-occurring with, dispersal events to result in later dehiscence in every extra-Australian genus. Correl (Midford and Maddison 2006) calculated an instantaneous transition rate of 24.199 for dispersal from Australia when dehiscence occurs at germination compared to a rate of 0.282 for dispersal from Australia when dehiscence occurs at fruit maturity. In the case of the second character,

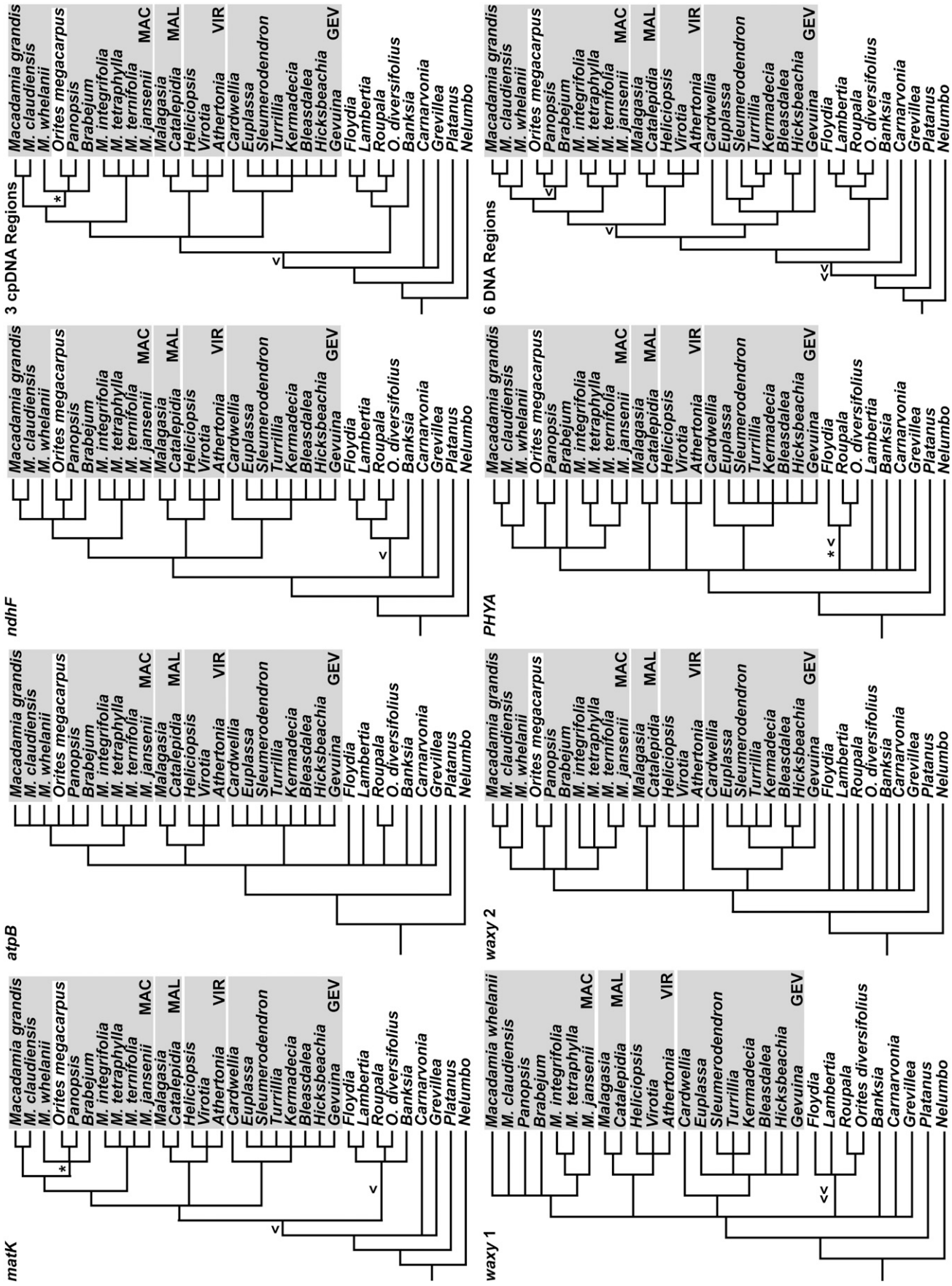
TABLE 3. Character state codings for 49 taxa. The consistency index is calculated on the tree inferred with the combined molecular and morphological data; that tree does not include all of the taxa given here. Percentage of taxa coded with "?" for each character ("% ?" as row) and percentage of characters coded with "?" for each taxon ("% ?" as column) given. Character and character state numbering corresponds to that used in Table 2.

		Character number																																																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Consistency index		0.2	0.5	0.7	0.3	0.2	0.5	1	0.2	1	1	0.3	0.2	0.3	0.2	0.2	1	0.3	0.3	0.4	0.3	0.2	0.3	1	0.3	1	0.3	0.3	0.2	0.3	0.3	0.3	0.2	0.4	0.5	0.3	1	0.3	1	0.5	0.2	0.6	0.2	0.3	0.3	0.3	1	0.5	-	-	0.3	0.3	0.3	1
	%?	39	37	41	39	39	39	22	10	49	69	49	0	0	10	0	10	0	33	12	2	0	0	73	0	65	0	2	0	0	2	2	0	0	0	2	0	0	0	8	8	20	12	6	20	10	53	55	55	55	12	12	14	69
Taxon																																																						
Mac. grandis	30	?	?	?	?	?	?	0	1	?	?	?	0	2	2	1	0	0	0	0	1	0	1	?	0	?	0	0	0	1	2	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0	?	?	?	?	1	2	2	?
Mac. claudiensis	21	1	0	0	1	1	0	0	1	?	?	?	0	2	2	1	0	0	?	0	1	0	1	?	0	?	0	0	0	0	2	0	1	1	0	0	1	1	0	1	0	1/5	0	0	0	0	?	?	?	?	0	2	2	?
Mac. whelanii	30	?	?	?	?	?	?	0	1	?	?	?	0	2	1	1	0	0	0	0	1	0	1	?	0	?	0	0	0	1	2	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	?	?	?	?	1	2	2	?
Mac. integrifolia	17	1	0	0	1	1	0	0	1	?	?	?	0	2	1	0	0	2	1	?	1	0	1	?	0	2	0	0	0	0	2	0	1	1	0	0	1	1	0	1	0	5	0	0	0	0	?	?	?	?	1	2	2	0
Mac. tetraphylla	15	1	0	0	1	1	0	0	1	?	?	?	0	2	0	0	0	2	1	0	1	0	1	?	0	2	0	0	0/1	0	2	0	1	1	0	0	1	1	0	1	0	5	0	0	0	0	?	?	?	?	1	2	2	0
Mac. ternifolia	19	1	0	0	1	1	0	0	1	?	?	?	0	2	0	0	0	2	1	0	1	0	1	?	0	?	0	0	0/1	0	2	0	1	1	0	0	1	1	0	1	0	5	0	0	0	0	?	?	?	?	1	2	2	?
Mac. jansenii	19	1	0	0	1	1	0	0	1	?	?	?	0	2	1	0	0	2	1	0	1	0	1	?	0	?	0	0	1	0	2	0	1	1	0	0	1	1	0	1	0	5	0	0	0	0	?	?	?	?	1	2	2	?
Mac. hildebrandii	49	?	?	?	?	?	?	?	?	?	?	?	0	2	?	1	0	1	0	0	1	0	1	?	0	?	0	0	1	0	2	0	0/1	1	0	0	1	1	0	1	0	?	?	0	?	?	?	?	?	?	?	?	?	?
Mac. erecta	51	?	?	?	?	?	?	?	?	?	?	?	0	2	?	1	0	0	?	0	1	0	1	?	0	?	0	0	0	0	2	0	1	1	0	0	1	1	0	1	0	?	?	0	?	?	?	?	?	?	?	?	?	?
P. cinnamomea	19	1	0	0	1	1	0	0	1	?	?	?	0	0/1	2	1	0	1	0	0	1	0	1	?	0	?	0	0	0	1	2	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	?	?	?	?	0	2	2	?
P. yolombo	34	?	?	?	?	?	?	?	1	?	?	?	0	1	2	1	0	0	0	?	1	0	1	?	0	?	0	0	0	2	2	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	?	?	?	?	0	2	2	?
P. ferruginea	55	?	?	?	?	?	?	?	1	?	?	?	0	0/1	2	2	0	0	?	?	1	0	1	?	0	?	0	0	0	1/2	2	0	1	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. lozanoi	42	?	?	?	?	?	?	?	1	?	?	?	0	0/1	2	2	?	0	0	?	1	0	1	?	0	?	0	0	0	1	2	0	1	0	0	0	1	1	0	1	0	?	?	0	?	0	?	?	?	?	0	2	2	?
P. pearcei	38	?	?	?	?	?	?	?	1	?	?	?	0	0/1	2	1	0	1	?	?	1	0	1	?	0	?	0	0	0	1	2	0	1	0	0	0	1	1	0	1	0	1	1	0	?	0	?	?	?	?	0	2	2	?
Br. stellatifolium	15	1	0	0	1	0	0	0	1	?	?	?	0	2	0	0	0	2	0	1	1	0	1	?	0	2	0	0	0	1	2	0	1	1	0	0	1	1	0	0	0	1	1	0	0	0	?	?	?	?	0	2	2	0
Mal. alticola	30	?	?	?	?	?	?	?	?	?	?	?	0	0	2	0	0	2	?	0	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	?	1	1	?	1	0	0	0	0	0	2	1	?
Cat. heyana	9	1	0	0	1	1	0	0	1	?	?	?	0	0	2	0	0	2	2	0	0	0	0	1	0	?	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	2/3	1	1	1	1	0	0	0	0	0	2	2	?
He. lanceolata	47	?	?	?	?	?	?	?	0	0	?	0	0	0	2	0	0	2	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
He. lobata	21	?	?	?	?	?	?	?	0	0	?	0	0	0	2	0	0	2	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	5	1	1	0	1	1	0	0	0	0	2	1	?
He. velutina	13	1	0	?	0	0	0	0	0	0	?	0	0	0	2	0	0	2	?	0	0/1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	1	1	0	1	1	0	0	0	0	2	?	?
A. diversifolia	4	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	4	1	1	0	1	1	1	0	0	0	2	1	?
V. neurophylla	9	0	0	3	0	0	0	0	1	?	?	?	0	0	2	0	0	2	2	0	0	0	0	0/1	0	?	0	0	0	0	2	0	0	0	0	0	1	1	0	0	1	2	1	1	0	1	1	1	0	0	0	2	1	?
V. leptophylla	4	0	0	2	0	0	1	0	0	0	?	0	0	0	1	1	0	2	2	0	0	0	0	0/1	0	?	0	0	0	0	2	0	0	0	0	0	1	1	0	0	1	2	1	1	0	1	1	1	0	0	0	2	1	1
V. rousselii	23	?	?	?	?	?	?	0	0	0	?	0	0	0	?	0	0	2	?	0	0	0	0	0/1	0	?	0	0	1	0	2	0	0	0	0	0	1	1	0	2	1	2	1	1	0	1	1	?	0	0	0	2	1	?
V. angustifolia	21	0	0	2	?	?	?	0	?	?	?	?	0	0	?	0	0	2	?	0	0	0	0	0/1	0	?	0	0	1	0	2	0	0	0	0	0	1	1	0	3	1	6	1	1	0	1	1	1	0	0	0	2	1	?

TABLE 3. Continued.

		Character number																																																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Consistency index		0.2	0.5	0.7	0.3	0.2	0.5	1	0.2	1	1	0.3	0.2	0.3	0.2	0.2	1	0.3	0.3	0.4	0.3	0.2	0.3	1	0.3	1	0.3	0.3	0.2	0.3	0.3	0.3	0.2	0.4	0.5	0.3	1	0.3	1	0.5	0.2	0.6	0.2	0.3	0.3	0.3	1	0.5	-	-	0.3	0.3	0.3	1
	%?	39	37	41	39	39	39	22	10	49	69	49	0	0	10	0	10	0	33	12	2	0	0	73	0	65	0	2	0	0	2	2	0	0	0	2	0	0	0	8	8	20	12	6	20	10	53	55	55	55	12	12	14	69
V. francii	26	0	0	2	0	0	1	0	?	?	?	?	0	0	1	0	0/1	2	?	0	0	0	0	0/1	0	?	0	0	1	0	2	0	0	0	0	0	1	1	0	0	1	?	1	1	?	1	1	1	?	?	?	?	?	?
V. vieillardii	47	?	?	?	?	?	?	0	0	0	?	0	0	0	?	0	0	2	?	0	0	0	0	0/1	0	?	0	0	0	0	2	0	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Card. sublimis	11	0	0	0	0	0	0	0	0	1	0	1	1	0	2	1	0	0	0	?	0	1	1	?	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	?	?	?	?	0	0	0	0
E. inaequalis	25	?	?	?	?	?	?	?	0	1	0	1	1	0	1	0	0	2	?	0	0	0	1	?	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	?	?	?	1	0	0	1	0	0	0	0	0	2	1	?
E. duquei	8	0	1	1	0	0	0	0	0	1	0	1	1	0	1	0	0	2	?	0	0	0	1	?	0	1	1	?	0	0	0	0	0	0	1	1	1	1	0	4	0	5	1	1	0	1	0	0	0	0	0	2	1	?
S. austrocal.	4	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	2	1	0	0	1	1	?	1	1	1	1	1	0	0	0	1	0	1	1	1	1	0	0	1	2	1	1	0	1	0	0	0	0	0	2	1	?
T. lutea	6	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	2	1	0	0	1	1	?	1	?	0	1	0	0	1	1	0	0	0	0	1	1	0	4	1	2	1	1	0	1	0	0	0	0	0	2	1	?
T. vitiensis	19	?	?	?	?	?	?	?	0	1	0	0/1	0	0	1	0	0	1	1	0	0	1	1	?	1	?	0	1	0	0	1	1	0	0	0	0	1	1	0	2	1	2	1	1	0	1	0	0	0	0	0	2	1	?
T. ferruginea	6	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	2	?	0	0	1	1	?	1	1	1	1	0	0	1	1	0	0	1	1	1	1	0	2	1	2	1	1	0	1	0	0	0	0	0	2	1	?
K. pronyensis	15	?	?	?	?	?	?	1	0	1	0	0	0	0	1	0	0	2	1	2	0	1	1	?	1	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0/1	2	1	1	0	1	0	1	0	0	0	2	1	?
K. elliptica	6	?	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0/1	2	1	2	1	0	1	?	1	?	0	0	0	0	1	1	1	0	0	0	1	1	0	0/2	0/1	2	1	1	1	1	0	1	1	1	0	2	1	0
K. sinuata	4	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0/1	2	1	2	1	0	1	?	1	?	0	0	0	0	1	1	1	0	0	0	1	1	0	2	1	2	1	1	1	1	0	1	1	1	0	2	1	0
K. rotundifolia	19	?	?	?	?	?	?	1	0	1	0	0	0	0	1	1	?	0	1	2	1	0	1	?	1	?	0	0	0	0	1	1	1	0	0	0	1	1	0	0/2	1	2	1	1	1	1	0	1	1	1	0	2	1	?
Bl. bleasdalei	4	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	1	?	1	1	1	1	0	0	1	1	0	0	1	1	1	1	0	1	0	2	1	1	0	1	0	0	0	0	0	2	2	?
Ge. avellana	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	1	1	?	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0	1	0	2	1	1	0	1	0	0	0	0	0	2	2	1
Hi. pinnatifolia	4	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	1	2	1	0	0	0	1	?	0	?	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	3	1	1	0	1	0	0	0	0	0	2	2	1
Ba. serrata	13	0	0	0	0	0	2	0	0	0	?	1	1	0	2	2	?	2	0	1	1	1	0	?	0	3	0	0	0	0	0	0	0	2	2	0	1	0	0	0	1	0	0	0	1	1	?	?	?	?	0	1	0	0
Carn. araliifolia	13	0	0	0	0	0	1	0	0	2	0	0	1	0	0/1	1	0	0	0/1	0	?	0	0	0	0	0	0	0	0	0	?	?	1	0	0	0	1	0	0	5	0	0	0	0	0	0	?	?	?	?	0	1	0	0
F. praealta	15	1	0	0	1	1	0	0	1	?	?	?	0	0	2	0	0	2	0/1	0	0	0	1	?	0	5	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	?	?	?	?	0	2	2	0
Gr. caleyi	17	0	0	?	0	1	2	0	0	0	?	0	1	0	2	2	?	2	0	0	1	0	1	?	1	4	1	0	0	0	1	1	1	1	0	1	1	0	0	0	1	5	0	0	1	0	?	?	?	?	0	2	1	?
L. formosa	17	0	0	0	0	0	0	0	1	?	?	?	0	2	2	2	?	2	2	1	1	1	1	?	0	6	0	0	1	0	2	0	1	0	0	0	1	1	0	6	1	1	0	0	0	1	?	?	?	?	0	0	0	0
O. diversifolius	30	?	?	?	?	?	?	0	1	?	?	?	0	0	1	1	0	2	1	1	1	1	1	?	0	?	0	0	0	0	0	0	1	0	0	?	1	0	0	0	1	0	0	0	1	0	?	?	?	?	0	1	0	0
O. megacarpus	21	0	0	0	0	0/1	0	0	1	?	?	?	0	0	2	1	0	0	?	0	1	0	1	?	0	?	0	0	0	1	2	0	1	0	0	0	1	0	0	2	0	1	0	0	0	0	?	?	?	?	0	1	1	?
R. montana	15	0	0	0	0	0	0/1	0	0	0	?	0	0	0	1	0	0	2	0/1	0	1	0	1	?	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	?	0	?	?	?	?	0	0	0	0

Notes: A. = Athertonia; Ba. = Banksia; Bl. = Bleasdalea; B. = Brabejum; Carn. = Carnarvonia; Card. = Cardwellia; Cat. = Catalepidia; E. = Euplassa; F. = Floydia; Ge. = Gevuina; Gr. = Grevillea; He. = Heliciopsis; Hi. =Hicksbeachia; K. = Kermadecia; L. = Lambertia; Mac. = Macadamia; Mal. = Malagasia; O. = Orites; P. = Panopsis; R. = Roupala; S. austrocal. = Sleumerodendron austrocaledonicum; T = Turrillia; V. = Virotia.


matK
atpB
ndhF
3 cpDNA Regions
waxy 1
waxy 2
PHYA
6 DNA Regions
Macadamia grandis
M. claudiensis
M. whelanii
Orites megacarpus
Panopsis
Brabejum
M. integrifolia
M. tetraphylla
M. ternifolia
M. jansenii
MAC
Malagasia
Catalepidia
MAL
Heliciopsis
Virotia
Athertonia
VIR
Cardwellia
Euplassa
Sleumerodendron
Turrillia
Kermadecia
Bleasdalea
Hicksbeachia
GEV
Gevuina
Floydia
Lambertia
Roupala
O. diversifolius
Banksia
Carnarvonia
Grevillea
Platanus
Nelumbo

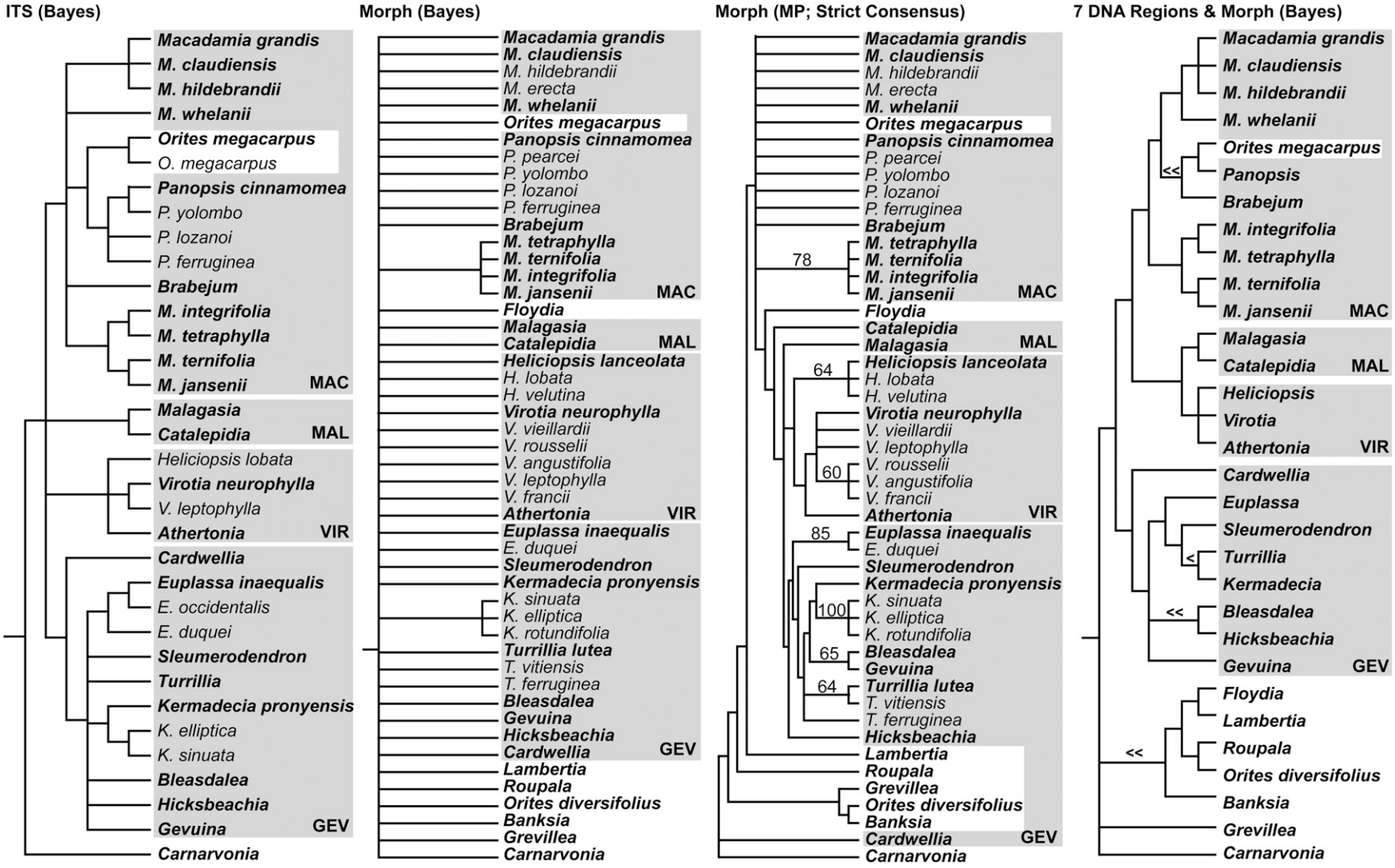
Fitch parsimony infers a state change to a succulent outer mesocarp immediately preceding, or potentially co-occurring with, the dispersal events occurring in subtribes Malagasiinae, Virotiinae, and Gevuininae, but not Macadamiinae (Fig. 5A). The program Correl calculated an instantaneous transition rate of 10.848 for dispersal from Australia when the outer mesocarp is succulent compared to a rate of 2.369 for dispersal from Australia when the outer mesocarp is dry. In the case of the third character, alternative reconstructions are equally parsimonious. A bony mesocarp arose either on the branch leading to the MRCA of the tribe and the outgroup clade that includes *Floydia*, with one loss on the branch leading to the MRCA of subtribe Macadamiinae and two losses within that outgroup clade, or it arose independently on the branches leading to the MRCA of subtribes Malagasiinae and Virotiininae, to the MRCA of subtribe Gevuininae, to *Lambertia*, and to *Banksia*. The latter scenario is similar, though not identical, to the ancestral reconstruction for the outer mesocarp succulence within the ingroup (Fig. 5A). Correl calculated an instantaneous transition rate of 7.343 for dispersal out of Australia when the inner mesocarp is strongly lignified and bony compared to a rate of 2.639 for dispersal out of Australia when the inner mesocarp is leathery. Cauliflory (character 16) is inferred to have arisen three separate times—once in each of *Virotia*, *Kermadecia*, and *Hicksbeachia* (Fig. 1G). The former two genera were recognized as producing typical bat fruits by Weston and Crisp (1996); cauliflory is often associated with bat pollination and/or dispersal (van der Pijl, 1972). Exocarp color (41) is quite labile and is discussed later in the context of synapomorphies. The optimization of testa thickness (50) is ambiguous in Macadamiinae and is also discussed later in the context of synapomorphies. Winged seeds (51) are inferred to have arisen twice in the tribe, in *O. megacarpus* and *Cardwellia* (Fig. 6).

Inference of ancestral states for characters 42, 43, and 45 on the chronogram using a likelihood approach is congruent with Fitch optimization of character state changes on the tree topology inferred using the combined molecular and morphological data. The two-parameter model of gain and loss does not result in a significant improvement in the likelihood of the data as compared to its likelihood with a one-parameter model for any of these characters. The pattern of fruit dehiscence (character 42) in extant taxa has a higher proportional likelihood when the MRCA of tribe Macadamieae is constrained to have fruit that dehisce at maturity (proportional likelihood = 0.785; proportional likelihoods given unless otherwise noted) vs. dehiscing at germination (0.215), though this difference is not statistically significant with the threshold chosen. Dehiscence at the time of maturity at the MRCA of subtribe Macadamiinae and dehiscence at the time of germination at the MRCA's of subtribes Malagasiinae and Virotiinae result in higher proportional likelihoods of the data when those nodes are constrained to have those states in turn (0.915, 0.932, and 0.958, respectively), and these differences are each statistically significant. The data have a statistically significant higher proportional likelihood when the MRCA of all of subtribe Gevuininae except *Cardwellia* is constrained to have dehiscence at the time of germination (0.999). The pattern of outer mesocarp succulence (character 43) in extant taxa has a statistically significant higher proportional likelihood when the MRCA of tribe Macadamieae is constrained to have a dry outer mesocarp (0.971). A dry outer mesocarp at the MRCA of subtribe Macadamiinae and a succulent mesocarp at the MRCAs of subtribes Malagasiinae, Virotiinae, and Gevuininae (minus *Cardwellia*) result in statistically significant higher proportional likelihoods of the data when those nodes are constrained to have those states, in turn (0.999, 0.981, 0.981, and 0.998, respectively). The pattern of inner mesocarp texture (character 45) in extant taxa has a higher proportional likelihood when the MRCA of tribe Macadamieae is constrained to have a strongly lignified and bony inner mesocarp (0.566), but this higher proportional likelihood is not statistically significant. A leathery inner mesocarp at the MRCA of subtribe Macadamiinae and a strongly lignified and bony inner mesocarp at the MRCAs of subtribes Malagasiinae, Virotiinae, and Gevuininae (minus *Cardwellia*) result in statistically significant higher proportional likelihoods of the data when those nodes are constrained to have those states, in turn (0.980, 0.980, 0.981, and 0.999, respectively).

Inference of ages—The mean and 95% credible interval of ages inferred for the 12 focal nodes discussed here varied when we systematically varied the age constraints (Table 4) and the assumed prior probability distributions for rtrate and brownmean (Table 5). However, only in those dispersal scenarios involving node 9—scenarios sensitive to the resolution of a trichotomy, as discussed—did the 95% credible interval for the ages of geographic disjunctions include or predate the last continental connection between the landmasses involved (Tables 4, 5; Fig. 6). Those landmasses, Australia and South America, are thought to have had the most recent continental connections among the fragments of Gondwana (via Antarctica; McLoughlin, 2001). Node 2 is unambiguously resolved to also involve an Australian/South American disjunction (Fig. 5), and the older boundary of the 95% credible interval for the age of that node is 20.8 Ma with our preferred set of prior assumptions (minimum age of MRCA of Gevuininae = 34 Ma, rtrate = 0.039, brownmean = 1.0; Table 4). That older boundary is 26.6 Ma when the minimum age of Gevuininae is increased to 49 Ma (Table 4), and it ranges as high 24.4 Ma when alternative priors for rtrate and brownmean are used with our preferred minimum age of Gevuininae. One of the three possible resolutions of node 8 (Resolution 1) results in the unequivocal inference of an Australian/South American disjunction first arising among the members of that node. However, optimizations on the other two resolutions of the node (2 and 3) resolve that scenario as equally parsimonious with one in which the Australian/South American disjunction arises first between *Cardwellia* and the stem leading to node 8 (node 9). As was found with node 2, none of the alternative assumptions shifted the older boundaries of the 95% credible intervals for the age of node 8 to include 29 Ma (Tables 4, 5). With one exception (when the minimum age constraint

←

Fig. 3. Phylogenies inferred for each of six regions analyzed separately, for the three chloroplast DNA (cpDNA) regions analyzed together, and for all six regions analyzed together. Only branches with 95% posterior probability or greater are shown. The asterisk (*) marks branches that are incongruent with the phylogeny inferred when all six regions were analyzed together. Branches marked with one (<) or two (<<) less-than symbols had bootstrap frequencies of 50–69% and <50%, respectively. All other branches had bootstrap frequencies from 70 to 100%. Previous circumscriptions of subtribes are indicated using the gray boxes and labeled as in Fig. 2.


ITS (Bayes)
Macadamia grandis
M. claudiensis
M. hildebrandii
M. whelanii
Orites megacarpus
O. megacarpus
Panopsis cinnamomea
P. yolombo
P. lozanoi
P. ferruginea
Brabejum
M. integrifolia
M. tetraphylla
M. ternifolia
M. jansenii
MAC
Malagasia
Catalepidia
MAL
Heliciopsis lobata
Virotia neurophylla
V. leptophylla
Athertonia
VIR
Cardwellia
Euplassa inaequalis
E. occidentalis
E. duquei
Sleumerodendron
Turrillia
Kermadecia pronyensis
K. elliptica
K. sinuata
Bleasdalea
Hicksbeachia
Gevuina
GEV
Carnarvonia
Morph (Bayes)
Macadamia grandis
M. claudiensis
M. hildebrandii
M. erecta
M. whelanii
Orites megacarpus
Panopsis cinnamomea
P. pearcei
P. yolombo
P. lozanoi
P. ferruginea
Brabejum
M. tetraphylla
M. ternifolia
M. integrifolia
M. jansenii
MAC
Floydia
Malagasia
Catalepidia
MAL
Heliciopsis lanceolata
H. lobata
H. velutina
Virotia neurophylla
V. vieillardii
V. rousselii
V. angustifolia
V. leptophylla
V. francii
Athertonia
VIR
Euplassa inaequalis
E. duquei
Sleumerodendron
Kermadecia pronyensis
K. sinuata
K. elliptica
K. rotundifolia
Turrillia lutea
T. vitiensis
T. ferruginea
Bleasdalea
Gevuina
Hicksbeachia
Cardwellia
GEV
Lambertia
Roupala
Orites diversifolius
Banksia
Grevillea
Carnarvonia
Morph (MP; Strict Consensus)
78
64
60
85
100
65
64
7 DNA Regions & Morph (Bayes)
<<
<
<<
<<

for subtribe Gevuininae was not used), the 95% credible intervals for the age of node 9 were consistently older than the period during which the latest continental connections between Australia and South America occurred (29–33 Ma BP; Tables 4, 5). The geographic disjunctions involving the earliest fragmentations of Gondwana (those involving Africa and Madagascar) occur at nodes 3 and 4. The older boundary of the 95% credible interval for the age of node 3 (a disjunction between Africa and Australia) is 29.0 Ma with our preferred set of assumptions (Table 4), less than a third of the age of the last continental connection between those two fragments. The older boundary of the 95% credible interval for the age of node 4 is 21.4 Ma with our preferred set of assumptions (Table 4), about a sixth of the age of the last continental connection between those two fragments.

The mean inferred age of the geographic disjunctions that are unambiguously inferred as such (nodes 1–7) with our preferred set of assumptions fall between 8.1 and 23.0 Ma, with the older boundary of the 95% credible intervals falling between 11.9 and 29.0 Ma (Table 4). Increasing the constraint on the minimum age of the MRCA of Gevuininae from 34 to 49 Ma increased the means of geographic disjunctions by just 3.5–6.3 Ma. Removing that constraint entirely reduced the mean ages of those nodes by 1.6–3.3 Ma (Table 4). The mean inferred age of the MRCA of *Macadamia* (node 10) and the MRCA of tribe Macadamieae (node 12; Fig. 6) increased by 8.1 Ma and 12.6 Ma, respectively, with the older constraint on the MRCA of Gevuininae and decreased by 4.3 Ma and 7.1 Ma, respectively, when the Gevuininae constraint was not used (Table 4). The analysis that did not use the MRCA of subtribe Gevuininae as a constraint produced a mean inferred age of 28.9 Ma for that node with a 95% credible interval (21.8–36.7 Ma) that included the preferred, 34 Ma minimum age constraint but not the older 49 Ma age constraint.

The mean inferred age of the geographic disjunctions (nodes 1–9) across alternative priors varied by as much as 4.7 Ma (for node 4) and as little as 1.8 Ma (for node 7; Table 5). The mean inferred age of the MRCA of *Macadamia* and tribe Macadamieae varied by 5.5 Ma and 10.6 Ma, respectively, across the alternative priors. The lowest mean ages for the nodes were inferred using the highest rtrate prior (0.39), the highest mean ages for the nodes was inferred using the lowest rtrate prior (0.0039; Table 5). This result is consistent with the sensitivity analyses of Wiegmann et al. (2003) and Bell et al. (2005).

Incrementally increasing the root age prior (rttm), the minimum and maximum age of the root, and the bigtime value up to values 110 Ma greater than our preferred values resulted in temporal shifts sufficient to include the age of last continental connections in the 95% credible intervals for nodes 2 and 8 (two nodes involved in disjunctions between Australia and South America, or potentially so). The mean inferred age of the other geographic disjunctions did not change enough across these alternative assumptions to change our conclusion regarding their origins. The 95% credible interval for the age of node 2 includes 29 Ma (the last continental connection between Antarctica and South America) when the root age prior (the age of the MRCA of Proteaceae and Platanaceae) is 185 Ma; the 95% credible interval for node 8 includes 29 Ma when the root prior is 215 Ma. The 95% credible interval for the age of node 9 no longer includes 33 Ma (the last continental connection between Antarctica and Australia) when the root age prior ≥175 Ma.

None of the mean or 95% credible intervals for nodes 1–12 differed by >1 Ma between any of the replicate pairs of MCMC analyses done using Multidivtime. All of the 95% credible intervals for the age of the MRCA of Malagasiinae and Virotiinae were older than the upper boundary of the Oligocene (23 Ma BP; Tables 4, 5), and we consider this to be congruent with the Oligocene age of the fossils that share derived sculpturing of the inner mesocarp with extant members of the Virotiinae (Rozefelds, 1992).

DISCUSSION

The monophyly of genera and subtribes—The phylogeny that we reconstruct here for the 16 genera of tribe Macadamieae (Fig. 6) is a major advance in our understanding the group's evolutionary relationships. The most recent prior phylogenetic hypothesis for the tribe (Weston and Barker, 2006) did not resolve relationships among the subtribes or among most genera within the subtribes. The most striking features of these newly resolved relationships are the paraphyly of *Macadamia* and the sister relationship of *Orites megacarpus* with *Panopsis*, rather than with *O. diversifolius* (Fig. 6). In this section, we will focus mainly on molecular and morphological support for these results, insofar as it is necessary to assess the congruence between these two sources of evidence for phylogenetic relationships and to decide which action to take to maintain monophyly at the generic rank. However, we also note that the phylogenetic relationships support the recent assertion (e.g., by Weston and Barker, 2006) that the five New Caledonian species with combinations in *Macadamia* are more closely related to the New Caledonian *Virotia leptophylla* (Figs. 1J, 4) and that *Floydia*, *Lambertia*, and *Roupala* should be excluded from tribe Macadamieae (Weston and Barker, 2006; cf., Johnson and Briggs, 1975; Fig. 6).

As currently circumscribed, *Macadamia* is composed of two clades—one subtropical Australian and one tropical Australian and Sulewesian—that are not each others' closest relatives (Fig. 6). The subtropical clade is composed of four species, including the two widely cultivated for their "nuts" (actually their embryos, *M. integrifolia* and *M. tetrapylla*) and the type species (*M. ternifolia*). These species have narrow distributions that are all found in a short (ca. 500 km) stretch of the eastern Australian coast (Gross, 1995) within, and immediately north of, the McPherson-Macleay area of endemism (Burbidge, 1960; Weston

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Fig. 4. Phylogenies inferred for the two internal transcibed spacers of the nuclear ribosomal DNA (ITS) analyzed together, for the morphological data (Morph), and for the seven DNA regions and morphological data analyzed together. The trees represent the results of Bayesian (Bayes) or parsimony (MP) analyses as indicated. Branches in trees inferred using the Bayesian method have 95% posterior probability or greater. The MP tree is the strict consensus of the most parsimonious trees for the data; bootstrap frequencies (as percentages) greater than 50% are given for that tree. Species in boldface are represented in the data analyzed for Fig. 3; genera in boldface are represented by the same species as they were in the data analyzed for Fig. 3. The MP result for the morphological data is unrooted because it is difficult to justify one position over another in the topology resolved. All the branches resolved in the ITS tree had a bootstrap frequency from 70 to 100%, as did those not marked with less-than symbols in the combined data tree. Less-than symbols are used in the combined data tree as in Fig. 3. Previous circumscriptions of subtribes are indicated using gray boxes and labeled as in Fig. 3.

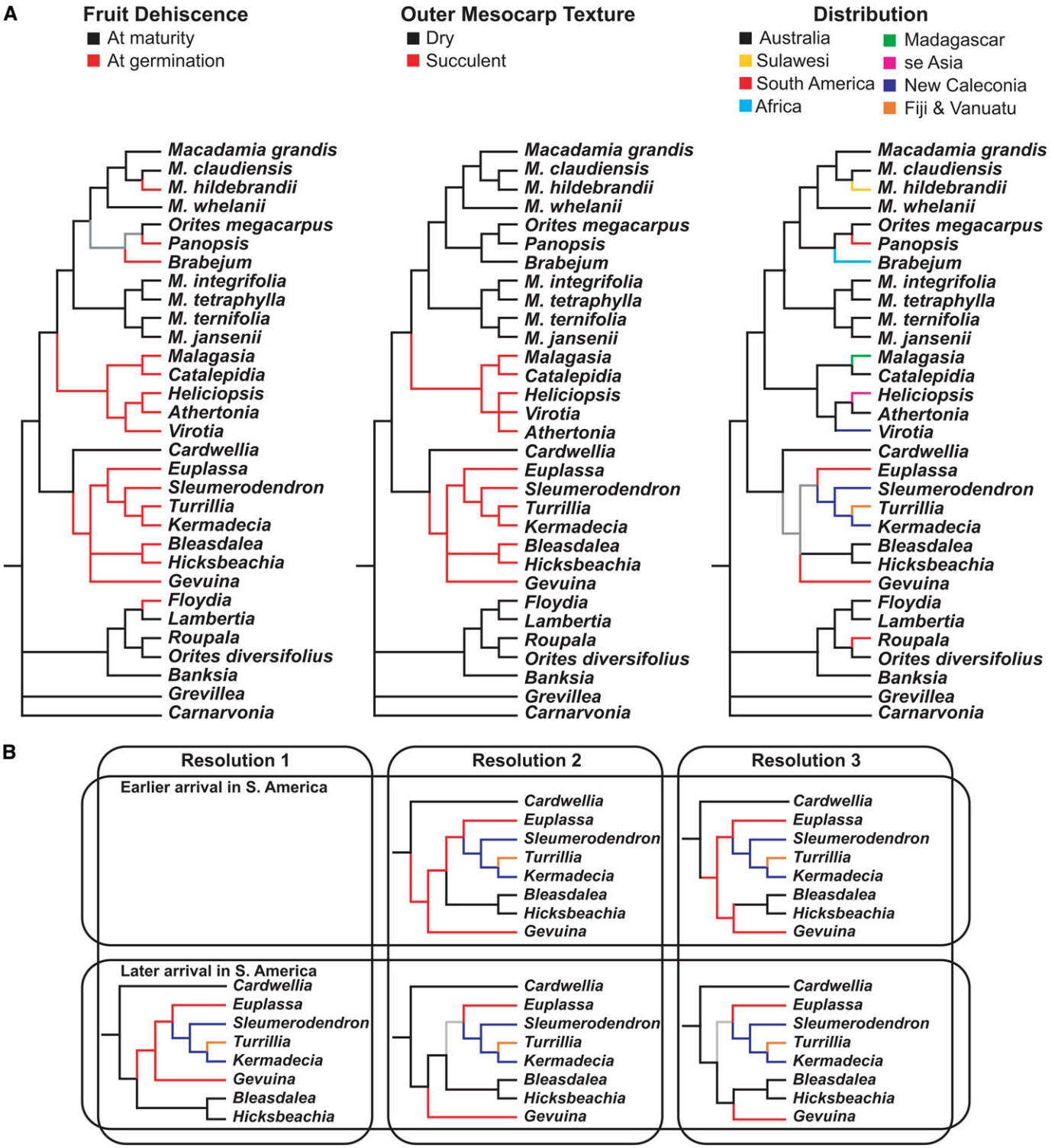


Fig. 5. Reconstructions of ancestral fruit morphologies and dispersal events. (A) Fruit dehiscence, outer mesocarp texture, and distributions are optimized using Fitch parsimony on the tree inferred with the combined DNA and morphological characters. Branches on which multiple states are inferred are gray. (B) The three possible resolutions of the trichotomy in subtribe Gevuininae with the inferred distributions of ancestors. For resolution 1, a single suite of dispersals is most parsimonious. For resolutions 2 and 3, two optimizations are equally parsimonious—one in which an earlier dispersal to South America occurs and one in which later dispersal to South America occurs.

and Crisp, 1994; Crisp et al. 1995). The "McPherson-Macleay overlap" was originally identified by Burbidge (1960) as a region where temperate and tropical Australian "migration tracks" overlap most conspicuously. Many otherwise tropical rainforest taxa have their southern limits of distribution here (e.g., *Macadamia*, *Hicksbeachia*, *Triunia* L.A.S.Johnson & B.G.Briggs, *Alloxylon* P.H.Weston & Crisp, and subtribe Floydiinae in the Proteaceae), and it is the northern limit of distribution of many predominantly temperate, often sclerophyllous taxa (e.g., *Telopea* R.Br., *Strangea* Meisn., and *Isopogon* R.Br. in the Proteaceae). More recently, though, the McPherson-Macleay overlap itself has been viewed as an area of endemism (e.g., Weston and Crisp, 1994; Crisp et al., 1995) that might have developed as such beginning in the early Miocene as mesic biomes contracted into wetter refugia along the eastern coast of Australia in response to the dramatic drying of Australia's climate. The tropical clade is composed of five, narrowly distributed species found in northeast Australia and Sulawesi—a range within ca. 1000 km of the subtropical clade. This tropical clade is not sister to the subtropical clade but to a widespread clade composed of the southern African genus *Brabejum* (1 sp.), the South and Central American genus *Panopsis* (25 spp.), and an Australian species not previously considered a part of tribe Macadamieae, *O. megacarpus.*

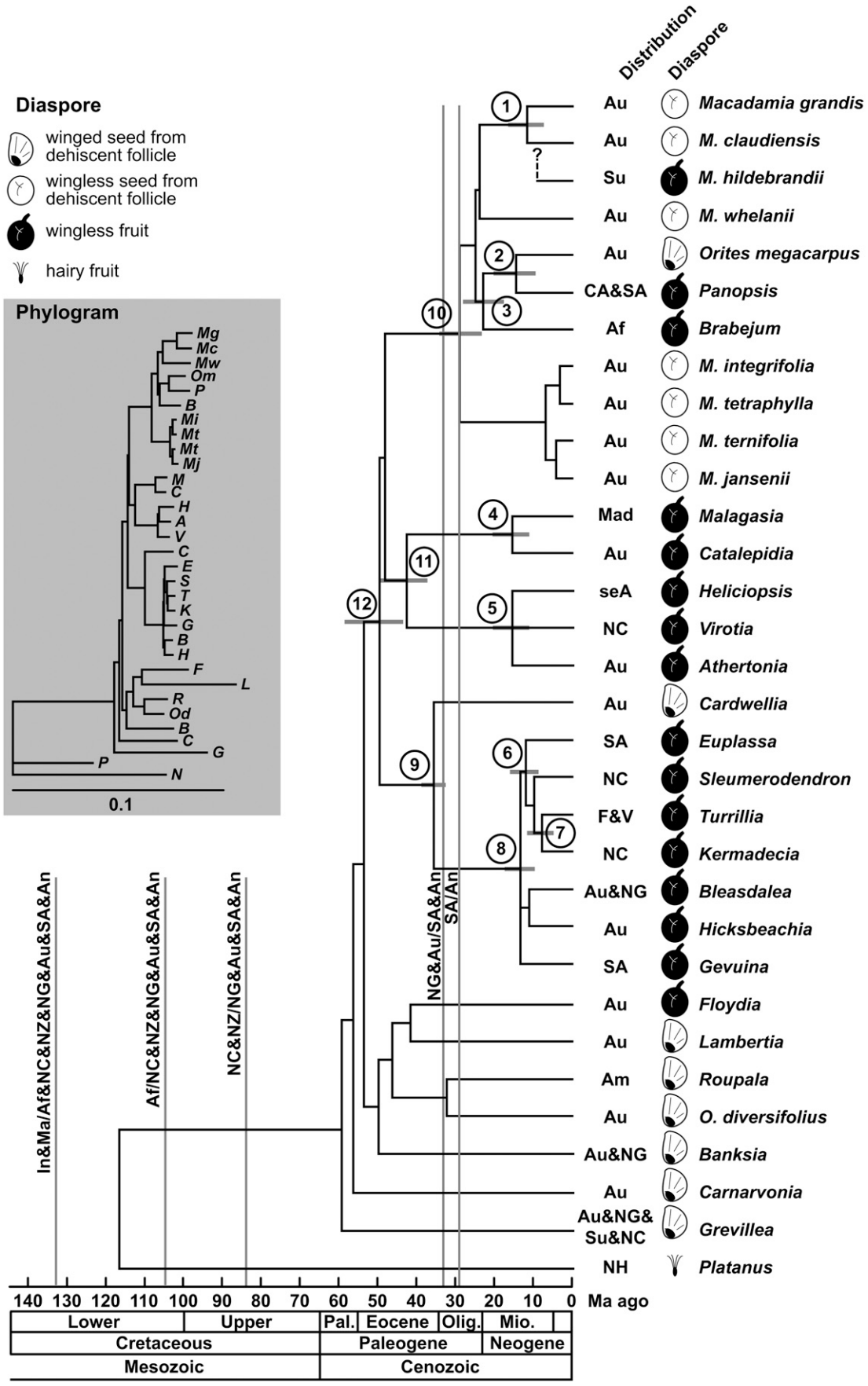
One of the striking features of the chronogram (Fig. 6) is the relative age of the MRCA of these subtropical and tropical clades of *Macadamia* (mean inferred age = 29.4 Ma; unless otherwise noted, we cite the mean inferred age from the analysis using our preferred set of prior assumptions; node 10, Table 4). With one exception, the MRCA is older than the divergence between any other taxon recognized at generic rank in tribe Macadamieae and its sister. For example, the divergence between *Panopsis* and *O. megacarpus* is about half the age of the MRCA of *Macadamia* (15.3 Ma; node 2, Table 4). The exception is the divergence between *Cardwellia* and the clade composed of the rest of subtribe Gevuininae (36.2 Ma; node 9, Table 4)—a divergence that approaches the period of time when the subtribes were diverging one from another (Fig. 6). Given the age of their MRCA, one might wonder how similar the two clades of *Macadamia* indeed are and how different they are from other members of the subtribe. We address that question, as well as discuss inferred synapomorphies, next.

The subtropical clade of *Macadamia* differs from most or all members of its sister clade (the tropical clade of *Macadamia* and its widespread sister clade) in six morphological characters (characters 14, 15, 17, 18, 29, and 41; Table 3). Fitch optimization unambiguously resolves a state of one of these, a "telopetal" direction of anthesis in the conflorescence (developing from the middle toward the base and tip; character 18), as providing a synapomorphy for the subtropical clade of *Macadamia.* Another state, the adnation of the staminal filament to the subtending tepal in its basal half only (character 29), provides a synapomorphy for the clade composed of the tropical macadamias and their widespread relatives, but this character reverses to more extensive adnation in *M. hildebrandii* and *M. claudiensis*. Character 41, the color of the mature exocarp, is sufficiently variable to make Fitch optimization of the states ambiguous at the base of the subtribe. However, the brown color seen in the tropical macadamias and their widespread relatives (polymorphic brown and green in *M. claudiensis*) is not seen elsewhere in the tribe and arguably provides a synapomorphy for the clade composed of the tropical macadamias and their widespread relatives, despite the ambiguity implied by the algorithm. For the remaining three characters (14, 15, 17), *Brabejum* (and *M. whelanii*, for character 14) shares the state of the subtropical clade of *Macadamia*, introducing ambiguity into the Fitch optimization.

Most or all members of the tropical clade of *Macadamia* differ from most or all members of its widespread sister clade in four morphological characters (13, 33, 42, 50; Table 3). Coincidentally, for each of these four characters, most or all members of the subtropical clade of *Macadamia* are scored with the same state as most or all members of the tropical clade of *Macadamia*. This character state distribution means that none of the four characters are inferred to provide an unambiguous synapomorphy for the tropical clade of *Macadamia*. While this might seem suggestive of a close relationship between the two clades of *Macadamia* to the exclusion of the widespread clade composed of *Brabejum*, *O. megacarpus*, and *Panopsis*, we point out that only one of these (a bony testa, character 50) is unambiguously resolved as a synapomorphy for *Macadamia* when the two clades are made sister to one another and that this is secondarily lost in the MRCA of *M. claudiensis* and *M. hildebrandii*. This single unambiguous synapomorphy can be compared to the two synapomorphies discussed earlier for a sister relationship between the tropical macadamias and their widespread relatives. None of these characters provide an unambiguous synapomorphy for the widespread clade either.

The absence of synapomorphies for the tropical clade of *Macadamia* and for its widespread sister clade might arise because the stems subtending their crown groups are inferred to be relatively short (Fig. 6), leaving little time for the origin and fixation of new phenotypes. The brevity of the stem lineages of both the tropical clade of *Macadamia* and its widespread sister clade is especially striking when compared to the stem subtending the crown group of the subtropical clade of *Macadamia* (Fig. 6). While short stem lineages for the former two clades might have led to an absence of morphological synapomorphies among extant members, it produced a larger window of opportunity for the generation of morphological diversity within these correspondingly older crown groups. This longer time period appears to have translated into greater morphological diversity in these groups. Members of the subtropical clade, with a mean inferred crown age of 7.1 Ma, vary in just two of the characters sampled in our study, but the tropical clade of *Macadamia* and its widespread sister clade, with mean inferred crown ages more than triple that (24.1 and 23.1 Ma, respectively), vary in eight and 13 characters, respectively.

The position of *O. megacarpus* within the clade that is otherwise composed of taxa from subtribe Macadamiinae was unexpected. This species differs spectacularly from subtribe Macadamiinae and other Proteaceae, including *Orites*, in its unusual fruit and seed morphology. Its obovoid, unripe fruits are almost globose, and thus superficially similar to those of most other Macadamiinae. However, the thick pericarp dehisces widely (Fig. 1E), quite unlike that of any other member of the Macdamiinae, releasing two, flat, narrowly winged seeds that are quite unlike the solitary, ±globose, wingless seed found in most Macadamiinae. That said, comparison of the flowers of *O. megacarpus* with that of some species of *Panopsis* (such as *P. cinnamomea* Pittier from Venezuela) reveals them to be remarkably similar. The species name was recently published by George and Hyland (1995) for a species found from 100–1200 m a.s.l. on three mountains in a small area of northern Queensland. They placed it in *Orites* without discussing alternative generic placements, and their note that "the linear bracts, villous


Distribution
Diaspore
Diaspore
winged seed from dehiscent follicle
wingless seed from dehiscent follicle
wingless fruit
hairy fruit
Phylogram
Mg
Mc
Mw
Om
P
B
Mi
Mt
Mt
Mj
M
C
H
A
V
C
E
S
T
K
G
B
H
F
L
R
Od
B
C
G
P
N
0.1
1
2
3
4
5
6
7
8
9
10
11
12
Au Macadamia grandis
Au M. claudiensis
Su M. hildebrandii
Au M. whelanii
Au Orites megacarpus
CA&SA Panopsis
Af Brabejum
Au M. integrifolia
Au M. tetraphylla
Au M. ternifolia
Au M. jansenii
Mad Malagasia
Au Catalepidia
seA Heliciopsis
NC Virotia
Au Athertonia
Au Cardwellia
SA Euplassa
NC Sleumerodendron
F&V Turrillia
NC Kermadecia
Au&NG Bleasdalea
Au Hicksbeachia
SA Gevuina
Au Floydia
Au Lambertia
Am Roupala
Au O. diversifolius
Au&NG Banksia
Au Carnarvonia
Au&NG& Su&NC Grevillea
NH Platanus
In&Ma/Af&NC&NZ&NG&Au&SA&An
Af/NC&NZ&NG&Au&SA&An
NC&NZ/NG&Au&SA&An
NG&Au/SA&An
SA/An
140 130 120 110 100 90 80 70 60 50 40 30 20 10 0 Ma ago
Lower
Upper
Pal.
Eocene
Olig.
Mio.
Cretaceous
Paleogene
Neogene
Mesozoic
Cenozoic

flowers and large, thick-walled fruits are distinctive" (George and Hyland, 1995, p. 348) leaves one wondering why they chose to place it in *Orites* (compare Fig. 1E and F). In our morphological data set, *O. megacarpus* differs from *O. diversifolius* (the type for *Orites*) in 12 characters and from all sampled members of its sister group, *Panopsis,* in seven characters. Five of the differences between *O. megacarpus* and *Panopsis* are resolved as autapomorphies for *O. megacarpus* (characters 1, 4, 37, 39, 52; Tables 2, 3), and for each of these, the state seen in *O. megacarpus* is not seen elsewhere in subtribe Macadamiinae. We could not score *O. diversifolius* for the first two of these five characters (1 and 4), but seedlings of *O. excelsus* examined by one of us (PHW) have the same states as *O. megacarpus* for these characters. Like *Panopsis*, *O. diversifolius* differs in state from *O. megacarpus* in the last two characters (39 and 52). The ovule morphology of both *O. megacarpus* and *O. diversifolius* is hemitropous (state 0, character 37), unlike all but one other species in tribe Macadamieae, *Cardwellia sublimis* F.Muell. However, hemitropous ovules are not an autapomorphy for *O. diversifolius* and thus are not a putative synapomorphy for *O. diversifolius* and *O. megacarpus* to the exclusion of other sampled taxa. In fact, none of the sampled characters provide unambiguous autapomorphies for *O. diversifolius.* Like other members of the clade composed of the tropical macadamias and their widespread relatives, *O. megacarpus* has staminal filaments adnate to the subtending tepals in their basal halves only (29) and fruit with a brown exocarp at maturity (41)—the two synapomorphies for the clade.

Several options exist for establishing monophyly at the generic rank in subtribe Macadamiinae, but we favor the creation of new genera for *O. megacarpus* (Fig. 1E, I) and the tropical clade of *Macadamia* (Fig. 1H). This choice seems reasonable, given that *O. megacarpus* has five character states not otherwise seen in subtribe Macadamiinae and it maintains *Panopsis* as a morphologically and geographically cohesive group. However, it does create a genus out of a clade, the tropical macadamias, for which we could not find a morphological synapomorphy. Alternatives to this include circumscribing a large genus composed of a broader clade—composed of the tropical clade of *Macadamia*, *O. megacarpus*, *Panopsis*, and *Brabejum*—called *Brabejum* (the oldest name at generic rank). This alternative would circumscribe a genus with two synapomorphies. However, it would be quite disruptive to the nomenclature of the group because it would result in 30 nomenclatural changes for the flora of South America, Australia, and Sulawesi. We make the new combinations in the last section.

Origin and timing of geographic disjunctions—The biogeographic scenario emerging from the results of this study turns the Gondwanan narrative for explaining biotic distributions of extant members of the tribe on its head. Most, or all, lineages extant during Gondwanan fragmentation did not "co-speciate" with the supercontinent and survive until the present, as previously accepted by many authors (e.g., Venkata Rao, 1971; Johnson and Briggs, 1975; Weston and Crisp, 1996; Prance and Plana, 1998; Prance et al., 2007). Instead, it was only after Gondwana had fully fragmented (Fig. 6) that dispersal events out of Australia (to begin with) led to an extant distribution that today stretches across the southern hemisphere. Most dispersal events in the tribe are inferred to have occurred between 23.1 Ma and 8.1 Ma BP (Table 4), at a time after the last continental connections between Australia, South America, and Antarctica (ending 29–33 Ma BP). While some topological resolutions (2 and 3; Fig. 5B) of a trichotomy in subtribe Gevuininae lead to an Australian/South American disjunction prior to the last continental connection between these fragments via Antarctica, another scenario in which the disjunction occurs well after the fragmentation is equally parsimonious. Note that we do not mean to imply that the fragmentation of Gondwana did not have an evolutionary impact on its biota or that the tribe was not distributed outside of Australia earlier than the dispersal events inferred here. Rather, our point is that the extant diversity on the continents other than Australia is not descended from the biota that existed on them at the time of their isolation from other fragments of Gondwana. In this section, we will consider the congruence of our results with those of Barker et al. (2007), and, in the next section, we will discuss biotic correlates (the evolution of the tribe's diaspores) and abiotic correlates (the advent of the Antarctic Circumpolar Current) to the dispersal events of the last 25 Ma.

The biogeographic scenario for subtribe Macadamiinae supported by our results fundamentally differs from that of Barker et al. (2007) in the mechanisms responsible for the disjunctions. We infer three dispersal events out of Australia in subtribe Macadamiinae: one to Sulawesi, one to South and Central America (mean inferred age = 15.2 Ma), and one to Africa (mean inferred age = 23.1 Ma; Table 4). We were unable to include the Sulawesian species *M. hildebrandii* and *M. erecta* in the six non-ITS data sets used for inferring the ages of disjunctions because of PCR failures (*M. hildebrandii*) and unavailability of tissue for DNA extractions (*M. erecta*). However, *Macadamia hildebrandii* and *M. claudiensis* are sister in the ITS results (PP 85%), and a sister relationship between *M. hildebrandii* and *M. erecta* is considered likely by McDonald and Ismail (1995) based on morphological evidence. This evidence leads us to believe that an ancestor of these species arrived by dispersal to Sulawesi less than 12.1 Ma (the mean age of the divergence between *M. grandis* and *M. claudiensis*; Table 4). A vicariance explanation for their position on Sulawesi then appears untenable. The tectonic plates that make up Sulawesi are thought to have fragmented from the Australia-New Guinea plate at much earlier times: in the Late Jurassic (ca. 160 Ma BP) and in the early Eocene (ca. 50 Ma BP; Audley-Charles, 1987; van Welzen et al., 2005). Furthermore, it appears that these plates have only emerged above sea level in the last 25 Ma (Hall, 2001), precluding their service as rafts for species from Australian-New Guinea (van Welzen et al., 2005). Perhaps corroborating this recent dispersal scenario is the observation that *M. hildebrandii* is most frequently found on ultramafic

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Fig. 6. Chronogram with the natural distribution of extant members of each taxon and characteristics of their diaspores. Position of node on *x*-axis is at the mean inferred age using a minimum age of 36 Ma for the most recent common ancestor of subtribe Gevuininae and rtrate = 0.039 and brownmean = 1. The 95% credible intervals are given for 11 focal nodes, as are the last continental connections between landmasses. The phylogram shows the mean branch lengths from the posterior probability density for the data. Taxa are vertically ordered as in the chronogram, but the first letter of the genus (or the genus and the specific epithet) is also given. An = Antarctica, Af = Africa, Au = Australia, CA = Central America, F = Fiji, Mad = Madagascar, NC = New Caledonia, NG = New Guinea, NH = widespread in the northern hemisphere, SA = South America, seA = southeast Asia, Su = Sulawesi, V = Vanuatu, Ma = Megayear.

TABLE 4. Ages inferred with alternative minimum ages for the most common recent ancestor of subtribe Gevuininae. The constraint was set at the most recent boundary of the Eocene, the maximum age of the fossil (according to Macphail in Carpenter and Pole, 1995), and removed in turn. The mean is followed by the 95% credible interval. Node numbering is as used as in Fig. 6.

	Gevuininae constraint		
Node	34 Ma	49 Ma	Removed
1	12.069 (8.243, 16.748)	15.515 (10.594, 21.438)	10.331 (6.882, 14.776)
2	15.259 (10.436, 20.810)	19.465 (13.404, 26.629)	13.083 (8.693, 18.390)
3	23.060 (17.798, 29.039)	29.434 (22.766, 36.638)	19.767 (14.505, 25.899)
4	15.632 (10.670, 21.361)	20.854 (14.255, 28.035)	13.072 (8.437, 18.671)
5	15.611 (10.960, 20.883)	20.484 (14.528, 27.243)	13.127 (8.703, 18.461)
6	12.285 (8.846, 16.490)	17.761 (12.912, 23.474)	9.726 (6.352, 14.118)
7	8.111 (4.931, 11.887)	11.625 (7.031, 16.887)	6.507 (3.700, 10.072)
8	13.594 (9.966, 17.901)	19.776 (14.804, 25.396)	10.711 (7.087, 15.376)
9	36.174 (34.074, 40.835)	50.179 (49.036, 53.117)	28.872 (21.827, 36.749)
10	29.396 (24.017, 35.344)	37.545 (31.051, 44.441)	25.109 (19.141, 31.956)
11	42.890 (36.898, 49.607)	54.318 (48.043, 60.854)	36.601 (28.882, 45.161)
12	50.225 (44.755, 56.700)	62.793 (57.606, 68.447)	43.117 (34.845, 52.080)

substrate of young age at low elevations (McDonald and Ismail, 1995). Barker et al. (2007) infer a topology in which the African *Brabejum* and the South American *Panopsis* are sister and these together are sister to the Australian and Sulewesian *Macadamia* (using one operational taxonomic unit, OTU, per genus). They conclude that this topology, in combination with their divergence age estimates, is partly consistent with the widely accepted model of Gondwanan fragmentation (McLoughlin,

TABLE 5. Ages inferred with alternative priors for brownmean and rtrate. The mean and credible intervals inferred for each of the 11 focal nodes are given with the alternative brownmean and rtrate combinations. Highest mean value for a node is in boldface; lowest mean value for a node is underlined. Node numbering is as used as in Fig. 6.

		Age		
		brownmean (brownsd)		
rtrate (rtratesd)	Node	0.1 (0.1)	1 (1)	10 (10)
0.0039 (0.0039)	1	**14.274** (10.017, 19.284)	13.942 (9.444, 19.320)	13.938 (9.366, 19.635)
	2	**18.145** (12.650, 24.496)	17.825 (12.124, 24.388)	17.828 (12.127, 24.826)
	3	**27.247** (21.202, 34.040)	26.742 (20.290, 34.309)	26.678 (20.188, 34.165)
	4	15.435 (10.332, 21.280)	17.416 (11.419, 24.236)	**18.203** (11.991, 25.435)
	5	15.695 (10.802, 21.398)	17.449 (11.917, 23.914)	**17.998** (12.264, 24.844)
	6	11.774 (8.438, 15.848)	13.032 (9.049, 18.011)	**13.467** (9.262, 18.909)
	7	7.966 (4.734, 11.658)	8.697(5.015, 13.105)	**8.989** (5.220, 13.571)
	8	12.875 (9.434, 17.178)	14.309 (10.091, 19.670)	**14.828** (10.449, 20.529)
	9	38.680 (34.262, 46.301)	39.421 (34.323, 47.626)	**39.672** (34.351, 48.223)
	10	**34.352** (28.081, 41.452)	33.941 (27.167, 41.960)	33.807 (26.921, 41.847)
	11	48.717 (41.197, 57.503)	**49.034** (41.128, 58.400)	48.911 (40.890, 58.231)
	12	**59.096** (51.494, 67.977)	57.418 (49.552, 66.749)	56.636 (48.787, 65.901)
0.039 (0.039)	1	12.427 (8.802, 16.593)	12.069 (8.243, 16.748)	12.132 (8.193, 16.992)
	2	15.879 (11.438, 21.117)	15.259 (10.436, 20.810)	15.287 (10.409, 21.131)
	3	24.031 (18.942, 29.555)	23.060 (17.798, 29.039)	23.009 (17.557, 29.098)
	4	13.903 (9.553, 19.013)	15.632 (10.670, 21.361)	16.363 (11.091, 22.403)
	5	14.350 (10.098, 19.138)	15.611 (10.960, 20.883)	16.083 (11.286, 21.730)
	6	11.011 (8.148, 14.432)	12.285 (8.846, 16.490)	12.794 (9.096, 17.237)
	7	7.348 (4.583, 10.488)	8.111 (4.931, 11.887)	8.445 (5.028, 12.454)
	8	12.057 (9.111, 15.566)	13.594 (9.966, 17.901)	14.204 (10.362, 18.827)
	9	35.988 (34.064, 40.286)	36.174 (34.074, 40.835)	36.223 (34.071, 41.253)
	10	30.278 (25.116, 36.083)	29.396 (24.017, 35.344)	29.240 (23.787, 35.413)
	11	43.393 (37.311, 50.178)	42.890 (36.898, 49.607)	42.569 (36.737, 49.316)
	12	52.738 (47.213, 59.119)	50.225 (44.755, 56.700)	49.230 (43.656, 55.895)
0.39 (0.39)	1	12.018 (8.518, 16.078)	11.960 (8.113, 16.419)	12.017 (8.037, 16.840)
	2	15.388 (10.943, 20.344)	15.093 (10.444, 20.675)	15.103 (10.231, 20.850)
	3	23.301 (18.418, 28.635)	22.874 (17.496, 28.937)	22.732 (17.279, 28.817)
	4	13.523 (9.266, 18.235)	15.540 (10.672, 21.281)	16.221 (10.941, 22.475)
	5	13.939 (9.790, 18.726)	15.460 (10.906, 20.738)	15.866 (11.121, 21.383)
	6	10.826 (8.032, 14.118)	12.304 (8.848, 16.419)	12.842 (9.202, 17.163)
	7	7.208 (4.421, 10.264)	8.131 (4.931, 11.793)	8.454 (5.088, 12.383)
	8	11.864 (8.958, 15.313)	13.625 (10.015, 17.852)	14.293 (10.487, 18.771)
	9	35.602 (34.046, 39.220)	36.070 (34.057, 40.885)	36.014 (34.052, 40.845)
	10	29.418 (24.458, 34.911)	29.113 (23.769, 35.208)	28.830 (23.294, 35.069)
	11	42.193 (36.468, 48.516)	42.557 (36.541, 49.438)	42.003 (36.267, 48.965)
	12	51.308 (46.112, 57.197)	49.865 (44.038, 56.542)	48.541 (43.085, 55.405)

2001). Their favored scenario begins with the MRCA of the subtribe widespread across Australia, Antarctica, and South America. That distribution is then disrupted with the loss of connections to Antarctica, isolating *Macadamia* on Australia and the ancestor of *Panopsis* and *Brabejum* on South America. Finally, a long-distance dispersal from South America to Africa leads to *Brabejum*. Barker et al. (2007) prefer this scenario because it invokes the fewest number of long-distance dispersal events by explaining disjunctions that can be explained by cospeciation of fragments and their biota in that way.

The incongruities in these two biogeographic scenarios primarily arise from differences in the inferred age of relevant divergence events. Barker et al. (2007) consistently estimated older ages for their divergence events, and these older age estimates sometimes include the last continental connections between relevant Gondwanan fragments when ours do not. For example, they inferred a mean age of the divergence between *Brabejum* and *Panopsis* at 43.8 (± 10.0 SD) Ma and that between these two genera and *Macadamia* at 53.9 (± 10.0) Ma. We inferred a mean age of divergence between *Brabejum* and *Panopsis* at 23.1 (17.8–29.0 = 95% credible interval) Ma, between these two and the tropical clade of *Macadamia* at 25.6 (20.4–31.4) Ma, and between these two and the subtropical clade of *Macadamia* at 29.4 (24.0–35.3) Ma (Table 4; Fig. 6). Ours is not the only study that inferred ages that are younger than Barker et al. (2007). For example, Barker et al. (2007) inferred a mean age of the crown group Proteaceae at 118.5 (± 8.2) Ma, while Anderson et al. (2005) inferred an age of 85 or 96 Ma for the crown group using *rbcL* data analyzed with penalized likelihood and nonparametric rate smoothing approaches, respectively.

A possible source of this difference is Barker et al.'s (2007) use of fossil pollen from the Upper Cenomanian (Dettman and Jarzen, 1998; interpreted as 93 Ma BP by Barker et al., 2007) as a minimum age constraint for the crown-group Proteaceae, despite its possession of only plesiomorphic characters of the family (H. Sauquet and D. Cantrill, personal communication in Barker et al., 2007). Barker et al. (2007) justify this by citing the age of the stem-group Platanaceae as 15 Ma older than 93 Ma and the age of fossils that share synapomorphies with an internal clade of Proteaceae at 82 Ma BP. However, neither of these observations support use of 93 Ma as a minimal age constraint for the crown-group Proteaceae. The age of the stem-group Platanaceae only suggests a minimum age for the stem-group Proteaceae, and fossils sharing synapomorphies with internal clades of Proteaceae would only justify using their age as the minimum age of crown-group Proteaceae, not an age 11 Ma earlier. Their estimate of the age of the crown-group Proteaceae at 118.5 (± 8.2) leaves little time between the appearance of the eudicots in the fossil record (125 Ma BP; Magallón et al., 1999) and the origin of the crown group Proteaceae, and explaining the long branch subtending the crown (Fig. 6; estimated to represent 23–25 Ma by Anderson et al. [2005]) is difficult with that time frame.

That said, other minimum ages used appropriately in Barker et al.'s (2007) study, but not used in our study, might also explain the older ages in their study. The second and third oldest minimum age constraints used by Barker et al. (2007) are 70 Ma for the stem-group Embothriinae and 65 Ma for the stem-group Banksieae, based upon synapomorphies shared by the respective fossils and their crown groups. We did not use these in our study because of our limited sampling of subfamily Grevilleoideae outside of tribe Macadamieae. However, among those taxa that we sampled, subtribe Embothriinae is most closely related to *Grevillea* R.Br. and *Banksia* is part of tribe Banksieae. The 95% credible intervals for the inferred age of the MRCA of *Grevillea* and its sister (52.7–68.0 Ma) and the MRCA of *Banksia* and its sister (44.2–57.7) do not include or predate the reconstructed ages of these fossils, suggesting that including them could affect the ages inferred with this data set, bringing them closer to the ages inferred by Barker et al. (2007). Thorough exploration of this will occur elsewhere (A. Mast et al., unpublished manuscript), but we began to explore this here. When we constrained the minimum age of these nodes to 70 and 65 Ma (and otherwise using our preferred set of assumptions), the mean inferred ages of nodes 1–8 increased by only 1.8–5.8 Ma, and the 95% credible intervals still did not include the last continental connections between landmasses involved in their respective disjunctions. The mean inferred age of the disjunction between *Brabejum* and its sister group using this approximation of Barker et al.'s second and third oldest minimum age constraints was 28.9 Ma (22.3–36.2)—still 14.9 Ma younger than the mean age inferred in that study.

An additional factor that likely affected age estimates more locally, in subtribe Macadamiinae, is the agglomeration of DNA sequence data in Barker et al. (2007) for *Macadamia*, a genus that we show here to be paraphyletic. In their study, Barker et al. (2007) combine new data that they generate with data from Hoot and Douglas (1998), and for some genera, they use data from different species for their OTUs at generic rank. As it turns out, their OTU *Macadamia* uses an *rbcL* sequence from *M. claudiensis* (a tropical species) and *atpB* and *atpB-rbcL* spacer sequences from *M. jansenii* (a subtropical species). This agglomeration combines data from clades of differing ages since divergence with *Panopsis* and *Brabejum* and presumably results in an age intermediate between the two actual ages of divergence.

It is not entirely clear how inclusion of *O. megacarpus* would have affected the biogeographic scenario favored by Barker et al. (2007) because their construction depended on the inferred ages of disjunctions, and we do not know if they would have inferred the divergence of *O. megacarpus* and *Panopsis* as earlier or later than 29–33 Ma BP with their data. However, exclusion of *O. megacarpus* from the tree on which we performed Fitch optimization of distributions would have left us with a far more ambiguous result. We note both that discovery of the sister relationship of *O. megacarpus* and *Panopsis* was fortuitous and not something that we expected a priori and that biogeographic inference, in general, can be sensitive to taxon sampling. For example, paraphyly of the moderately large *Panopsis* (25 spp.) with respect to *O. megacarpus* would alter our interpretation of the dispersal events in this subtribe. However, we do not expect this to be the case because the four sampled species of *Panopsis* form a monophyletic group in the phylogeny inferred with ITS, the species are morphologically very similar (Prance and Plana, 1998; Prance et al., 2007), and the diaspore morphology of *O. megacarpus* is not consistent with the morphology of other diapsores thought to undergo long-distance dispersal in this group (with delayed dehiscence, as discussed later).

In subtribe Gevuininae, only the inferences that *Bleasdalea* dispersed from Australia to New Guinea and that *Turrillia* arose following a dispersal from New Caledonia to Fiji and Vanuatu are unambiguous. We sampled the Australian species *Bleasdalea bleasdalei* (F.Muell.) A.C.Sm. & J.E.Haas but not the New Guinean species *Bleasdalea papuana* (Diels) Domin. So, we did not infer an age for the disjunction between these two areas. However, we infer that it originated recently because the mean inferred

age for the divergence between *Bleasdalea* and its sister, the Australian genus *Hicksbeachia,* is 11.5 Ma. There have been a number of terrestrial connections between Australia and New Guinea via sea level fluctuations in the shallow Torres Strait, and the latest of these occurred just 18 000 yr ago (Veevers, 1991; Hope, 1994). The mean inferred age of the disjunction between *Turrillia* and its sister on New Caledonia, *Kermadecia,* is 8.1 Ma (Table 4). This age corresponds to a time after the origin of the volcanic ridges that make up the archipelagos of Fiji (Late Eocene) and Vanuatu (Late Oligocene) and the origin of the North Fiji Basin that separates the two island chains (11–12 Ma BP; Schellart et al., 2006). It is also well after the rifting of the 'Eua Ridge from New Caledonia at 41 Ma BP and its subsequent accretion to Fiji at about 6 Ma BP—events postulated by Kroenke (1996). Weston and Crisp (1996) suggested that vicariance has likely played a larger role in the biota of Fiji and Vanuatu than previously recognized, based on the distributional limit of many "primitive" taxa at Fiji (e.g., Proteaceae, Winteraceae, Fagaceae, Balanopaceae, Magnoliales, and conifers). However, it now seems clear that, in the case of *Turrillia*, the timing of the relevant tectonic events substantially predated the biological event that they were supposed to explain. The trichotomy inferred in subtribe Gevuininae leads to an inability to discriminate between an early Australia/South America disjunction arising at node 9 or a later disjunction arising at node 8 (Figs. 5B, 6). The later Australia/South America disjunction at 13.6 Ma BP (node 8; Table 4) would bring that dispersal into a period of time during which all of the other disjunctions represented in today's biota were originating.

Diaspore evolution and dispersal—Prior to asking if there are any correlates to this apparent increase in vagility starting ca. 25 Ma BP, it is important to note that extant distributions are a product of both dispersal and survival to the present. It is possible that the tribe dispersed as frequently from one landmass to another prior to 25 Ma BP as it did after that time but that these early immigrants are no longer represented in the biota of those continents due to extinction. However, a fossil record of earlier immigrants has not been discovered. The only extra-Australian fossil attributable to the group using synapomorphies is the fossil cuticle of subtribe Gevuininae from the early Miocene (ca. 23 Ma BP) of New Zealand mentioned earlier (Carpenter, 1994; Pole, 1998). In the absence of fossil evidence suggesting a more widespread lineage prior to 25 Ma BP, we will consider both the biotic and abiotic events occurring prior to, or at the same time as, this period of dispersal events that are represented in the extant biota.

The diaspores in the tribe vary from the winged seeds of *Cardwellia* to the wingless seeds protected by a hard testa in *Macadamia*, to the wingless fruits that have a (typically) succulent outer mesocarp and bony inner mesocarp in the majority of remaining taxa (Fig. 6). It is this third diaspore type that appears to be related to the greatest expansions in distributions (Fig. 5A). Dehiscence of the fruit at seed germination, rather than at fruit maturity, occurs in every extra-Australian genus in the tribe, as well as some Australian members. It is inferred to have arisen independently 4–5 times, and in each case this was prior to, or as early as the time of, each of the dispersal events (Fig. 5A), and the character state changes are significantly correlated with dispersal out of Australia, as determined using Pagel's (1994) method. We conclude that the pericarp might then have served one or more important functions in the dispersal events. These might include initial attraction of the disperser (when it is an organism), protection of the seed during long periods under harsh conditions (e.g., in a gut or in seawater), or provision of buoyancy in water. Two other characters were also significantly correlated with dispersal out of Australia: the texture of the outer and inner mesocarp. A succulent outer mesocarp and bony inner mesocarp in subtribes Malagasiinae, Virotiinae, and Gevuininae undoubtedly makes them more attractive to vertebrate dispersers, such as birds, bats, and less vagile organisms (e.g., agoutis; Prance et al., 2007) and protects the seed from destruction by these dispersers, respectively. And these might be the common dispersers in those subtribes (Johnson and Briggs, 1975; Weston and Crisp, 1996).

However, we propose that a dispersal mechanism inconsistent with that suggested by the morphology of these fruits—dispersal by seawater as buoyant fruit or on natural rafts—might have played the greatest role in dispersing seeds of the tribe across the southern hemisphere. We suggest this for three reasons. First, the hard kernel (the inner mesocarp or the testa) of the fruits in the group is larger (>1 cm) than those known to be ingested by bats and vagile birds (reviewed by Whittaker and Jones, 1994; Shilton et al., 1999). This fact suggests that seeds do not pass through the guts of these organisms but are instead discarded short distances from the source trees. Whittaker and Jones (1994) considered colonization of Krakatau from adjacent islands—a distance much shorter than that between Australia and South America—via movement of seeds that are orally ejected to be highly unlikely. Furthermore, Higgins et al. (2003) found in a meta-analysis of available data sets that the relationship between morphological dispersal syndromes and long-distance dispersal is poor, in part because of the role that nonstandard dispersal mechanisms play in primary and secondary dispersal (e.g., movement by water after oral ejection of a kernel at a riparian perch). Second, some of the extra-Australian genera are known to be dispersed by water or live in riparian habitats and are presumed to be dispersed by water, suggesting ecological signatures that persist from the original dispersal event. For example, the South American genus *Panopsis* includes species dispersed by water (Prance et al., 2007), and the African genus *Brabejum* occurs mainly along permanent water courses (Rourke, 1998). And finally, 25 Ma BP is shortly after the onset of the Antarctic Circumpolar Current (ACC)—a powerful ocean current that rotates eastward around an isolated Antarctica. The ACC is assumed to have had a significant impact on intercontinental dispersal of the southern hemisphere biota and is used to explain asymmetry in the rates of dispersal between pairs of southern continents (e.g., Winkworth et al., 2002; Sanmartín et al., 2007). While the Australian genera are today in the northeast of that continent—outside of the latitudes in which the ACC is found—we point out that rainforest was much more widespread in Australia in earlier times and that lower latitude currents interact with the ACC. Subtribe Gevuininae is known to have occurred along the southern coast of Australia in the Eocene (Carpenter and Pole, 1995). And, while the drying of Australia began with the onset of the ACC, it was only ca. 15 Ma BP that the major northerly shift across the continent of anticyclonic high-pressure cells that block rain-bearing low-pressure cells occurred (Bowler, 1982). Thus, there seems to have been opportunity for the tribe to use the ACC for the dissemination of its diaspores across the greatest distances.

Establishing monophyly at the generic rank—Here, we establish two new names at generic rank and make new combinations for relevant species in those genera, as justified earlier. We also make new combinations for the New Caledonian species of *Macadamia* in *Virotia* because they are more closely related to the type of *Virotia* than *Macadamia* (Fig. 4).

New generic names—***Nothorites*** P. H. Weston & A. R. Mast, **gen. nov.**

Description: Arbores. Hypocotylus evolutus. Trichomata simplicia. Folia alterna, simplicia, integra. Conflorescentia lateralis vel terminalis, ramosa. Par florum pedunculum communem deficiem, bractea lineari subtentum. Flores ebracteati, pedicellati, hermaphroditi. Perianthium actinomorphum. Glandes hypogynae connatae, annulatae, cupulatae. Ovarium breviter stipitatum; ovula 2, hemitropa, lateraliter inserta; stylus inter tepala ante anthesin non protrudens; pollenophorum plus minusve tumidum, plus minusve actinomorphum; stigma terminale. Fructus obovoideus, plene dehiscens, complanatus post dehiscentia; mesocarpium externum crassum, coriaceum, fibris dense radiantibus; mesocarpium internum tenue. Semina 2, plana, elliptica vel fere orbicularia, ala angusta marginali circumcincta; testa tenuis, chartacea.

Trees. Hypocotyl developed. Trichomes simple. Leaves alternate, simple, entire. Conflorescence terminal or lateral, branched. Flower pair lacking a common peduncle, subtended by a linear bract. Flowers ebracteate, pedicellate, hermaphrodite, actinomorphic. Hypogynous glands connate, annular, cuplike. Ovary shortly stipitate; ovules 2, hemitropous, laterally inserted; style not protruding between the tepals before anthesis; pollen presenter slightly swollen, more or less radially symmetrical; stigma terminal. Fruit obovoid, fully dehiscing, flattened after dehiscence; outer mesocarp thick, leathery, with dense radiating fibers; inner mesocarp thin. Seeds 2, flat, elliptic to almost orbicular; surrounded by a narrow, marginal wing; testa thin, chartaceous.

Type: *Nothorites megacarpus* (A. S. George & B. Hyland) P. H. Weston & A. R. Mast.

Derivation of name: from the Greek *nothos* (bastard, baseborn) and *Orites* (the genus in which this species was originally placed), indicating the inappropriate original generic placement of this species.

Lasjia P. H. Weston & A. R. Mast, **gen. nov.**

Description: Arbores. Hypocotylus vestigialis. Trichomata simplicia. Folia adulta verticillata, simplicia, integra. Conflorescentia lateralis vel terminalis, plerumque ramosa, raro simplex. Par florum pedunculum communem deficiem, bracteatum. Flores ebracteati, pedicellati, hermaphroditi. Perianthium actinomorphum. Glandes hypogynae connatae, annulatae, cupulatae. Ovarium breviter stipitatum; ovula 2, orthotropa, pendula; medium styli inter tepala ante anthesin protrudens; pollenophorum non tumidum vel plus minusve basaliter tumidum, plus minusve actinomorphum; stigma terminale. Fructus globosus, tarde dehiscens; mesocarpium externum crassum, coriaceum, fibris dense radiantibus; mesocarpium internum tenue. Semen plerumque solitarium, globosum, non alatum; testa tenuis chartaceaque vel crassa osseaque.

Trees. Hypocotyl vestigial. Trichomes simple. Adult leaves whorled, simple, entire. Conflorescence terminal or lateral, usually branched, rarely simple. Flower pair lacking a common peduncle, bracteate. Flowers ebracteate, pedicellate, hermaphroditic. Perianth actinomorphic. Hypogynous glands connate, annular, cuplike. Ovary shortly stipitate; ovules 2, orthotropous, pendulous; middle of style protruding between the tepals before anthesis; pollen presenter not swollen or slightly swollen basally; stigma terminal. Fruit globose, tardily dehiscent; outer mesocarp thick, leathery, with dense radiating fibers; inner mesocarp thin. Seed usually solitary, globose, wingless; testa thin and chartaceous or thick and bony.

Type: *Lasjia claudiensis* (C. L. Gross & B. Hyland) P. H. Weston & A. R. Mast.

Derivation of name: formed from the initials of the late Dr. Lawrence Alexander Sidney Johnson (L.A.S.J.) to honor his outstanding contribution to our knowledge of the evolution and biogeography of the family Proteaceae.

New combinations—***Nothorites megacarpus*** (A. S. George & B. Hyland) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Orites megacarpus* A. S. George & B. Hyland (as "*Orites megacarpa*"), *Fl. Australia,* 16: 497. 1995.

Lasjia grandis (C. L. Gross & B. Hyland) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Macadamia grandis* C. L. Gross & B. Hyland, *Austral. Syst. Bot.* 6: 347. 1993.

Lasjia claudiensis (C. L. Gross & B. Hyland) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Macadamia claudiensis* C. L. Gross & B. Hyland, *Austral. Syst. Bot.* 6: 343. 1993.

Lasjia whelanii (F. M. Bailey) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Helicia whelanii* F. M. Bailey, *Report on New Plants, Preliminary to General Report on Botanical Results on Mestons Expedition to the Bellenden-Ker Range.* p. 2. 1889.

Lasjia hildebrandii (Steenis) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Macadamia hildebrandii* Steenis, *Reinwardtia* i: 475. 1952.

Lasjia erecta (J. A. McDonald & Ismail R.) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Macadamia erecta* J. A. McDonald & Ismail R., *Harvard Pap. Bot.* 7: 7. 1995.

Virotia angustifolia (Virot) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Macadamia angustifolia* Virot, *Fl. N. Caled. & Depend.* 2: 120. 1968.

Virotia francii (Guillaumin) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Roupala francii* Guillaumin (as "*Rhopala francii*"), *Bull. Mus. Hist. Nat. Paris.* Ser. II. 5: 325. 1933.

Virotia neurophylla (Guillaumin) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Kermadecia neurophylla* Guillaumin, *Bull. Mus. Hist. Nat. Paris.* Ser. II. 5: 325. 1933.

Virotia rousselii (Vieill.) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Roupala rousselii* Vieill. (as "*Rhopala rousselii*"), *Bull. Soc. Linn. Normand.* 9: 394. 1865.

Virotia vieillardi (Brongn. & Gris) P. H. Weston & A. R. Mast, **comb. nov.**

Basionym: *Roupala vieillardii* (as "Rhopala vieillardi") Brongn. & Gris, *Bull. Soc. Bot. France* 10: 229. 1863.

Conclusions—The results presented here both fundamentally change our views on the evolutionary history of tribe Macadamieae and nicely illustrate the sensitivity of conclusions to assumptions made with limited knowledge. The most dramatic example of this was the discovery that *O. megacarpus*, a species not previously considered to be part of the tribe, is sister to *Panopsis*. This discovery shifts the origin of the disjunction between South America and Australia 10 Ma closer to the present (Fig. 6), making it much younger than the last continental connection between these Gondwanan fragments (via Antarctica). In another example, we show that Barker et al.'s (2007) assumption of monophyly in *Macadamia* permitted them to agglomerate

data that turned out to be from two clades with different ages of divergence from their sister groups. This inappropriate agglomeration presumably produced an overestimate of the age of a disjunction between Australia and other fragments of Gondwana in their analysis. Our creation of a separate genus for the tropical macadamias, *Lasjia*, and our combinations in *Virotia* for the New Caledonian species previously discussed as macadmias (e.g., Virot, 1968) should lead to fewer mistakes of this sort in the future. For our part, we have assumed that moderately large genera (e.g., *Panopsis* and *Euplassa*) are monophyletic. Future results to the contrary have the potential to either strengthen or weaken the dispersal scenario that is supported in this study, as well as to resolve some of the ambiguity in our results (were *Euplassa* found to be paraphyletic with respect to genera resolved here as sister to it).

Our conclusion that most or all of the extra-Australian range of the tribe is the result of dispersal across substantial water barriers is generally robust across a wide range of alternative assumptions (Tables 4, 5). However, it does not remain valid for the Australian-South American disjunctions when the root age prior and the root's minimum and maximum age constraints are increased by 70 Ma (for node 2) or 100 Ma (for node 8). These alternative assumptions move the origin of the Proteaceae back into the Jurassic and Triassic—a period during which Croizat (1962) thought they originated, but that we recognize today as much earlier than their first occurrence in the fossil record. Of course, if, for example, tricolpate pollen is later found that documents the eudicots at a time 70 Ma or more before their current earliest occurrence, then our assumptions would change sufficiently to conclude that the data do not reject a vicariance scenario for one or both of these nodes. But changes in the earliest occurrence of tricolpate pollen is unlikely because it is distinctive and pollen is abundant in sedimentary rocks (Crane, 1989).

We still have a lot to learn about this arguably underexploited group. For example, chromosome number proved to be among the poorest known characters in the study. And future work is warranted. *Macadamia* is the principle orchard crop in Hawaii (Nagao and Hirae, 1992), and its embryos have the highest oil content (78%) of any "nut" on the market (Strohschen, 1986a). However, other promising genera—*Brabejum*, *Gevuina*, *Heliciopsis*, *Hicksbeachia*, *Kermadecia*, and *Athertonia*—are still only exploited locally, and little is known of their reproductive biology.

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APPENDIX 1. Voucher specimens for DNA and GenBank accession numbers.

Taxon—Voucher specimen, GenBank accession numbers for *matK*, *atpB*, *ndhF*, *PHYA*, *waxy* locus 1, *waxy* locus 2, internal transcribed spacers of the nuclear ribosomal DNA.

Athertonia diversifolia (C.T.White) L.A.S.Johnson & B.G.Briggs; *P.H. Weston 2760* (NSW702013); EU642699, EU642729, EU642668, EU642760, EU649765, EU649735, —. *P.H. Weston 1859* (NSW368736); —, —, —, —, —, —, EU642793.

Banksia serrata L.f.; *A. R. Mast, D. S. Feller & P. D. Hind 225* (WIS); AY823169, AY837794, EU642656, EU642748, AY829483, EU649723, —. ***Bleasdalea bleasdalei*** (F.Muell.) A.C.Sm. & J.E.Haas; *P. H. Weston 891* (NSW208555); EU642693, EU642723, EU642662, EU642754, EU649759, EU649729, EU642786**.** ***Brabejum stellatifolium*** L.; *A. R. Mast 449* (BOL); EU642707, EU642737, EU642677, EU642769, EU649771, EU649744, —. *P.H. Weston 2044* (NSW403139); —, —, —, —, —, —, EU642803.

Cardwellia sublimis F.Muell.; *P. H. Weston 1824* (NSW360127); EU642688, EU642718, EU642657, EU642749, EU649754, EU649724, EU642777**.** ***Carnarvonia araliifolia*** F.Muell.; *P. H. Weston 2762* (NSW700972); EU642685, EU642715, EU642653, EU642745, EU649752, EU649720, EU642774**.** ***Catalepidia heyana*** (F.M.Bailey) P.H.Weston; *P. H. Weston 2472* (NSW445879); EU642700, EU642730, EU642669, EU642761, EU649766, EU649736, —. *P.H. Weston 2008* (NSW397447); —, —, —, —, —, —, EU642794.

Euplassa duquei Killip & Cuatrec.; *V. Plana 52* (NSW666085, K); —, —, —, —, —, —, EU642779**.** ***E. inaequalis*** Engl.; *B. Walter 2741* (NY); EU642689, EU642719, EU642658, EU642750, EU649755, EU649725, EU642778**.** ***E. occidentalis*** I.M.Johnst.; *V. Plana 8* (NSW666087, K); —, —, —, —, —, —, EU642780.

Floydia praealta (F.Muell.) L.A.S.Johnson & B.G.Briggs; *P.H. Weston 1857* (NSW368734); EU642682, EU642712, EU642650, EU642742, EU649749, EU649717, —.

Gevuina avellana Molina; *E. E. Reed s.n.* (UC); EU642694, EU642724, EU642663, EU642755, EU649760, EU649730, EU642787**.** ***Grevillea caleyi*** R.Br.; *P. H. Weston 2885* (NSW750430); EU642709, EU642739, EU642679, EU642771, EU649773, EU649730, —.

Heliciopsis lanceolata (Koord. & Valeton) Sleumer; Cult. Hort. Bogor III-B-11. (BO); EU642696, EU642726, EU642665, EU642757, EU649762, EU649732, —. ***H. lobata*** (Merr.) Sleumer; *P. H. Weston 2014* (NSW438593); —, —, —, —, —, —, EU642789. ***Hicksbeachia pinnatifolia*** F.Muell.; *P. H. Weston 2761* (NSW700971); EU642697, EU642727, EU642666, EU642758, EU649763, EU649733, —; *P. H. Weston 2015* (NSW397463); —, —, —, —, —, —, EU642790.

Kermadecia elliptica Brongn. & Gris; *P. H. Weston 1639* (NSW238939); —, —, —, —, —, —, EU642784**.** ***K. pronyensis*** (Guillaumin) Guillaumin; *P. H. Weston 1661* (NSW240123); EU642692, EU642722, EU642661, EU642753, EU649758, EU649728, EU642783**.** ***K. sinuata*** Brongn. & Gris; *P. H. Weston 1844* (NSW368719); —, —, —, —, —, —, EU642785.

Lambertia formosa Sm.; *A. R. Mast & D. S. Feller 218* (NSW421323); EU642683, EU642713, EU642651, EU642743, EU649750, EU649718, —.

Macadamia claudiensis C.L.Gross & B.Hyland; *LCR 865525* (NSW 397498); EU642703, EU642733, EU642673, EU642765, EU649768, EU649740, EU642799**.** ***M. grandis*** C.L.Gross & B.Hyland; *K. H. Downs 95* (NSW410462); EU642701, EU642731, EU642670, EU642762, —, EU649737, EU642796**.** ***M. hildebrandii*** Steenis; Acc. HMAC35 from Steiger et al. (2003); —, —, —, —, —, —, EU642795**.** ***M. integrifolia*** Maiden & Betche; *FTG 355A* (WIS); AY823204, AY837827, EU642672, EU642764, EU649739, AY829522, —; P. H. Weston 2055 (NSW410513); —, —, —, —, —, —, EU642798**.** ***M. jansenii*** C.L.Gross & P.H.Weston; *P. H. Weston 1860* (NSW368737); EU642706, EU642736, EU642676, EU642768, EU649770, EU649743, EU642802. ***M. ternifolia*** F.Muell.; *P. H. Weston 2798* (NSW746281); EU642705, EU642735, EU642675, EU642767, —, EU649742, —; *P.H. Weston 1961* (NSW397476); —, —, —, —, —, —, EU642801**.** ***M. tetraphylla*** L.A.S.Johnson; *P. H. Weston 2853* (NSW750090); EU642704, EU642734, EU642674, EU642766, EU649769, EU649741, —; *K. H. Downs 94* (NSW410460); —, —, —, —, —, —, EU642800. ***M. whelanii*** (F.M.Bailey) F.M.Bailey; K. H. Downs 96 (NSW410463); EU642702, EU642732, EU642671, EU642763, EU649767, EU649738, EU642797**.** ***Malagasia alticola*** (Capuron) L.A.S.Johnson & B.G.Briggs; *Schatz 3586* (MO); EU642695, EU642725, EU642664, EU642756, EU649761, EU649731, EU642788.

Nelumbo lutea Pers.; Braun et al. s.n. (FSU); EU642710, EU642740, EU642680, EU642772, EU649747, EU649747, —.

Orites diversifolius R.Br.; *J. Allen s.n.* (NSW701096); EU642686, EU642716, EU642654, EU642746, EU649753, EU649721, —. ***O. megacarpus*** A.S.George & B.Hyland; *P. H. Weston 3011* (NSW745445); EU642687, EU642717, EU642655, EU642747, —, EU649722, EU642775. *A. Ford 4795* (QRS); —, —, —, —, —, —, EU642776.

Panopsis cinnamomea Pittier; P. Kater s.n. (NSW408045); EU642708, EU642738, EU642678, EU642770, EU649772, EU649745, EU642804**.** ***P. ferruginea*** Pittier; *V. Plana 34* (K); —, —, —, —, —, —, EU642807**.** ***P. lozanoi*** L.E.Gutiérrez-H.; *V. Plana 37* (K); —, —, —, —, —, —, EU642806**.** ***P. yolombo*** (Posada) Killip; *V. Plana 47* (NSW461816, K); —, —, —, —, —, —, EU642805**.** ***Platanus occidentalis*** Hook. & Arn.; *A. R. Mast s.n.* (FSU); EU642711, EU642741, EU642681, EU642773, EU649748, EU649748, —.

Roupala montana Aubl.; *P. H. Weston 2038* (NSW399358); EU642684, EU642714, EU642652, EU642744, EU649751, EU649719, —.

Sleumerodendron austrocaledonicum (Brongn. & Gris) Virot; *P. H. Weston 2505* (NSW471678); EU642690, EU642720, EU642659, EU642751, EU649756, EU649726, EU642781.

Turrillia lutea (Guillaumin) A.C.Sm.; *E. A. Brown s.n.* (NSW750450); EU642691, EU642721, EU642660, EU642752, EU649757, EU649727, —. *P. Kater* (NSW365783); —, —, —, —, —, —, EU642782.

Virotia leptophylla (Guillaumin) L.A.S.Johnson & B.G.Briggs; *P. H. Weston 2763* (NSW702017); —, —, —, —, —, —, EU642792**.** ***V. neurophylla*** P.H.Weston & A.R.Mast; *P. Kater s.n.* (NSW417651); EU642698, EU642728, EU642667, EU642759, EU649764, EU649734, EU642791.

APPENDIX 2. Exemplar specimens used to code the morphological data matrix.

Taxon—Specimens for (1) seedling characters; (2) juvenile foliage characters; (3) adult foliage and flowers characters; (4) fruit characters.

Athertonia diversifolia (C.T.White) L.A.S.Johnson & B.G.Briggs; *P. Kater* (NSW365777); *P. H. Weston 2760* (NSW700970, NSW 702012-5); *B. Gray 5416* (NSW537419); *B. Gray 3302* (NSW621526).

Banksia serrata L.f.; *P. Kater* (NSW415551); —; *R. Coveny 5360* (NSW638695); *P. Hind 5656* (NSW212825). ***Bleasdalea bleasdalei*** (F.Muell.) A.C.Sm. & J.E.Haas; *P. H. Weston 932a* (NSW666093); *P. H. Weston 1823* (NSW360126); *P. H. Weston 806* (NSW225397); *C. L. Gross 92-87* (NSW395160). ***Brabejum stellatifolium*** L.; *P. Kater* (NSW391575); *P. H. Weston 2044* (NSW403139); *J. P. Rourke 3321* (NSW652981); *H. Kurzweil 1501* (NSW652983).

Cardwellia sublimis F.Muell.; *P. H. Weston 1819* (NSW297061); *L. A. S. Johnson* (NSW511564); *P. H. Weston 3018* (NSW750758); *B. J. Wallace 83141* (NSW222963). ***Carnarvonia araliifolia*** F.Muell.; *P. H. Weston 1822* (NSW360125); *P. H. Weston 951* (NSW208594); *B. Gray 1250* (NSW561658); *B. Hyland 11336* (NSW699177). ***Catalepidia heyana*** (F.M.Bailey) P.H.Weston; *P. H. Weston 937* (NSW208584); *P. H. Weston 2008* (NSW397447); *P. H. Weston 793* (NSW666080); *P. H. Weston 937* (NSW208584).

Euplassa duquei Killip & Cuatrec.; *V. Plana 52* (NSW666085); —; *V. Plana 53* (NSW666092); *V. Plana 52* (NSW666085). ***E. inaequalis*** Engl.; —; —; *J.A. Ratter 435* (NSW666086); —.

Floydia praealta (F.Muell.) L.A.S.Johnson & B.G.Briggs; *P. Kater* (NSW391695); —; *W. Bauerlen* (NSW168163); *L.A.S. Johnson* (NSW372615).

Gevuina avellana Molina; *P. Kater* (NSW391571); *P. H. Weston 1992* (NSW397516); *J. Allen* (NSW471558); *C. S. Sargent* (NSW666091). ***Grevillea caleyi*** R.Br.; *P. Kater* (NSW415572); —; *R. O. Makinson 594* (NSW279580); *G. D'Aubert 634* (NSW223650).

Heliciopsis lobata (Merr.) Sleumer; —; *P.H. Weston 2014* (NSW438593); —; —. ***H. velutina*** (Prain) Sleumer; *E. F. deVogel 1074* (L); *J. Sinclair 9976* (L); *A. J. G. H. Kostermans 4364* (L); *E. F. deVogel 1074* (L). ***Hicksbeachia pinnatifolia*** F.Muell.; *P. Kater* (NSW415573); *L. S. Smith 5114* (BRI183089); *P. H. Weston 2015* (NSW397469-397470); *P. H. Weston 2550* (NSW477121).

Kermadecia elliptica Brongn. & Gris; *P. H. Weston 1639* (NSW232260); *P. H. Weston 1639* (NSW238939); *G. McPherson 1945* (NSW 666095, NSW666097); —. ***K. pronyensis*** (Guillaumin) Guillaumin; —; *P. H. Weston 1661* (NSW240123); *P. H. Weston 1661* (NSW239094); *J. M. Veillon 6467* (NSW666098). ***K. rotundifolia*** Brongn. & Gris; —; *Odricourt 830* (NOU); *G. McPherson 2977* (NSW666096); —. ***K. sinuata*** Brongn. & Gris; *P. Kater* (NSW240331-2, NSW240334-5); *P. H. Weston 1668* (NSW239211); *P. H. Weston 1673* (NSW232139, NSW232256); *P. H. Weston 1673* (NSW239223).

Lambertia formosa Sm.; *P. Kater* (NSW392460); —; *P. H. Weston 2021* (NSW399134); *T. James 52* (NSW571765).

Macadamia claudiensis C.L.Gross & B.Hyland; *P. Kater* (NSW415577); *P. H. Weston 1974* (NSW397498); *B. Gray 3236* (NSW264497, 264650); *B. P. M. Hyland 12424* (NSW264507). ***M. erecta*** J.A.McDonald & Ismail R.; —; —; *M. M. J. van Balgooy 3393* (NSW261961, L); *H. Iking 8* (L); —. ***M. grandis*** C.L.Gross & B.Hyland; —; *P. H. Weston 988* (NSW256081); *G. C. Stocker 1720* (NSW264501); *B. Gray 2864* (NSW264506). ***M. hildebrandii*** Steenis; —; —; *M. M. J. van Balgooy 3832* (NSW261981, NSW261983, L); *Boschproefel Cel/III-23* (L). ***M. integrifolia*** Maiden & Betche; *P. Kater* (NSW415504); *J. G. Tracey* (NSW257872); *C. W. E. Moore* (NSW256079); *P. H. Weston 2055* (NSW410513). ***M. jansenii*** C.L.Gross & P.H.Weston; *P. Kater* (NSW415576); *P. H. Weston 1860* (NSW368737); *P. H. Weston 3040* (NSW749921); *R. C. Jansen* (NSW257721). ***M. ternifolia*** F.Muell.; *P. H. Weston 1961* (NSW397476); *P. H. Weston 2798* (NSW746281); *P. I. Forster 27495* (NSW674596); *I. McConochie* (NSW395729). ***M. tetraphylla*** L.A.S.Johnson; —; *K. M. Downs 94* (NSW410460); *A. G. Floyd 1349* (NSW256103); *R. F. Thorne 25898* (NSW130633). ***M. whelanii*** (F.M.Bailey) F.M.Bailey; —; *P. H. Weston 990* (NSW208622); *P. I. Forster 29793* (NSW536827); *B. P. M. Hyland 11483* (NSW264513). ***Malagasia alticola*** (Capuron) L.A.S.Johnson & B.G.Briggs; —; —; *R. Capuron 18360* (K); —.

Orites diversifolius R.Br.; —; *R. Parsons 125/87* (NSW203027); *P. H. Weston 2997* (NSW735001); *P. H. Weston 2000* (NSW397524). ***O. megacarpus*** A.S. George & B.Hyland; *A. Ford* (QRS); *P. H. Weston 3011* (NSW745445); *M. Godwin C2960* (NSW 562525); *B. Hyland 14090* (NSW541387).

Roupala montana Aubl.; *P. Kater* (NSW415507); *P. H. Weston 2038* (NSW399358); *M. Saldias 740* (NSW666089); *B. Manara* (NSW666090).

Sleumerodendron austrocaledonicum (Brongn. & Gris) Virot; *P. Kater* (NSW240337); *P. H. Weston 1638* (NSW2368938); *G. McPherson 6357* (NSW666088); *P. H. Weston 1662* (NSW239206).

Turrillia ferruginea (A.C.Sm.) A.C.Sm.; *P. Kater* (NSW391705); *A. C. Smith 8567* (BISH); *A. C. Smith 8227* (BISH); *A. C. Smith 8797* (GH). ***T. lutea*** (Guillaumin) A.C.Sm.; *P. Kater* (NSW391704); *P. Kater* (NSW365778); *A. N. Gillison RSNH3513* (NSW666100); *P. Cabalion 893* (NSW666099). ***T. vitiensis*** (Turrill) A.C.Sm.; —; —; *H.U. Stauffer 5823* (NSW82301); *S. Vodonaivalu* (NSW417900).

Virotia angustifolia P.H.Weston & A.R.Mast; —; —; *M. Mackee 1966* (NSW666081); —. ***V. francii*** P.H.Weston & A.R.Mast; *P. H. Weston 1679* (NSW232292); *P. H. Weston 1679* (NSW232295); *P. H. Weston 1677* (NSW239229); *P. H. Weston 1679* (NSW239231). ***V. leptophylla*** (Guillaumin) L.A.S.Johnson & B.G.Briggs; *P. H. Weston 1640* (NSW238940); *P. H. Weston 1640* (NSW232257); *P. H. Weston 2763* (NSW702017); *G. McPherson 3220* (NSW666101). ***V. neurophylla*** P.H.Weston & A.R.Mast; *P. Kater s.n.* (NSW417651); —; *P. H. Weston 1676* (NSW 232290); *P. H. Weston 1676* (NSW 239228). ***V. roussellii*** P.H.Weston & A.R.Mast; —; *G. McPherson 2868* (NSW666082); *M. Vieillard 2153* (NSW666103); *H. S. McKee* (NSW666102). ***V. vieillardii*** P.H.Weston & A.R.Mast; —; —; *G. McPherson 6289* (NSW666083), —.