



REVIEW ARTICLE

Spatio-temporal history of the endemic genera of Madagascar

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Madagascar is renowned for its unparalleled species richness and levels of endemism, which have led, in combination with species extinction caused by an unprecedented rate of anthropogenic deforestation, to its designation as one of the most important biodiversity hotspots. It is home to 10 650 species (84% endemic) of angiosperms in 1621 genera (19% endemic). During the last two centuries, botanists have focused their efforts on the provision of a taxonomic framework for the flora of the island, but much remains to be investigated regarding the evolutionary processes that have shaped Madagascan botanical diversity. In this article, we review the current state of phylogenetic and biogeographical knowledge of the endemic angiosperm genera. We also propose a new stratified biogeographical model, based on palaeogeographical evidence, allowing the inference of the spatio-temporal history of Madagascan taxa. The implications of past climate change and extinction events on the evolutionary history of the endemic genera are also discussed in depth. Phylogenetic information was available for 184 of the 310 endemic genera (59.3%) and divergence time estimates were available for 67 (21.6%). Based on this evidence, we show the importance of phylogenetic clustering in the assemblage of the current Madagascan diversity (26% of the genera have a sister lineage from Madagascar) and confirm the strong floristic affinities with Africa, South-East Asia and India (22%, 9.1% and 6.2% of the genera, respectively). The close links with the Comoros, Mascarenes and Seychelles are also discussed. These results also support an Eocene/Oligocene onset for the origin of the Madagascan generic endemic flora, with the majority arising in the Miocene or more recently. These results therefore de-emphasize the importance of the Gondwanan break-up on the evolution of the flora. There is, however, some fossil evidence suggesting that recent extinctions (e.g. Sarcocollaenaceae, a current Madagascan endemic, in southern Africa) might blur vicariance patterns and favour dispersal explanations for current biodiversity patterns. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **171**, 304–329.

ADDITIONAL KEYWORDS: biodiversity hotspot – biogeography – conservation – divergence time estimation – molecular phylogenetics – taxonomy.

INTRODUCTION

Madagascar is located in the south-western Indian Ocean and is a significant distance from other large landmasses, such as Africa (450 km), India (3800 km), Indonesia (5600 km) and Australia (6800 km). The

unique richness of the Madagascan biodiversity and its unparalleled levels of endemism have been acknowledged since the first naturalists set foot on the island in the 1700s (see, for example, Perrier de la Bâthie, 1936; Goodman & Benstead, 2005; Yoder & Nowak, 2006). As an example of this unique diversity, Madagascar is home to 11 220 species of vascular plants, > 80% of which are endemic (Callmander *et al.*,

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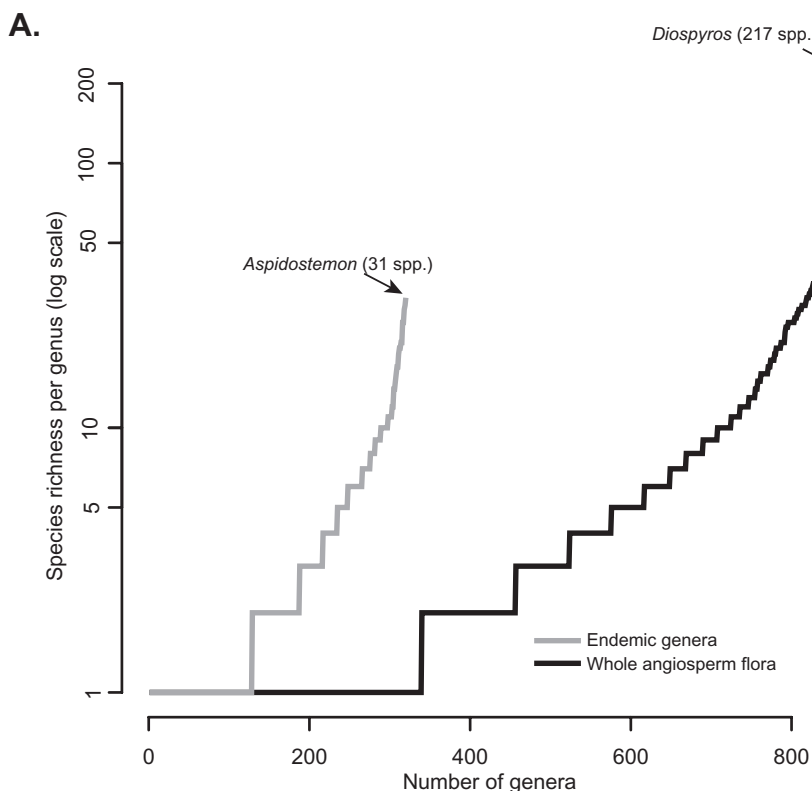


Figure 1. A, Comparison of species richness per genus between the Madagascan endemic genera (in grey) and the whole angiosperm flora on this island (in black). There are some nonendemic genera that were not included in this plot because of a lack of taxonomic knowledge leading to unreliable species richness estimations. The y axis was log transformed. See Table 1 for data on the Madagascan endemic genera and the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue, 2012) for the other genera. B, Phylogenetic positions of the endemic Madagascan genera following the Angiosperm Phylogeny Group (APG) III system (APG III, 2009). The number of families per order is also provided in parentheses, as well as the endemic families (including Didiereaceae).

2011). The angiosperm component represents 95% of the whole flora, 10 650 species (84% endemic) distributed in 1621 genera (19% endemic) (Callmander *et al.*, 2011). Madagascar has been designated one of the most important biodiversity hotspots, mainly because of the unprecedented rate of deforestation that threatens the survival of its biodiversity and therefore the sustainability of its ecosystems (Myers *et al.*, 2000). The island retains < 10% of its natural habitats compared with their original extent before the arrival of the first humans about 2000 years ago (Goodman & Benstead, 2005; for a description of vegetation types, the factors which threaten them and their conservation importance, see Moat & Smith, 2007).

During the last two centuries, botanists have focused mainly on providing a taxonomic framework, and little is known about the evolutionary processes involved in shaping the extant Madagascan flora. The main barrier preventing a better understanding

of these processes is the limited availability of well-supported molecular phylogenetic inferences that have been dated using robust calibrations from the fossil record. In this article, we provide a first step towards achieving this aim by reviewing the current state of knowledge of the endemic angiosperm genera. According to Callmander *et al.* (2011) and the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue, 2012), there are 310 endemic genera of angiosperms in Madagascar (c. 19% of the generic diversity), comprising 1227 species (11.5% of the species richness) (Table 1). In these genera, one-third have only one species, but there are a few genera with > 20 species (e.g. *Aspidostemon* Rohwer & H.G.Richt., Lauraceae, with 31 species; Fig. 1A). We focus on these taxa because the current taxonomic and phylogenetic knowledge of the Madagascan angiosperm flora remains limited. Only species-level phylogenetic trees will allow a more accurate estimation of the number of colonization events to

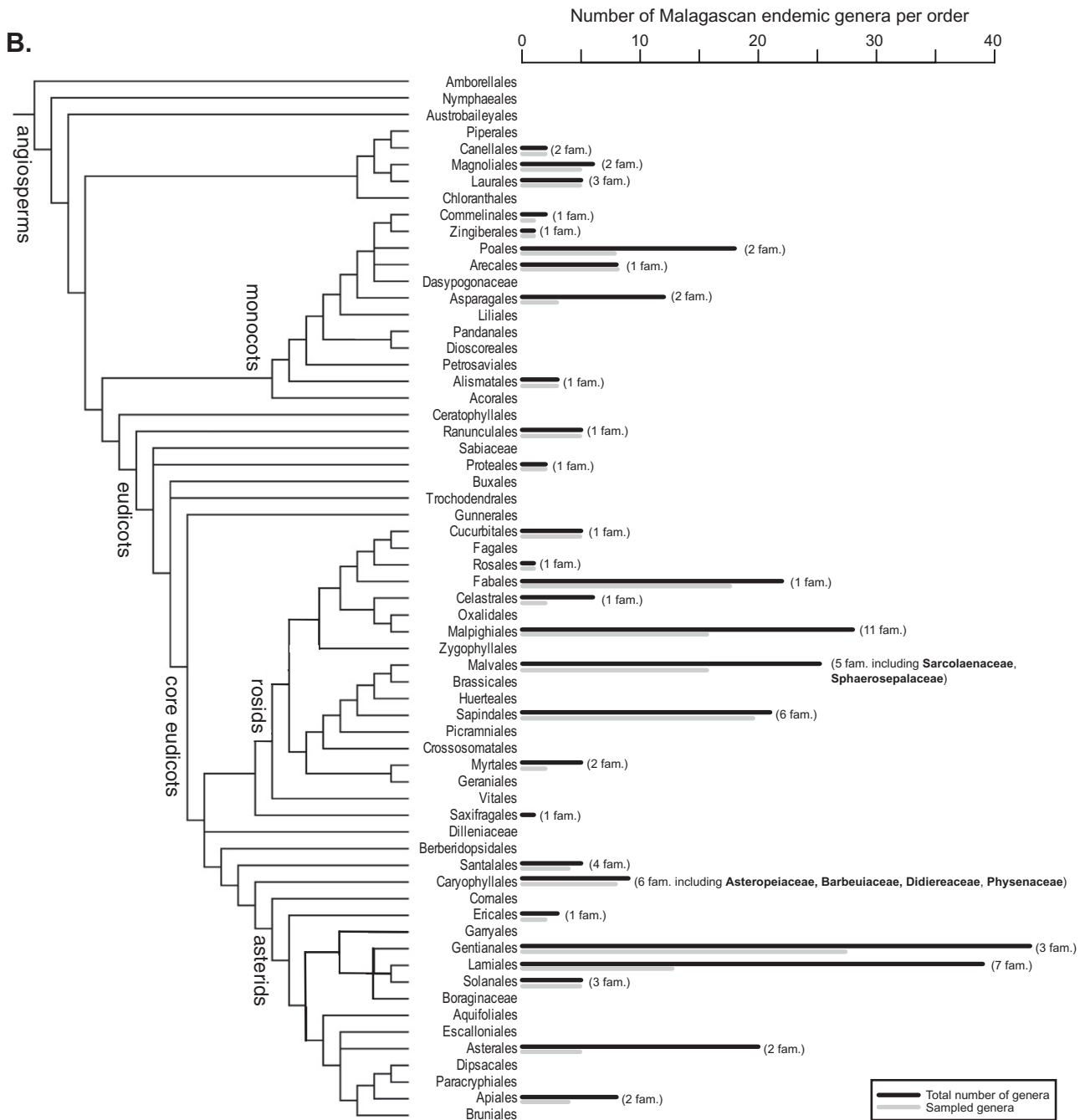


Figure 1. *Continued*

Madagascar by species of more widespread genera. For instance, results from the species-rich genera *Pandanus* Parkinson (Pandanales; Buerki *et al.*, 2012a) and *Impatiens* L. (Balsaminaceae; Yuan *et al.*, 2004) involved one and several events of colonization to the island, respectively. Therefore, by focusing on the endemic genera, we maximize the chances of addressing these issues using only monophyletic plant radiations. To infer the biogeographical affini-

ties of this element of the flora with other areas, only the genera already included in a phylogenetic framework and retrieved as monophyletic will be considered further. In this review, we also propose a worldwide stratified biogeographical model, based on palaeogeographical evidence, that will prove fundamental to infer the spatio-temporal history of the Malagascan flora. Finally, the implications of past climate change on the origin of these elements of the

flora are discussed in depth based on palaeobotanical evidence and divergence time estimation data.

MATERIAL AND METHODS AND PRELIMINARY RESULTS

For this review, the list of the 310 endemic Madagascan genera was compiled based on the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue, 2012). At the generic level, the phylogenetic position of the endemic Madagascan genera appears to be well distributed over the Angiosperm Phylogeny Group (APG) phylogenetic tree (in 28 of the 63 orders; APG III, 2009; Fig. 1B). The five orders with the highest generic diversity are Gentianales (43 genera), Lamiales (39 genera), Malpighiales (28 genera), Fabales (22 genera) and Sapindales (21 genera) (see Table 1 for more details). The endemic families Asteropeiaceae and Physenaceae and the endemic subfamily Didiereoideae (Didiereaceae) belong to Caryophyllales, whereas Sarcocaulaceae and Sphaerosepalaceae are included in Malvales (Fig. 1B). With the exception of Didiereaceae (Arakaki *et al.*, 2011), the understanding of phylogenetic relationships in these families remains limited and further work is needed (Fig. 1B; Table 1). Phylogenetic information for 184 endemic genera was compiled by querying the GenBank database (last accessed 26 October 2012), and DNA sequences for ten additional genera that were not included in any published phylogenetic studies (Table 1) were found. In most of the studies considered, the main aim of the analysis of the Madagascan endemic genera was to support systematic work (i.e. generic and species circumscriptions and the assessment of the position and monophyly of a particular genus). Consequently, there are very few studies investigating the spatio-temporal histories of these taxa (but see, for example, Renner *et al.*, 2010, Monimiaceae; Wikström *et al.*, 2010, Rubiaceae; however, the latter study lacks a dating framework), and data on divergence time estimates are also scarce; we have compiled this type of data for only 67 genera.

If the taxon sampling used in a particular study to infer phylogenetic relationships was judged to be adequate (i.e. sampling covering the whole distribution of the family, reasonable phylogenetic resolution and a monophyletic genus), the distribution of the sister lineage was scored using area circumscriptions defined as follows: (A) Madagascar region (including Madagascar, the Seychelles archipelago, Mascarenes and Comoros); (B) India (including Sri Lanka); (C) mainland Africa; (D) Australia, New Guinea, New Caledonia and New Zealand; (E) South-East Asia and the Pacific islands; (F) Eurasia; (G) South America;

and (H) North America. This area circumscription was used to propose a new worldwide biogeographical model (adapted from Buerki *et al.*, 2011a; see below) to constrain ancestral area reconstructions based on palaeogeography. To assess the biogeographical affinities of the Madagascan endemic genera with the other regions, we further split area A into two subareas: (A) Madagascar and (A') Mascarenes, Comoros and Seychelles. Data on the distribution of the genera were retrieved either from the source publication (see Table 1) or from the general literature (e.g. Schatz, 2001; Mabberley, 2008). Biogeographical affinities of the Madagascan genera with the other areas were assessed by assigning a score of 1.0 to the area in which the sister lineage was found. This value of 1.0 was divided by the number of areas in which a sister lineage was found if the latter had a widespread distribution (i.e. found in more than one area). This scoring scheme differed from that used by Yoder & Nowak (2006), which assigned a score of 1.0 to all areas. By the application of this approach, we minimized the effect of widespread taxa on the estimations of affinities between areas. In addition to scoring the distribution of the sister lineage, we also reported the name of its component(s) (Table 1). Based on this matrix, the distribution of the Madagascan sister lineages was assessed (as percentages). This biogeographical approach does not allow for the assessment of dispersal directionality, but quantifies affinities between floras/areas. The examination of the symmetry (or asymmetry) of dispersals between areas through time can only be inferred using biogeographical methods (see Buerki *et al.*, 2011a). If available, we recorded the stem age of the endemic Madagascan genera and the age of the node subtending it. We have recorded these two ages because, without inferring the biogeographical scenario (and taking extinction into account), it remains difficult to estimate the time of dispersal of the lineage to the island. In addition, as further discussed below, many endemic Madagascan genera tend to share a common ancestor (i.e. they form clades), and therefore this approach provided a conservative estimate of the colonization of the whole lineage on the island. Finally, as a first attempt to investigate the effect of ecology on the evolutionary history of the Madagascan endemics, genera were assigned to one of three habitat types: (1) humid forest (including mountain forest); (2) dry forest; and (3) spiny bush (Moat & Smith, 2007).

A BIOGEOGRAPHICAL MODEL WITH COMMENTS ON THE ESTABLISHMENT OF BIOMES

In this section, we focus on the assessment of the influence of abiotic factors in shaping the current

Madagascan flora, based on palaeogeographical and palaeoclimatic evidence (Figs 2, 3). We also propose a worldwide stratified biogeographical model (adapted from Buerki *et al.*, 2011a) to investigate the spatio-temporal history of the Madagascan flora. The model is subdivided into four time slices as follows: (1) Early to Late Cretaceous (145–80 Mya); (2) Late Cretaceous to early Palaeocene (80.0–61.7 Mya); (3) middle Palaeocene to late Eocene (61.7–33.9 Mya); and (4) early Oligocene (33.9 Mya) to present (Figs 2, 3). The area circumscriptions used in this model are as described above. In the model, the Madagascan satellite islands are included in area A (mainly because of their relatively recent origin), but we refer to them separately when relevant. With the exception of the granitic Seychelles (estimated to have originated *c.* 85 Mya; Braithwaite, 1984), the other islands originated from the late Miocene onwards (Warren *et al.*, 2010; Fig. 2). In cases in which biogeographical reconstructions are to be inferred on taxa originating during this period (i.e. late Miocene onwards) and exhibiting high species richness in the region, the model could be modified by the addition of a fifth time slice. This would reflect the successive emergence of these islands and their implications in connecting areas, especially in the Quaternary (see Warren *et al.*, 2010). The biogeographical model described here will prove to be useful to constrain ancestral area reconstructions according to palaeogeographical evidence, using software such as Lagrange (Ree & Smith, 2008), and will be applicable to all plants. We describe below the rationale behind the proposed time slice delimitation.

TIME SLICE 1 (EARLY TO LATE CRETACEOUS, FIGS 2, 3A)

During this period, Pangaea was subdivided into two distinct continents isolated by the Tethyan Seaway: Laurasia and Gondwana (see Buerki *et al.*, 2011a and references cited therein). Movements between Laurasian and Gondwanan landmasses were practically impossible at that time, but dispersal across all areas within these landmasses was possible. South-East Asia (area E) did not come into existence until the early Palaeocene (60 Mya), and thus this area was not included in time slice 1 (for more details, see Metcalfe, 1998). During this period, Madagascar had already separated from Africa as a result of continental drift, but remained in close proximity to India (forming the Indo/Madagascan subcontinent) until the Late Cretaceous (Figs 2, 3A). At that point, the Indo/Madagascan subcontinent broke apart and India started to drift north-eastwards towards the Eurasian plate, but dispersals between these two areas might have remained possible via the Seychelles archipelago (Braithwaite, 1984; Fig. 3). During its northern

migration, the position of India greatly influenced the rainfall regime on Madagascar by blocking the moisture coming from the east in the Proto-Indian Ocean (Yoder & Nowak, 2006). There is also a growing body of evidence suggesting possible dispersals between Madagascar and South America via Antarctica until about 80 Mya, despite the fact that these regions were not in direct contact (see Fig. 2; Yoder & Nowak, 2006). Based on this evidence, it is now widely accepted that vicariance-mediated speciation was the main biogeographical process that shaped the Madagascan flora prior to 80 Mya, whereas dispersal-mediated speciation became predominant from this point onwards (Fig. 2).

TIME SLICE 2 (LATE CRETACEOUS TO EARLY PALAEOCENE, FIGS 2, 3B)

Gondwanan landmasses, despite ongoing fragmentation during this period, remained in contact until the early Palaeocene, with the exception of South America and Africa as a result of the expansion of the South Atlantic Ocean (Buerki *et al.*, 2011a; Fig. 3B). In the case of Madagascar, India, Africa and Australia, this connection was mediated by the Kerguelen Plateau (and Antarctica), acting as a land bridge between these areas until the end of the Cretaceous (see Sanmartin & Ronquist, 2004 and references cited therein). Likewise, South America, Australia, New Zealand and New Caledonia remained connected with Antarctica until the Late Cretaceous (65–60 Mya), when New Zealand and New Caledonia drifted away from West Antarctica, breaking land connections with Australia and South America (Sanmartin & Ronquist, 2004). Finally, proto-South-East Asia (the south-east part of the Malaysian peninsula and south-west Borneo) was in place in the Late Cretaceous–early Palaeocene (see Fig. 2 in Metcalfe, 1998), such that dispersal between Eurasia and this part of South-East Asia was possible (Fig. 3B; see Buerki *et al.*, 2011a).

TIME SLICE 3 (MIDDLE PALAEOCENE TO LATE EOCENE; FIGS 2, 3C)

During the Palaeocene, India mediated dispersals between proto-South-East Asia, Madagascar and Africa, whilst drifting rapidly northwards, heading for an imminent collision with Eurasia. Several studies have discussed the similarities between the Madagascan and Indian floras by invoking a direct pathway of dispersal via islands in the Indian Ocean (e.g. Schatz, 1995); the continental dispersal route via Arabia–Socotra (Africa) was largely neglected, but it is now modelled here. This route was inferred by Yuan *et al.* (2005) to explain the current distribution

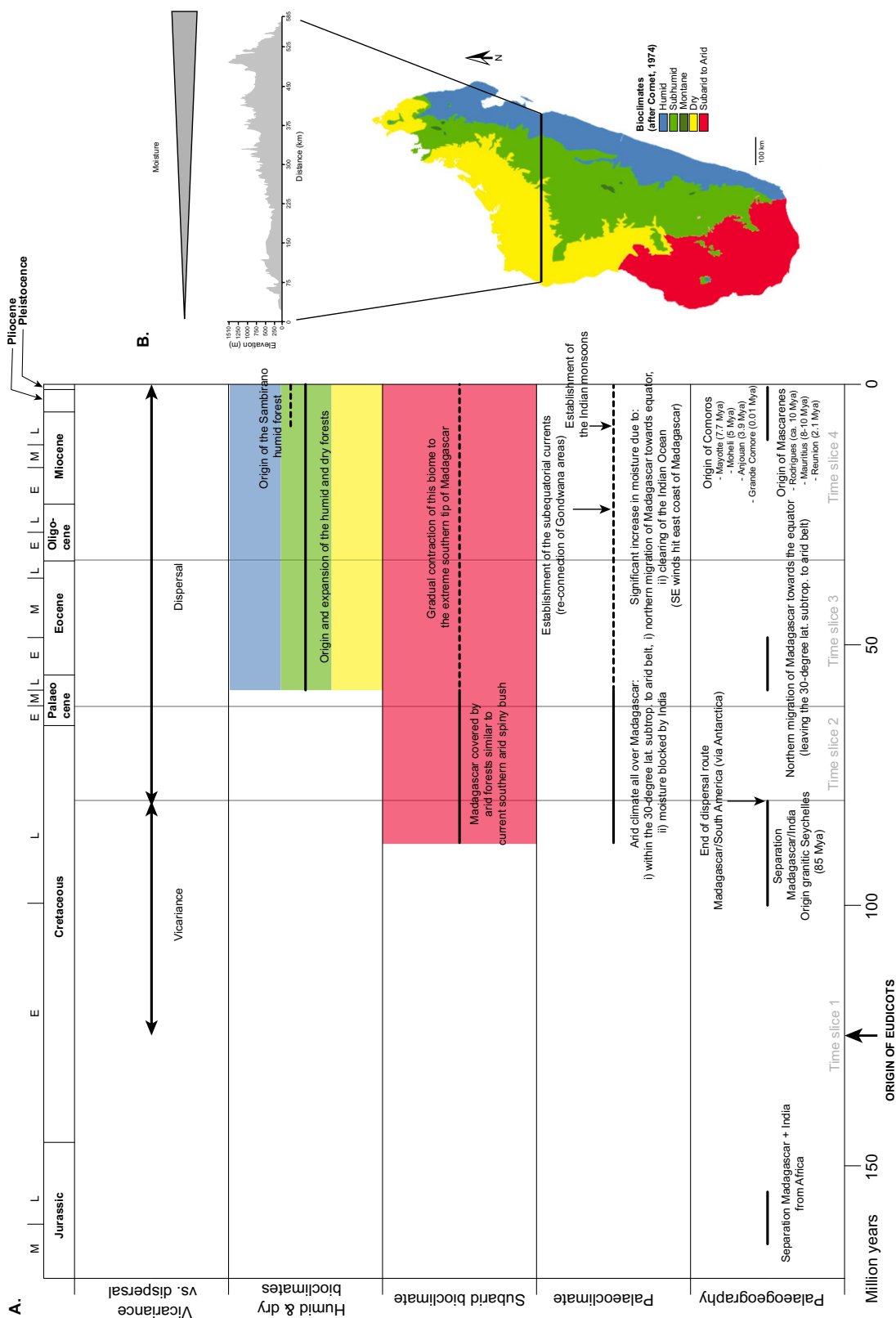
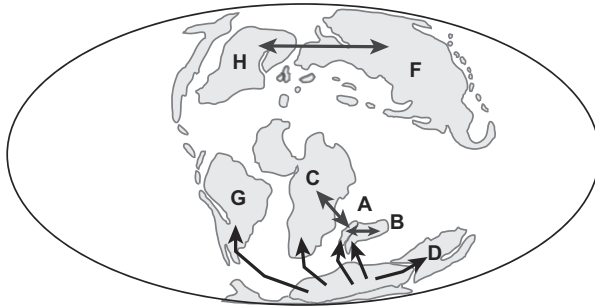
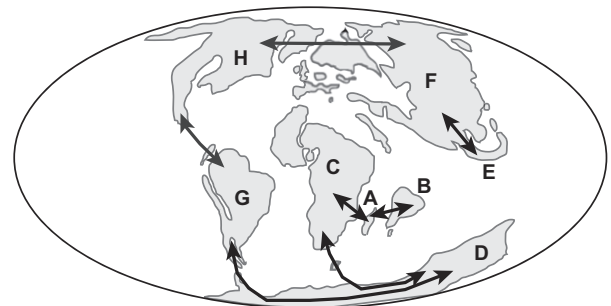


Figure 2. A, Palaeogeographical history of Madagascar showing the establishment of bioclimates and biomes (see text for more details). B, The five major bioclimates (Cornet, 1974, adapted by Schatz, 2000) in Madagascar and an elevation profile.

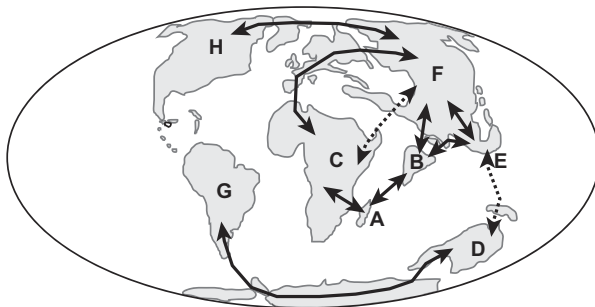
A. Timeslice 1: Early to Late Cretaceous (145 to 80 Mya)



B. Timeslice 2: Late Cretaceous to early Palaeocene (80 to 61.7 Mya)



C. Timeslice 3: middle Palaeocene to late Eocene (61.7 to 33.9 Mya)



D. Timeslice 4: early Oligocene (33.9 Mya) to present

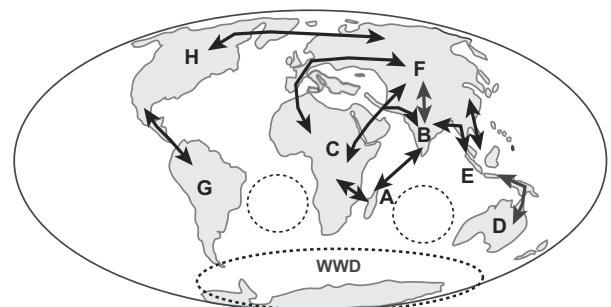


Figure 3. Stratified worldwide biogeographical model adapted from Buerki *et al.* (2011a). The model is subdivided into four time slices. Abbreviations of the biogeographical areas: (A) Madagascar region (including Madagascar, the Seychelles archipelago, Mascarenes and Comoros); (B) India (including Sri Lanka); (C) mainland Africa; (D) Australia, New Guinea, New Caledonia and New Zealand; (E) South-East Asia and the Pacific islands; (F) Eurasia; (G) South America; and (H) North America. The full lines refer to dispersal probabilities of unity in the model, whereas broken lines refer to probabilities of 0.5 (for more details, see Buerki *et al.*, 2011a).

of *Exacum* L. (Gentianaceae). Also during this period, Africa and Madagascar started a northward migration towards the equator (which created a path of dispersal between Gondwanan and Laurasian landmasses), leaving the subtropical and arid belt at 30° latitude (Wells, 2003; Fig. 2). This northward migration greatly influenced the vegetation on Madagascar, causing a shift from a dry/arid to a more humid environment (Wells, 2003; Fig. 2). Before it drifted north, Madagascar had a much drier climate because of its geographical position and the limited amount of moisture reaching the island from the Proto-Indian Ocean (Fig. 2; Yoder & Nowak, 2006 and references cited therein). According to Wells (2003), the conjunction of these abiotic factors resulted in the emergence of arid forests all over Madagascar that were similar in nature to the extant spiny bush vegetation (referred to as the subarid bioclimate by Cornet, 1974) currently confined to the southern part of the island (Fig. 2). The dramatic shift in rainfall regime that took place during the Eocene and onwards led

to the gradual replacement of the arid forests by three main bioclimate types from the humid biome (Fig. 2; Wells, 2003). These three ecotypes are the product of the orographic processes that led to the current Madagascan topography, which includes a steep eastward-facing slope on the eastern coast (ranging from sea level to *c.* 1500 m) and a more gentle slope that gradually descends to sea level on the western coast (Fig. 2B; Cornet, 1974).

TIME SLICE 4 (EARLY OLIGOCENE TO PRESENT; FIGS 2, 3D)

During this phase, climatic conditions on Earth shifted and there was a change from a relatively ice-free world to one with glacial conditions in polar regions, characterized by the presence of substantial ice sheets (Bowen, 2007). This glaciation resulted in a drastic drop in sea level (leading to the emergence of islands between Madagascar and India that could have acted as stepping stones for dispersal; Warren

et al., 2010), induced drought in southern regions (especially in Africa and Australia; Bowen, 2007) and a subsequent reduction in the width of the tropical belt (see Morley, 2003). In the same time span, the collision of the Australian and Eurasian plates resulted in intensive volcanic activity (Buerki *et al.*, 2011a and references cited therein) and created most of the islands in South-East Asia (e.g. Sumatra, part of Borneo, Celebes, the Inner Banda Arc). These climatic and geological events (especially the emergence of South-East Asia) opened up new pathways of dispersal, allowing plants to colonize various parts of the world, including Madagascar. After the Miocene climatic optimum (Zachos *et al.*, 2001), a second drought period was recorded, persisting until the Pleistocene, and this correlated with the establishment of several deserts, C₄ grasslands and the radiation of major succulent lineages (see Micheels, Eronen & Mosbrugger, 2009; Arakaki *et al.*, 2011 and references cited therein).

This period also coincided with the establishment of the Mediterranean climate in the Cape region (South Africa; Buerki *et al.*, 2012b and references cited therein), which replaced a continuous subtropical humid forest shared between this region, Madagascar, Antarctica and South America (Coetzee & Muller, 1984). For instance, Nilsson, Coetzee & Grafstrom (1996) described fossil pollen grains from this region assigned to an extinct species of Sarcolaenaceae that is morphologically similar to extant species of the family currently viewed as endemic to Madagascar. This pattern suggests a wider distribution for this family before the middle Miocene, followed by extinctions driven by climate change in the region. This example is unlikely to be unique (for a discussion of New Caledonia, see, for example, Pillon, 2012) and, consequently, further palaeobotanical studies (with particular focus on the eastern coast of Africa) are critically needed to understand the biogeographical history of the Madagascan flora. Parametric biogeographical methods would need to be amended to take into account the distribution of fossil taxa. This need is well exemplified in the case of Sarcolaenaceae, where current biogeographical methods would infer Madagascar as the cradle of this family, which would be clearly ruled out if the fossil record were to be taken into account. Finally, the use of such new methods, together with the biogeographical model presented here, would allow the inference of more accurate and realistic dispersal routes.

Sometime during the Miocene onwards, the establishment of the equatorial and west wind drift currents allowed a certain level of reconnection between previously isolated Gondwanan areas via long-distance dispersal (Fig. 3D; Buerki *et al.*, 2011a). During the late Miocene (*c.* 8 Mya), an onset of heavy seasonal

rains was initiated, especially in the north-western Sambirano region in Madagascar, as a result of the establishment of the Indian monsoons (Fig. 2; Yoder & Nowak, 2006). This onset of heavy rain was advocated to be the cause of the expansion of the humid forest in the Sambirano region (Yoder & Nowak, 2006). Finally, the Comoros and Mascarene islands originated during the late Miocene and might have facilitated dispersals between Madagascar and Africa (via the Comoros) and Madagascar and India (Mascarenes and Seychelles) (Warren *et al.*, 2010; Fig. 2).

BIOGEOGRAPHY AND TEMPORAL FRAMEWORK OF THE ENDEMIC MADAGASCAN GENERIC FLORA

BIOGEOGRAPHICAL AFFINITIES OF THE ENDEMIC MADAGASCAN GENERA

The biogeographical patterns and divergence time estimates retrieved here are displayed in Figures 4 and 5. A lack of information on the biogeography and palaeobotany of each group has prevented what was initially intended, namely the combination of these data to infer the main routes of dispersal through time, based on palaeogeography. Consequently, we only discuss biogeographical affinities between areas and investigate the impact of past climate change on the origin of Madagascan endemic genera.

As demonstrated previously (e.g. Yoder & Nowak, 2006), the Madagascan endemic genera share extensive biogeographical affinities with African taxa (22.4%; Fig. 4). This affinity could easily be explained by the close geographical proximity of these areas through time, and agrees with past (Leroy, 1978) and current (Gautier *et al.*, 2012) floristic views. This floristic similarity was even higher before the establishment of the Mediterranean climate in the Cape region (during the middle Miocene; Coetzee & Muller, 1984), as demonstrated by the discovery of fossils of Sarcolaenaceae in this region. The strong connections between the Madagascan, South-East Asian (9.1%; see Schatz, 1995) and Indian (6.2%; Warren *et al.*, 2010) biota are also confirmed by our data (Fig. 4). In this context, India could have acted as a land bridge, but further dated inferences are required to assess this hypothesis. In addition, further data will also be crucial to investigate the importance of the African continental route of dispersal connecting Madagascar with India and, to some extent, South-East Asia via Arabia and Socotra (see above; Figs 3, 4). Finally, in the Madagascar region, the Mascarenes exhibit the highest biogeographical affinity with Madagascar (58.3%), followed by the Comoros (37.5%) and Seychelles (4.1%) (Fig. 4). These figures were compiled by considering sister lineages restricted to a maximum of

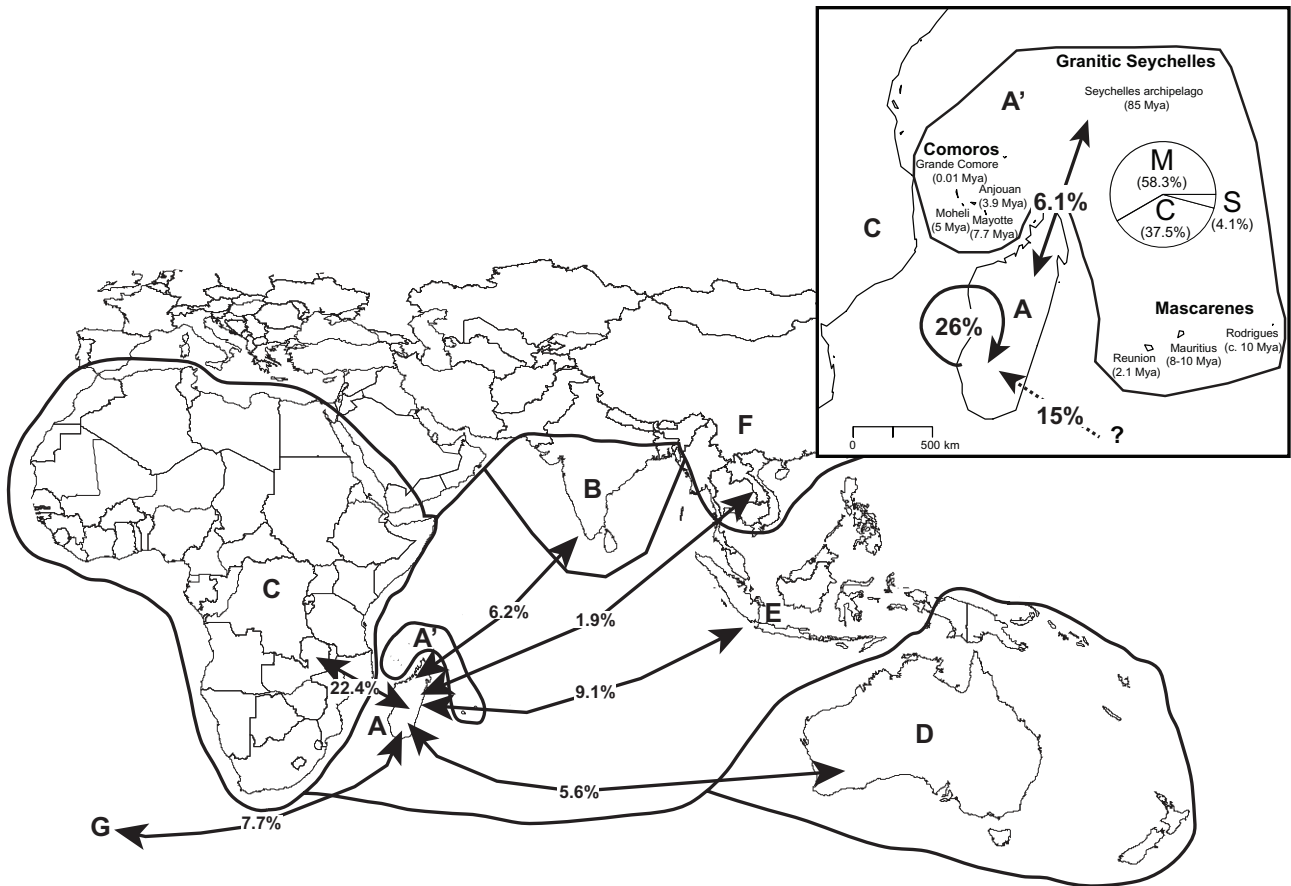


Figure 4. Biogeographical affinities of the Madagascan endemic genera (in percentages). See text for details related to the compilation of the data used here and in Table 1. The pie chart in the inset refers to the occurrence of sister lineages in the Mascarenes (M), Comoros (C) and the Seychelles (S) based on sister lineages occurring in a maximum of three areas (see text). The biogeographical affinities of some widespread genera (15% of cases) remain unclear.

three areas (most of the time, these areas were Africa, Madagascar and one of these islands). It should be noted, however, that the relationship between the Madagascan, Mascarene and Comoros floras is most certainly underestimated by this analysis, as it is limited to genera endemic to Madagascar. Indeed, these satellite islands share a lot of diversity with Madagascar, such as *Didymeles* Thouars (Buxaceae; Schatz, 2001) and *Oncostemum* A.Juss. (Primulaceae; Bone *et al.*, 2012) with the Comoros, *Molinaea* Comm. ex Juss. (Sapindaceae; Buerki *et al.*, 2011b) with the Mascarenes and *Martellidendron* (Pic. Serm.) Callm. & Chassot (Pandanaeae; Callmander *et al.*, 2003; Buerki *et al.*, 2012a) with the granitic Seychelles. In addition, to further demonstrate the affinities between these floras, Wikström *et al.* (2010) inferred the origin of almost all the taxa of Rubiaceae found in these satellite islands to be Madagascar. Further studies focusing on the biogeography and tempo of diversification of the Madagascan flora will need to consider these additional genera [for an example on

Psiadia Jacq. (Asteraceae), see Strijk *et al.*, 2012], but, for the moment, the information required to undertake such a task is not available.

TEMPO OF ORIGIN OF THE MADAGASCAN ENDEMIC GENERA

With the exception of *Hazomalania* Capuron (Hernandiaceae) and *Dilobeia* Thouars (Proteaceae), which originated during the Cretaceous, the current data suggest that the endemic Madagascan genera originated from the middle Eocene/Oligocene onwards, with most of the genera appearing in the Miocene (Fig. 5). These results confirm the current trend in ruling out the importance of the Gondwanan break-up on shaping the current Madagascan flora (as proposed by Leroy, 1978). One of the only genera that might have been sufficiently old (> 80 Mya; Fig. 2) to have been influenced by vicariance speciation triggered by the break-up of Gondwana is *Takhtajania* Baranova & J.-F. Leroy (Winteraceae;

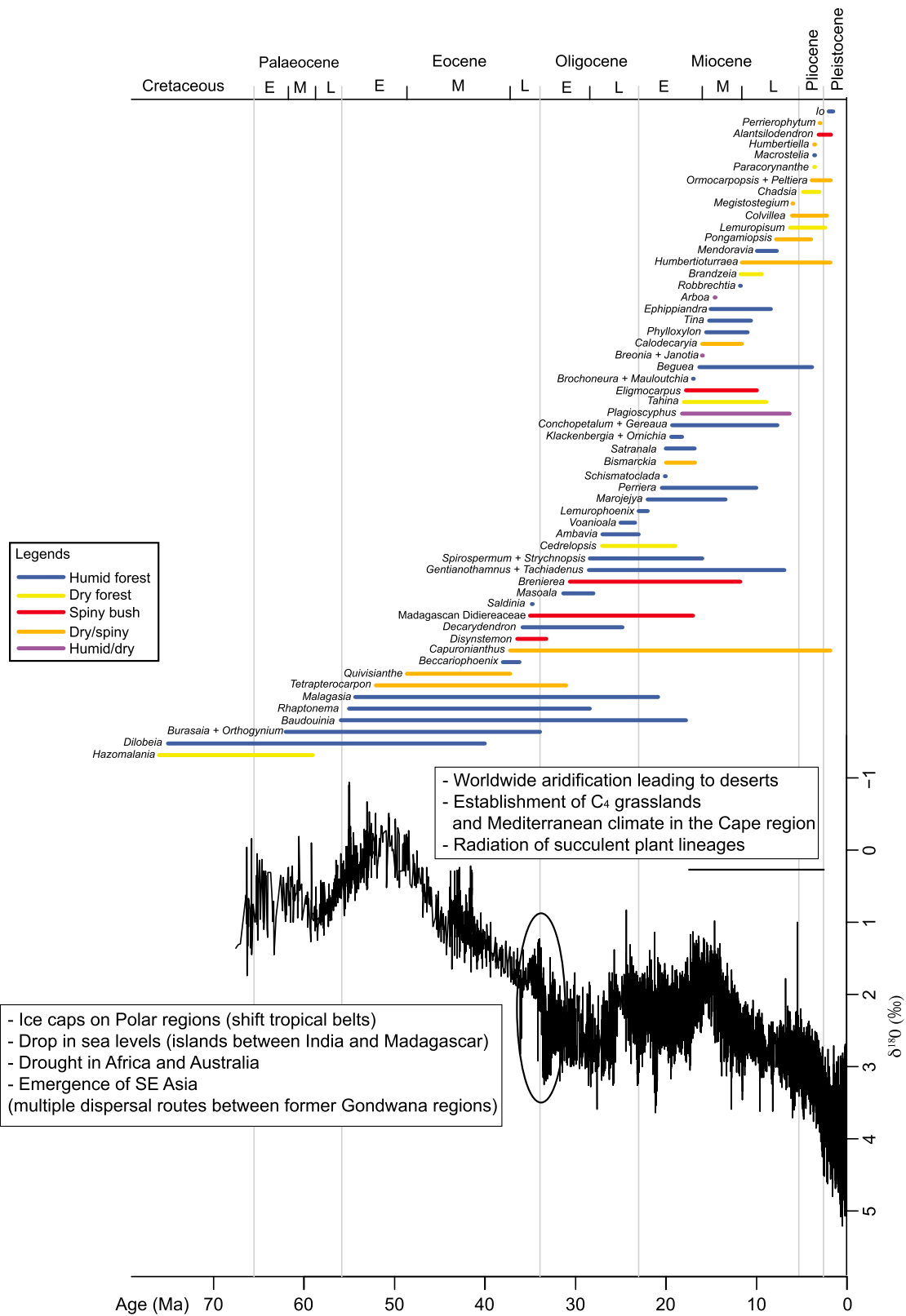


Figure 5. See caption on next page.

Figure 5. Plot of the tempo of origin of the 67 endemic Madagascan genera for which divergence time estimates are available. For each genus, the ages of its stem and the node subtending it are displayed as intervals (see text for more details). The estimations of climatic oscillations through time are displayed based on the variation of ^{18}O concentration (Zachos *et al.*, 2001) and major abiotic events (see text for more details). Data for Fabaceae are based on unpublished data from a study of phylogenetic diversity patterns in the family in Madagascar (S. Buerki *et al.*, unpubl. data). For Rubiaceae, the only age estimates available were at the tribal level; these values overestimate the actual age of the genera (see Table 1). The distribution of the genera in the main vegetation types is also provided.

c. 120 Mya; Marquinez *et al.*, 2009; Table 1). In this context, this element of the flora (i.e. the endemic genera) was mainly shaped by dispersal events and relatively recent climate change. However, we would like to draw attention to the importance of putative extinction events in the assemblage of the current species distributions and the subsequent interpretations that arise from them. Extinction events could lead to the loss of the signature of vicariance, thus favouring dispersal as an explanation for current distributions and, consequently, increase the assignment of endemism (e.g. the case of Sarcolaenaceae; see above). Further studies inferring spatio-temporal histories of the endemic Madagascan lineages, based on the fossil record, to calibrate molecular phylogenetic trees and provide evidence of past distributions are crucial to provide more accurate estimates for the dispersal routes (Figs 2–5).

STRONG PHYLOGENETIC CLUSTERING OF THE MADAGASCAN ENDEMIC GENERA

One of the particular features of the Madagascan endemic genera is their high level of phylogenetic clustering in families (i.e. genera generally form monophyletic clades confined to the island), low species richness per genus and frequent occurrence of narrow endemics (Madagascar Catalogue, 2012; Table 1; Fig. 1A). The data compiled here show that 26% of the endemic genera have sister lineages that are also restricted to the island (Fig. 4). Based on this evidence, these taxa can be: (1) simply an artefact of taxonomic over-splitting; (2) relicts of extinct lineages resulting, for instance, from abrupt mass extinctions induced by climate change on Madagascar and elsewhere, and therefore creating the observed genetic and morphological discontinuities; or (3) the result of recent ‘rapid’ radiations potentially caused by, for example, co-evolutionary processes and/or abrupt climate change that cleared or created new niches for colonization. In the latter case, the observed pattern resulted from a rapid geographical or phenological barrier and speciation is ongoing. To address these lines of investigation fully, we need robustly dated phylogenetic trees based on almost complete taxon sampling (at least at the generic level) and knowledge

of the fossil record. Below, we assess the importance of each of these factors in explaining the current distribution and diversity of the endemic genera.

Recently, phylogenetic inferences have suggested cases of taxonomic over-splitting in the Madagascan flora, particularly in Acanthaceae, in which several endemic genera have been shown to be nested in more widespread genera (e.g. *Conocalyx* Benoist, clustered in the Afro-Madagascan genus *Isoglossa* Oerst.; Kiel *et al.*, 2006). However, there are also cases in which phylogenetic studies have supported the description of Madagascan endemic genera segregated from more widely distributed genera (e.g. *Andringitra* Skema segregated from *Dombeya* Lam., Malvaceae; Skema, 2012). Consequently, taxonomic over-splitting is not a satisfactory explanation to account for the pattern observed in Madagascan endemic genera, and so, although it may have an effect, it must be ruled out as a general explanation.

We have already shown the role played by extinction during the middle Miocene in explaining the apparent endemism of Sarcolaenaceae (see above). This is one of many potentially similar pieces of evidence supporting the option that this process could have been one of the main driving forces involved in shaping current Madagascan diversity. Additional fossil data are necessary to fully assess this situation. The African and Madagascan family Didiereaceae potentially provides another example in which extinction events could have led to the current diversity. The family is estimated to have originated sometime during the Eocene, but the 11 species assigned to four genera forming the Madagascan clade only diversified during the middle Miocene (Arakaki *et al.*, 2011; Fig. 5). This long temporal interval between the stem and crown ages for this group is putatively indicative of extinction events in Madagascar (and, to some extent, in Africa, see Fig. 3) caused by the contraction of the subarid biome from the Eocene onwards as a result of the northward drift of Madagascar (Figs 2, 5). The time of origin of the Madagascan Didiereaceae coincides with the same aridification events that led to the establishment of deserts, C_4 grasslands, the radiation of succulent plant lineages and the establishment of the Mediterranean climate in the Cape region (see Micheels *et al.*, 2009; Arakaki *et al.*, 2011; Buerki *et al.*, 2012b and

references cited therein; Fig. 5). Although this biome was under contraction, this period of aridification could have mimicked the former climatic conditions of the end of the Cretaceous and triggered the emergence of these taxa. Finally, this period is also synchronous with the origin of other major elements of the spiny bush flora of southern Madagascar, such as the Fabaceae, Malvaceae and Meliaceae (Fig. 5). In this case, the subarid biome could have served as a second geographical centre of diversification for these plants, as they were better adapted to dry ecosystems.

Finally, preliminary results of DNA-based divergence time estimates showed that most of the examined genera originated recently (Fig. 5). Most of these genera have few species, with the exception of *Tina* Schult. (Sapindaceae) which contains *c.* 25 species (Table 1). This genus originated and diversified in the last ten million years (Buerki *et al.*, 2011a, b), most probably in response to the onset of heavy seasonal rains as a result of the establishment of the Indian monsoons (Figs 1, 5), and has successfully colonized the humid forests (from the eastern coast to the highlands, with a high species richness in the Sambirano region) and also diversified into the drier areas of the island. Further investigations are required to confirm this hypothesis and test it over a set of taxa widely represented in the Sambirano region. The implications of the last glaciation on the Madagascan flora also deserve to be investigated, especially with regard to the preliminary results suggesting the origin of several endemic lineages during this period (Fig. 5).

CONCLUSION AND PERSPECTIVES

Although we have been able to gather data for 184 endemic genera, there is still a long way to go to sample

all the genera endemic to the Madagascan flora and to obtain extensive spatial and temporal information. The network of DNA and tissue banks (particularly those housed at the Royal Botanic Gardens, Kew, and Missouri Botanical Garden, which have important Madagascar programmes) could support the completion of this task, but extensive fieldwork in target areas will also need to be conducted. Such a task will also require sampling in areas with the strongest biogeographical links with Madagascar (particularly Africa, India and South-East Asia, as shown here) to obtain robust phylogenetic frameworks and reliable timescales at the species level for as many groups as possible. These dated phylogenetic trees will subsequently be employed to perform biogeographical analyses using the model presented here. This work will be instrumental in allowing the evaluation of the hypotheses presented in this review, especially the effect of climate change on the diversification of the Madagascan flora as a whole.

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Table 1. List of the Madagascan endemic genera of angiosperms based on the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue, 2012). Abbreviations of the biogeographical areas: (A) Madagascar; (A') the Seychelles archipelago, Mascarenes and Comoros; (B) India (including Sri Lanka); (C) mainland Africa; (D) Australia, New Guinea, New Caledonia and New Zealand; (E) South-East Asia and the Pacific islands; (F) Eurasia; (G) South America (Fig. 4). The species richness per genus refers to estimates performed by the *Catalogue of the Vascular Plants of Madagascar*'s team. When several genera were clustered together in the phylogeny, we also scored the distribution of their sister lineage (see Araceae family below for an example). We also provide indications of when the phylogenetic status of the endemic genus was dubious and required further investigation (in this case, the genus was not included for the biogeographical inference). Finally, when a clade had a large range of distribution and included several genera, we did not provide the names of all the taxa

Order	Family	Genus	N species	Sister lineage(s)			Reference(s)
				Taxa	Distribution		
Alismatales	Araceae	<i>Arophyton</i>	7	<i>Carlephyton</i> , <i>Colletogyne</i>	A	Cabrera <i>et al.</i> (2008)	
	Araceae	<i>Carlephyton</i>	3	<i>Colletogyne</i>	A	Cabrera <i>et al.</i> (2008)	
	Araceae	<i>Colletogyne</i>	1	<i>Carlephyton</i>	A	Cabrera <i>et al.</i> (2008)	
	Araceae	<i>Arophyton</i> + <i>Carlephyton</i> + <i>Colletogyne</i>		<i>Typhonodorum</i>	AA'C	Cabrera <i>et al.</i> (2008)	
Apiales	Apiaceae	<i>Andriana</i>	3	<i>Pseudocarum</i>	AC	Nicolas & Plunkett (2009)	
	Apiaceae	<i>Anisopoda</i>	1	—	—	—	
	Apiaceae	<i>Billburitia</i>	2	African lineages of <i>Peucedanum</i> (all new genera)	C	Magee <i>et al.</i> (2009)	
	Apiaceae	<i>Cannaboides</i>	2	—	—	—	
	Apiaceae	<i>Phellolophium</i>	2	<i>Cryptotaenia</i>	C	Spalik & Downie (2007)	
	Apiaceae	<i>Pseudocannaboides</i>	1	—	—	—	
	Apiaceae	<i>Tana</i>	1	—	—	—	
	Torrnellaceae	<i>Melanophylla</i>	7	<i>Aralidium</i>	E	Plunkett <i>et al.</i> (1996)	
	Areaceae	<i>Beccariophoenix</i>	2	<i>Jubaeopsis</i> , <i>Voanioala</i> , <i>Jubaea</i> , <i>Butia</i> , <i>Parajubaea</i> , <i>Cocos</i> , <i>Attalea</i> , <i>Allagoptera</i> , <i>Syagrus</i> , <i>Lytocaryum</i>	ACDEG	Baker <i>et al.</i> (2009); Baker and Couvreur (in press)	
	Asparagales	Areaceae	<i>Bismarckia</i>	1	<i>Satranala</i>	A	Baker <i>et al.</i> (2009); Baker and Couvreur (in press)
Areaceae		<i>Lemurophoenix</i>	1	<i>Marojejya</i> , <i>Dypsis</i>	AA'C	Baker <i>et al.</i> (2009); Baker and Couvreur (in press)	
Areaceae		<i>Marojejya</i>	2	Taxa distributed in the Old World	AA'BDEF	Baker <i>et al.</i> (2009); Baker and Couvreur (in press)	
Areaceae		<i>Masoala</i>	1	<i>Bismarckia</i>	A	Baker <i>et al.</i> (2009); Baker and Couvreur (in press)	
Areaceae		<i>Satranala</i>	1	<i>Kerriodoxa</i>	E	Dransfield <i>et al.</i> (2008)	
Areaceae		<i>Tahina</i>	1	<i>Jubaea</i> , <i>Butia</i> , <i>Parajubaea</i> , <i>Cocos</i> , <i>Attalea</i> , <i>Allagoptera</i> , <i>Syagrus</i> , <i>Lytocaryum</i>	DEG	Baker <i>et al.</i> (2009); Baker and Couvreur (in press)	
Areaceae		<i>Voanioala</i>	1	<i>Hyphaene</i> , <i>Medemia</i>	BC	—	
Areaceae		<i>Bismarckia</i> + <i>Satranala</i>		—	—	—	
Asparagaceae		<i>Herrertopsis</i>	1	—	—	—	
Orchidaceae		<i>Ambrella</i>	1	—	—	—	
Orchidaceae		<i>Cymbidiella</i>	3	<i>Cyrtopodium</i>	G	van den Berg <i>et al.</i> (2002)	
Orchidaceae		<i>Erasanthe</i>	1	—	—	—	
Orchidaceae		<i>Eulophiella</i>	6	—	—	—	
Orchidaceae	<i>Grammangis</i>	2	—	—	—		
Orchidaceae	<i>Imernaea</i>	1	<i>Anguloa</i> , <i>Maxillaria</i> , <i>Adiptye</i> , <i>Paphina</i> , <i>Houletia</i> , <i>Treuvia</i> , <i>Jumellea</i>	AA'CDEG	Gorniak <i>et al.</i> (2010)		
Orchidaceae	<i>Lemuroorchis</i>	1	—	—	—		
Orchidaceae	<i>Megalorchis</i>	1	—	—	—		
Orchidaceae	<i>Paralophia</i>	2	—	—	—		
Orchidaceae	<i>Physoceras</i>	10	—	—	—		
Orchidaceae	<i>Tylostigma</i>	8	—	—	—		

Asterales	Asteraceae	<i>Apodocephala</i>	10	-	-	-	-
	Asteraceae	<i>Catata</i>	2	-	-	-	-
	Asteraceae	<i>Centauropsis</i>	8	C	-	Keeley <i>et al.</i> (2007)	-
	Asteraceae	<i>Cloiselia</i>	4	C	-	Ortiz (2006)	-
	Asteraceae	<i>Colobanthera</i>	1	-	-	-	-
	Asteraceae	<i>Decastyllocarpus</i>	1	-	-	-	-
	Asteraceae	<i>Diaphractanthus</i>	1	-	-	-	-
	Asteraceae	<i>Exomiocarpon</i>	1	-	-	-	-
	Asteraceae	<i>Gladiopappus</i>	1	-	-	-	-
	Asteraceae	<i>Grangeopsis</i>	1	-	-	-	-
	Asteraceae	<i>Humeocline</i>	1	-	-	-	-
	Asteraceae	<i>Io</i>	1	AA'	-	Pelser <i>et al.</i> (2010)	-
	Asteraceae	<i>Madagaster</i>	6	AA'CDEG	-	Karaman-Castro & Urbatsch (2009)	-
	Asteraceae	<i>Oliganthes</i>	10	-	-	-	-
	Asteraceae	<i>Psiadiella</i>	1	-	-	-	-
	Asteraceae	<i>Rochonia</i>	4	-	-	-	-
	Asteraceae	<i>Stenocline</i>	2	-	-	-	-
	Asteraceae	<i>Syncephalum</i>	5	-	-	-	-
	Asteraceae	<i>Vernoniopsis</i>	3	-	-	-	-
	Campanulaceae	<i>Dialypetalum</i>	5	AA'CDEFG	-	Tank & Donoghue (2010)	-
Canellales	Canellaceae	<i>Cinnamosma</i>	11	C	-	Marquinez <i>et al.</i> (2009)	-
	Winteraceae	<i>Takhtajania</i>	1	CDEG	-	Marquinez <i>et al.</i> (2009)	-
Caryophyllales	Amaranthaceae	<i>Henonia</i>	1	-	-	-	-
	Asteropeiaceae	<i>Asteropeia</i>	8	A	-	Brockington <i>et al.</i> (2009)	-
	Barbuiaceae	<i>Barbeuia</i>	1	-	-	Cuenoud <i>et al.</i> (2002)	-
	Didiereaceae	<i>Alluaudia</i>	6	A	-	Arakaki <i>et al.</i> (2011)	-
	Didiereaceae	<i>Alluaudiopsis</i>	2	A	-	Arakaki <i>et al.</i> (2011)	-
	Didiereaceae	<i>Decarya</i>	1	A	-	Arakaki <i>et al.</i> (2011)	-
	Didiereaceae	<i>Didierea</i>	2	A	-	Arakaki <i>et al.</i> (2011)	-
	Didiereaceae	<i>Alluaudia + Alluaudiopsis + Decarya + Didierea</i>	2	C	-	-	-
	Physenaceae	<i>Physena</i>	2	A	-	Brockington <i>et al.</i> (2009)	-
	Talinaceae	<i>Talinella</i>	12	G	-	Applequist & Wallace (2001)	-
Celastrales	Celastraceae	<i>Brexilla</i>	5	-	-	-	-
	Celastraceae	<i>Evonymopsis</i>	1	-	-	-	-
	Celastraceae	<i>Hartgiopsis</i>	1	BCDE	-	Simmons <i>et al.</i> (2012)	-
	Celastraceae	<i>Polycardia</i>	12	AA'C	-	Simmons <i>et al.</i> (2012)	-
	Celastraceae	<i>Ptelidium</i>	2	-	-	-	-
	Celastraceae	<i>Salvadoropsis</i>	1	-	-	-	-
Commelinales	Commelinaceae	<i>Pseudoparis</i>	2	-	-	-	-
	Commelinaceae	<i>Rhopalephora</i>	1	CG	-	Evans <i>et al.</i> (2003)	-
Cucurbitales	Cucurbitaceae	<i>Ampelosycios</i>	5	AC	-	Kocyan <i>et al.</i> (2007)	-
	Cucurbitaceae	<i>Lemurosycios</i>	1	BEF	-	Kocyan <i>et al.</i> (2007)	-
	Cucurbitaceae	<i>Seyrigia</i>	6	A	-	Kocyan <i>et al.</i> (2007)	-
	Cucurbitaceae	<i>Trochomeriopsis</i>	1	A	-	Kocyan <i>et al.</i> (2007)	-
	Cucurbitaceae	<i>Seyrigia + Trochomeriopsis</i>	6	AA'BCDE	-	-	-
	Cucurbitaceae	<i>Xerosycios</i>	6	G	-	Kocyan <i>et al.</i> (2007)	-
Ericales	Sapotaceae	<i>Capurodendron</i>	25	C	-	Anderberg & Swenson (2003); Smedmark & Anderberg (2007)	-
	Sapotaceae	<i>Fauchera</i>	11	-	-	Anderberg & Swenson (2003)	-
	Sapotaceae	<i>Tsebona</i>	1	-	-	-	-

Table 1. Continued

Order	Family	Genus	N species	Sister lineage(s)		Reference(s)	
				Taxa	Distribution		
Fabales	Fabaceae	<i>Alantsilodendron</i>	9	Nested within <i>Dichrostachys</i>	ABCD	Hughes <i>et al.</i> (2003)	
	Fabaceae	<i>Baudouinia</i>	6	<i>Eligmocarpus</i>	A	Bruneau <i>et al.</i> (2001, 2008)	
	Fabaceae	<i>Brendzeia</i>	1	<i>Daniellia</i>	C	Bruneau <i>et al.</i> (2001, 2008)	
	Fabaceae	<i>Brenierea</i>	1	<i>Bauhinia</i> clade s.s.	AA'BCDEFG	Sinou <i>et al.</i> (2009)	
	Fabaceae	<i>Chadisia</i>	9	<i>Mundulea</i>	ABC	Hu <i>et al.</i> (2002)	
	Fabaceae	<i>Colvillea</i>	1	<i>Delonix, Lemuropisum</i>	ABC	Bruneau <i>et al.</i> (2001, 2008)	
	Fabaceae	<i>Disystemon</i>	1	<i>Indigoferaceae</i>	AA'BCDEG	Schrire <i>et al.</i> (2009)	
	Fabaceae	<i>Dupuya</i>	2	–	–	–	
	Fabaceae	<i>Eligmocarpus</i>	1	<i>Baudouinia</i>	A	Bruneau <i>et al.</i> (2001, 2008)	
	Fabaceae	<i>Lemurodendron</i>	1	–	–	–	
	Fabaceae	<i>Lemuropisum</i>	1	<i>Delonix</i>	BC	Bruneau <i>et al.</i> (2001, 2008)	
	Fabaceae	<i>Mendoravia</i>	1	<i>Koompassia</i>	DE	Bruneau <i>et al.</i> (2001, 2008)	
	Fabaceae	<i>Neopaloxylon</i>	3	Not provided in the manuscript	–	Fougere-Danezan <i>et al.</i> (2007)	
	Fabaceae	<i>Neoharmsia</i>	2	Not provided in the manuscript	–	Edwards & Hawkins (2007)	
	Fabaceae	<i>Ormocarpopsis</i>	6	<i>Ormocarpum</i>	ABCDE	Lavin <i>et al.</i> (2001)	
	Fabaceae	<i>Peltiera</i>	2	–	–	J. N. Labat & M. Lavin (unpubl. data)	
	Gentianales	Fabaceae	<i>Phylloxylon</i>	7	<i>Indigoferaceae</i>	AA'BCDEG	Schrire <i>et al.</i> (2009)
		Fabaceae	<i>Pongamiopsis</i>	3	<i>Neodunnia</i>	–	Hu <i>et al.</i> (2002)
		Fabaceae	<i>Pyranthus</i>	6	–	–	–
		Fabaceae	<i>Saboanala</i>	2	–	–	–
Fabaceae		<i>Syloichadisia</i>	4	<i>Fordia</i>	BEF	Schrire <i>et al.</i> (2009)	
Fabaceae		<i>Tetrapterocarpon</i>	2	<i>Acrocarpus</i> (but weak relationship)	BE	Bruneau <i>et al.</i> (2001, 2008)	
Fabaceae		<i>Baudouinia</i> + <i>Eligmocarpus</i>	2	Sister to Dialinae (excl. <i>Poeppegia</i>)	ABCDEG	–	
Apocynaceae		<i>Baroniella</i>	9	<i>Pentopetia</i>	AA'	Ionta & Judd (2007)	
Apocynaceae		<i>Calyptranthera</i>	10	–	–	–	
Apocynaceae		<i>Craspidospermum</i>	1	<i>Melodinus</i>	BDE	Simoes <i>et al.</i> (2007)	
Apocynaceae		<i>Cryptostegia</i>	2	<i>Camptocarpus</i>	AA'	Ionta & Judd (2007)	
Apocynaceae		<i>Ischnolepis</i>	1	<i>Cryptostegia, Camptocarpus</i>	AA'	Ionta & Judd (2007)	
Apocynaceae		<i>Plectaneta</i>	3	<i>Pteralyxia, Alyxia</i>	BDE	Livshultz <i>et al.</i> (2007)	
Apocynaceae		<i>Secamonopsis</i>	2	<i>Secamone, Pervillaea</i>	AC	Lahaye <i>et al.</i> (2005)	
Apocynaceae		<i>Stapelanthus</i>	6	–	–	B. Gravendeel <i>et al.</i> (unpubl. data)	
Apocynaceae		<i>Stephanotis</i>	2	–	–	–	
Apocynaceae		<i>Stephanotis</i>	5	Used as outgroup taxon	–	Wanntorp <i>et al.</i> (2011)	
Gentianaceae		<i>Gentianothamnus</i>	1	<i>Tachiaenus</i>	A	Kissling (2007); Kissling <i>et al.</i> (2009)	
Gentianaceae		<i>Klackenbergia</i>	2	<i>Ornichia</i>	A	Kissling (2007); Kissling <i>et al.</i> (2009)	
Gentianaceae		<i>Ornichia</i>	3	<i>Klackenbergia</i>	A	Kissling (2007); Kissling <i>et al.</i> (2009)	
Gentianaceae	<i>Tachiaenus</i>	11	<i>Gentianothamnus</i>	A	Kissling (2007); Kissling <i>et al.</i> (2009)		
Gentianaceae	<i>Gentianothamnus</i> + <i>Klackenbergia</i> + <i>Ornichia</i> + <i>Tachiaenus</i>	2	<i>Exacum</i>	ABCDE	–		
Rubiaceae	<i>Amphistemon</i>	2	<i>Thamnodendlandia</i>	A	Groeninckx <i>et al.</i> (2010a)		
Rubiaceae	<i>Astiella</i>	1	<i>Phialiphora</i>	A	Groeninckx <i>et al.</i> (2010b)		
Rubiaceae	<i>Breonia</i>	20	<i>Gyrostipula, Janotia</i>	AA'	Bremer & Eriksson (2009); Manns & Bremer (2010)		
Rubiaceae	<i>Canephora</i>	5	<i>Polysphaeria</i>	AA'C	Davis <i>et al.</i> (2007)		
Rubiaceae	<i>Carphalea</i>	6	Used as outgroup taxon	–	Groeninckx <i>et al.</i> (2009a)		
Rubiaceae	<i>Chapelieria</i>	2	–	–	–		
Rubiaceae	<i>Flagenium</i>	6	–	–	–		
Rubiaceae	<i>Gallienia</i>	1	–	–	–		
Rubiaceae	<i>Gomphocalyx</i>	1	<i>Phylolhydrax, Gomphocalyx</i>	AC	Groeninckx <i>et al.</i> (2010a)		

Rubiaceae	<i>Homollea</i>	3	-	-	-	-
Rubiaceae	<i>Homoliella</i>	1	-	-	-	Bremer & Eriksson (2009); Manns & Bremer (2010)
Rubiaceae	<i>Janotia</i>	1	-	AA'	-	
Rubiaceae	<i>Jovetta</i>	1	-	-	-	Kainulainen <i>et al.</i> , unpublished data
Rubiaceae	<i>Landiopsis</i>	1	-	-	-	Groeninckx <i>et al.</i> (2009b)
Rubiaceae	<i>Lathraeocarpa</i>	2	-	AC	-	
Rubiaceae	<i>Lemyrea</i>	4	-	-	-	
Rubiaceae	<i>Mantalania</i>	3	-	-	-	
Rubiaceae	<i>Nematostylis</i>	1	-	A	-	Kainulainen <i>et al.</i> (2009)
Rubiaceae	<i>Paracorymanthe</i>	2	-	BCEF	-	Bremer & Eriksson (2009); Manns & Bremer (2010)
Rubiaceae	<i>Payera</i>	10	-	-	-	Kruger <i>et al.</i> (2012)
Rubiaceae	<i>Phialiphora</i>	2	-	A	-	Groeninckx <i>et al.</i> (2010b)
Rubiaceae	<i>Pseudomantalania</i>	1	-	-	-	
Rubiaceae	<i>Pyragra</i>	2	-	-	-	
Rubiaceae	<i>Razafimandimbisonia</i>	5	-	A	-	Kainulainen <i>et al.</i> (2009)
Rubiaceae	<i>Robbrechtia</i>	2	-	-	-	Bremer & Eriksson (2009)
Rubiaceae	<i>Saldinia</i>	21	-	-	-	Bremer & Eriksson (2009); Rydin <i>et al.</i> (2008)
Rubiaceae	<i>Schismatoclada</i>	19	-	AA'C	-	Bremer & Eriksson (2009); Rydin <i>et al.</i> (2008)
Rubiaceae	<i>Schizenterospermum</i>	4	-	-	-	
Rubiaceae	<i>Thamnodendlandia</i>	1	-	A	-	Groeninckx <i>et al.</i> (2010a)
Rubiaceae	<i>Amphistemon</i> + <i>Thamnodendlandia</i> + <i>Astiella</i> + <i>Phialiphora</i>	1	-	G	-	
Rubiaceae	<i>Nematostylis</i> + <i>Razafimandimbisonia</i>	1	-	C	-	
Acanthaceae	<i>Ambongia</i>	1	-	-	-	
Acanthaceae	<i>Benoicanthus</i>	2	-	-	-	
Acanthaceae	<i>Boutonia</i>	1	-	-	-	
Acanthaceae	<i>Canarotea</i>	2	-	A	-	McDade <i>et al.</i> (2008)
Acanthaceae	<i>Celerina</i>	1	-	-	-	
Acanthaceae	<i>Danguya</i>	1	-	-	-	
Acanthaceae	<i>Dolichostachys</i>	1	-	-	-	
Acanthaceae	<i>Forcipella</i>	6	-	A	-	McDade <i>et al.</i> (2008)
Acanthaceae	<i>Ionacanthus</i>	1	-	-	-	
Acanthaceae	<i>Lasiocladius</i>	7	-	AC	-	McDade <i>et al.</i> (2008)
Acanthaceae	<i>Leandriella</i>	2	-	A	-	McDade <i>et al.</i> , (2008)
Acanthaceae	<i>Melittacanthus</i>	1	-	-	-	
Acanthaceae	<i>Pericalypta</i>	1	-	-	-	
Acanthaceae	<i>Podorungia</i>	4	-	-	-	
Acanthaceae	<i>Populina</i>	2	-	-	-	
Acanthaceae	<i>Pseudodidicliptera</i>	4	-	-	-	
Acanthaceae	<i>Pseudoruellia</i>	1	-	-	-	
Acanthaceae	<i>Ritonia</i>	4	-	-	-	
Acanthaceae	<i>Sphacanthus</i>	2	-	-	-	
Acanthaceae	<i>Vavara</i>	1	-	-	-	
Acanthaceae	<i>Vindasia</i>	1	-	-	-	
Acanthaceae	<i>Zygoruella</i>	1	-	-	-	
Acanthaceae	<i>Canarotea</i> + <i>Forcipella</i> + <i>Leandriella</i>	2	-	AC	-	
Bignoniaceae	<i>Perichlaena</i>	1	-	-	-	
Bignoniaceae	<i>Phylloctenium</i>	9	-	-	-	
Lamiaceae	<i>Adelosa</i>	1	-	-	-	
	<i>Chlamydacanthus</i>		-	-	-	

Table 1. Continued

Order	Family	Genus	N species	Sister lineage(s)		Distribution	Reference(s)
				Taxa	Taxa		
Laurales	Lamiaceae	<i>Capitanopsis</i>	3	<i>Dauphinea</i>	A	Paton <i>et al.</i> (2004)	
	Lamiaceae	<i>Dauphinea</i>	1	<i>Capitanopsis</i>	A	Paton <i>et al.</i> (2004)	
	Lamiaceae	<i>Madlabium</i>	1	–	–	–	
	Lamiaceae	<i>Capitanopsis</i> + <i>Dauphinea</i>	3	<i>Aeollanthus</i>	C	E. Fischer <i>et al.</i> (unpubl. data)	
	Orobanchaceae	<i>Leucosalpa</i>	1	–	–	–	
	Orobanchaceae	<i>Pseudomelasma</i>	5	–	–	–	
	Orobanchaceae	<i>Radamaea</i>	1	–	–	–	
	Orobanchaceae	<i>Rhaphispermum</i>	1	–	–	–	
	Orobanchaceae	<i>Sieversandreas</i>	1	–	–	–	
	Orobanchaceae	<i>Tetrastidium</i>	1	–	–	–	
	Pedaliaceae	<i>Uncarina</i>	14	Used as outgroup taxon	–	–	
	Plantaginaceae	<i>Hydrotriche</i>	4	The taxon sampling is not appropriate	–	–	
	Scrophulariaceae	<i>Androya</i>	1	<i>Myoporium</i>	D	Schaeferhoff <i>et al.</i> (2010)	
	Scrophulariaceae	<i>Barthlottia</i>	1	The taxon sampling is not appropriate	–	–	
Scrophulariaceae	<i>Ranipisosa</i>	1	–	–	–		
Laurales	Hernandiaceae	<i>Hazomalania</i>	1	<i>Illigera</i>	ABCE	Michalak <i>et al.</i> (2010)	
	Lauraceae	<i>Aspidostemon</i>	31	<i>Beilschmiedia</i> , <i>Endiandra</i> , <i>Potameia</i> , <i>Cryptocarya</i>	AA'BCDEFG	Chanderbali <i>et al.</i> (2001)	
	Lauraceae	<i>Potameia</i>	29	<i>Beilschmiedia</i> (might need to be included in this genus)	AA'BCDEFG	Chanderbali <i>et al.</i> (2001)	
	Monimiaceae	<i>Decarydendron</i>	4	<i>Tambourissa</i> , <i>Ephippiandra</i>	AA'	Renner <i>et al.</i> (2010)	
	Monimiaceae	<i>Ephippiandra</i>	7	Nested within <i>Tambourissa</i>	AA'	Renner <i>et al.</i> (2010)	
	Annonaceae	<i>Ambavia</i>	4	<i>Cleistopholis</i> , <i>Mezzettia</i> , <i>Tetrameranthus</i>	CDE	Chatrou <i>et al.</i> (2012); Pirie and Doyle (2012)	
	Annonaceae	<i>Fenerivia</i>	10	Weak relationship, but sister to <i>Maasia</i>	E	Saunders <i>et al.</i> (2011)	
	Myristicaceae	<i>Brochoneura</i>	5	<i>Mauloutchia</i>	A	Doyle <i>et al.</i> (2004); Sauquet <i>et al.</i> (2003)	
	Myristicaceae	<i>Doyleanthus</i>	2	–	–	–	
	Myristicaceae	<i>Haematodendron</i>	1	<i>Bicuiba</i>	G	Sauquet <i>et al.</i> (2003)	
Malpighiales	Myristicaceae	<i>Mauloutchia</i>	9	<i>Brochoneura</i>	A	Doyle <i>et al.</i> (2004); Sauquet <i>et al.</i> (2003)	
	Myristicaceae	<i>Brochoneura</i> + <i>Mauloutchia</i>	3	<i>Cephalosphaera</i>	C	–	
	Achariaceae	<i>Prockiopsis</i>	11	<i>Agrostistachys</i> , <i>Pseudagrostistachys</i>	BDE	Wurdack <i>et al.</i> (2005)	
	Euphorbiaceae	<i>Anyrea</i>	1	–	–	–	
	Euphorbiaceae	<i>Anomostachys</i>	3	–	–	–	
	Euphorbiaceae	<i>Benoistia</i>	1	–	–	–	
	Euphorbiaceae	<i>Bossera</i>	1	–	–	–	
	Euphorbiaceae	<i>Cladogelonium</i>	1	<i>Suregada</i>	AA'BCDE	Wurdack <i>et al.</i> (2005)	
	Euphorbiaceae	<i>Claoxylopsis</i>	3	–	–	–	
	Euphorbiaceae	<i>Conosapium</i>	2	–	–	–	
	Euphorbiaceae	<i>Parapantadenia</i>	1	–	–	–	
	Euphorbiaceae	<i>Radcliffea</i>	1	–	–	–	
	Hypericaceae	<i>Eliea</i>	1	<i>Cratoxylum</i>	BE	Wurdack & Davis (2009)	
	Malpighiaceae	<i>Digoniopterys</i>	1	<i>Rhynchochloa</i> , <i>Madagasikaria</i> , <i>Microsteira</i>	A	Davis and Anderson (2010)	
Malpighiales	Malpighiaceae	<i>Madagasikaria</i>	1	<i>Rhynchochloa</i> (might need to be merged with the former)	A	Davis and Anderson (2010)	
	Malpighiaceae	<i>Microsteira</i>	28	<i>Rhynchochloa</i> , <i>Madagasikaria</i>	A	Davis and Anderson (2010)	
	Malpighiaceae	<i>Digoniopterys</i> + <i>Rhynchochloa</i> + <i>Madagasikaria</i> + <i>Microsteira</i>	3	<i>Triaspis</i> + <i>Caucanthus</i>	C	Davis and Anderson (2010)	
	Passifloraceae	<i>Arboa</i>	4	<i>Mathurina</i>	A'	Thulin <i>et al.</i> (2012)	

Phyllanthaceae	<i>Blotia</i>	5	<i>Petalodiscus</i>	AC	Wurdack <i>et al.</i> (2004)
Phyllanthaceae	<i>Leptonema</i>	2	<i>Hieronyma, Martretia, Apodiscus</i>	CG	Wurdack <i>et al.</i> (2004)
Picrodendraceae	<i>Stachyandra</i>	4	—	—	—
Picrodendraceae	<i>Voatamalo</i>	2	—	—	—
Podostemaceae	<i>Endocaulos</i>	1	<i>Thelethylax</i>	A	Koi <i>et al.</i> (2012)
Podostemaceae	<i>Paleodieracia</i>	1	—	—	—
Podostemaceae	<i>Thelethylax</i>	2	<i>Endocaulos</i>	A	Koi <i>et al.</i> (2012)
Podostemaceae	<i>Endocaulos + Thelethylax</i>	—	Sister to an Asian and Australian clade	DE	—
Rhizophoraceae	<i>Macarisia</i>	4	<i>Cassipourea</i>	ABCEG	Schwarzbach and Riecklefs (2000)
Salicaceae	<i>Bembicia</i>	2	—	—	M. Alford (unpubl. data)
Salicaceae	<i>Calanica</i>	10	—	—	M. Alford (unpubl. data)
Salicaceae	<i>Tisonia</i>	21	—	—	M. Alford (unpubl. data)
Trigonaceae	<i>Humbertioidendron</i>	1	—	—	—
Bixaceae	<i>Diegodendron</i>	1	<i>Bixa</i>	G	Fay <i>et al.</i> (1998)
Malvaceae	<i>Andringitra</i>	6	<i>Helmiopsiella, Hemioipsis, Eriolaena</i>	ABEF	Skema (2012)
Malvaceae	<i>Helicteropsis</i>	1	<i>Hibiscus grandidieri, Jumelleanthus</i>	—	Koopman and Baum (2008)
			(some incongruence between the nuclear and plastid data)		
Malvaceae	<i>Helmiopsiella</i>	4	<i>Eriolaena</i>	BEF	Skema (2012)
Malvaceae	<i>Helmiopsis</i>	10	<i>Helmiopsiella, Eriolaena</i>	ABEF	Skema (2012)
Malvaceae	<i>Humbertiella</i>	6	<i>Kostetetzky, Perrierophytum</i>	A	Koopman and Baum (2008)
Malvaceae	<i>Jumelleanthus</i>	1	<i>Hibiscus grandidieri, Helicteropsis</i>	—	Koopman and Baum (2008)
			(some incongruence between the nuclear and plastid data)		
Malvaceae	<i>Macrostelia</i>	3	Australian <i>Hibiscus</i> spp.	—	Koopman and Baum (2008)
Malvaceae	<i>Megistostegium</i>	3	<i>Humbertiella, Kostetetzky, Perrierophytum</i>	A	Koopman and Baum (2008)
Malvaceae	<i>Paramelhania</i>	1	<i>Trochetiopsis</i>	C	Bayer <i>et al.</i> (1999)
Malvaceae	<i>Perrierophytum</i>	9	Malagasy species of <i>Kostetetzky</i>	—	Koopman and Baum (2008)
Malvaceae	<i>Pseudocochorus</i>	6	—	—	—
Sarcolaenaceae	<i>Eremolaena</i>	2	—	—	—
Sarcolaenaceae	<i>Leptolaena</i>	8	<i>Sarcolaena</i>	A	Ducousso <i>et al.</i> (2004)
Sarcolaenaceae	<i>Mediusella</i>	2	—	—	—
Sarcolaenaceae	<i>Pentachlaena</i>	3	—	—	—
Sarcolaenaceae	<i>Perrierodendron</i>	5	—	—	—
Sarcolaenaceae	<i>Rhodolaena</i>	7	<i>Leptolaena</i>	A	Ducousso <i>et al.</i> (2004)
Sarcolaenaceae	<i>Sarcolaena</i>	14	—	—	—
Sarcolaenaceae	<i>Schizolaena</i>	20	—	—	—
Sarcolaenaceae	<i>Xerochlamys</i>	8	—	—	—
Sarcolaenaceae	<i>Xyloaena</i>	5	—	—	—
Sarcolaenaceae	<i>Dialyceras</i>	3	Dipterocarpaceae	BE	van der Bank <i>et al.</i> (2002)
Sphaerosepalaceae	<i>Rhopalocarpus</i>	17	Used as outgroup taxon	—	Alverson <i>et al.</i> (1998)
Thymelaeaceae	<i>Atemnosiphon</i>	1	Not a good taxon sampling	—	—
Lythraceae	<i>Capuronia</i>	1	<i>Galpinia</i>	C	Graham <i>et al.</i> (2005)
Lythraceae	<i>Koehneria</i>	1	<i>Woodfordia</i>	ABCEF	Graham <i>et al.</i> (2005)
Melastomataceae	<i>Amphorocalyx</i>	5	—	—	—
Melastomataceae	<i>Dionycha</i>	3	—	—	—
Melastomataceae	<i>Rousseauxia</i>	17	—	—	—

Table 1. Continued

Order	Family	Genus	N species	Sister lineage(s)		Reference(s)	
				Taxa	Distribution		
Poales	Cyperaceae	<i>Trichoschoenus</i>	1	–	–	–	
	Poaceae	<i>Camusiella</i>	2	–	–	–	
	Poaceae	<i>Catharistostachys</i>	2	<i>Decaryochloa</i>	A	Clark <i>et al.</i> (2007)	
	Poaceae	<i>Chasechloa</i>	3	–	–	–	
	Poaceae	<i>Cyphochloa</i>	2	<i>Oplismenus</i>	AA'BCDEFG	Morrone <i>et al.</i> (2012)	
	Poaceae	<i>Decaryella</i>	1	–	–	–	
	Poaceae	<i>Decaryochloa</i>	1	<i>Catharistostachys</i>	–	Clark <i>et al.</i> (2007)	
	Poaceae	<i>Hitchcockella</i>	1	–	–	–	
	Poaceae	<i>Lecomitella</i>	1	–	–	–	
	Poaceae	<i>Neostapfiella</i>	3	–	–	–	
	Poaceae	<i>Perrierbambus</i>	2	<i>Valiha</i> , <i>Decaryochloa</i> , <i>Catharistostachys</i>	A	Clark <i>et al.</i> (2007)	
	Poaceae	<i>Pseudolasiacis</i>	3	–	–	–	
	Poaceae	<i>Schizostachyum</i>	2	<i>Cephalostachyum</i>	BCEF	Clark <i>et al.</i> (2007)	
	Poaceae	<i>Sirochloa</i>	1	<i>Perrierbambus</i> , <i>Hickelia</i> , <i>Valiha</i> , <i>Decaryochloa</i> , <i>Catharistostachys</i>	AC	Clark <i>et al.</i> (2007)	
	Proteales	Poaceae	<i>Toitara</i>	1	–	–	–
		Poaceae	<i>Valiha</i>	3	<i>Decaryochloa</i> , <i>Catharistostachys</i>	A	Clark <i>et al.</i> (2007)
		Poaceae	<i>Viguierella</i>	1	–	–	–
Poaceae		<i>Yvesia</i>	1	–	–	–	
Proteaceae		<i>Dilobeia</i>	2	–	–	–	
Proteaceae		<i>Malagasia</i>	1	–	–	–	
Ranunculales		Menispermaceae	<i>Burasaia</i>	6	<i>Orthogynium</i>	A	Hoot <i>et al.</i> (2009); Wang <i>et al.</i> (2012)
		Menispermaceae	<i>Orthogynium</i>	1	<i>Burasaia</i>	A	Hoot <i>et al.</i> (2009); Wang <i>et al.</i> (2012)
		Menispermaceae	<i>Rhaptomena</i>	7	<i>Strychnopsis</i>	A	Hoot <i>et al.</i> (2009); Wang <i>et al.</i> (2012)
		Menispermaceae	<i>Spirospermum</i>	2	<i>Strychnopsis</i>	A	Wang <i>et al.</i> (2012)
	Menispermaceae	<i>Strychnopsis</i>	1	<i>Rhaptomena</i>	A	Hoot <i>et al.</i> (2009); Wang <i>et al.</i> (2012)	
	Menispermaceae	<i>Burasaia</i> + <i>Orthogynium</i>	1	<i>Dioscoreophyllum</i> , <i>Jateorhiza</i> , <i>Tinospora</i> , <i>Rhigiocarya</i> , <i>Kolobopetalum</i> , <i>Chasmanthera</i> , <i>Leptoterantha</i> , <i>Syntriandrium</i> , <i>Odontocarya</i>	BCDEG	–	
	Rosales	Menispermaceae	<i>Rhaptomena</i> + <i>Strychnopsis</i> + <i>Spirospermum</i>	7	<i>Cyclea</i> , <i>Cissampelos</i> , <i>Perichasma</i> , <i>Stephania</i>	AA'BCDEFG	–
		Rhamnaceae	<i>Bathiorhammus</i>	7	<i>Doerpfeldia</i> , <i>Ampelozizyphus</i>	G	Richardson <i>et al.</i> (2000)
		Aptandraceae	<i>Phanerodiscus</i>	3	<i>Anacolosa</i> , <i>Cathedra</i>	ACE	Malecot & Nickrent (2008)
		Balanophoraceae	<i>Ditepalanthus</i>	1	–	–	–
Loranthaceae		<i>Socratina</i>	2	<i>Vanuykia</i>	C	Vidal–Russell & Nickrent (2008)	
Santalaceae		<i>Pilgerina</i>	1	<i>Staufferia</i> , <i>Scleropyrum</i> , <i>Okoubaka</i>	ABCDE	Rogers <i>et al.</i> (2008)	
Santalaceae		<i>Staufferia</i>	1	<i>Scleropyrum</i> , <i>Okoubaka</i>	BCDE	Rogers <i>et al.</i> (2008)	

Sapindales	Anacardiaceae	<i>Abrahamia</i>	15	<i>Micronychia, Rhus, Protorhus</i>	AC	Pell (2004); Pell <i>et al.</i> (2008)
	Anacardiaceae	<i>Fageitia</i>	1	<i>Trichoscypha</i>	C	Pell (2004); Pell <i>et al.</i> (2008)
	Anacardiaceae	<i>Micronychia</i>	9	<i>Micronychia, Rhus, Protorhus</i>	AC	Pell (2004); Pell <i>et al.</i> (2008)
	Anacardiaceae	<i>Poupartopsis</i>	1	Weak support, but sister to South American species of <i>Antrocaryon</i>	G	Mitchell <i>et al.</i> (2006)
	Burseraceae	<i>Ambiloba</i>	1	A pantropical clade	AA'BCDEFG	Thulin <i>et al.</i> (2008)
	Meliaceae	<i>Astrotrichilia</i>	16	A pantropical clade	AA'BCDEFG	Mueller <i>et al.</i> (2003, 2006)
	Meliaceae	<i>Calodacarya</i>	2	<i>Humbertioturraea, Turraea</i>	ABCDE	Mueller <i>et al.</i> (2003, 2006)
	Meliaceae	<i>Capuronianthus</i>	2	<i>Lovoa</i>	C	Mueller <i>et al.</i> (2003, 2006)
	Meliaceae	<i>Humbertioturraea</i>	11	<i>Turraea</i>	ABCDE	Mueller <i>et al.</i> (2003, 2006)
	Meliaceae	<i>Neobegonia</i>	3	<i>Toona, Cedrela, Swietenia, Khaya, Carapa, Lovoa, Capuronianthus</i>	ACDEF	Mueller <i>et al.</i> (2003, 2006)
	Meliaceae	<i>Quinisianthe</i>	2	<i>Elkebergia</i>	AC	Mueller <i>et al.</i> (2003, 2006)
	Rutaceae	<i>Cedrelopsis</i>	8	<i>Ptaeroxylon</i>	C	Appelhans <i>et al.</i> (2012); Razafimandimbison <i>et al.</i> (2010)
	Sapindaceae	<i>Begonia</i>	7	<i>Macphersonia</i>	AA'C	Buerki <i>et al.</i> (2010, 2011a)
	Sapindaceae	<i>Chouxia</i>	6	<i>Pseudopteris</i>	A	Buerki <i>et al.</i> (2010)
	Sapindaceae	<i>Conchopetalum</i>	2	<i>Gereaua</i>	A	Buerki <i>et al.</i> (2010, 2011a)
Sapindaceae	<i>Gereaua</i>	1	<i>Conchopetalum</i>	A	Buerki <i>et al.</i> (2010, 2011a)	
Sapindaceae	<i>Plagioscyphus</i>	10	<i>Pappea</i>	C	Buerki <i>et al.</i> (2010, 2011a)	
Sapindaceae	<i>Pseudopteris</i>	3	<i>Chouxia</i>	A	Buerki <i>et al.</i> (2010)	
Sapindaceae	<i>Tina</i>	25	<i>Molinaea</i>	AA'	Buerki <i>et al.</i> (2011a, b)	
Sapindaceae	<i>Tsingya</i>	1	–	–	–	
Sapindaceae	<i>Chouxia + Pseudopteris + Gereaua + Conchopetalum</i>	2	<i>Macphersonia, Begonia</i>	AA'C	–	
Simaroubaceae	<i>Perriera</i>	2	<i>Gymnostemon</i>	C	Appelhans <i>et al.</i> (2012); Clayton <i>et al.</i> (2007)	
Saxifragales	Crassulaceae	<i>Perrierosedum</i>	1	–	–	
Solanales	Convolvulaceae	<i>Cardioclarys</i>	2	<i>Poranopsis, Cordisepalum</i>	E	Stefanovic <i>et al.</i> (2002)
	Convolvulaceae	<i>Humberia</i>	1	Most early lineage within the family	AA'BCDEFG	Stefanovic <i>et al.</i> (2002)
Zingiberales	Convolvulaceae	<i>Rapona</i>	1	<i>Dipteropeltis</i>	C	Stefanovic <i>et al.</i> (2002)
	Montiniaceae	<i>Kaliphora</i>	1	–	–	N. F. Refulio-Rodriguez & R. G. Olmstead (unpubl. data)
Zingiberales	Solanaceae	<i>Tsoala</i>	1	<i>Metternichia</i>	G	Olmstead <i>et al.</i> (2008)
	Strelitziaceae	<i>Ravenala</i>	1	<i>Phenakospermum, Strelizia</i>	CG	Cron <i>et al.</i> (2012)

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