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Gondwanan origin of the Dipterocarpaceae-Cistaceae-Bixaceae is supported by fossils, areocladograms, ecomorphological traits and tectonic-plate dynamics

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Abstract

There is disparity between the estimated time of origin of the 'superclade' Dipterocarpaceae *sensu lato*, that includes Sarcolaenaceae, Cistaceae, *Pakaraimaea*, Bixaceae, Cochlospermaceae and Sphaerosepalaceae, as determined by recent molecular phylogenies (100–85 million years ago, Ma) and its strongly tropical, South American-African-Madagascan-SE Asian distribution that indicates an older Gondwanan origin (>110 Ma). We used several paleobiogeographic approaches, including recently reported fossil records, to explore the hypothesis that Dipterocarpaceae *sl* has a Gondwanan/early-Cretaceous origin.

We created molecular phylogenies for this group, assigned each genus/family to the tectonic plate on which it is extant, and subjected the cladogram to areogram analysis. We also assessed ecological, mycotrophic and morphological traits, and global circulation patterns, as these might affect this group's distribution.

The initial analysis (omitting fossil evidence) showed that the crown of Dipterocarpaceae *sl* occurred concurrently on the South American and Madagascan plates. Including fossils from Africa and India changed this to a South American-African origin. Collectively, these origins represent NorthWest Gondwana with South America, Africa and Madagascar remaining conjoined until ≥105–115 Ma, setting the minimum age for this superclade with some evidence that it may be much older. We also show that the immediate ancestors of the three daughter lineages [Dipterocarpaceae-Sarcolaenaceae (in Africa/Madagascar, ≥115 Ma), Cistaceae-*Pakaraimaea* (South America/Africa/Eurasia, ≥105 Ma) and Bixaceae-*Cochlospermum*-Sphaerosepalaceae (South America/Africa, ≥105 Ma)] also arose in NorthWest Gondwana.

The immediate ancestors or basal species in Sarcolaenaceae, Sphaerosepalaceae, Dipterocarpaceae (both its subfamilies) and Bixaceae migrated from (South America)/Africa to Madagascar and we propose that the Dipterocarpoideae proceeded from Africa to India while still linked to Madagascar. In addition, much subsequent diversification of this superclade has occurred on the Eurasian, Indian, SE Asian (Sunda) and North American plates post-Gondwanan breakup.

This long vicariant history is supported by fossil, ecological, mycotrophic and morphological traits, and global circulation patterns that show negligible propensity for transoceanic dispersal to explain this clade's wide intercontinental distribution.

We conclude that all these areocladogram/plate-breakup/ecomorphological/circulation features are consistent with a Gondwanan/early-Cretaceous (>115 Ma) origin for the Dipterocarpaceae-Cistaceae-Bixaceae superclade plus its three daughter clades. Future analyses at the species level, exploring alternative diversification dates from both fossils and plate-tectonic dynamics, are needed to refine these findings.

Highlights

- It was proposed 40 years ago that the iconic Dipterocarps of Asia had a Gondwanan origin.
- Yet current phylogenies place the origin of the Dipterocarpaceae and associated lineages at 100–85 million years ago, when all but a few Gondwanan plates had long since separated.
- We created a molecular phylogeny for the superclade, Dipterocarpaceae-Sarcolaenaceae-Cistaceae-*Pakaraimaea*-Sphaerosepalaceae-Bixaceae-Cochlospermaceae, submitted it to areogram analysis, and then related this to when the major Gondwanan plates separated, with further support from fossil-morphological-ecological data and historic global circulation patterns.
- We show that South America, Africa and Madagascar-India must have still been fused at the time this superclade arose and its three lineages must have arisen in various parts of NorthWest Gondwana (well) over 115 million years ago.
- We conclude that all Dipterocarp-related clades had an African or South American origin with the Asian Dipterocarps originating in India overland via Africa and Madagascar.
- Our results add to the growing body of evidence that Gondwana has been a major cradle for many flowering-plant clades now spread throughout the globe and point to a much earlier origin for Angiosperms than is generally accepted, since the Dipterocarpaceae (Malvales) is not even considered a basal clade.

Keywords: areogram, Cistaceae, Cretaceous fossils, Dipterocarpaceae, ectomycorrhizas, Gondwanan breakup, tectonic plate, transoceanic transport

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Introduction

It has long been held that the iconic family Dipterocarpaceae originated in Gondwana during the Early Cretaceous Period (100–145 million years ago, Ma) due to its strongly intercontinental distribution in the tropical regions of the world (Ashton 1982, Ashton et al. 2021). In the light of this claim, we examined the biogeographic history of this clade and its sisters, that form a natural superclade within the Malvales (Dipterocarpaceae *sl*), consisting of Dipterocarpaceae, Sarcolaenaceae, Cistaceae, *Pakaraimaea*, Bixaceae, Cochlospermaceae and Sphaerosepalaceae (Hernández-Gutiérrez and Magallón 2019). The confirmation that *Pseudomonotes* in the Amazon, South America, is sister to *Monotes* (Monotoideae, Dipterocarpaceae) in Central Africa adds further weight to the assertion of a Gondwanan origin for this family (Morton et al. 1999). The assumption is so strong that it appears Moyersoen (2006) was able to entitle their paper, "*Pakaraimea dipterocarpacea* is ectomycorrhizal, indicating an ancient Gondwanaland origin for the ectomycorrhizal habit in Dipterocarpaceae", without objection from others. Yet the dated molecular phylogeny of Heckenhauer et al. (2017) gives the origin of this species at just 42 Ma; and Hernández-Gutiérrez and Magallón (2019) estimate it at 56 Ma. The full list of papers that have examined the biogeographic history of the Dipterocarpaceae and various members of its superclade, and their findings, are given in Table S1.

Ducousso et al. (2004) concluded that the Sarcolaenaceae (with all 80 species endemic to Madagascar), sandwiched between the two subfamilies of Dipterocarpaceae according to Heckenhauer et al. (2017) and Hernández-Gutiérrez and Magallón (2019), must have split from the Dipterocarpoideae (endemic to Asia) at least 88 Ma, because they were shown to share ectomycorrhizal symbionts and Madagascar separated from India 88 Ma (Bossuyt and Milinkovitch 2001, Reeves 2018). However, this logic is not convincing as it assumes that a) the common ancestor could/did not migrate to either location at a later stage and b) suitable mycobionts were not already present in both locations, and would not therefore have needed to be carried there by their hosts. A later date is possible since transoceanic transport was not considered and there is no evidence that these fungi are specific to their parent clade. Ducousso et al. (2004) were also unaware of research on the fossil pollen of Sarcolaenaceae in South Africa and discussions on its likely African origin (Coetzee and Muller 1984, Nilsson et al. 1996, Randrianasolo and Miller 1999) and incorrectly stated that the family had no history there. Therefore, using the same arguments as Ducousso et al. (2004), if Sarcolaenaceae, or its ancestor, was present in Madagascar before it separated from Africa ~115 Ma (Reeves 2018), then the origin of the Sarcolaenaceae-Dipterocarpaceae must be even earlier (>115 Ma) when Gondwana was still intact. Fossil pollen of Sarcolaenaceae has since been recorded much earlier in northeast Africa from 97 Ma, as several tetrad types (Cole et al. 2017; Morley, 2018), and also India at 78–68.5 Ma (Prasad et al. 2018, Ashton et al. 2021) and cannot be ignored when examining the phylogenetics of this superclade. Bansal et al. (2022) omitted this family from their analysis so that Madagascar was (unfortunately) excluded from any possible role in the migratory history of the Dipterocarpaceae.

Evolutionary biologists estimate the age of divergence events in the form of dated phylogenies known as chronograms. The molecular clocks are invariably set to the dates fossil pollen grains were deposited in sedimentary layers or amber of known age and are compared against the extent of nucleotide differences at nodes in the relevant lineage. Setting the root (base of the stem) of a lineage at the node of the age of the oldest pollen of known identity is fraught with uncertainties (Lamont et al. 2019). In particular, there is no guarantee that this is the time it separated from its sister lineage and it is sure to have been earlier, sometimes much earlier. Further, correct identification of pollen to genus level is difficult (partly because they are rarely located with the parent plant) and even numerical taxonomic analyses can come up with different answers (e.g., see Sauquet et al. 2009 and He et al. 2016 for differences over the correct identity of *Beaupreaidites orbiculatus*, a key palynomorph in the origin of *Beauprea*). Bell et al. (2010) set the split of Dipterocarpoid Dipterocarpaceae from its sister, Sarcolaenaceae, at 38 Ma. This was based on the date obtained by Cavagnetto and Anadón (1996) for Cistaceae (aff. *Helianthemum*) pollen that they gave as 38 Ma. Aparicio et al. (2017) used 42 Ma that they obtained by combining this date with that of a fruit in amber (*Cistinocarpum roemeri,* aff. Cistaceae) at 46 Ma.

Convinced that such dates were too young and unreliable, Heckenhauer et al. (2017) abandoned fossil records altogether. They adopted a strict biogeographic approach and used 88 Ma for the crown of the Sarcolaenaceae-Dipterocarpaceae from Ducousso et al. (2004), coinciding with the possible final date of the separation of Madagascar from the Indian plate. Their subsequent chronogram gave the estimated median for the crown of Dipterocarpaceae *sl* as 91 Ma, and origins of Sarcolaenaceae and dipterocarpoid Dipterocarpaceae as 87 Ma, monotoid Dipterocarpaceae as 77 Ma, and *Pakaraimaea* and Cistaceae as 42 Ma. Using the complete fossil record, Hernández-Gutiérrez and Magallón (2019) estimated that Dipterocarpaceae *sl* separated from its sister clade 100 Ma, Sarcolaenaceae from Dipterocarpaceae 75 Ma, and *Pakaraimaea* from Cistaceae at 56 Ma. These estimates are moderately into the Cretaceous and after the breakup of Gondwana, with the final separation of northwest Africa from northern South America estimated at 110–100 Ma (Hay et al. 1999, McLoughlin 2001, Lawver et al. 2011). More recently, Ashton et al. (2021) estimated the crown of the superclade (excluding Bixaceae and Sphaerosepalaceae) at 99 Ma and the crown of Monotoideae-Dipterocarpoideae at 86 Ma. They gave a central place to *Periretisyncolpates phosphaticus* pollen recorded in the Sudan and Somalia by Cole et al. (2017) and placed by Morley (2018) into *Dipterocarpus* and dated at 78–68.5 Ma.

A key paper is Bansal et al. (2022) that gives the crown of the Monotoideae-Dipterocarpoideae at 102.9 Ma, the Monotoideae at 72.1 Ma, and the Dipterocarpoideae at 94.6 Ma. Even using the oldest 95% HPD age for the most-recent common ancestors, *Trillesanthus* (syn. *Marquesia*, endemic to Africa) and *Pseudomonotes* (endemic to South America) of 85 Ma, this would require transAtlantic-Ocean migration in one direction or the other. Bansal et al. (2022) used highly restrictive assumptions in their analysis as follows: 1) constrained the age of Dipterocarpaceae to a maximum of 110 Ma; 2) pre-assigned Africa as the continent of origin, as the oldest fossil found so far (*P. phosphaticus* noted above) is from there; 3) rejected an Indian origin as it was too far south and consequently the climate too dry for the Dipterocarpaceae as currently distributed; 4) opted for 80–70 Ma as the time of migration to India as by then the climate in greater India and North Africa were considered both perhumid; 5) rejected Madagascar as having any role in the biogeography of Dipterocarpaceae by a) merging it with Africa and b) ignoring Sarcolaenaceae, currently endemic there; and 6) omitted from the analysis other sister clades with a non-African affinity, especially *Pakaraimaea* in South America and Sphaerosepalaceae in Madagascar (Heckenhauser et al. 2017, Hernández-Gutiérrez et al. 2019). From their chronogram we see that 8−9 lineages of the Dipterocarpoideae would have had to migrate ~2,000 km of ocean to reach India 75 Ma (that had now moved east, not yet north, of Madagascar), including two genera whose seeds are wingless. And this means there would have been 8−9 lineages in Africa at the time under supposedly matched climates as well – where there is currently none. Thus, such a migratory history appears far too late and points to the need for a different approach that might give greater support to its conjectured Gondwanan origin. As Tedersoo and Brundrett (2017) comment, “Given the slow evolution and continental disjunctions in these woody plants, the age of Dipterocarpaceae *sl*, Cistaceae and *Pakaraimaea* is almost certainly (greatly) underestimated”.

Since Heckenhauser et al. (2017) have set the precedent of using biogeographic knowledge to identify key events in the evolution of Dipterocarpaceae clades, we took the opportunity to apply a similar approach using modern biogeographic techniques to help resolve the origin of the Dipterocarpaceae *sl.* We incorporated fossil evidence of its historical presence on a given plate without paying particular attention to its age as areogram techniques only have a spatial, not temporal, component. This approach mirrors that adopted by He et al. (2016) who demonstrated an autochthonous origin for *Beauprea* in New Caledonia. Thus, we asked: did the Dipterocarpaceae *sl* and its daughter clades originate in Gondwana before the tectonic plates that they currently occupy begin to separate? We erected a molecular phylogeny at the level of family and genus for the entire Dipterocarpaceae *sl*. This enabled us to give more attention to the possible location of the most-recent common ancestor (stem) of sister clades, rather than current analyses that concentrate on their node of separation (crown). To further explore this superclade’s possible Gondwanan/early-Cretaceous origin, relevant ecological and dispersal traits were identified from the literature and compared across its daughter clades. These ecomorphological traits were used to provide support for, or against, the co-occurrence of the clades before separation of conjoined plates. The combined fossil, areocladogram, tectonic-plate dynamics and ecomorphological data were overwhelmingly consistent with the presence of Dipterocarpaceae *sl* in the Lower Cretaceous, well before the Gondwanan elements of Africa, Madagascar and South America separated. More detailed work would be required at finer scales to confirm that this was the actual biogeographic pathway taken by this superclade.

Materials & Methods

Phylogenetic analyses

We constructed a molecular phylogeny at the species level for Dipterocarpaceae *sl.* Molecular phylogenies for families in the Malvales were examined as a guide to what taxa to include in our analysis: Dayanandan et al. (1999), Morton et al. (1999), Ducousso et al. (2004), Guzmán and Vargas (2009), Heckenhauer et al. (2017), Johnson-Fulton and Watson (2017), and Hernández-Gutiérrez and Magallón (2019). The taxa studied are given in Table S2. A GenBank search was performed using SUMAC (Freyman 2015). Sequences available for Dipterocarpaceae sl were the loci internal transcribed spacers *mat*K, *ndh*F, *psb*A, *rbc*L, *trn*L, *trn*L-*trn*F, *atp*B-*rbc*L, *rpo*B, and these were downloaded and aligned. The alignments were concatenated with SequenceMatrix (Vaidya et al. 2011) and then phylogenetically analysed using maximum-likelihood (ML), with the RAxML Blackbox tool using a GTR + Gamma + I partition model on each locus in the CIPRES portal (http://www.phylo.org). The resulting species-level tree was saved as a nexus file and then manually trimmed using Mesquite (Maddison 2009) to a genus-level phylogeny where each genus terminal was represented by a randomly selected species. Table 1 gives all genera that we included in our analyses and for purposes of discussion we refer to this group as Dipterocarpaceae *sl*.

Areocladogram analyses

We obtained a map of the Earth divided into its major tectonic plates (shapefile from https://github.com/fraxen/tectonicplates#readme and based on Bird 2003). The Somalia plate, composed of the eastern side of Africa and Madagascar, did not suit our purposes when defining genera distributions, because Somalia and the rest of Africa have never separated, whereas Madagascar drifted away in the mid-Cretaceous and contains a highly endemic flora. Thus, for genera distribution, we treated the western side of the Somalia plate as part of the African plate and the eastern side, separated by the Mozambique Channel, as the Madagascan plate. This

Table 1. Summary of outcomes of areocladogram analyses in Figure 2 for the three daughter lineages of Dipterocarpaceae *sl* whose origin is Madagascar-S America when the African fossils are not taken into account and S America-Africa-Madagascar when they are included.

Attribute	1. Bixaceae clade	2. Cistaceae clade	3. Dipterocarpaceae clade
Members at generic level	Amoreuxia, Bixa, Cochlospermum, *Dialyceras*, Diegodendron, *Rhopalocarpus*	*Cistus*, *Crocanthemum*, *Fumana*, *Halimium*, *Helianthemum*, *Hudsonia*, *Lechea*, *Pakairamaea* (sometimes considered a subfamily or even monotypic sister family), *Tuberaria*	*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Eremolaena*, *Hopea*, *Leptolaena*, *Mediusella*, *Monotes*, *Neobalanocarpus*, *Parashorea*, *Pentachlaena*, *Perrierodendron*, *Pseudomonotes*, *Rhodolaena*, *Sarcolaena*, *Schizolaena*, *Shorea*, *Stemonoporus*, *Trillesanthus*, *Upuna*, *Vateria*, *Vateriopsis*, *Vatica*, *Xerochlamys*, *Xyloolaena*
Origin (no fossil data included)	Madagascar-South America	South America	Madagascar
Origin (with African and Indian fossil data)	Africa-South America	Africa-South America	Africa-India-South America (stem), Africa-India (crown)
Other plates represented (postGondwanan)	SE Asia, Australia, N America	Eurasia, North America	SE Asia, Sunda, Seychelles, Australia

resulted in eight plates for which all terminals in the phylogeny were scored. Geographic locations for all species used in the phylogeny were obtained from GBIF records (https://www.gbif.org/) and accuracy tested using http://www.plantsoftheworldonline.org/ and http://www.worldfloraonline.org/ and spot-checked against other geographically restricted web sources. Extra taxonomic and distribution details were obtained from Londoño et al. (1995), Lemmens (2011) and Catarino et al. (2013). The tectonic plate associated with each species location was identified from the supplementary animation by Young et al. (2019; https://ars.els-cdn.com/content/image/1-s2.0-S1674987118301373-mmc1.mp4). Synonyms were removed (mostly *Helianthemum* to *Crocanthemum*) and records for cultivated and invasive species were identified and deleted. Extant distributions of each terminal species were parsimoniously traced onto the phylogenies using Mesquite. Phylogenies of the entire Dipterocarpaceae *sl* at family level, and subset genus level phylogenies for Cistaceae and Dipterocarpoid Dipterocarpaceae, were parsimoniously analysed and then summarized in the overall areocladogram (conceptual distinctions between cladograms and areocladograms are illustrated in Figure 1). The exception was *Cochlospermum* that had to be treated at species level as it is spread over six plates (Johnson-Fulton and Watson, 2017). Data were obtained from the literature on the likely dates that the various plates at that node separated or merged. A search for fossils of Dipterocarpaceae *sl* no longer extant on a tectonic plate revealed Sarcolaenaceae, Sphaerosepalaceae and Dipterocarpoideae in Africa and *Monotes*, Dipterocarpoideae and Sarcolaenaceae in India (Bancroft 1933, 1935, Couper 1958, Srivastava and Binda 1991, Bamford and de Wit 1993, Goodman and Jungers 2014, Aubriot et al. 2016, Cole et al. 2017, Prasad et al. 2018 and Morley 2018). These fossils were incorporated as terminals in the phylogeny at

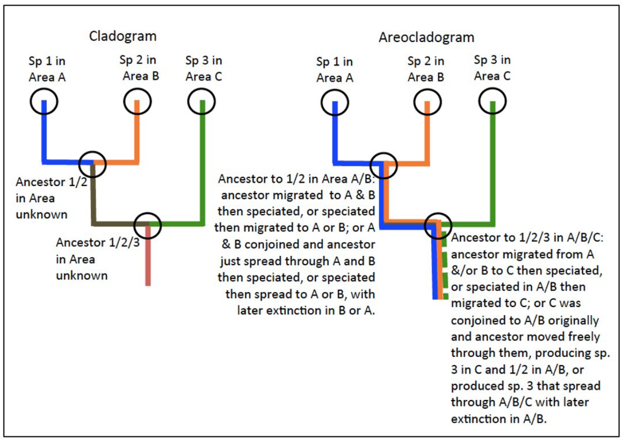


Figure 1. Interpretation of cladograms (left) and areocladograms (right). Ancestor refers to the single, most recent common ancestor (MRCA) to the daughter clades. Note that a MRCA can occur in multiple areas (plates, in our case) that implies it has spread to them or, in fact, that they are the same area (plates yet to separate, in our case).

the ancestral sister positions of their respective clades in a second overall areogram.

Barriers to migration

We applied a paleobiogeographic model of the probability of connectivity (plant or animal migration) between pairs of tectonic plates using the methods of Buerki et al. (2011) and Estrella et al. (2019). Each pair of adjacent plates was assigned as follows: H (high), no barriers to overland migration; M (moderate), some or occasional physiographic barriers (climate, topography) to migration or where a second region has to be traversed via the ocean; or L (low), substantial barriers to migration (wide ocean, a third region has to be traversed). Migration was noted as more or less likely in the direction of the sequence in the pair being compared according to the Coriolis effect on wind direction (over land as well as water; see Bush and Philander, 1997) and ocean currents (Renner 2004). Criteria for ranking pairs from highest (1) to lowest (12) probability of occurring also included: when two regions are joined, distance from their centres is more important than the Coriolis effect; and when two regions are separated, the Coriolis effect is considered more important than their distance apart.

Trait assignments

To further explore this superclade's possible Gondwanan/early-Cretaceous origin, 13 traits that relate to its ecology and dispersal were identified from the literature. These were applied to nine key clades to assist comparisons in the next phase where five clades, with one part of them currently, or historically, on a different plate from others, were chosen for closer analysis. These were used to test the hypotheses that:

1. Sarcolaenaceae was in Africa before it split from Madagascar where it currently occurs;
2. Monotoideae was present in Africa and South America before they split;
3. Monotoideae was present in Africa before it split from Madagascar;
4. Cistaceae was present in Africa-Eurasia before it split from South America where its sister *Pakaraimaea* currently occurs; and
5. Bixaceae-Sphaerosepalaceae-Cochlospermaceae had a Gondwanan origin centred on Africa with all its lineages vicariant, except *Amoreuxia* (Central-South America).

Six or seven sources of evidence that could provide support for, or against, co-occurrence before the plates split were applied to these subclades/clades. The strength of each set of arguments was assessed in a trinary way (yes, no, uncertain) and conclusions drawn on the likelihood of each scenario. Knowing the approximate dates that the various tectonic plates separated within the cladogram, an idea of when Dipterocarpaceae *sl*, and of its three key lineages, arose became possible. Dispersal traits were obtained from Augspurger (1986), Bollen et al. (2005) and Thapliyal and Phartyal (2005). Data for mycorrhizal status was obtained from Giovannetti and Fontana (1982), Malloch and Thorn (1985), Allen et al. (2005), Comandini et al. (2006), Ducousso et al. (2008), Massicotte et al. (2010), Bâ et al. (2011), Barbieri et al (2011), and Smith et al. (2013).

Results

Phylogenetic analyses

The phylogenies produced by the ML analysis revealed three major and seven minor clades: 1) Sarcolaenaceae (comprising Sarcolaenaceae in Madagasacar, monotoid Dipterocarpaceae in Africa and dipterocarpoid Dipterocarpaceae in India, Asia); 2) Cistaceae (*Pakaraimaea* in South America and Cistaceae in Eurasia, Africa, N America); and 3) Bixaceae (Sphaerosepalaceae in Madagascar, Bixaceae-Cochlospermaceae in South America, Africa, Madagascar, India and Asia).

Areocladogram analyses

Areocladogram analysis showed that, when fossils were omitted from the phylogeny, the most recent common ancestor (MRCA) of the Dipterocarpaceae *sl* was located on the South American-Madagascan plates (Figure 2a). When fossils were included, the origin switched strongly to South America-Africa (Figure 2b). The three lineages arising from the deepest diverging ancestor have slightly different origins using the latter, more comprehensive, analysis: 1) the Bixaceae clade is spread across these three plates; 2) the Cistaceae clade is African-South American; and 3) the Dipterocarpaceae clade has a South American-African-Indian origin at its stem and African-Indian origin at its crown (Table 1). While Sphaerosepalaceae has a Madagascan-African origin, its MRCA also occurred in South America whether or not the African fossils were included. Africa was added to South America as the MRCA for the *Pakairamaea*-Cistaceae clade when the African fossils were incorporated into the other two daughter clades. The MRCA for the Dipterocarpaceae clade switched from Madagascar to South America-Africa-India when the African-Indian fossils were added, but South America is not represented among the MCRAs for the Dipterocarpoideae, Sarcolaenaceae or Monotoideae.

The Madagascan and African plates remained fused until ~115 Ma when the Madagascan plate slipped south along the SE margin of the African plate and west margin of the Indian plates, detaching from the former but remaining attached to the latter (Figure 3; Reeves 2018). The Monotoid Dipterocarpaceae has genera in Africa (*Monotes*, *Trillesanthus*), Madagscar (*Monotes*) and South America (*Pseudomonotes*). These merge with Sarcolaenaceae, currrently endemic to Madagascar, but the family has convincing fossil records in SE and NE Africa (Coetzee and Muller 1984, Nilsson et al. 1996, Randrianasolo and Miller 1999, Cole et al. 2017, Prasad et al. 2018). The most basal lineage of the Dipterocarpaceae is the Dipterocarpoideae that occurs on five plates, but SE Asia dominates the areal patterns

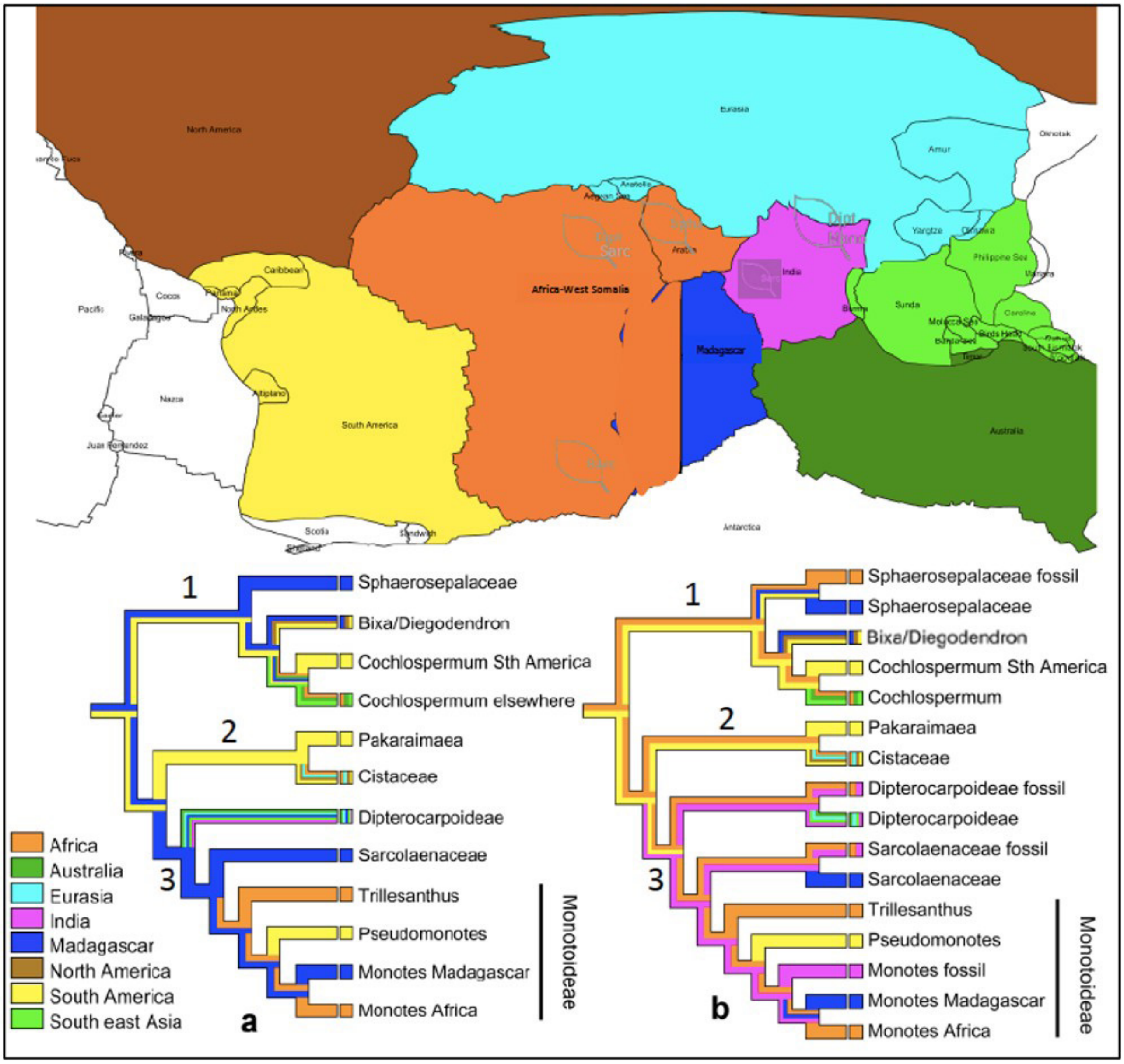


Figure 2. World map of tectonic plates (from https://github.com/fraxen/tectonicplates#readme, see Methods) and two areocladograms for Dipterocarpaceae *sl*. **a**: phylogeny for entire Dipterocarpaceae *sl*. **b**: Dipterocarpaceae *sl* with fossil occurrences in Africa included in the analysis. The plates occupied at a node are indicated by the colours of the adjoining stem to the right. Number 1 refers to the Bixaceae daughter clade, 2 to the Cistaceae clade, and 3 to the Dipterocarpaceae clade (see Tables 1 and S1 for included genera). Note that the Somalian plate has been bisected and the west section re-allocated to the east section of the African plate and the remainder referred to as the Madagascar plate. The Gondwanan plates given here are therefore S America, Africa-Arabia, Madagascar (Somalia, minus E Africa), India and Australia. Fossil records (leaf symbol: Dipt, Dipterocarpoid Dipterocarpaceae; Mono, Monotoideae; Spha, Sphaerosepalaceae; Sarc, Sarcolaenaceae) were added at their approximate locations on the world map.

with 10 of 13 genera analysed on the plates of this region. Since the Indian plate accounts for two basal genera and six other genera have species there, the net result is that the MRCA was located on the Indian/SE-Asian plates when fossil records were omitted (Figure S1). An Asian origin for the Dipterocarpoid Dipterocarpaceae when analysed alone is replaced by an African-Indian origin when compared with the overall cladogram, even though Africa currently lacks any Dipterocarpoid Dipterocarpaceae.

The Dipterocarpaceae clade node links to Cistaceae such that the crown occurs on the Madagascan, African and South American plates (Figure 2). These plates were joined as part of NW Gondwana up to ~115 Ma (Figure 4). NW Africa and NE South America were linked until ~105 Ma (Hay et al. 1999, Brownfield &

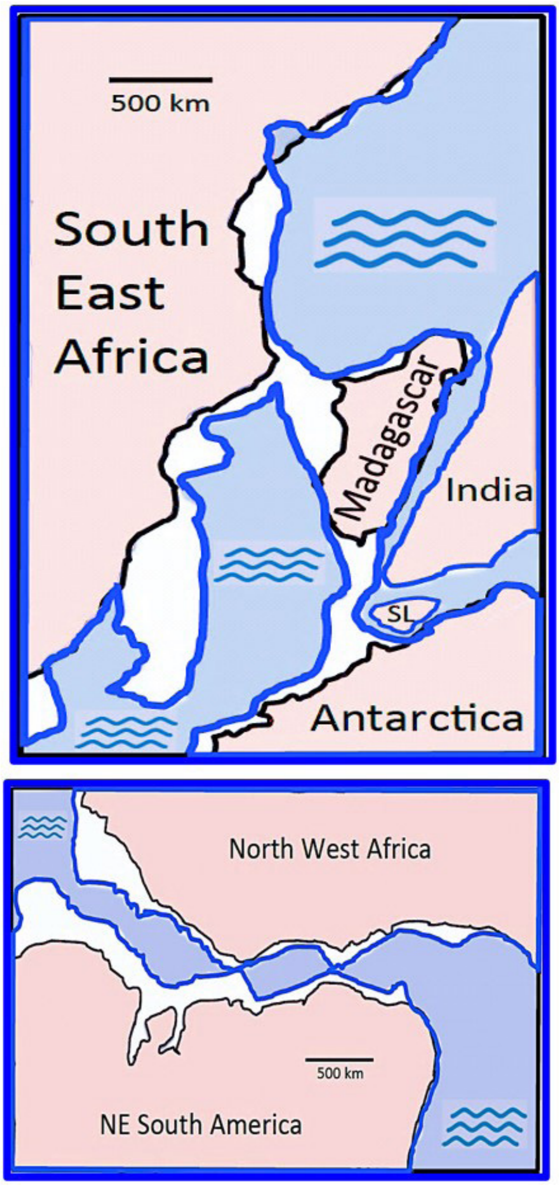


Figure 3. Adjacent plates at times close to their separation. Cratons of plates (pink) are separated by oceans (blue) and extended continental shelves (white), that later became submerged. Blue lines bound areas generally above sea level at the time. **Upper:** SouthEast Africa connected to Madagascar via the extended continental shelf (120–115 Ma; adapted from Reeves, 2018). **Lower**: NorthEast South America about to separate from NW Africa, with incursions of the Atlantic Ocean and lagoons well developed (100 Ma; adapted from Brownfield & Charpentier 2006). Note, Figure 2 in Hay et al. (1999) shows three (rather than two) conjunction points at this time.

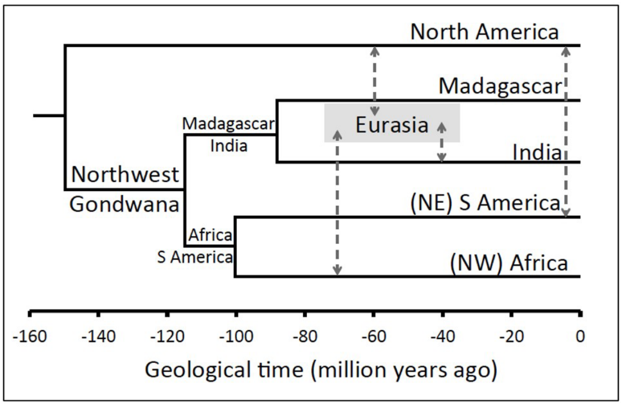


Figure 4. Current understanding of the final separation (or merging – broken lines) of plates associated with NorthWest Gondwana. Mean dates have a ~5 million variance term and were collated from Fisher and Sclater (1983), Hay et al. (1999), Morley (2003), Sanmartíin and Ronquist (2004), Brownfield & Charpentier (2006), Graham (2011), Lawver et al. (2011), Wilf et al. (2013), Reeves (2018), Young et al. (2019) and Earthworks (2021). Note that there have been several North Atlantic landbridges between Europe and N America formed and lost over the Cenozoic – only the oldest is given here. Parentheses refer to the fact that the node represents those parts of South America and Africa that separated last (Figure 3).

Charpentier 2006; Figure 3). Considering Cistaceae-*Pakaraimaea* independently of the overall cladogram shows that the MRCA was located on the South American, African and Eurasian plates (Figure S1). The MRCA for just the Cistaceae alone occupied Africa-Eurasia, having lost South America while separating from *Pakaraimaea*. The MRCA became Africa-South America in the overall cladogram plus fossils, implying an African origin for the Cistaceae since the only connection to South America is the recent migration of *Crocanthemum* from North America (Figure S1).

The MRCA of the Sphaerosepalaceae-Bixaceae *sl* occurred on the South American-African-Madagascan plates (Figure 2). Including the fossil record of the Sphaerosepalaceae in Saudi-Arabia **(**Srivastava and Binda 1991; Figure 2**)** in this analysis provides land continuity between South America and Madagascar, assuming that this family remained in Africa up to 115 Ma (Figures 2–4). Bixaceae *sl* is also rooted in the Madagascan/South American plates, with *Bixa* in South America and *Diegodendron-Dialycerus* in Madagascar. *Cochlospermum* is basal in South America with other species on the (Central) North American, (W) African, Indian, SE Asian and Australian plates, and, via *Amoreuxia*, in South and Central America as well (Johnson-Fulton and Watson, 2017). Oscillations within *Cochlospermum* between S America and Africa are consistent with migrations ≥ 105 Ma, whereas migrations to SE Asia, India and Australia are best explained by post-Gondwanan processes.

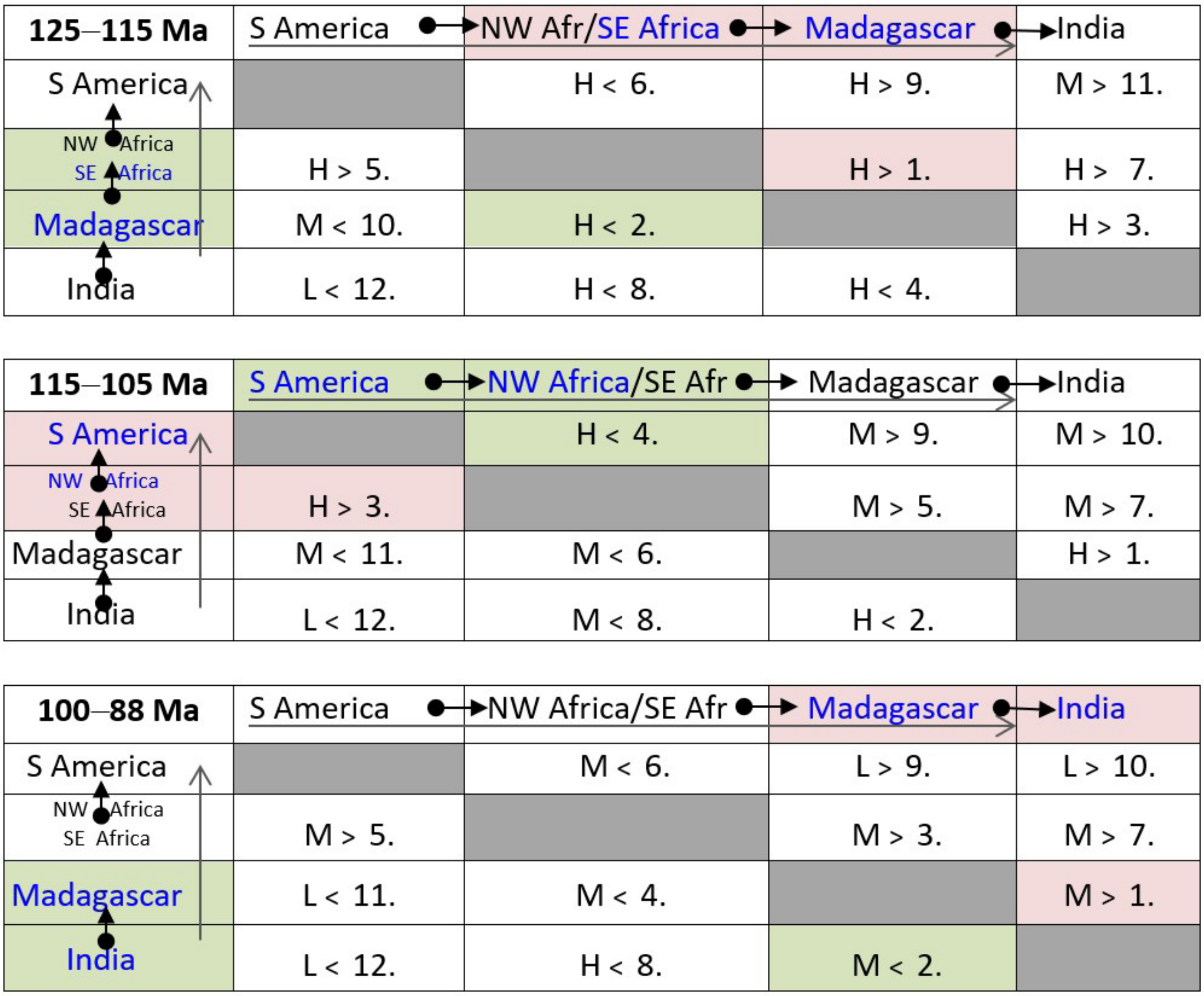
Barriers to migration

Application of the paleobiogeographic model of the probability of connectivity between 12 pairs of (sub) plates (after Buerki et al. 2011 and Estrella et al. 2019) showed that, in the period 125–115 Ma, the probability of organisms migrating was highest from SE Africa to

Madagascar, with the second highest probability from Madagascar to SE Africa (Figure 5). Madagascar–India exchange had the highest probability 115–105 Ma, followed by NW Africa to South America, then South America to NW Africa. Madagascar to India had the highest probability at 100–88 Ma, and India to Madagascar the next highest.

Trait assignments

Fossil records, phylogenetic relations from earlier analyses, and ecological/mycotrophic/ morphological traits of nine major clades in the Dipterocarpaceae *sl* are given in Table S3. The extent to which these traits support a preGondwanan-split origin for five pairs of clades on different tectonic plates are given in Tables S4–7 and are summarized in Table 2. Four lines of evidence support, and two are uncertain (evidence insufficient), regarding the proposition that Sarcolaenaceae and Dipterocarpoid Dipterocarpaceae were present in Africa before it split from Madagascar. There was the same level of support for the proposition that the Monotoideae was present in Africa and



125–115 Ma	S America	NW Afr/SE Africa	Madagascar	India
S America		H < 6.	H > 9.	M > 11.
NW Africa SE Africa	H > 5.		H > 1.	H > 7.
Madagascar	M < 10.	H < 2.		H > 3.
India	L < 12.	H < 8.	H < 4.	

115–105 Ma	S America	NW Africa/SE Afr	Madagascar	India
S America		H < 4.	M > 9.	M > 10.
NW Africa SE Africa	H > 3.		M > 5.	M > 7.
Madagascar	M < 11.	M < 6.		H > 1.
India	L < 12.	M < 8.	H < 2.	

100–88 Ma	S America	NW Africa/SE Afr	Madagascar	India
S America		M < 6.	L > 9.	L > 10.
NW Africa SE Africa	M > 5.		M > 3.	M > 7.
Madagascar	L < 11.	M < 4.		M > 1.
India	L < 12.	H < 8.	M < 2.	

Figure 5. Probability of connectivity between pairs of plates that would facilitate migration during three geological periods during breakup of Gondwana. The first row and column of each matrix (geological period) describes the alternative migration directions. The probability of migration is ranked (1-12) based on: (a) the likelihood of migration (high to low) based on barriers to dispersal, and (b) the likely direction of migration (> or <) according to wind and ocean currents. The events of interest involve the separation of pairs of plates (blue) at the end of each period causing the final separation of: northern S America from NW Afr(ica); Madagascar from India; and their separation from South-eastern Africa (see Figure 3). Colour cells highlight the most likely scenario for the plates of interest at that time (pink) and the next most likely scenario (green). *Barriers to migration*: H (high), no barriers to overland migration; M (moderate), some or occasional physiographic barriers (climate, topography) to migration or where a second region has to be traversed via the ocean; or L (low), substantial barriers to migration (wide ocean, a third region has to be traversed). *Direction of migration*: >, more likely in the direction indicated; or <, less likely in the direction indicated.

Table 2. Summary of evidence from fossils and ecomorphological traits to support a preGondwanan-split origin for pairs of clades in the Dipterocarpaceae *sl*. Based on evidence presented in Supplementary Tables S4–S8.

1. Evidence in favour of Sarcolaenaceae and Dipterocarpaceae present in Africa before it split from Madagascar	**Level of Support**
Fossil pollen present at this time	uncertain
Suitable savanna/rainforest habitats available	uncertain
Inability for fruits or seeds to disperse long distances by air or ocean	yes
Suitable ectomycobionts available	yes
Unable to colonize coastal dunes	yes
A 125–115 Ma split between the two continents relative to the origin of flowering plants reasonable	yes
2. Evidence in favour of Monotoideae present in Africa and South America before they split	
Fossil pollen present at this time	uncertain
Suitable savanna/rainforest habitats available	uncertain
Inability for fruits or seeds to disperse long distances by air or ocean	yes
Suitable ectomycobionts available	yes
Unable to colonize coastal dunes	yes
A 110–100 Ma split between the two continents relative to the origin of flowering plants reasonable	yes
3. Evidence in favour of Monotoideae present in Africa and Madagascar before they split	
Fossil pollen present at this time	uncertain
Suitable savanna/rainforest habitats available	uncertain
Inability for fruits or seeds to disperse over the Mozambique Channel by air or ocean	yes
Suitable ectomycobionts available	yes
Unable to colonize coastal dunes	yes
A 125–115 Ma split between the two landmasses relative to the origin of flowering plants reasonable	yes
4. Evidence in favour of Cistaceae present in Africa and *Pakaraimaea* in South America before they split	
Fossil pollen present at this time	uncertain
Suitable vegetation types available in Cretaceous	yes
Fire-proneness of habitats and fire adaptations	yes
Inability for fruits or seeds to disperse long distances by air or ocean	yes
Suitable ectomycobionts available	yes
Unable to colonize coastal dunes	yes
A 115–105 Ma split between the two continents relative to the origin of flowering plants reasonable	yes
5. Evidence in favour of Bixaceae-Sphaerosepalaceae-Cochlospermaceae in Africa and/or S America before they split	
Fossils present at this time	uncertain
Suitable vegetation types available in Cretaceous	yes
Fire-proneness of habitats and suitable fire adaptations evident	yes
Inability of fruits or seeds to disperse long distances by air or ocean	yes
Suitable mycobionts available	yes
Unable to colonize coastal dunes	yes
A 115–105 Ma split between the two continents relative to the origin of flowering plants reasonable	yes

South America before these plates split; also that Monotoideae was present in Africa and Madagascar before they split. Six lines of evidence support, and one is uncertain, for the proposition that the Cistaceae was present in Africa and *Pakaraimaea* in South America before these plates split. There was the same level of support for the proposition that the Bixaceae-Sphaerosepalaceae-Cochlospermaceae were in Africa and/or South America before they split. Most of the 32 trait propositions were supported with eight traits of uncertain status.

Discussion

The combination of evidence from phylogenetics, fossils, functional traits, and spatial and temporal relations points to an origin of the Dipterocarpaceae *sl* in NorthWest Gondwana at least 115 Ma, i.e., before South America, Africa and Madagascar-India separated. The logical conclusion from the areocladogram analysis, showing that the most recent common ancestor (MRCA) was present in all three plates, must be that they were still fused at the time. Africa formed the basal dispersal route throughout, South America to a lesser extent, and, later, Madagascar-India (Figure 2b). Below we systematically unpack all evidence and reasoning behind five scenarios among the major lineages within this superclade that leads to our overarching conclusion.

1. Sarcolaenaceae had an African-Madagascan origin while they were still connected ≥ 115 Ma (Figure 6)

Sarcolenaceae has a well-established fossil presence in Africa (four sites) and lesser extent India (one site), yet today it is endemic to Madagascar. Figure 2b shows that the MRCA occurred in Africa and India and reached Madagascar either via Africa or India.

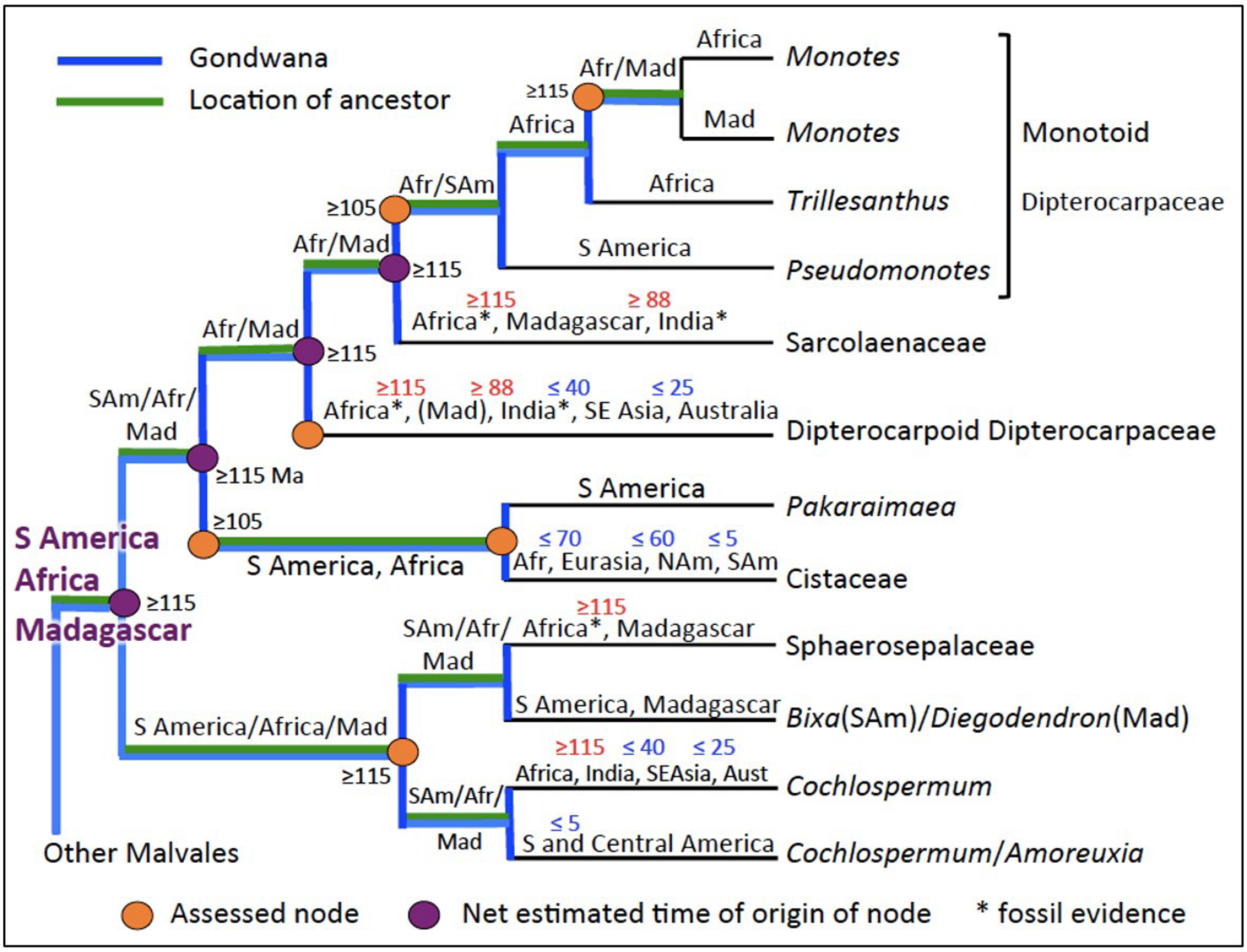


Figure 6. Areocladogram (based on Figures 2–4) with fossil records (*) for Dipterocarpaceae-Cistaceae-Bixaceae and dates of tectonic-plate-breakups added. The minimum ages (in Ma) of origin for five key lineages (●) are based on conclusions from the present study. The minimum ages of origin for four key nodes (●) are based on outcomes for the supporting pair of stems taking the older as minimum. Values in colour are the ages of separation (red) or merging (blue) of the plates to either side. Note that branch lengths are arbitrary as this is not a chronogram, which must await further molecular work. Afr = Africa, Aust = Australia, Mad = Madagascar (Malagasy), NAm = N America, SAm = South America.

Fruits of Sarcolaenaceae are (currently) dispersed by lemurs, are considered too heavy to respond to wind uplift, and the seeds are short-lived and saltwater-intolerant (Tables 2, S3). No taxa in this family are known to colonize coastal dunes, as required for successful transoceanic transport (Crisp et al. 2009). These data indicate that transoceanic dispersal is unlikely, meaning that the MRCA must have travelled overland before Africa and India separated. The most recent time that these plates were linked directly was 200–180 Ma (Young et al. 2019). Accepting that the family is younger than that (there is no *a priori* reason for doing so, as evidence is mounting of a Permian origin (> 250 Ma) for flowering plants, He and Lamont 2022), then the most likely path is from SE Africa to Madagascar ≥ 115 Ma (Figures 3, 4) then to India before it separated from Madagascar 88 Ma. The reverse pathway is not possible as India is only terminal in the areocladogram (Figure 2b). In further support of a common original habitat, Sarcolaenaceae shares numerous Cretaceous-active ectomycobionts with both Dipterocarp subfamilies in Africa (Table S3). Therefore, Sarcolaenaceae, or its MRCA with Monotoid or Dipterocarpoid Dipterocarpaceae (Heckenhauer et al. 2017, Hernández-Gutiérrez and Magallón 2019; Figure 2b), must have arisen in Africa-Madagascar ≥ 115 Ma, i.e., before Gondwana began to break up (Figures 4, 6).

The absence of Dipterocarpoid Dipterocarpaceae in Madagascar implies that the MRCA with the Sarcolaenaceae clade may have arisen in Africa. An Asian origin for the Dipterocarpoid Dipterocarpaceae when analysed alone (Figure S1) is replaced by an Africa-India origin at their common node when compared with the overall cladogram (Figure 2b). This is due to the effects of adding fossils from both plates and presence of Africa among the two sister clades. This result is consistent with Ducousso et al. (2004) for a Madagascar origin but it clear that it should include Africa, especially when the Monotoideae is included. We do not consider the rich post-Gondwana history of the Dipterocarpaceae here that must await more detailed analyses.

2. Pseudomonotes (endemic to S America) and Monotes (endemic to Africa/Madagascar) arose from an ancestor that moved freely through South America-Africa when they were still connected ≥ 105 Ma (Figure 6).

This scenario is described in Figure 2b and can be explained most convincingly via two options. Either, *Pseudomonotes*, or its MRCA with *Monotes*, migrated from Africa to South America over the North Atlantic Ocean (Figure 5). Or, the northern-most plate components were still joined and *Pseudomonotes* (or its MRCA) spread from NW Africa to NW South America, bearing in mind that the basal sister, *Trillesanthus*, is African. We ignore the Indian option as it is only present in the MRCA because of the inclusion of a *Monotes* fossil in India (it may be interpreted as indicating that Africa and India were still linked when *Pseudomonotes* separated from *Monotes*). *Pseudomonotes* has recalcitrant seeds (Smith et al. 2015) – they must germinate within two weeks of release or perish. This lack of seed dormancy, coupled with saltwater-intolerance, helps to rule out the first option that requires transoceanic dispersal (Tables 2, S3, S5). However, the fruits are strongly winged (Table S3), making wind transport possible. If the arrival of the MRCA to South America occurred 40 Ma (i.e., the age of fossil pollen found in Peru; Prasad et al. 2018), then it would need to migrate aerially from tropical rainforests in NW Africa (e.g., Congo, the centre of diversification for *Monotes*; Meerts et al 2017), west to the coast, cross ~4,000 km of Atlantic Ocean (the distance at ~40 Ma) and then traverse ~3000 km terrestrially to Peru. Even assuming that all seeds were not lost (the fruit is tardily dehiscent) during the shortest likely distance that might lead to establishment (perhaps 5,000 km), the journey duration would exceed seed longevity. Were the fruits to be carried in the stratosphere, such non-dormant seeds would lose viability to the freezing temperatures anyway.

The more likely scenario is that the MRCA spread across Africa/South America before Gondwana split 115−105 Ma (Figure 3) to yield *Pseudomonotes* in S America and *Monotes* in Africa. Since *Monotes* is positioned at the crown of this lineage (Figure 2b), it is likely that the MRCA was spread through Africa-South America to produce *Pseudomonotes* in South America and *Monotes* in Africa later. This helps to explain why there is no fossil evidence of *Pseudomonotes* in Africa although there is for *Monotes*. A Gondwanan origin for the clade is further supported by the most basal clade in the Monotoideae, *Trillesanthus,* residing in West Africa, implying that it also originated >105 Ma, when it separated from the *Pseudomonotes-Monotes* ancestor that was spread widely through the two plates (Figure 6). In further support of a common original habitat, these genera in different continents share many ectomycobionts (Table S3).

3. Monotes spread from Africa to Madagascar before they separated ≥ 115 Ma.

Monotes is terminal in a lineage that has a long history in Africa/Madagascar stretching back to the origin of Sarcolaenaceae (Figures 2, 6). This means that the clade has either had two matched phylogeny histories on separate plates during this time, or more likely, that they existed on the presplit plate during that time. Nevertheless, *Monotes* in Madagascar could have diverged after the two plates separated via an ancestor traversing the Mozambique Channel < 115 Ma (Figure 5), or by basal *Monotes* (or their MRCA) spreading into Madagascar prior to the separation ≥ 115 Ma (Figures 3, 4). Bansal et al. (2022) has four African *Monotes* (of the > 25 species) genetically isolated from the single Madagascan *Monotes* whose origin is only 15 Ma that is consistent with either interpretation. Suitable mycobionts are currently on both landmasses and these have a history that stretches back to the Cretaceous (Berbee and Taylor

2001, Hackel et al. 2014), and lack of host specificity means that the MRCA could have been widespread across the two plates before separation. However, this evidence does not allow dismissal of post-split migration as a possibility. Although *Monotes* fruits are winged, Humbert (1944) considers them too heavy to be caught up by wind vortices. Also a post-split arrival in Madagascar is inconsistent with the inability of seeds to survive in seawater, the ocean current sweeping through the Mozambique Channel rather than across it, the genus occurring strictly in savanna/rainforest, and having no known ability to colonize coastal vegetation (Tables 2, S3, S6). At face value, India and Madagascar appear as alternative routes for *Monotes* to reach Africa, except that both are only terminal in the phylogeny. Assuming that Africa and India were not fused at the time *Monotes* arose (see under topic 1 above) to explain the presence of the Indian fossil (63 Ma, Bansal et al. 2022), then it is more likely that *Monotes* reached Madagascar from Africa ≥ 115 Ma and then to India > 88 Ma. Overall, it seems reasonable to conclude that the common ancestor, or basal species, of *Monotes* existed across Africa-Madagascar before they split ~115 Ma.

4. Old World Cistaceae were unable to reach South America directly from Africa and Pakairamaea was unable to reach S America from Africa such that their ancestor must have evolved before these plates separated ≥ 105 Ma (Figure 6).

When the common node for the N South American endemic, *Pakaraimaea*, and the predominantly Old World Cistaceae is considered, the stem representing their MRCA resides in Africa and South America (Figure 2). Two possible interpretations emerge to explain this scenario. Their MRCA migrated across the N Atlantic Ocean from North Africa to NE South America after their plates finally separated ~105 Ma. This would allow the MRCA to exist earlier in South America than in Eurasia that merged with N Africa ~70 Ma (Figure 4). Further analysis at the species level shows that the basal species occur in Africa and the terminal species in Eurasia (unpublished), such that the MRCA must be > 70 My old (i.e., before the Africa–Eurasia merger). Alternatively, the MRCA spread across the African and South American plates before they separated ≥ 105 Ma.

There is little support for the post-Gondwanan scenario (Tables 2, S3, S7). Since the Coriolis effect strongly favours east to west transport here (Figure 5), most attention needs to be given to the possibility of the *Pakaraimaea* MRCA migrating from Africa to South America. Fruits of both clades dehisce at maturity, seeds are wingless, spheroid and small, get buried readily, and are known for their limited dispersability (Table S7). Consequently, the seeds are unlikely to be lifted up from the ground by wind vortices nor attach to pterosaurs/birds for transoceanic dispersal. Their ability to float, or survive, in seawater for many months is unknown, but any non-dormant seeds are unlikely to survive if that were possible. The habitat and response to fire of *Pakaraimaea* are also inconsistent with transoceanic dispersal. The genus occurs in frequently burnt savanna or rainforest margins, it resprouts after fire and its predominantly hard seeds require fire-type heat to break dormancy (Maguire and Ashton 1980). There is no evidence that it can colonize coastal dune vegetation, that is typically non-fireprone, as would be required if the seeds were to survive transoceanic dispersal (Crisp et al. 2009).

Both clades are essentially adapted to fireprone woodlands with a strongly seasonal climate and the likelihood of aerially or marine-dispersed seeds arriving to suitable fireprone vegetation following transcontinental dispersal appears fanciful at best. *Pakaraimaea* accepts a wide range of ectomycobionts (29 species; Vasco-Palacios 2016) that indicates a long association with the South American flora, although the seven genera in common with African mycorrhizal fungi (Lee 1998) also support its historical link there via its MRCA. Having already dated the origin of the sister clade (Dipterocarpaceae-Sarcolaenaceae) above at ≥ 115 Ma this gives additional support to dating this clade at ≥ 115 Ma (sister clades cannot have different times of origin). Overall, there is little support for a post-Gondwanan origin of *Pakaraimaea*-Cistaceae and more support for a pre-Gondwanan-breakup origin with the MRCA spread through NE South America and NW Africa before they finally split. We do not explore the rich post-Gondwanan history of Cistaceae here that must await more detailed analyses.

5. The Bixaceae-Sphaerosepalaceae-Cochlospermaceae had a Gondwanan origin with all its basal lineages vicariant, except Amoreuxia.

The Sphaerosepalaceae is currently endemic to Madagascar, but a convincing palynomorph has been identified in Saudi-Arabia (African plate) at 56 Ma (Table S3). And because Bixaceae occurs in Madagascar and is widespread in N South America, this lineage is given a South America-Africa-Madagascar origin according to the areocladogram (Figure 2). Cochlospermaceae is basally N South American, with speciation oscillations between W Africa and South America over time, and later intrusions into India, SE Asia, Australia and Central America (Johnson-Fulton and Watson 2017) that we do not explore here. This places the MRCA of Bixaceae-Sphaerosepalaceae-Cochlospermaceae in South America-Africa-Madagascar. Again, we must confront the possibility of transoceanic transport between the plates. We note that Johnson-Fulton and Watson (2017) gave the origin of this clade at ~100 Ma using the fossil leaves of *Bixa* and *Cochlospermum previtifolium* in Patagonia at 52 Ma to set the molecular clock for their phylogeny. However, Hernández-Gutiérrez and Magallón (2019) dated these same fossils at 66–56 Ma. The latter estimate would then place the clade in South America-Africa at ~110 Ma – tenuously prior to their final separation but would allow the MRCA to spread between these plates without the need for transoceanic dispersal. The question then becomes: could the MRCA also have spread from Africa to Madagascar ≥ 115 Ma, or was transoceanic dispersal possible, allowing more recent immigration?

Since the Cochlospermaceae has no fossil or extant record in Madagascar it is only necessary to consider how the Bixaceae-Sphaerosepalaceae got there. The fruits and seeds are wingless and fleshy, and considered too heavy and spheroidal to be lifted by wind vortices (Humbert 1944). Seeds have a prominent, lychee-like aril attractive to vertebrate dispersers – currently lemurs and birds (Horn 2004). There is a distribution mismatch between frugivorous birds that consume seeds adapted for endozoochory in forests and omnivorous seabirds on the coast that might rarely be caught up by hurricanes to spread seeds to other lands (He et al. 2016). Thus, we can dismiss birds/pterosaurs as possible transoceanic dispersal agents. Seeds of most species are nondormant and short-lived (Table S3), although *Dialyceras* (Sphaerosepalaceae) is hard-seeded (has a water gap, as befits its fireprone savanna habitat), but *Diegodendron* (Bixaceae) is not (Table S3). Fruits might float in water (never tested), but they gradually disintegrate (Schatz and Lowry II 2006). Species are strictly in savanna or rainforest and are unknown as colonizers of coastal dunes, but *Rhopalocarpus* may occur in stable coastal vegetation in SE Madagascar (Table S8). The fact that all 20 or so species in Sphaerosepalaceae only occur on the east side of Madagascar, i.e., furthest from the wet African coast (see Ohba 2016 for the late Cretaceous climate), also decreases the likelihood of trans-Mozambique-Channel transport. Certainly, suitable savanna (fireprone) and rainforest (non-fireprone) climates existed during the Cretaceous that would have allowed for lineage spread (Axelrod and Raven 1978; Table S8). Since all species in this clade are endomycorrhizal (for which host specificity is unknown) and suitable fungi are present in all ecosystems (Table S8), this does not present a barrier to inter-plate diversification. We conclude that the case for a post-Gondwana-split (i.e., transoceanic migration) origin for the Bixaceae-Sphaerosepalaceae-Cochlospermaceae is weak. Having independently shown that the clade, Cistaceae-Dipterocarpaceae-Sarcolaenaceae, is likely to have arisen ≥ 115 Ma, we accept that this is also true for its sister clade.

Overall patterns

Figure 6 summarizes the results in Figure 2 and puts them in the context of Gondwana. The entire Dipterocarpaceae-Sarcolaenaceae lineage shows a South American-African-Indian origin with terminal branches in Africa, South America, Madagascar, India, Eurasia, SE Asia and Australia, whose locations are consistent with the breakup sequence of Gondwana (clade 3 in Figure 2b). This means that the minimum ages of 105 Ma through parts of the phylogeny interspersed with the older estimated dates ≥ 115 Ma can be replaced by ≥ 115 Ma throughout. Interestingly, South America is present in the stem to the lineage in the areogram but drops out at the crown to leave Africa-India to give rise to the Dipterocarpoideae and Sarcolaenaceae-Monotoideae. This places *Pseudomonotes* in isolation without a direct connection to South America in the areogram. But, since the entire lineage is shown to have existed ≥ 115 Ma, this implies that *Pseudomonotes* arose ≥ 115 Ma via Africa (given as a possible location for its MRCA) with which it was still connected.

The sister lineage (clade 2 in Figure 2b) also shows a sequence consistent with a Gondwanan breakup from South America-Africa at ≥ 115 M with one branch to *Pakaraimaea* and the other to Cistaceae. The MRCA of the Sphaerosepalaceae-Bixaceae-Cochlospermaceae (clade 1 in Figure 2b) dated to ≥ 115 Ma was also located in South America-Africa. One branch of this clade includes Madagascar (Sphaerosepalaceae), indicating its passage to Madagascar via Africa. And the other branch, *Cochlospermum*-Bixaceae, is strongly South American-African, but later reached Madagascar, India, SE Asia and Australia, with *Amoreuxia* in South-Central America. Since our cladogram has yet to be converted into a chronogram we are not able to comment on the further timing of these later events. Thus, omitting the ultimate stems, Figure 6 shows that all lineages were initially located in South America (seven stems), Africa (six stems) and Madagascar (seven stems) that can together be considered part of NorthWest Gondwana. All 12 ultimate stems are also present on these plates, but may include the descendants of taxa that separated at the nodes that can be assigned to a preGondwanan-breakup. In addition, four of these stems lie on postGondwanan-breakup plates, especially Eurasia, SE Asia, and, to a lesser extent, N-Central America and Australia (actually New Guinea).

We note that Bansal et al. (2022) have the Dipterocarpoideae reaching India from Africa 76−71 Ma. According to their chronogram, at that time, 8−9 lineages of the Dipterocarpoideae would have needed to migrate over 1500 km of ocean to reach India, including two genera that are wingless. And this means there would have been 8−9 lineages in Africa then as well – where there is currently none. Thus, even without the counter evidence presented here, such a passage appears far too late – diversification in the Dipterocarpoideae at this scale can only have occurred since it departed from Africa. As shown by their chronogram, and confirmed here, India has had a major role in the biogeographic and evolutionary history of the Dipterocarpoideae. But, as we note, the two plates have been separated since the Lower Cretaceous. Since we show that transoceanic dispersal lacks ecomorphological support, we have to confront the issue of how this clade got from Africa to India. It is not inconsistent with our findings (a MRCA for Dipterocarpoideae extending ≥ 115 Ma) that this clade may have arisen >180 Ma when the two plates were still fused and possessed a suitable ever-wet climate at that time (Scotese et al. 2021). Accepting that such an earlier possibility is at present poorly supported, we see that the origin of Sphaerosepalaceae, Sarcolaenaceae, *Monotes* and *Diogendendron* (Bixaceae) can all be accounted for by them, or their MRCAs, migrating to Madagascar from SE Africa (Figure 2b).

Consistent with these findings, we propose that the Dipterocarpoideae reached India from Africa via Madagascar. This conclusion has some affinity with Ducousso et al. (2004) although there is no evidence that Dipterocarpoideae split from Sarcolaenaceae coinciding with India separating from Madagascar 88 Ma, and Dipterocarpoideae and Sarcolaenaceae had already arisen before migration to Madagascar. We also note that Sri Lanka is considered to have separated from India in the early Cretaceous (145–100 Ma; Katz 2000). This implies that the Dipterocarpoideae (via at least the endemic *Stemenoporus*) was already present in India at that time, consistent with our findings, although not excluding the Jurassic link between Africa and India as a pathway if this clade existed then. It requires acceptance that transoceanic dispersal was not an option for *Stemonoporu*s, with its wingless, recalcitrant seeds (Thompsett 1998). Our proposed pathway is identical to that recently proposed for the passage of *Phylica* from the Cape, South Africa to the West Burma plate 100 Ma (and thence to Myanmar) that was probably attached to Greater India at that time (He and Lamont 2022, Shi et al. 2022). We note that Bansal et al. (2022) dismissed from the outset any role for Madagascar in the paleobiogeography of Dipterocarpoideae. It is unfortunate that Madagascar has never been a source of fossils for any of the clades considered here.

Figure 7 integrates the most likely direction of overland migration (spread) based on Figure 5 with data from Figures 3−4 to recognize nine general migration pathways, although other scenarios are possible. NorthWest Gondwana comprised the tectonic plates of South America, Africa, Madagascar and India that embraced all species of Dipterocarpaceae *sl* from ≥ 115 Ma. This ceased ~70 Ma when N Africa merged with Eurasia and provided a multidirectional pathway for the Cistaceae to spread from Europe

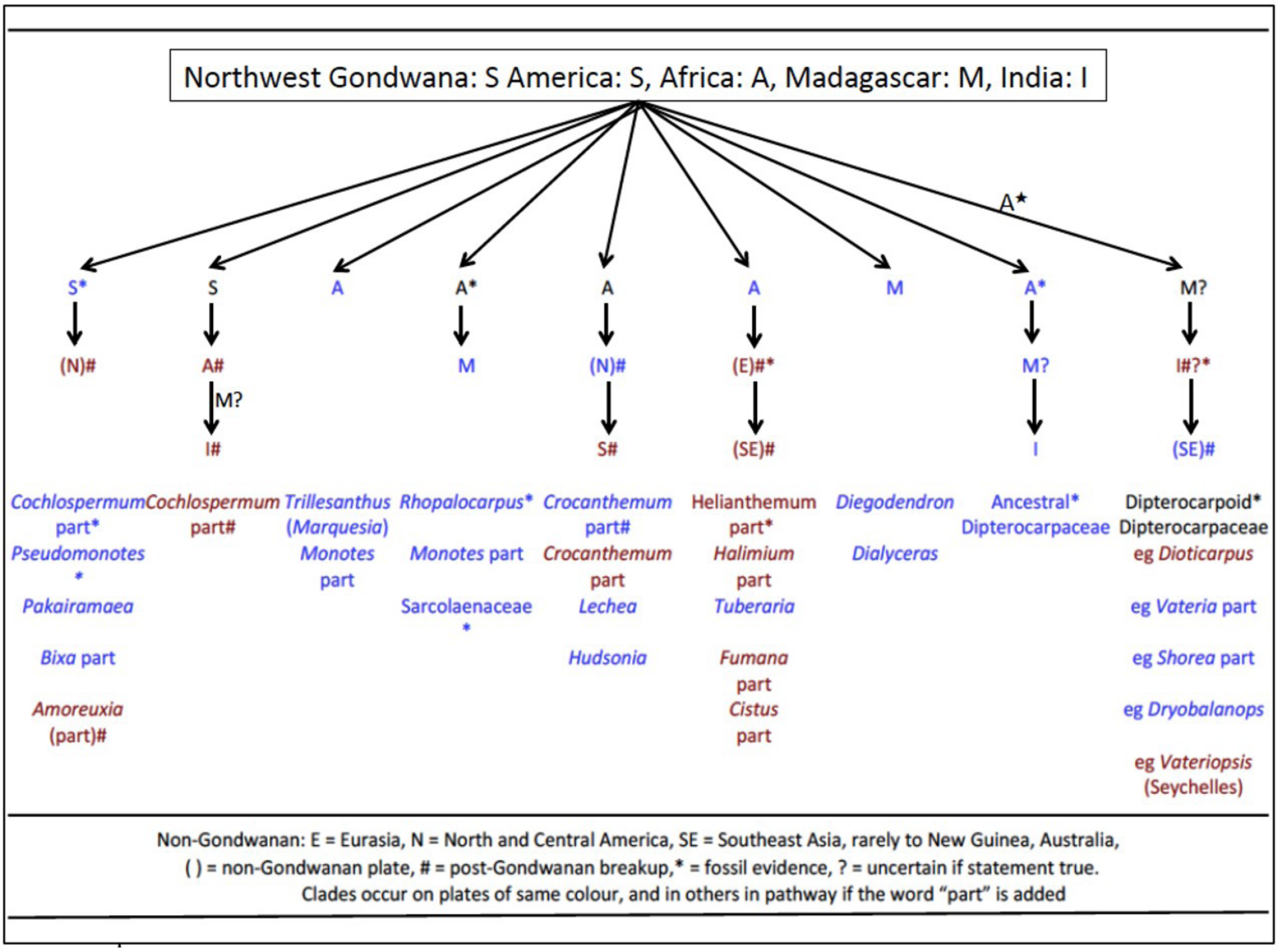


Figure 7. Nine sequences interpreted as the most likely migration pathways taken by lineages in the Dipterocarpaceae-Sarcolaenaceae-Cistaceae-*Pakaraimaea*-Sphaerosepalaceae-Bixaceae-Cochlospermaceae superclade, based on Figures 2 and 6. The most likely parent tectonic plate for the first step in each pathway is Gondwanan, whereas subsequent steps, representing more recent migratory events, may, or may not be, on Gondwanan plates. Fossils related to a given lineage and its associated plate are noted (*) and these are assumed to be ancestral. The meaning of other symbols and colours are explained on the figure. The only uncertain aspects of the pathways are a) the complex history of *Cochlospermum* outside of South America and b) the complex history of Dipterocarpoids following their apparent secondary origin in Madagascar/India, neither of which was of primary interest in this study.

to: a) North America and finally South America (to complete the loop) ~5 Ma, and b) Russia, central Asia and finally NW China < 5 Ma (Su et al. 2017). Cistaceace established itself via these pathways in each region through which it passed. Africa holds the key to the distribution pattern, possibly being the ancestral plate for nine of the pathways. *Cochlospermum* (endemic species), *Pakaraimaea* and *Pseudomonotes* appear autochthonous in N South America. *Trillesanthus* and *Monotes* appear autochthonous in tropical Africa, with one (extant) species of *Monotes* reaching Madagascar ≥ 115 Ma. To support the spread of Sarcolaenacae and *Rhopalocarpus* from Africa to Madagascar ≥ 115 Ma, fossil evidence must be included. *Diegodendron* and *Dialycerus* are possibly autochthonous in Madagascar. Widespread in SE Asia, the Dipterocarpoid Dipterocarpaceae has speciated more than any other clade. While there are convincing fossil records in NE Africa, this clade does not at present occur in Africa or Madagascar. However, it is reasonable to conclude that this subfamily arose in Africa and reached India via Madagascar ≥ 115 Ma. This conclusion is based on ectomycobionts endemic to Madagascar that establish on Dipterocarpoid Dipterocarpaceae and its sister, Sarcolaenaceae (Ducousso et al. 2004), and our evidence for the inability of Dipterocarpoid Dipterocarps to undertake, or survive, transoceanic dispersal (Tables S3, S4). It remained on the Indian plate (e.g., *Dioticarpus* and *Vateriopsis* in the Seychelles) or migrated to one (e.g., *Shorea*) or more (e.g., *Vateria*) Asian–Australian tectonic plates, whose history we do not explore further here. All 30 examples we give in Figure 7 are consistent with the phylogeny of the lineage and the breakup history of Gondwana. We detected no exceptions, although there were several cases of ambivalence.

Our aim was to show that the immediate ancestors of the three key lineages of Dipterocarpaceae *sl*: Dipterocarpaceae-Sarcolaenaceae (in Africa/Madagascar), Cistaceae-*Pakaraimaea* (South America-Africa-Eurasia) and Bixaceae-*Cochlospermum*-Sphaerosepalaceae (South America/Madagascar) could also have occurred concurrently in the supercontinent, NorthWest Gondwana, that remained intact ≥115 Ma. The areocladograms demonstrated that the three major tectonic plates on which these clades are extant (South America, Africa, Madagascar) co-occurred along their basal stems (Figures 2, 6). (India enters the areogram later but will have been there all the time, attached to Madagascar until 88 Ma). Having shown for all taxa that transoceanic transport and recruitment are essentially untenable (Tables S3-8), we accept the alternative explanation that this group has a preGondwanan-breakup origin. Although our aims did not include developing a chronogram, which must await more detailed work, it is instructive to compare this date with previous chronograms. Heckenhauer et al. (2017), using the separation of India from Madagascar to set their molecular clock, gave the 95% highest posterior density range for Dipterocarpaceae-Sarcolaenaceae as 103−85 Ma, and Cistaceae-*Pakaraimaea* as 60−25.5 Ma. Note how this will decrease the accuracy of speciation rates for clades older than 88 Ma and that the problem increases using just fossils to set the clock, as all their fossils are dated < 65 Ma. Hernández-Gutiérrez and Magallón (2019), using comprehensive fossil evidence, gave 85−65 Ma and 70−43 Ma for the same comparisons. For Bixaceae-*Cochlospermum*-Sphaerosepalaceae, Johnson-Fulton and Watson (2017) obtained 101−96 Ma, which they constrained "according to past molecular clock estimates" so this lacked independence. Interestingly, had they used the same dates for their fossils as Hernández-Gutiérrez and Magallón (2019), this would have increased the origin of this clade to ~110−105 Ma. Relying on *Dipterocarpus*-like pollen in NE Africa, dated at 68.5 Ma (although records actually extend to 78 Ma), Bansal et al. (2022) obtained a mean for the crown of Dipterocarpaceae (ignoring Sarcolaenaceae) in Africa at 103 Ma, compared with our findings for its two subfamilies of ≥115 Ma as the very minimum.

These disparate dates, considerably younger than our estimates (although sometimes comparable), highlight the problems of using only fossils from the Cenozoic to calibrate the clock when the hypothesis is that the clade has a Mesozoic origin − too much extrapolation is required. Also, relevant ecomorphological traits were almost never considered, as if there are no biological constraints to dispersal. Transoceanic dispersal is typically treated as the default option as though this is without any impediments whatever the direction required, even when apparent distances apart are vast, and often unnecessarily so because the fossil record (especially for Antarctica) is ignored (Sauquet et al. 2009, He et al. 2016). For example, by basing the origin of Cistaceae-*Pakaimaea* on a Cistaceae-like palynomorph from NE Europe (estimated at 42 Ma; Aparicio et al. 2017), the South American endemic, *Pakairamaea*, is assigned the same date without questioning its veracity (Heckenhauer et al. 2017). Yet we have here a monotypic outlier 4,000 km from the deepest diverging Cistaceae (*Fumana*) in Africa-Eurasia. Its dehiscent fruits and seeds are wingless and occur in dense savannas or marginal rainforest (unknown habitat among *Fumana*), so that they are unlikely to be lifted by wind vortices. Also seed dormancy is broken by fire-type heat that would need to be encountered immediately by the pioneer seeds on reaching coastal dunes in South America via the ocean or dropping into vegetation that is essentially non-fireprone (Amazon rainforest). And the species is a small tree that resprouts after fire, further traits unknown among basal *Fumana* (Table S7). While its breeding system is not known, multiple viable seeds within interplant dispersal distances would likely be required to produce a viable pioneering population.

Older fossils than those currently used for setting molecular clocks are increasingly reported, pushing the origin of flowering plants even further back. For example, flowering shoots of *Phylica*, essentially endemic to southern Africa, have been described from 100-My-old Burmese amber, some 80 My older than its origin as used in current phylogenies

(Shi et al. 2022). New research shows that flowering plants are more likely to have arisen in the Permian than the Cretaceous or even Triassic, at 250 Ma or beyond (Li et al. 2019, Silvestro et al. 2021, He and Lamont 2022). Earlier, Hochuli and Feist-Burkhardt (2013) identified six ‘angiosperm-like’ polynomorphs at 241−239 Ma in Switzerland. Thus, confidence is growing that such dates as ours, which would have appeared unreasonable even in the recent past, are becoming acceptable. Further, there is evidence that land links may have been maintained for much longer than current dates of plate separations indicate (e.g., based on the distribution of frogs that do not tolerate seawater, Van Bocxlaer et al. 2006).

Limitations

There are four possible sources of error with our biogeographic approach. The areas of occupancy allocated to each stem depend greatly on: a) what taxa are included in the cladogram, b) what plate separations are used (e.g., Heckenhauer et al. (2017) only used the Madagascar-India separation, Bansal et al. (2022) omitted Madagascar), c) whether or not fossil data are added, and d) treating the fossil data as sister to extant lineages in the absence of an actual age dimension to the areogram. Estimates of the dates of separation of the plates vary greatly between models, and the wide gap between when separation started and finished adds to the uncertainty. Identification problems and whether locations of accessions are accurate or represent the complete distribution of the taxon (we had to take extra care to delete the many records of cultivated plants among the GBIF data) add to the limitations. Also the ecomorphological dimension requires a thorough knowledge of ancestral traits, global circulation patterns and habitat environments. Extra empirical data would also help confirm some of the conclusions – e.g., demonstrating that seeds of *Pakaraimaea* and basal Cistaceae do not remain afloat or viable in seawater for any length of time, although no one trait was considered critical in making the conclusions drawn here.

A reviewer pointed out that terminal taxa may have lost dispersability traits more recently, giving the false impression of their inability to disperse transoceanically. That is certainly possible. Related work has shown how this superclade has passed through various climates and vegetation types, including fire-prone savannas that promoted evolution of various fire-related traits (Lamont 2022, Pausas and Lamont 2022). Even so, there is no evidence that clades currently in rainforests had a substantially different biogeographic history. On this point, Bansal et al. (2022) undertook an ancestral-trait assignment analysis for wingedness in the Dipterocarpaceae that they calculated arose ~103 Ma. The ancestral condition was a wing length of 1–10 cm. By 40–50 Ma, wing length was > 10 cm in *Dipterocarpus* and *Shorea*, but 40 million years earlier, there was a >50% probability that *Stemenoporus* was wingless and 100% probability that *Vateriopsis* was wingless. Their chronogram has these two genera yet to reach their current locations at that time. Apart from this lack of correlation between wingedness and apparent long-distance dispersal, many other seed traits are given in Table S3 (recalcitrance, seawater intolerance, animal dispersal) that render transoceanic transport unacceptable as a general explanation for any of the extant biogeographic patterns, and they cannot all have only recently evolved.

Conclusions

If the boundary between the Upper and Lower Cretaceous is taken as 100 Ma (Gradstein et al. 2004), the outcome of our analysis is that the Dipterocarpaceae *sl* superclade arose well into the Lower Cretaceous (> 115 Ma) when the South American, African and Madagascan-Indian components of NorthWest Gondwana were still intact. However, this does not necessarily mean that the African and South American Monotoid Dipterocarps, the Madagascan Sarcolaenaceae, the Asian Dipterocarpoid Dipterocarps, or Mediterranean Basin Cistaceae are of Gondwanan origin, just that their most recent common ancestors were. Exceptions to this uncertainty might exist among what appear to be basal autochthonous genera on these tectonic plates, such as *Pakaraimaea* in N South America that implies a Gondwanan origin for it sister clade, Cistaceae, whose oldest genera are in North Africa-Europe (Figure 7). Only a comprehensive phylogenetic/molecular-clock-type analysis at the individual species level might demonstrate the actual locations of the oldest crown species in these daughter clades.

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Author Contributions

B.L. conceived and guided the project, A.T. undertook the areocladogram analyses, prepared Figs. 2 and S1 and contributed to the Methods, D.K. collated the distribution data from GBIF and other websites and prepared Table S2, B.L. prepared all other figures and tables, reviewed the literature, interpreted the results, and wrote the initial drafts, D.K. edited the figures and tables and formatted the manuscript, and all authors edited and approved of the submitted manuscript.

Data Availability

All distribution data were obtained from Global Biodiversity Information Facility (GBIF Secretariat 2021) and are summarized in Table S2, all DNA data were obtained from GenBank, and the sources of all geological dates, ecomorphological/ mycotrophic traits and global circulation patterns are cited under the relevant figures and tables and given in the reference list.

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb:

Figure S1. Areocladogram for a) Cistaceae-Pakaraimaea and b) dipterocarpoid Dipterocarpaceae.

Table S1. Historical phylogenetic treatments of Dipterocarpaceae sl.

Table S2. Taxa in the Dipterocarpaceae-Sarcolaenaceae-Cistaceae superclade analysed in this study.

Table S3. Attributes of nine taxa in the Dipterocarpaceae-Cistaceae-Bixaceae superclade of the Malvales that might shed light on their evolutionary history.

Table S4. The case for and against Sarcolaenaceae and Dipterocarpaceae being present in Africa before it split from Madagascar.

Table S5. The case for and against Monotoideae being present in Africa and South America before they split.

Table S6. The case for and against Monotoideae being present in Africa before it split from Madagascar.

Table S7. The case for and against Cistaceae being present in Africa before it split from South America where its sister Pakaraimaea currently occurs.

Table S8. The case for and against the Bixaceae-Sphaerosepalaceae-Cochlospermaceae clade having a Gondwanan origin centred on Africa.

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