Biogeography and ecology in a pantropical family, the Meliaceae

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ABSTRACT. This paper reviews the biogeography and ecology of the family Meliaceae and maps many of the clades. Recently published molecular phylogenies are used as a framework to interpret distributional and ecological data. The sections on distribution concentrate on allopatry, on areas of overlap among clades, and on centres of diversity. The sections on ecology focus on populations of the family that are *not* in typical, dry-ground, lowland rain forest, for example, in and around mangrove forest, in peat swamp and other kinds of freshwater swamp forest, on limestone, and in open vegetation such as savanna woodland. Information on the altitudinal range of the genera is presented, and brief notes on architecture are also given. The paper considers the relationship between the distribution and ecology of the taxa, and the interpretation of the fossil record of the family, along with its significance for biogeographic studies. Finally, the paper discusses whether the evolution of Meliaceae can be attributed to 'radiations' from restricted centres of origin into new morphological, geographical and ecological space, or whether it is better explained by phases of vicariance in widespread ancestors, alternating with phases of range expansion.

Keywords. Altitude, limestone, mangrove, rain forest, savanna, swamp forest, tropics, vicariance

Introduction

The family Meliaceae is well known for its high-quality timbers, especially mahogany (*Swietenia* Jacq.). The family also has a diverse phytochemistry with many bioactive compounds, and different species are used in the production of cosmetics, medicines (antifungal, antiviral, and antibacterial), and poisons (such as insecticides). Some are important for their edible fruit. Most Meliaceae species are tropical trees with compound leaves, and the family includes the largest-known tree in Africa — an *Entandrophragma excelsum* Sprague, 81.5 m high on Mt Kilimanjaro (Hemp et al., 2017).

Meliaceae comprise about 48 genera and 700 species. The family is widespread through the tropics and also occurs in some temperate areas. Most members occupy lowland tropical rain forest on dry ground (termed 'terra firme' forest in Brazil), but the family is also present in mangrove swamp, freshwater swamp forest, montane forest, drier forest, woodland, and open savanna. It is often present in secondary vegetation, and several species are invasive weeds. The family occurs up to subalpine forest at the tree line (some members are frost-tolerant), but it is absent from true alpine vegetation.

Previous models of Meliaceae biogeography

Spatial analysis

It has long been assumed that taxa originate in a restricted area and attain their distribution by moving out from there. Many different criteria have been proposed in order to locate a group's centre of origin. For example, it has been placed at the site of a group's centre of diversity, of its oldest fossil, or of its phylogenetically 'basal' group. (A 'basal' group is simply the smaller of the two main groups at the basal phylogenetic node; both clades are equally basal in the phylogeny, and strictly speaking it is the node, not either one of the clades, that is basal).

Previous studies on the biogeography of Meliaceae have proposed a localised centre of origin for the group. Using 'ancestral area' programmes, these studies have calculated an Old World centre of origin, either in Africa (Koenen et al., 2015) or in Madagascar-India (Koenen, 2011). However, the programmes used will often calculate centres of origin, even in cases where this is unlikely or at least questionable. For example, if members of a basal paraphyletic grade occur in the same region, the programmes will always find a centre of origin there. However, a group with a phylogeny Old World (Old World (Old World (New World))) has a basal paraphyletic grade in the Old World, but may not have had a centre of origin there. In the example shown here (Fig. 1), differentiation has taken place entirely by vicariance. The ancestor was cosmopolitan, as is the modern group.

In the case of subfamily Melioideae, for example, the phylogeny is: Old World (Old World (Old World (Old World (Old World and New World)))). The paraphyletic group in the Old World means that ancestral area programmes will calculate a centre of origin there. However, there is no need for any trans-Atlantic dispersal in the Melioideae if Meliaceae were already global before the origin of the two modern subfamilies (cf. Fig. 1).

Likewise, for the family as a whole, Koenen et al. (2015) wrote that: "The topology indicates an Old World origin for the family, as the Palaeotropical taxa in the family are paraphyletic with respect to Neotropical lineages (figs 1, S1)". The phylogeny shows that New World Meliaceae are secondary in a sense, but this does not necessarily mean they are the result of trans-Atlantic dispersal.

Chronological analysis

Establishing the time tree of phylogeny of a group is traditionally based on the fossil record of the group and its relatives. Muellner et al. (2006) wrote that "Fossils supporting a Gondwanan range are available for only few of the many pantropical eudicot families. Some workers have therefore taken the absence of Cretaceous fossils to attribute tropical range disjunctions to long-distance dispersal…". An alternative possibility is that the fossil record is very incomplete. Previous studies on the biogeography of Meliaceae have all calibrated the phylogeny with the fossil record alone, although Koenen et al. (2015) admitted that the fossil record of Meliaceae is "sparse".
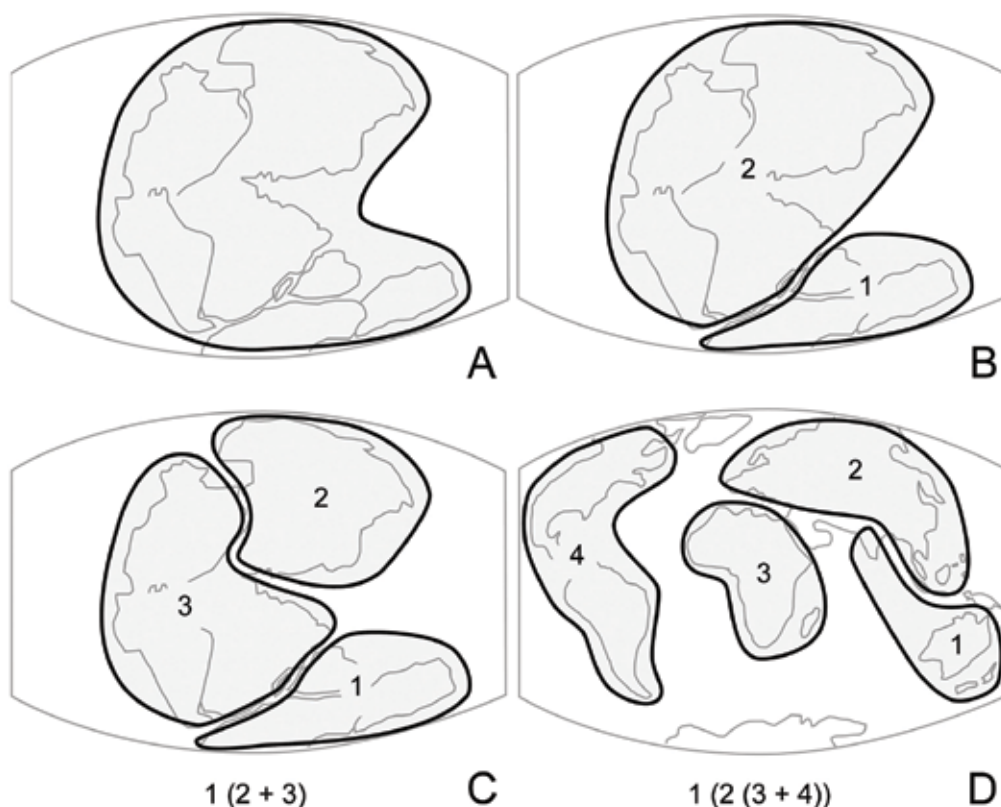
Fig. 1. Differentiation of a hypothetical, global group by vicariance, not by radiation from a centre of origin. **A.** A cosmopolitan ancestor of the group. **B.** Division into two groups. **C.** A second division gives three groups, one in what will become Africa and America. **D.** With the opening of the Atlantic, the America-Africa group is divided. The phylogeny is: Old World (Old World (Old World + New World)). There is a basal, paraphyletic grade in the Old World, but there was not a centre of origin there.

Individual fossils provide a fabulous wealth of data on extinct organic form, but the fossil record itself, and the stratigraphic sequence of taxa in it, cannot be taken at face value. Even at high taxonomic levels there are large gaps. For example, Grande (2016) highlighted three orders of fishes. In lampreys (order Petromyzontiformes; 38 living species), the youngest fossil is 120 million years old. In hagfishes (order Myxiniformes; 20 living species), the only fossil is 300 million years old. In coelacanths (order Coelacanthiformes; two living species, 150 extinct fossil species), the youngest fossil is 65 million years old. These marine animals live in conditions that are much more conducive to fossilisation than land plants such as Meliaceae.

Fossils (assuming palaeontologists agree on their identification) can provide a very useful *minimum* age for a clade, while actual clade ages can be estimated on the basis of biogeography and tectonics. If the boundary between clades correlates spatially with a tectonic feature, the age of the clades can be equated with the age

of activity on that feature. If a coherent synthesis can be obtained using many such correlations, the argument for a causative relationship is strengthened.

Muellner et al. (2006) wrote that reliable age estimates depend on "completeness of the fossil record of a plant group… uncontroversial geology and age of the fossils… unambiguous assignment of the fossil taxa to extant taxa… and unambiguous, well-supported positions of the corresponding extant taxa in the phylogenetic trees". In the Meliaceae alliance, the authors proposed that two taxa fulfilled all these requirements, *Ailanthus* Desf. (Simaroubaceae) and *Toona* (Endl.) M.Roem. (Meliaceae). However, the oldest *Ailanthus* fossils are "virtually identical" (Pfeil & Crisp, 2008) to modern plants, and they appear in the fossil record without any obvious precursors. The simplest explanation is that the record is very incomplete.

Fossil fruit from the Early Eocene London Clay comprise capsules with winged seeds, typical of Meliaceae subfamily Cedreloideae, and they have been described as *Toona sulcata* (Bowerb.) E.Reid & M.Chandler (Reid & Chandler, 1933; Collinson, 1983). Other authors have interpreted the fossils as intermediate between *Toona* and *Cedrela* P.Browne and have placed them on the crown node of tribe Cedreleae (*Toona* and *Cedrela*) (Muellner et al., 2010). However, Koenen et al. (2015) wrote that the fruits of extant species of *Toona* and *Cedrela* are more elongate than the globose fossil fruits, "making the placement in Cedreleae [*Toona* and *Cedrela*] doubtful". Pigg et al. (2014) wrote that the generic assignment of the London Clay fossils "is in need of reevaluation".

Fossils from the Late Cretaceous of Wyoming have been identified as an extant genus of Meliaceae, *Guarea* L., that is widespread in tropical America. Muellner et al. (2006) described the identification as 'controversial'. Nevertheless, both the experts that they consulted (T.D. Pennington and K.B. Pigg) gave personal communications that the identification "may be correct". Muellner et al. did not use the fossil in their analysis, as this calibration produced "unrealistically old ages" for clades.

Fruits and seeds described from the Late Cretaceous (Campanian/Maastrichtian boundary) of Senegal were assigned to Meliaceae and considered to be similar to the genera *Carapa* Aubl. and *Trichilia* P.Browne (Monteillet & Lappartient, 1981). However, Pigg et al. (2014) considered that the specimens need to be reevaluated.

Based on a fossil-calibrated phylogeny of the family, Muellner et al. (2006) argued that Meliaceae originated in Africa and dispersed from there to Eurasia, then North America, and finally South America (see discussion in Heads, 2012). Vicariance was ruled out because the family was thought to be too young: fossil-calibrated divergence estimates "indicate that Meliaceae originated *after* the last known connection between Africa and South America" (Muellner et al., 2006; italics added).

However, fossils can only indicate that a clade evolved *before*, not after, a particular date. Muellner et al. (2006) eliminated trans-Atlantic vicariance, but only by treating the minimum (fossil-calibrated) clade ages as maximum clade ages. Interpreting the clade ages in this way is not logical, and so the idea of dispersal that is based on these interpretations is dubious.

Muellner et al. (2006: 246) wrote: "Although we are aware that our calculated values are minimum estimates our fossil calibration points would have to be at least

30–40 million years older to make the oldest Old–New World divergence events within the Meliaceae consistent with a continental break-up scenario". There is no reason why there should not be at least 30–40 million years of sampling error in a group's fossil record (see the three orders of fishes cited above), and so vicariance in Meliaceae with continental breakup is not falsified by the fossil record.

Muellner et al. (2006: 247) concluded: "Investigations employing new tools… have shown that long-distance, transoceanic dispersal may have played a major role in shaping the distribution of many taxa…". But the new data from sequencing studies, fossils, and geology all need to be interpreted. The studies that Muellner et al. (2006) cited have indeed supported traditional, centre of origin/dispersal theory, but only by treating fossil-calibrated, minimum clade ages as maximum ages.

Muellner-Riehl et al. (2016) referred to "the only direct (primary) information that the fossils provided, namely the minimum age of the respective clade…". To obtain actual clade ages with fossil calibrations "generally requires setting a maximum constraint [for at least one clade] that, in a strict form, does not exist as fossils only provide minimum ages". This is correct. However, the authors neglected their own advice, as they continued: "Using the absence of fossils for a maximum age constraint can only be justified in cases of a dense fossil record of multiple groups appearing in a sequence reflecting their evolutionary relationship. This applies to the eudicotyledons (eudicots), where the succession of the appearance and geographical spread of early angiosperm pollen (monosulcate, Hauterivian–Valanginian), early eudicot pollen (tricolpate, Barremian–Aptian), and derived eudicot pollen (tricolporate, late Albian) justifies the assumption that eudicots originated not much earlier than the appearance of their fossil pollen record…". Koenen et al. (2015) agreed with this: tricolpate pollen "is perhaps the only angiosperm fossil that can be used as a hard maximum age constraint as it is a plant part that is produced in abundance, fossilises easily and appears all over the fossil record shortly after its [putative] first appearance… Consequently, it seems unlikely that eudicots will be much older".

However, there are several problems with this, as discussed elsewhere (Heads, 2014: 67). Smith et al. (2010: 5897) concluded instead: "Using the first appearance of tricolpate pollen as a fixed calibration may underestimate the origin of eudicots and, by extension, other age estimates that have relied on this constraint. Tricolpate grains first appear in separated geographical areas and the grains themselves are not uniform in morphology…, both observations implying that the tricolpate clade originated some time before its appearance in the fossil record…".

Although the oldest tricolpate (eudicot-type) pollen is dated as about 125 Ma, excellent macrofossil material from 123 to 126 Ma shows closest affinities with the eudicot family Ranunculaceae (Sun et al., 2011), suggesting that modern eudicot families, or their immediate precursors, already existed by then. This indicates a prior history for eudicots as a whole.

A further problem with the dating of eudicots from fossils is the fact that while most eudicots have tricolpate or 'tricolpate-derived' pollen, some do not. One example is *Duparquetia* Baill., a liane from West Africa that is near-basal in the phylogeny of legumes. It has bizarre pollen that in some features is "unique in the Fabales and

eudicot clades, resembling more closely the monosulcate pollen found in monocots and basal angiosperms" (Banks et al., 2006: 107). It is doubtful that this pollen, if known only from fossils, would be identified as a eudicot.

In their clock study of eudicots, Anderson et al. (2005) noted that the tricolpate pollen of eudicots may have evolved *after* the split of eudicots from their sister group, for example, by parallel evolution in the main eudicot lineages. In another clock study, Smith et al. (2010) estimated that eudicots evolved in the Late Jurassic. They wrote: "our results suggest that the first appearance of tricolpate grains at ca. 125 Myr underestimates the origin of the tricolpate clade by perhaps 3 to 22 Myr. This finding is problematic because the record of fossil pollen is judged to be very good through this time period…". But the pollen record is very good only in relation to the fossil record of other plant parts, not in an absolute sense. Smith et al. concluded (p. 5900): "we favour the use of 125 Myr as a *minimum* age for the origin of the eudicot crown clade".

The study by Smith et al. (2010) was fossil-calibrated, and the age of eudicots they suggested is still only a minimum. Yet their extension of the age of eudicots from Early Cretaceous to Late Jurassic means that eudicot groups would have been exposed to critical, tectonic and paleogeographic events in Earth history.

Modern Bayesian dating studies (e.g. Muellner-Riehl et al., 2016) often acknowledge that, in theory, fossils can give only minimum clade ages. However, in practice they stipulate just how much older a clade can be than its oldest fossil, in the 'priors' (stipulated prior to any analysis). The problem is that the priors are subjectively chosen and are usually very narrow, that is, a clade is assumed to be not much older than its oldest fossil. With priors that are too narrow, the analysis will often produce clade ages that are much too young, and this is especially likely in a group with such a sparse fossil record as Meliaceae.

Priors are crucial. As Hauenschild et al. (2018) observed, vicariance is often ruled out for clades in which reconstructed age estimates are younger than continental breakup. However, they noted that the young ages estimated "may also be due to overly small highest posterior density intervals of the time estimated *based on too narrowly set priors*, and vicariance thereby may be erroneously ruled out (Beaulieu et al., 2013). If the importance of vicariance in the course of the Gondwanan breakup is to be evaluated via the pragmatic criterion of mismatch between age estimates and geological history, the priors defining the molecular dating analyses have to be solid" (italics added). Yet the priors used in practice are both subjective and narrow, an inheritance from the earlier, simplistic idea that a group's age is the age of its oldest fossil.

Biologists setting priors often do not appreciate that there is a secular trend to fossil preservation, as younger periods of time are represented by larger volumes of sedimentary rock. In addition, the quality of younger rocks for fossil preservation increases, as older rocks are more likely to be deformed. Finally, younger fossils are more similar to modern groups and are more likely to have been identified correctly.

Holland (2016) discussed 'the pull of the recent', whereby the quality of the fossil record declines with geological age. He concluded: "Although minimum ages of clades are given by the oldest preserved fossil, these underestimate the true age,

which must be bracketed by probabilistic methods… Although most of these methods assume uniform preservation rates, this assumption is unsupported over geological timescales…".

Bromham (2019) suggested that molecular clock dating "requires us to believe six impossible things before breakfast". Many of the assumptions "are based on statistical tractability rather than being informed by improved understanding of molecular evolution, yet changing the assumptions can influence molecular dates. … If our assumptions are wrong, then our inference could be misleading, however much data we have…. All molecular dating analyses require us to make statements of belief, irrespective of whether we call them models, assumptions, or priors. We need to recognise that while some disagreements between molecular dates are due to differences in data or method, many are due to different beliefs codified in the analyses…".

To summarise, a fossil gives a minimum age for its clade, and we do not know how much older than this date the actual clade age is. Biogeographic calibrations suggest that many clades are much older than their oldest fossil (Heads, 2014).

Koenen et al. (2015) used four fossils to calibrate a phylogeny of Meliaceae, including *Toona sulcata* from the London Clay. All four fossil calibration points were assigned uniform priors with the fossil ages as a minimum age and the maximum age constrained to the same age as the root height prior. But how old is the root? Koenen et al. (2015) wrote: "the shape of the chosen prior distribution is often subjective. Choosing an informed prior distribution based on palaeobiological evidence… would be better, but this is not possible given the sparse fossil record of Meliaceae…".

Koenen et al. (2015) ran three analyses with different maximum age priors, as follows: 1. Using a fossil-calibrated crown age for Sapindales (c. 71 Ma) as a hard maximum bound; 2. Using a fossil-calibrated stem age of Sapindales (98 Ma) as a hard maximum bound; 3. Using the age of the first tricolpate pollen (127 Ma) as a hard maximum bound for the age of eudicots.

The authors regarded the third method as most likely. Nevertheless, the authors found that in scenarios 2 and 3, the crown age of the Sapindales becomes 'unrealistically old', especially when the tricolpate pollen age is used. (Using tricolpate pollen, the authors calculated that Sapindales originated at 120 Ma and Meliaceae at 80 Ma, but biogeography indicates that this last date is still much too young).

By stipulating such narrow priors and thus calculating such young clade ages, the authors were able to support traditional chance dispersal over vicariance: "… Old World/New World disjunctions are indeed substantially *too young* (Oligocene or younger) for vicariant explanations… [Thus] Our results indicate [Oligocene or younger] trans-Atlantic dispersal from Africa to the New World…" (Koenen et al., 2015). Again, this simply reflects the very narrow priors that were imposed. The time and place of origin of Meliaceae can be regarded as open questions.

Twenty years ago, most authors argued that species had their origin in the Pleistocene (since 2.6 Ma). The argument that species could ever be Cretaceous (before 65 Ma), made on the basis of treating fossils as minimum clade ages and on biogeography (Craw et al., 1999), was controversial. Now, most authors accept that

species may be as old as Miocene (5–20 Ma). However, recent molecular studies have proposed that species of plants, such as *Gunnera herteri* Osten (Bacon et al., 2018), and animals, such as petalurid dragonfly species and the frog *Leiopelma hochstetteri* (Ware et al., 2014; Carr et al., 2015), date back to the Cretaceous (65 Ma).

Global distribution of Meliaceae and allied families

The family Meliaceae is widespread in tropical Africa, Asia and America (Fig. 2), and so it can be described loosely as 'pantropical'. However, it also has significant representation outside the tropics in South Africa, Australia, New Zealand, Pakistan, northern India, Nepal, and central China (north to Gansu). The highest latitude reached by the family is about 43°S (*Dysoxylum spectabile* Hook.f. at the Hurunui River in New Zealand; see www.NZPCN).

In addition to their presence in some temperate forests, native Meliaceae are absent in a large part of the wet tropics, as they do not occur in the central Pacific (Hawaii and southeastern Polynesia). The reason for this curious anomaly is discussed further below.

As already mentioned, fossils suggest that Meliaceae were formerly distributed further north, in Europe, Japan, and North America. However, because of problems with the identifications, the putative fossil Meliaceae are not shown in Fig. 2. Also missing from Fig. 2 are the many naturalised species of Meliaceae, including invasive weed trees. In modern times, species of Meliaceae have naturalised far beyond the indigenous limits of the family, especially in North America, Eurasia, and the central Pacific islands.

Most Meliaceae inhabit 'lowland tropical rain forest' of some kind (540 species), but 162 species are in drier, deciduous forest and savanna (Koenen et al., 2015). Also, many occur at higher elevations, in distinctly montane forest. Together with the extra-tropical species, this shows that the group does not require the hot, wet conditions of lowland tropical rain forest, and the distribution of these conditions does not explain the distribution of the family.

Distribution of Meliaceae and related families in the Pacific
Meliaceae have maximum species numbers in tropical Asia and Malesia (303 species), with fewer in the Neotropics (189 species), Madagascar (107 species), and tropical Africa (102 species). However, despite their abundance in Malesia and parts of the south-west Pacific, such as Fiji, Meliaceae are absent from a vast area of the central Pacific (Fig. 2). This area of absence includes Hawaii (where there are five naturalised species), the Galapagos (with one naturalised, invasive species), Juan Fernandez Islands, the Marquesas Islands (one naturalised species), the Society Islands and the Cook Islands. This absence exists despite the fact that the family includes mangroves (*Xylocarpus* J.Koenig, which ranges east to Tonga) and many weedy species.

When explaining absences in groups it is often useful to consider the distribution of the groups' relatives. Meliaceae (48 genera, 700 species) form a well-supported
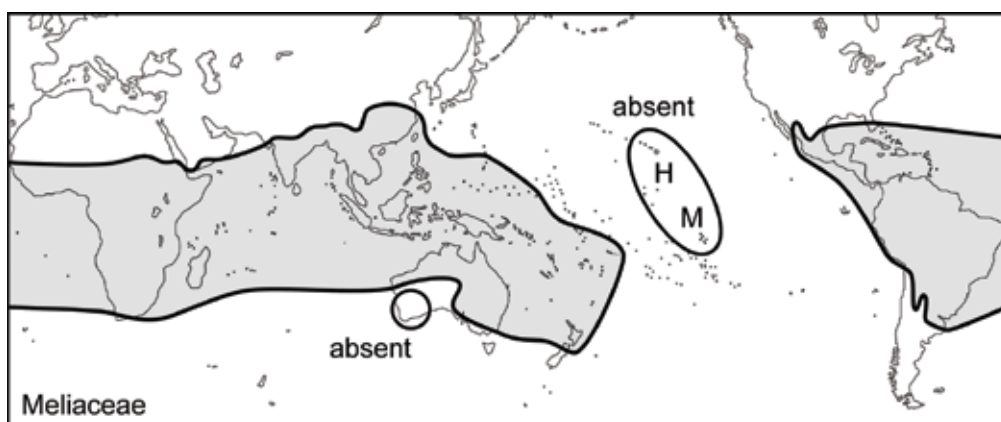
Fig. 2. Global distribution of Meliaceae (grey fill), and large regions where Meliaceae are absent (unfilled) (Stevens, 2001 onwards). H = Hawaiian Islands; M = Marquesas Islands. Extralimital fossils occur in the northern hemisphere but are not shown. Anthropogenic introductions are also not shown.

clade with the smaller, pantropical family Simaroubaceae (22 genera, 100 species) (Koenen et al., 2015; Muellner-Riehl et al., 2016). This pair is closest to Rutaceae (153 genera, 1975 species). Simaroubaceae are 'pantropical', as they are present in Africa, Asia and America. However, as with Meliaceae, they are absent from Hawaii, the Galapagos, Juan Fernandez Islands, and SE Polynesia. In contrast, native Rutaceae are present in all four of these areas, and are notably diverse in Hawaii (58 species) and the Marquesas (7 species) (the Marquesas have only 4% of the land area of Hawaii). The absence of Meliaceae from many very small islands in the central Pacific, such as Rapa or Rarotonga, might be the result of regional extinction with continuing subsidence (as the plate moves away from the central Pacific spreading ridge and cools). However, the absence from Hawaii and the Marquesas seems more significant, as the closely related Rutaceae are so diverse there.

The central Pacific allopatry between the two clades, Meliaceae + Simaroubaceae, vs Rutaceae, especially on the Hawaii–Marquesas sector, can be explained as a trace of the original allopatry caused by vicariance between the two clades. If this is correct, similar patterns should occur in other groups.

The Hawaiian biota is well known for the high diversity of groups such as honeycreepers, drosophilids and lobeliads. However, there are also many conspicuous absences (Heads, 2012). In the Hawaiian flora, many tropical plants, including mangroves, are absent, despite having very efficient means of dispersal. Other plants that characterise tropical shorelines and small islands, either globally (such as *Calophyllum* L., *Terminalia* L., *Hernandia* L., *Salicornia* L., and *Atriplex* L.) or through the Old World and Pacific (such as *Barringtonia* J.R.Forst. & G.Forst.), are also absent from the Hawaiian indigenous flora. Nevertheless, species of most of these genera thrive in Hawaii as introduced weeds.

Transport to Hawaii in mud on birds' feet is often proposed to explain groups' presence on the islands. Yet some of the most characteristic marsh plants, such as Eriocaulaceae and *Juncus* L., are absent from the indigenous flora (although several introduced *Juncus* species are now widespread). In the same way, many diverse, pantropical groups that are abundant in rain forest elsewhere are absent from the indigenous flora of Hawaii. These include Cyatheaceae, Araceae sensu stricto, Zingiberales (Zingiberaceae, Marantaceae etc.), Melastomataceae, *Ficus* L. (figs), and *Piper* L. (members of all these groups are naturalised). Thus, although the absence of Meliaceae, including the mangrove *Xylocarpus*, from Hawaii seems strange, it conforms to a standard pattern that requires a general explanation, and regional vicariance is suggested here. Meliaceae are also absent from southwestern Australia (as native plants), again, in a region where Rutaceae have high diversity.

Phylogeny and biogeography in Meliaceae

Koenen et al. (2015) sequenced all the genera of Meliaceae and 254 (c. 34%) of the species. The phylogeny that they proposed (Fig. 3) is adopted here, with the single exception of the *Xylocarpus–Carapa* group, discussed below.

Two subfamilies are now accepted for Meliaceae: Cedreloideae (previously known as Swietenioideae) with 14 genera, and Melioideae with 34 genera. The xylem anatomy in each of the two subfamilies is distinctive (Pennington & Styles, 1975), and the genera that are most highly rated for their timber, some of the most sought after in the world, are mainly in subfamily Cedreloideae. These include true mahogany (*Swietenia* in America), African mahogany (*Khaya* A.Juss. and *Entandrophragma* C.DC.), Spanish cedar (*Cedrela*) and toon (*Toona*).

Subfamily Cedreloideae
Subfamily Cedreloideae comprises three primary clades (Fig. 3). The first is a trans-Pacific pair, *Chukrasia* A.Juss. and *Schmardaea* H.Karst. The second and third groups are pantropical. The second main clade comprises another trans-Pacific pair (*Toona* and *Cedrela*) and genera of Africa and Madagascar. In the third main clade (*Soymida* A.Juss. etc.), the phylogenetic/geographic sequence is distinctive: India – Madagascar – Africa – America – widespread. This could represent either a series of dispersal events or a sequence of vicariance events in an already widespread ancestor.

Each of the three main groups in Cedreloideae includes both Old World and New World members, suggesting early differentiation of the three, followed by their range expansion (by normal dispersal) and widespread overlap around the globe. These two phases are obscure, and their geography is 'buried' beneath the last round of differentiation, *within* each of the three clades. The biogeography at that level is much clearer.
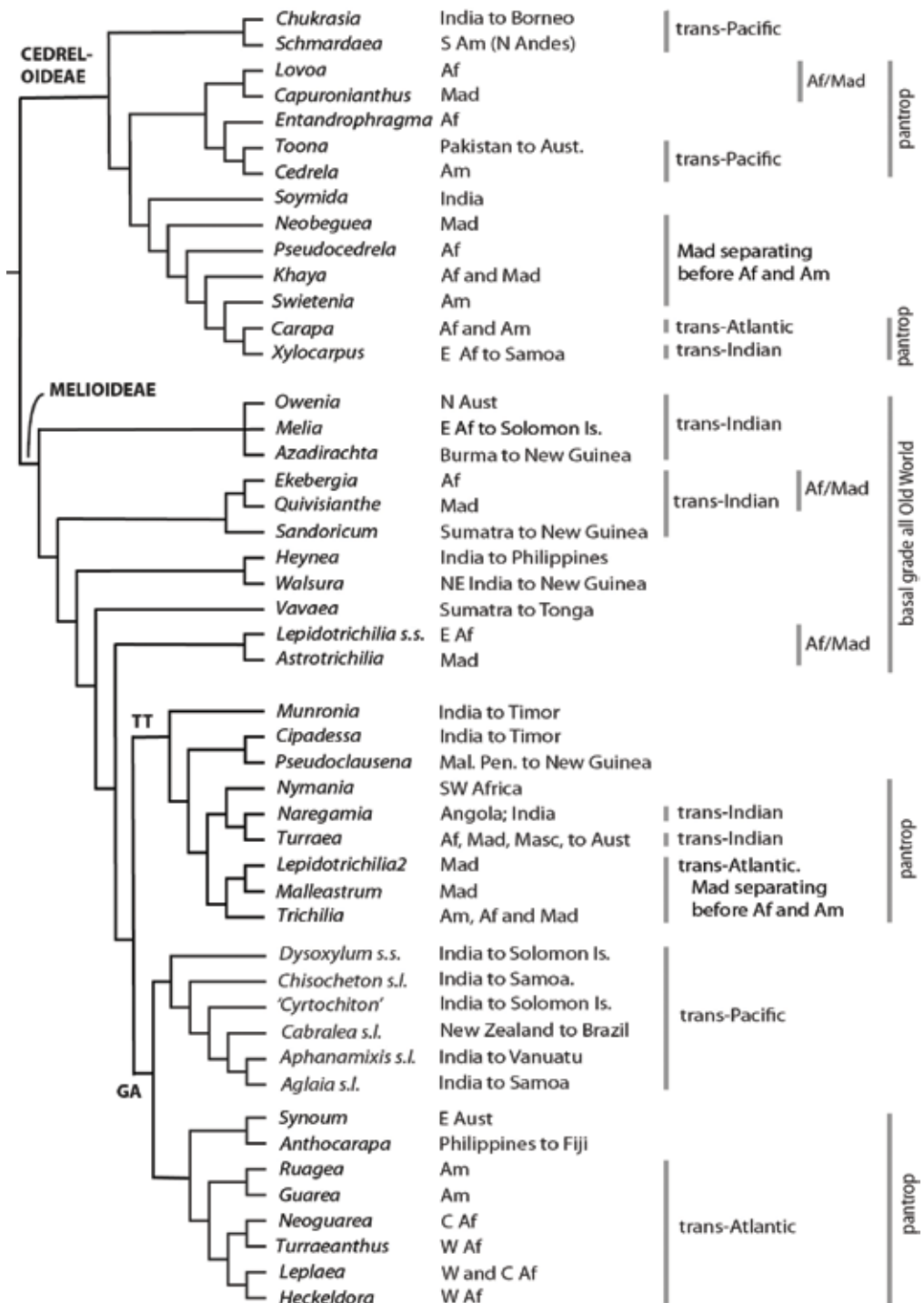
Fig. 3. Phylogeny and distribution of Meliaceae. TT = *Turraea–Trichilia* clade; GA = *Guarea–Aglaia* clade.

Subfamily Melioideae
Subfamily Melioideae comprises a basal, paraphyletic grade made up of five clades (all restricted to the Old World) and two large, Old World-New World sister groups, the TT and GA clades.

In the basal grade, the two basal clades (the *Owenia* F.Muell. group and the *Ekebergia* Sparrm. group) both have trans-Indian Ocean disjunctions; in the first it appears to be East Africa – India, in the second: Madagascar – Sumatra. Of the next three clades, two are around the eastern Indian Ocean (India to the Philippines and New Guinea), and one is around the western Indian Ocean (East Africa and Madagascar).

The remainder of Melioideae comprises the *Turraea–Trichilia* (TT) clade and its sister, the *Guarea–Aglaia* (GA) clade. Both are distinct in the family because of the large numbers of species in each. Both could be described as 'pantropical', but there are significant differences between them. The geographic differences are of special interest, and it is suggested that they represent traces of the original allopatry that existed between the two at the time of their origin.

Pantropical groups in Meliaceae
Meliaceae are not simply a pantropical group, as the family includes four, separate pantropical groups, two in each subfamily. Thus Meliaceae, a complex of several pantropical groups, stand in contrast with other 'pantropical' groups, such as primates, in which there is only one pantropical clade, the group itself, and the primary subclades are geographically restricted.

As suggested above, the fact that there are multiple pantropical clades in Meliaceae implies early phases of diversification followed by large-scale range expansion leading to clade overlap. The range expansion was not necessarily the result of rare, chance dispersal, and is more likely to have involved normal dispersal, as part of a community, mediated by geological changes which affected many different groups in similar ways. For example, the last, very large-scale marine transgressions, in the Cretaceous, would have meant that any groups with a maritime or tidal ecology and a tendency to weediness would have expanded their range considerably.

Trans-Atlantic distributions
Within the pantropical clades of Meliaceae (Fig. 3), several groups each straddle one of the major ocean basins. Trans-Atlantic disjunctions are evident in three clades: *Khaya–Carapa*; *Lepidotrichilia*2–*Malleastrum–Trichilia* (with *Lepidotrichilia*2 being a segregate of *Lepidotrichilia* T.D.Penn. & Styles sensu stricto); and *Ruagea–Guarea–Neoguarea–Turraeanthus–Leplaea–Heckeldora*. Likewise, in the sister group of Meliaceae, the Simaroubaceae, trans-Atlantic groups include *Quassia* L. of West Africa and tropical America, and also *Pierreodendron* Engl. of West Africa + *Simarouba* Aubl. of tropical America (Clayton et al., 2009).

Trans-Indian Ocean distributions
These occur in five clades of Meliaceae: *Xylocarpus*; *Owenia–Melia–Azadirachta*; *Ekebergia–Quivisianthe–Sandoricum*; *Naregamia*; and *Turraea*. In Simaroubaceae,

similar patterns occur in *Samadera* Gaertn. (Madagascar, India, Sri Lanka, and Burma to the Solomon Islands) and *Soulamea* Lam. (Seychelles, and Borneo to Fiji).

Trans-Pacific distributions

Trans-Pacific affinities in tropical groups are common, but they are much less well known than trans-Atlantic and trans-Indian Ocean affinities. In Meliaceae they occur in three clades: *Chukrasia–Schmardaea*; *Toona–Cedrela*; and *Dysoxylum–Chisocheton–Cabralea–Aphanamixis–Aglaia*. These trans-Pacific affinities include the 'basal' clade of the 'basal' subfamily (*Chukrasia–Schmardaea*). Likewise, in the Simaroubaceae, the 'basal' clade comprises *Picrasma* Blume: India to the Solomon Islands, also in tropical America, plus *Castela* Turpin + *Holacantha* A.Gray of tropical and subtropical America (including the Galapagos; Clayton et al., 2009). Other trans-Pacific groups include the family Heliconiaceae (Sulawesi to Fiji and widespread in tropical America) and the tribe Moutabeeae (Polygalaceae) (Heads, 2014: 271–274). A recently documented example is the tribe Anomospermeae (Menispermaceae) (Lian et al., 2019).

The biogeographic connections across the tropical Pacific can be accounted for by tectonic change. As Mabberley (1992: 17) noted: "… much of the land accreted along the western coast of the Americas since the Middle Jurassic comprises various fragments, some from far away in the Pacific". There is now good evidence that parts of the large igneous plateaux that formed in the West Pacific (Ontong Java, Hikurangi and Manihiki Plateaux) were subaerial (Heads, 2014: 205; Buchs et al., 2018; Hochmuth et al., 2019), and that components of the Manihiki Plateau collided with western Colombia (Hochmuth & Gohl, 2017).

Madagascar

Madagascar has long been known for its high levels of endemism in Meliaceae, and six of the eight genera present are endemic. The morphology-based taxonomy of Pennington & Styles (1975) proposed that two of the Madagascar endemics, *Capuronianthus* J.-F.Leroy and *Quivisianthe* Baill., represent monotypic subfamilies (the only subfamilies that were accepted apart from Cedreloideae and Melioideae). The molecular phylogeny of Koenen et al. (2015) does not support this, but the earlier classification does indicate the great morphological distinction of these Madagascar genera.

Three clades display an Africa–Madagascar sister group relationship: *Lovoa–Capuronianthus*, *Ekebergia–Quivisianthe*, and *Lepidotrichilia* sensu stricto–*Astrotrichilia*. Rather than the Madagascar group being nested in an otherwise African group, perhaps sister to a form in Mozambique, the Madagascar group is sister to Africa as a whole, consistent with an early differentiation.

In two cases, a Madagascar clade separates from a widespread, intercontinental group before Africa and America separate from each other (*Lepidotrichilia*2 and *Malleastrum* (Baill.) J.-F.Leroy in Madagascar vs. *Trichilia* in America, Africa, Madagascar and Asia; and *Neobeguea* J.-F.Leroy in Madagascar vs. *Pseudocedrela* Harms in Africa, *Swietenia* in America, and others). Again, this suggests an early differentiation.

India

India appears as a boundary or centre of endemism in 13 clades, especially in the *Dysoxylum* Blume group. A boundary at NE India (Assam in the broad sense) occurs in *Walsura* Roxb. and *Chisocheton* Blume, and in the widespread species *Dysoxylum mollissimum* Blume.

Phylogeny and ecology of Meliaceae

Meliaceae are often abundant and conspicuous. In the lowland primary forests of Malesia they make up to 17% of all trees with trunks over 10 cm diameter (Mabberley et al., 1995). In West Africa they can dominate forests in the same way that legumes dominate some South American rain forests, and dipterocarps dominate some in Malesia. Meliaceae are poorly represented at higher altitudes, but they are sometimes conspicuous in lower montane forest and a few species occur near the tree line in the Andes and East Africa. Many species inhabit secondary forest, and drier, more open vegetation, with a few in semidesert. As White (1986) commented, "In its ecology the Meliaceae is more diverse than most tropical families of comparable size…".

Apart from rain forest giants, the family also includes understorey treelets (with a single trunk) and shrubs with varied architecture. Subfamily Melioideae also includes a few straggling, scandent and climbing shrubs, a liane (*Turraea laurentii* De Wild. in the Congo basin), rhizomatous subshrubs, and geoxylic subshrubs with more or less herbaceous sucker shoots that resprout annually from a woody rootstock.

Reconstructions of ancestral ecology

Most Meliaceae are evergreen trees and treelets in lowland rain forests. However, an analysis using BAYESTRAITS reconstructions (Pagel & Meade, 2007) concluded that the most recent common ancestor of Meliaceae was a deciduous species that inhabited either savannas, dry forest, or montane forest (Koenen et al., 2015). The programmes that reconstruct ancestral morphology and ecology, as with the ancestral area programmes (see above), assume that a paraphyletic basal grade displays the primitive condition. However, the idea that the ancestor was geographically, morphologically and ecologically restricted and uniform in this way (as an ideal, Platonic entity) is rejected here. The biogeography of the family instead indicates widespread ancestors, and widespread groups are much more likely to be heterogeneous genetically, morphologically and ecologically. There is no reason to assume that the direct ancestor of Meliaceae was a uniform species, or that it was restricted to a single area or habitat type.

Have Meliaceae evolved by radiation?

It is sometimes suggested that the evolutionary history of Meliaceae has been one of radiation. Koenen et al. (2015) concluded that the family as a whole evolved by "recent radiations", while Pennington & Clarkson (2013) proposed recent radiation in *Guarea*, Clarkson et al. (2016) proposed "recent rapid radiation" in *Trichilia*, and

Grudinski et al. (2014a) discussed the "major radiation" in *Aglaia* Lour.

The idea of 'evolutionary radiation' implies a restricted morphological, ecological and geographical centre, and, as noted, Koenen et al. (2015) proposed that the Meliaceae radiated from 'a deciduous species that inhabited seasonal habitats… in the Old World'. Their paper was a contribution in a volume dedicated to 'adaptive radiations' (Hetherington, 2015). This concept was popularised by the authors of the Modern Synthesis (Simpson, 1953), and it proposes that groups originate at a centre and radiate out from there, invading new morphological, ecological and geographic space. However, the acceptance of vicariance as a mode of speciation means there is another mode of differentiation, one that does not involve radiation. Hence authors now make a clear distinction between adaptive radiation and geographic speciation (Givnish, 2015), and accept non-ecological, allopatric speciation as well as non-adaptive radiations (Czekanski-Moir & Rundell, 2019).

The process that has resulted in many 'adaptive radiations' is not only not adaptive, it is also not a radiation. In a vicariance event, there is not necessarily any ecological difference between the descendants, and there is no radiation from a centre; rather, there is a *break* at the centre, in a widespread ancestor. Thus examples of 'adaptive radiations', such as Meliaceae, are probably neither adaptive nor radiations, but are more likely to be the result of alternating phases of differentiation by allopatric vicariance, and range expansion by dispersal. The latter is not the result of chance, but is mediated by tectonics and climatic change.

Givnish (2015) pointed out that there is much confusion about 'adaptive radiation'. Soulebeau et al. (2015) described it as a 'pivotal concept' in evolutionary biology, but found that it is 'hazy', and "usually used in a misleading way, implying a range of hypotheses and corollaries in the best case and serving as an 'empty bag' in many others". One thing that 'radiation' must imply is a central point of origin (morphological, ecological and geographic), from which the radiation takes place. As Givnish (2015) recognised, the core issue in adaptive radiation has always been: "… the invasion of additional volumes of morphospace and ecospace [the 'adaptive zones' of Simpson (1953)]". Volume of ecospace is, in large part, 'kind of habitat'.

The key point here is that a clade invades one or more new ecospaces from a centre of origin in another. This differs from a vicariance model, in which different habitats are *inherited*, not invaded, by descendant clades, from a widespread ancestor that *already* occupied a range of habitats before the new clades diverged.

Adaptive radiation is a component in a process termed the CODA model (Lomolino & Brown, 2009), as it is based on centre of origin, dispersal and adaptation. In this model, a clade moves out from its centre of origin by dispersal to a new locality and habitat. Here it faces new *extrinsic needs* and changes its morphology and physiology in response to these, bringing about adaptation. It is usually taken for granted that adaptation is the main factor in structural evolution, although this has been questioned by some tropical botanists (e.g. Corner, 1952; Van Steenis, 1981; Hay & Mabberley, 1991), and instead of structure being determined by function and extrinsic needs, structure may determine function. For example, the morphology of an animal's teeth determines many aspects of its diet; the diet does not determine the

teeth. If the teeth evolve (or fall out), the diet changes. In this model, morphological evolution is driven not by adaptation (which is the result, not the cause), but by non-random mutation (Nei, 2013). In mutation-driven evolution, selection may prune some of the products of mutation, but it is a secondary process, not an all-powerful mechanism that can produce whatever new morphology is required. Modern studies are now questioning even classical examples of adaptation, such as bill morphology in birds (Navalón et al., 2019) and body size in squamates (Slavenko et al., 2019).

In the model of ecological evolution suggested here, the ancestor of Meliaceae was *already* widespread globally, morphologically diverse, and ecologically diverse before the modern groups began to differentiate. Differentiation of such a global group by vicariance does not require a centre of origin, or a radiation, and the trajectory of morphological evolution is primarily the result of non-random mutation, not selection.

Habitats occupied by Meliaceae

Meliaceae are in 'lowland rain forest', but this is difficult to define and grades off into other types of forest in cooler, drier, wetter, and more saline sites. Many Meliaceae occur in typical lowland forest, but are also present in one or more of the other forest types, and several are restricted to these. Niche studies often concentrate on the ecological relationships of species, but the focus in this paper is on the distributional and ecological range of genera. Within the genera, the species often occur in different habitats and form ecophyletic series. Aspects of the ecology of Meliaceae genera are shown in Fig. 4.

Mangrove and associated vegetation

In Meliaceae, *Xylocarpus* is recognised as a true mangrove, and mangrove associates occur in 10 other genera, scattered through the different clades. Likewise, in a phylogenetic study of halophytes, Bromham (2015) was "…surprised to find that, rather than clustering in groups of related species, salt-tolerant grass species [200 spp.] were scattered throughout the phylogeny… Many of the other families tested showed a similar (non-significant) pattern of many independent origins [of salt tolerance]". However, the scattering of salt-tolerance through the phylogeny would not be surprising if the feature were a primitive one and the present-day occurrences relictual.

Mangrove plants are characterised by their intertidal habitat and a high frequency of certain morphological features, such as stilt roots, pneumatophores, and vivipary. However, these are far from constant, even in classic mangroves. For example, *Rhizophora* L. does not have pneumatophores, *Bruguiera* Lam. does not have stilt roots, and *Sonneratia* L.f. is not viviparous (even though it is often a pioneer mangrove; Van Steenis, 1958). This suggests that the features are not new adaptations to new needs, but relictual features of early seed plant architecture, and that mangroves did not invade the shore but originated there.

Stilt roots are recorded in two Meliaceae, both species of lowland forest in Malesia: *Chisocheton tomentosus* Mabb. of the Malay Peninsula and Sumatra (lowland and hill dipterocarp forest, to 400 m altitude), and *C. polyandrus* Merr. of Borneo (lowland and hill dipterocarp forest, 150-300 m altitude) (Mabberley et al., 1995).
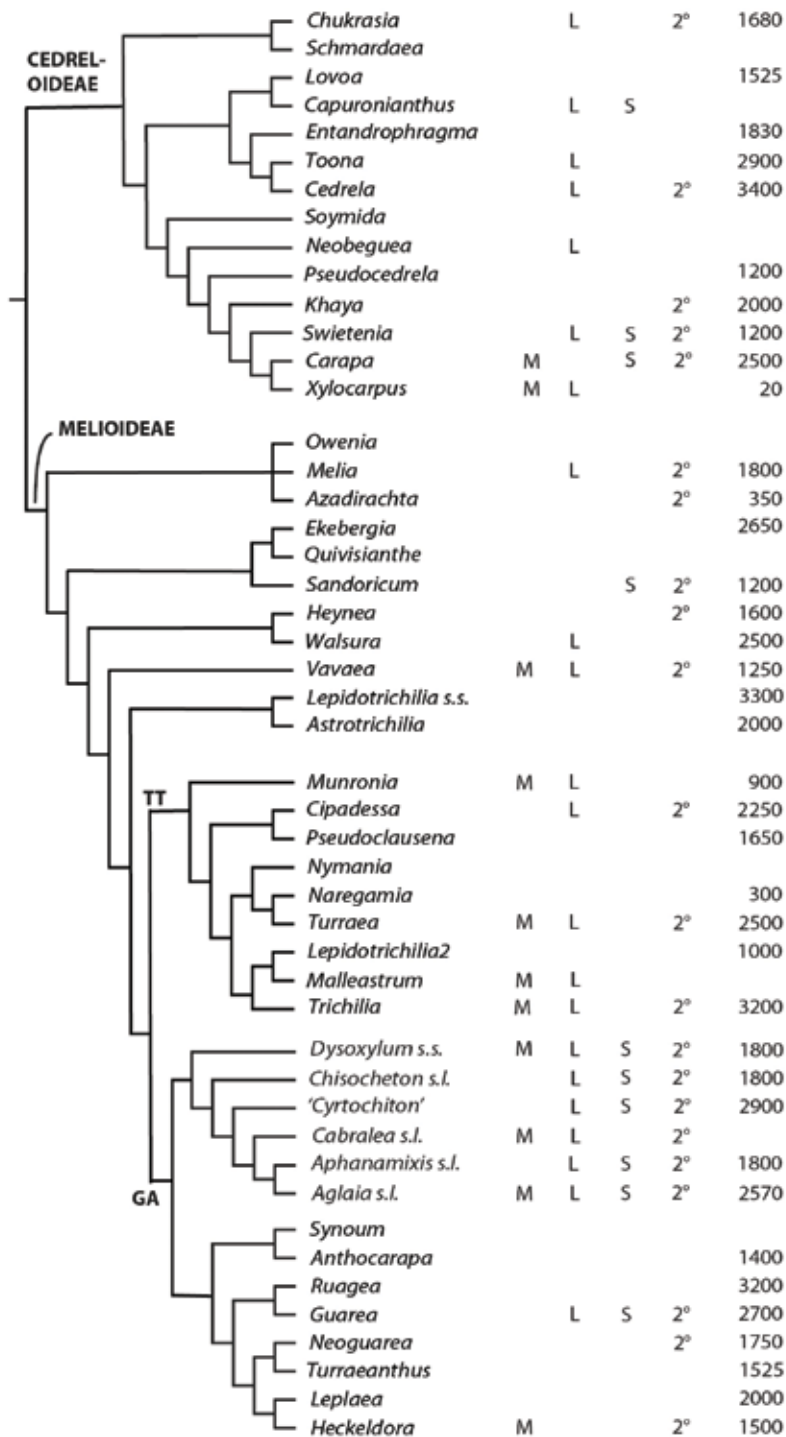
Fig. 4. Phylogeny and ecology of Meliaceae. M = in or near mangrove; L = on limestone; S = in swampy forest; 2° = in secondary forest; upper elevational limit given (in metres) where documented. Most genera are also in the lowlands. The figure does not include all species in *Dysoxylum* Blume sensu lato, including the 2580 and 3000 m records, as their precise clade is not known.

Pneumatophores and extended, ribbon-like buttresses occur in the mangrove *Xylocarpus*. Another member of Meliaceae, *Aglaia cucullata* Pellegr., is a tree with plank buttresses up to 3 m high; it also has pneumatophores up to 60 cm high and up to 7 m away from the bole. The species ranges from the Ganges delta in Bangladesh to New Guinea, and inhabits mangrove, back-mangrove, tidal estuaries, *Nypa* Steck palm swamp, riverine forest, and lowland evergreen forest, at 0–50 m altitude (Mabberley et al., 1995).

A third morphological feature seen in many mangroves is vivipary. In most angiosperm seeds, growth is suppressed for some time and can involve a lengthy phase of dormancy. This suppression does not occur in viviparous seeds. Tomlinson (1986: 26) suggested that "vivipary among seed plants… is well-developed only in mangroves". However, it occurs in many species other than those given in the latest list (Farnsworth, 2000), such as 53 species of Cactaceae (Cota-Sánchez et al., 2011) and a spectacular, stilt-rooted member of Asteraceae, *Fitchia speciosa* Cheeseman (pers. obs, in Rarotonga, Cook Islands). Lloyd (1902) described vivipary in *Podocarpus* Pers. and other groups, and concluded that vivipary "…is by no means the unusual condition it is often supposed to be".

Another plant missing from Farnsworth's (2000) list is a viviparous member of Meliaceae, *Dysoxylum mollissimum* Blume. This large tree (up to 58 m high) inhabits primary and secondary forests, including coastal forests behind mangrove, up to 1900 m altitude, and Mabberley et al. (1995) wrote that "the seeds may germinate before the fruits are dispersed from the tree". In contrast, the 'true mangrove' member of Meliaceae, *Xylocarpus*, is not truly viviparous, but the embryos, like those of the mangroves *Avicennia* L. and *Laguncularia* C.F.Gaertn., are well developed when they fall and emerge as seedlings soon afterwards (Mabberley et al., 1995).

A poorly known aspect of architecture in mangroves is the development of runners. In mangroves such as *Avicennia*, *Rhizophora* and *Sonneratia*, the lower branches may recline under their own weight and root distally; in *Sonneratia alba* Sm., individual axes have been traced to a length of 37 m (Tomlinson, 1986). These runners or stolons are similar morphologically to rhizomes, which are present in Meliaceae such as *Naregamia* Wight & Arn., *Trichilia*, and possibly *Turraea* L. Likewise, rooting of reclining branches is observed in *Carapa*. Runner development here, as in the mangroves, is interpreted as archaic. Thus the construction of the trees and treelets of most Meliaceae has involved the suppression of the horizontal system of runners in favour of a single, main, erect axis. Adventitious rooting in many trees is suppressed, but it has been found to be more common in tree branches (under epiphyte mats) than was realised (Nadkarni, 1981). Fully developed stilt roots also occur in mossy montane forest, in groups such as *Pandanus* Parkinson.

A critical feature of mangroves is their tolerance of frequent physical disturbance by the tides. Tomlinson (1986: 24) noted that mangroves display "clearly pronounced characteristics of pioneer species in their reproductive biology…" and "we might characterise mangroves as pioneer species…". Likewise, many genera and species of Meliaceae occur in secondary vegetation (see 'Secondary forest', below), and some species are gregarious.

Back-mangrove

The inner, landward edge of the mangrove (the 'back-mangrove') is one of the more diverse communities in the tropics, but it is seldom discussed. There are many kinds of adjacent terrestrial communities, and a large number of 'mangrove-associate' species.

Guppy (1906: 43) described Fijian shore plants under three headings, 'beach formation', 'mangrove formation', and 'intermediate formation'. He observed that "The mangrove formation comprises . . . many plants other than mangroves", and that "It is not possible to draw a definite line between the plants of the mangrove swamp and those of the tracts around" (p. 551). Whitmore (1984) agreed: "there is no sharp demarcation between beach vegetation of sandy and rocky coasts, mangrove forest of muddy coasts, and brackish water forests . . .". In Queensland, Dowling & McDonald (1982) wrote: "In some instances it is difficult to decide which species are 'true' mangroves and which are not. The problem mainly exists for marginal species that occur in brackish areas and which may occasionally behave as a 'true' mangrove in some situations and as land based plants in others".

The back-mangrove may grade into beach forest or thicket, to periodically or permanently inundated freshwater swamp forest and peat swamp forest, to lowland rain forest, to "a particularly rank and luxuriant vegetation where the Scitamineae [Zingiberaceae, Marantaceae, etc.] often take a leading part" (Guppy, 1906: 485), to open, arid salinas occupied by halophytic herbs or shrubs (Chapman, 1976), or to other kinds of open habitat and secondary vegetation. There is often no sharp line between mangrove and these communities, or, rather, there is often a small-scale mosaic of species typical of the different communities in different microhabitats. A small area in inner mangrove vegetation that is raised by just a few centimetres can bear typical dry land species, even if it is only a few square metres in extent (cf. Van Steenis, 1958: 432). The situation is much more complex than the zonation patterns illustrated in text-book accounts of the outer mangrove.

It is usually assumed that angiosperms 'invaded' the mangrove habitat (and the morphology) rather than inheriting it. However, "the oldest coniferoid gymnosperms [Cordaitales] had stilt-roots and a combination of anatomical features today seen only in some mangrove trees" (Mabberley, 1992: 18). In order to provide a coherent explanation for angiosperm evolution, it was suggested that the ancestral forms were mangroves or mangrove associates that could tolerate high levels of disturbance (Heads, 2003, 2006). Because of these pre-adaptations, the main clades became widespread with the marine transgressions of the Mesozoic. Following the retreat of the seas, many mangroves and mangrove associates were left stranded inland, for example in the Amazon and Congo basins, and in central Australia. In regions that underwent mountain-building (orogeny), populations were subject to passive uplift (Heads, 2019). This model recalls Church's (1919) ideas on land plant evolution: "… a continental area could not have been lifted out of the sea in the first place without taking some life with it [p. 8]… The discussion of any theory of 'migration' should be preceded by the examination of the probabilities of a mechanism of '*transition* in situ' (= transmigration) [p. 12]".

The 'stranding' model predicts that Meliaceae may retain some characters associated with mangroves or mangrove associates on carbonate platforms and limestone. Limestone and mangrove floras, especially those with a 'weedy' tendency, would have provided widespread, genetically diverse, ancestral species from which modern species of freshwater swamp forest, lowland rain forest, dry forest, secondary forest, thicket, and montane forest could have been derived.

In Meliaceae, an ecophyletic series spanning mangrove and dry land forest is seen in the sister genera *Xylocarpus* (in mangrove, or at least maritime) and *Carapa* (on the edge of mangrove to montane). A similar range is seen in many other angiosperms. For example, it is well known that Rhizophoraceae inhabit the outer belt of mangrove (i.e. mangrove in the strict sense), but the family also includes large trees of dry land rain forest, such as *Anopyxis* Engl. of West Africa, and *Carallia* Roxb. of Madagascar, tropical Asia and Australia. In another example, Combretaceae include *Conocarpus* L. and *Laguncularia* of mangroves and saline swamps, but the family is also a major component of African savannah woodland and rain forest. One of the genera, *Terminalia* L., inhabits mangrove, freshwater swamp forest, dry land rain forest, and savanna-woodland. In another family, Chrysobalanaceae, *Chrysobalanus icaco* L. subsp. *icaco* is one of the most characteristic members of coastal thicket and the landward side of mangrove swamps on both sides of the Atlantic. However, it also occurs in open vegetation on waterlogged soils up to 200 km inland in Africa and 600 km inland in South America, and the inland populations can be attributed to the advance and recession of inland seas. The second subspecies, *Chrysobalanus icaco* subsp. *atacorensis* (A.Chev.) F.White, is widely distributed on river banks in tropical Africa and can be explained in the same way.

Distinguishing 'true mangroves' from plants that are 'not true mangroves' is simply a matter of academic definition. Many species occur in mangrove but are not restricted to it; likewise, there is often no real difference between the 'inner' or 'back mangrove' and 'forest immediately behind the mangrove'. Rather than trying to define discrete ecological entities, the aim here is to trace the ecophyletic connections of plants in the mangrove.

For example, the trees of Sabah and Sarawak in northwestern Borneo include many species in mangrove or closely associated with it, and eight of these illustrate the main links between this vegetation and various others (Soepadmo et al., 1995–2014): 1. *Cerbera odollam* Gaertn. (Apocynaceae). In, or on the edge of, mangrove and riverine forest; 2. *Cynometra elmeri* Merr. (Leguminosae). Back mangrove and freshwater swamp forest, up to 300 m; 3. *Cynometra ramiflora* L. var. *ramiflora* (Leguminosae). Forest just behind mangrove, also in inland forest up to 400 m; 4. *Ilex cymosa* Blume (Aquifoliaceae). Mangrove, peat swamp forest, coastal *padang* shrubland on white sands, riverine forest, and dipterocarp forest, up to 1200 m; 5. *Pouteria obovata* (R.Br.) Baehni (Sapotaceae). Mangrove, kerangas (heath forest), hill forest on limestone; 6. *Cordia dichotoma* G.Forst. (Boraginaceae). At the back of mangroves, coastal hills below 100 m, inland forest along rivers and on limestone. Both *Pouteria obovata* and *Cordia dichotoma* have 'invaded' the hinterland by normal dispersal along the shores of earlier seas in which the limestones were deposited. Some

of the regions were later uplifted; 7. *Ganophyllum falcatum* Blume (Sapindaceae). Inner edge of mangroves, river banks, primary and secondary forest on well-drained or periodically inundated level-lands, on slopes, clay and limestone, to 1200 m; 8. *Guioa bijuga* Radlk. (Sapindaceae). Mangroves, peat swamp forest, riverbanks, primary and secondary kerangas, mixed dipterocarp forest, roadsides (i.e. highly disturbed sites); sometimes on ultramafics.

In Sabah and Sarawak a complete sequence from mangrove to montane occurs in many tree genera. Examples include *Barringtonia* (Lecythidaceae), known from mangrove, beach forest and swamp forest at sea level, and dipterocarp forest, up to 2000 m. Outside the region the complete mangrove-to-montane sequence occurs in individual species, including four members of Meliaceae. These are: 1. *Munronia pinnata* (Wall.) W.Theob. Just behind the mangrove, up to 900 m in Malesia and 1800 m in China; 2. *Trichilia emetica* Vahl. *Combretum* forest on coral limestone, up to 1850 m; 3. *Dysoxylum mollissimum*. Forests behind mangrove (sometimes viviparous), up to 1900 m; and 4. *Trichilia dregeana* Harv. & Sond. Behind mangrove, up to 2100 m.

Munronia pinnata, with higher altitude populations at higher, rather than lower, latitudes (in China), displays an 'anti-ecological' trend. The same phenomenon is also seen in other groups such as the odd-nosed primates (mangrove of Borneo to mountains of China; Heads, 2019). The trend can be explained by passive uplift of populations in southern China.

In standard 'ancestral area' algorithms, a large family with all genera in Africa and one, deeply nested, in Madagascar will always indicate that the group dispersed from Africa to Madagascar. But this overlooks the possibility of widespread ancestral biogeography (cf. Fig. 1). Likewise, in a large family with only one mangrove, deeply nested in the phylogeny, the mangrove habitat is assumed to be derived. However, this overlooks the possibility of ancestral polymorphism ('incomplete lineage sorting').

The idea that ancestral angiosperms and Meliaceae were mangroves and mangrove associates is not derived from standard ancestral habitat algorithms. These are flawed, as they assume that the ancestral condition is that held by a paraphyletic basal 'group', and this cannot be justified (cf. Fig. 1). Instead, a mangrove ancestry is suggested in order to group and explain many different aspects of the plants' biogeography, morphology and ecology, as well as their phylogeny.

Freshwater swamp forest
The best description of freshwater swamp forest is Corner's (1978) account for the southern Malay Peninsula, which includes 40 spectacular plates. Corner described the tidal flooding: "Salt water from the estuary banks up the brackish water to a depth of several feet and the effect is carried upstream… The water would rise in the creeks and spill over into the swamp-forest with a slight gurgling and hissing as the air was driven out" (Corner 1978: 9). As well as the tidal flooding (which varies through the year), there is also seasonal flooding with the annual rains. At Jason Bay, "For 2–3 miles inland from the coast there was a confusion of brackish and freshwater swamp-forest and remains of former coastal dunes" (Corner 1978: 49).

Corner (1978: 8) noted that while stilt roots are well known in the mangrove family Rhizophoraceae, "…even now few botanists realise that stilt-rooted trees of many genera of other families abound in freshwater swamp-forest". The swamp forest at Sedili contained 75 species with stilt roots, 75 with prominent buttresses, and 36 with pneumatophores. Eighteen species had both stilt roots and pneumatophores. One of the formations in the freshwater swamp forest is the mempisang (*Polyalthia sclerophylla* Hook.f. & Thomson) belt, "distinguished by the variety of trees and shrubs and by the presence of erect pneumatophores, which in places were so dense that passage was impossible…" (Corner 1978: 16). Thus freshwater swamp forest and mangrove are closely related in their flooding regime, in the structure of their trees, and in their floras.

Ten genera of Meliaceae are recorded in freshwater forest that is either permanently or periodically flooded (Fig. 4). In the Sedili region of the Malay Peninsula, Corner (1978) recorded 40 species of Meliaceae, and as many as 26 of these (65%) occurred in freshwater swamp forest. Corner compared this forest with a distinct type of swamp forest in Borneo and Sumatra that is built on peat.

Peat swamp forest

Peat soils are formed by the build-up of partially decomposed organic matter under waterlogged, anoxic conditions. Corner (1978: 85) wrote: "Peat swamp-forest is considered to be an outcome of freshwater swamp-forest, behind the mangrove and nipa, where for some reason the water-logged soil is no longer subject to tidal inundation or disturbed by the passage of streams". Thus there is no enrichment of the soil with silt. Peat swamp can also develop from old mangrove cut off from the sea, and in some ways peat swamp forest is the acidic-soil equivalent of alkaline-soil mangrove. Corner continued: "The forest debris accumulates into peat which raises the soil into a convex mound or dome, even up to 16 m in depth in Sarawak and Brunei, and becomes eventually so poor for plant-growth that a rather low forest of small trees… survives, along with a little undergrowth and *Sphagnum*".

In Malesia, two species of Meliaceae are more or less restricted to peat swamp forest. These are *Sandoricum beccarianum* Baill. (Thailand, Malay Peninsula, Sumatra and Borneo) and *Chisocheton amabilis* Miq. (Malay Peninsula, Sumatra and Borneo; also in riparian forest) (Mabberley et al., 1995). Six other Malesian Meliaceae are recorded in peat swamp but are not restricted to it (*Chisocheton lansiifolius* Mabb., *Dysoxylum cyrtobotryum* Miq., *Aglaia rubiginosa* (Hiern) Pannell, *A. lawii* (Wight) C.J.Saldanha, *A. korthalsii* Miq. and *A. glabriflora* Hiern).

In the central part of the Congo basin, the Cuvette Centrale, peat does not occur beneath terra firme forest, seasonally flooded forest or savanna (Dargie et al., 2017). However, peat does underlie swamp forest that covers about 145,500 km^2 in the basin, and this is the most extensive area of peatland in the tropics. Dargie et al. (2017) described two main types of peat swamp forest in this basin; one is dominated by the hardwoods *Carapa procera* DC. (Meliaceae), *Uapaca paludosa* Aubrév. & Leandri (Phyllanthaceae) and *Xylopia rubescens* Oliv. (Annonaceae), and one by a palm, *Raphia laurentii* De Wild.

Riverbank communities and rheophytes

Riverine or riparian forest is intermediate between freshwater flooded forest and dry land forest. In the tropics, riparian forest often includes rheophytes, plants distinguished by their long, narrow, willow-like leaves, tough, flexible stems, and their habitat, in or by rivers. Their morphology enables them to withstand heavy floods, and herbarium specimens often include debris left after floods. On river banks the branches of rheophytes typically project horizontally over the water.

Worldwide, Borneo has by far the highest diversity of rheophyte species (Van Steenis, 1981). In Meliaceae, Van Steenis listed five rheophytes, all in Malesia. More recent taxonomy recognised the following (Mabberley et al., 1995; Pannell, 2007): *Aglaia yzermannii* Boerl. & Koord. (Sumatra and Malay Peninsula), *A. rivularis* Merr. (Borneo), *A. lancifolia* Harms (Borneo), *Dysoxylum angustifolium* King (Malay Peninsula) and *Sandoricum borneense* Miq. (Borneo). *Dysoxylum angustifolium* is a common component of the *neram* (*Dipterocarpus oblongifolius* Blume) vegetation of rivers, growing amongst the rocks and on the banks, and overhanging the water. *Sandoricum borneense* inhabits riparian forest, subject to inundation down to just above tidal influence, overhanging the water like *Dipterocarpus oblongifolius*.

Heath forest in Malesia – kerangas

A distinctive, open heath forest called kerangas (or *kerengas*) occurs in coastal and lowland Borneo and other parts of Malesia. In Borneo, it can occur between peat-swamp forest and lowland dipterocarp forest. It is found on acidic, nutrient-poor, white sands that are strongly podzolised or even seasonally waterlogged, often on raised beach terraces and sandstone plateaux that are periodically inundated. On increasingly poor sites, kerangas is replaced by open shrubland (*padang*), but this is not inhabited by Meliaceae. Seventeen Meliaceae species are recorded from kerangas: *Sandoricum dasyneuron* Baill.*, S. caudatum* Mabb., *Dysoxylum crassum* Mabb.*,* and 14 species of *Aglaia* sensu lato.

There is a close relationship between kerangas and peat swamp; for example, of the four species of *Aglaia* sensu lato recorded in peat swamp forest, three are also in kerangas. Another example is the tree *Combretocarpus* Hook.f. (Anisophylleaceae), distributed from Sumatra to Borneo and restricted to coastal peat swamp forest and kerangas (Ding Hou, 1958). There is also a close link between these two forest types and montane forest. For example, *Castanopsis foxworthyi* Schottky (Fagaceae) inhabits peat swamp forest, kerangas, and montane forest up to 2400 m (Soepadmo, 1972).

Savanna woodland

The floristic affinities between lowland rain forest and open savanna woodland are closer than might be expected based on their very different appearance. In the lowland tropics, the same families of trees characterise both rain forest (closed forest with evergreen trees) and savanna woodland (open vegetation with deciduous trees). These families include Meliaceae, along with Anacardiaceae, Sapindaceae, Burseraceae, Leguminosae, Rubiaceae, Myrtaceae, Annonaceae, Chrysobalanaceae, Moraceae, Combretaceae, and Ebenaceae.

High altitude forest

Five genera of Meliaceae are recorded at or above 3000 m altitude, 13 others at or above 2000 m, and 11 others above 1500 m (the approximate upper limit of lowland rain forest). Thus 29 genera, more than half the genera in the family, extend above the lowlands. The genera of Meliaceae that reach the highest altitudes are: 1. *Cedrela* at 3400 m (*C. lilloi* C.DC. of SW Peru, NW Argentina and SE Brazil. *Cedrela montana* Turcz., is recorded at 3100 m and in subpáramo, in the Andes north of *C. lilloi*); 2. *Trichilia* at 3300 m (*T. multifoliola* C.DC. of Bolivia); 3. *Lepidotrichilia* sensu stricto at 3300 m (*L. volkensii* Styles & F.White of East Africa); *Ruagea* H.Karst. at 3200 m (*R. hirsuta* (C.DC.) Harms of Bolivia to Ecuador); and *Schmardaea* at 3000 m (Andes), a monotypic genus known only above 1500 m and the only genus of Meliaceae that does not occur in the lowlands.

Secondary forest

Meliaceae are often thought of as trees of primary rain forest, but as many as 22 genera are recorded from secondary vegetation. Six of these (*Cedrela*, *Swietenia*, *Chukrasia*, *Melia* L., *Azadirachta* A.Juss. and *Trichilia*) include species regarded in places as troublesome weeds and invasives. In the largest genus in the family, *Aglaia* sensu lato, 52 of the 127 species (41%), are recorded in secondary forest (Pannell, 1992, 2004; Mabberley et al., 1995).

Weeds are the plants of the future. The plants of 20 million years from now will be descended from today's widespread weeds of secondary forest, not today's restricted endemics of 'climax' vegetation. Weediness is an archaic feature, a relic ecology and not a recently derived one, but it is not necessarily preserved in an old clade. If evolution works largely by recombination of older features rather than evolution of new characters (as suggested for many Meliaceae), old features can be preserved in younger taxa.

Limestone

In the genera of Meliaceae, 22 out of 48, or 46%, have been reported from limestone. In the largest genus of the family, *Aglaia* sensu lato, 44 of the 127 species, or 35%, are recorded on it. The close connection between Meliaceae and limestone is probably an ancient one. Epicontinental limestone formed during past marine incursions, and as the seas receded (with either uplift or climatic change) it would have been colonised by the local coastal flora.

In Meliaceae, the genus *Xylocarpus* is present in mangrove and also on limestone rocks just above the mangrove. This close link between mangrove forest and limestone vegetation occurs in many other groups. For example, in Fiji, 39 indigenous plant species are recorded in or around mangrove and also on limestone (Heads, 2006). The presence of calcium ions in the soil water dramatically reduces the damage that would otherwise be done to a plant by an excess of sodium ions (see references in Heads, 2006). The evidence from biogeography, ecology and physiology suggests that the mangrove–limestone connection is an old one.

Mangroves are often most conspicuous growing in mud. It has been suggested that "Rocky coasts or coasts with exposed coral are unsuited to mangroves except where plants can root in silt-filled depressions" (Tomlinson, 1986: 5), and even that coral reefs are an 'extreme' habitat for mangroves (Tomlinson, 1986: 333). However, Van Steenis (1958) described the habitat of mangroves as "muddy shores,… along sandy or rocky beaches, and on old coral reefs covered with a thin sheet of sand or mud". Mangroves such as *Rhizophora stylosa* Griff. often occur in pure white coral sand (e.g. on Vanua Mbalavu Island in Fiji; pers. obs.). In Malesia, the species is recorded "Exclusively along sandy shores and coral terraces, facing the open sea, obviously resisting the surf better than the other species" (Ding Hou, 1958). The mangrove *Sonneratia alba* (cited above for its runners) occurs in: "Shallow parts of calm seas, seashores, along the mouth of tidal creeks… [and] grows as well on a sandy or rocky as on a muddy soil, *not rarely on coral terraces*. Often gregarious…" (Backer & Van Steenis, 1951; italics added).

Ultramafic substrate
Cedrela, Walsura, *Dysoxylum* and *Aglaia* are recorded in soil developed on ultramafic parent material (including weathered ultramafic rock, serpentine). *Walsura monophylla* Merr. of the Philippines (Palawan) and *Dysoxylum minutiflorum* C.DC. of New Caledonia are restricted to it. Four species occur on both limestone and ultramafics: 1. *Cedrela cubensis* Bisse. Cuba. On serpentine and limestone sites (Puentes, 2005); 2. *Dysoxylum nutans* (Blume) Miq. Sumatra to Moluccas. Primary and secondary forest, very common especially near streams, parent material of the sites includes ultrabasics and limestone; to 1600 m (Mabberley et al., 1995); 3. *Aglaia grandis* Korth. Indochina to Sulawesi. Primary forest, sometimes on ultrabasic rock and limestone; sea level to 1700 m (Mabberley et al., 1995); 4. *Aglaia elaeagnoidea* Benth. India to Samoa. In New Caledonia on beaches, and on calcareous and serpentine soil (Mabberley, 1988).

The affinity between limestone and ultramafics is also seen within genera, such as *Walsura*: *W. monophylla* is largely restricted to ultrabasic soils, while *W. grandifolia* Ridl. is apparently restricted to limestone. The relationship is also evident in other families. For example, in the *Alocasia* (Schott) G.Don species (Araceae) of west Malesia, *A. melo* A.Hay et al. is confined to ultramafics, six other species are restricted to limestone, and *A. cuprea* (K.Koch & Bouché) K.Koch of Sabah is found on sandstone, limestone and ultramafics (Hay, 1998). West Indian Euphorbiaceae (Jestrow et al., 2012) include the sister pair *Lasiocroton* Griseb. (7 species) in coastal Cuba, Bahamas, western Hispaniola and Jamaica on limestone, and *Leucocroton* Griseb. (26 species) in inland Cuba, on serpentine soils.

Soils on both ultramafics and limestone are characterised by being drought-prone and showing high base saturation (in limestone soils the exchange complex is dominated by calcium, in ultramafic habitats by magnesium). However, the physiological, ecological and phylogenetic affinity between limestone and ultramafic floras also reflects the tectonic relationship between the two types of rock. Both characterise belts of subduction and accretion (plate margins), where taxa of uplifted

coral reefs and carbonate platforms are pre-adapted for life on the basic soils of obducted ultramafic terranes (Heads, 2014). Taxa that are able to survive on ultramafics and limestone will thrive around active plate margins and persist around extinct ones.

Habitat restriction
Most Meliaceae species inhabit lowland tropical forest, but within this some species have a specific habitat type and also a localised geographic distribution. In Malesia, for example, certain species are restricted to flooded sites by rivers (*Dysoxylum angustifolium* of the Malay Peninsula), peat swamp forest (*Sandoricum beccarianum* of Thailand, Malay Peninsula, Sumatra and Borneo), peat swamp forest and riparian forest (*Chisocheton amabilis* in Sumatra, Malay Peninsula, and Borneo), limestone (*Chisocheton ruber* Ridl. of Borneo) and ultramafic rocks (*Walsura monophylla* in the Philippines) (Mabberley et al., 1995). It might be assumed that what appear to be specific habitat requirements have determined the distribution. However, limestone and ultramafics are widespread, and other species with very localised distributions have no obvious ecological restrictions, e.g. *Dysoxylum boridianum* Mabb. from Boridi, Papua New Guinea. In practice, many individual species occur in many habitat types.

Generic Treatment

Information has been compiled from the general treatments and floras of Harms (1940), Keay (1958), Staner & Gilbert (1958), White & Styles (1963), Van Balgooy (1971), Pennington & Styles (1975), Pennington et al. (1981), White & Styles (1986), Styles & White (1991), Mabberley (1988, 1995, 2011, 2013, 2017), Mabberley et al. (1995), Peng et al. (2008), Wongprasert et al. (2011), and African Plant Database (2019). These are cited explicitly only in particular cases. Other sources of information are listed under individual genera.

The first two genera, *Chukrasia* and *Schmardaea*, form a clade that straddles the Pacific basin.

1. *Chukrasia* A.Juss.

Distribution. One species in India and Sri Lanka to southern China, Indochina, Malay Peninsula, northern Sumatra and SW Borneo (Fig. 5; Kalinganire & Pinyopusarerk, 2000). Three allopatric forms have been proposed, based on bark and leaf morphology: one in Sri Lanka, one in Myanmar and Thailand, and one in China, Laos, Vietnam, and Malaysia (Kalinganire et al., 2002).

Ecology. Trees in evergreen rain forest, semi-deciduous forest, and deciduous forest, sparse forests in hilly regions (China); occasionally as a colonist of bare ground, including road cuttings; recorded on limestone. Up to 1680 m altitude (in Thailand;
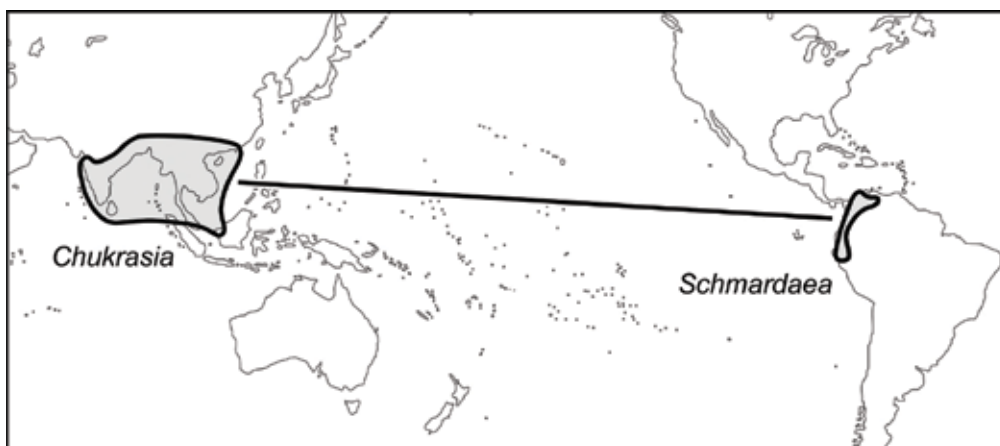
Fig. 5. Distribution of *Chukrasia* A.Juss. and *Schmardaea* H.Karst.

Wongprasert et al., 2011). *Chukrasia tabularis* A.Juss. is capable of invading gaps in the forest and is often gregarious. It is common in former shifting cultivation areas (Kalinganire & Pinyopusarerk, 2000). In Australia, it is an aggressive species that produces large seed crops and may form pure stands in disturbed forest. It has become naturalised on parts of the Atherton Tablelands where it was initially established in plantations (Kalinganire & Pinyopusarerk, 2000).

2. *Schmardaea* **H.Karst.**

Distribution. One species in the Andes of NW Peru, W Ecuador, NW Colombia, and NW Venezuela (Fig. 5).

Ecology. A small tree or multistemmed shrub which coppices readily (Styles & Bennett, 1992). Confined to evergreen montane and submontane cloud forest; 1500–3000 m (Pennington et al., 1981).

The next clade comprises five genera (Fig. 6): *Lovoa* Harms (Africa), *Capuronianthus* J.-F.Leroy (Madagascar), *Entandrophragma* (Africa), *Toona* (India to Australasia) and *Cedrela* (America). The five genera are all allopatric except for *Lovoa* and *Entandrophagma*, which overlap in Africa. The overall pattern is consistent with vicariance of a pantropical ancestor, followed by dispersal of *Lovoa* or *Entandrophragma*, or both, within Africa.

In the clade of five genera as a whole, *Lovoa* and *Capuronianthus* form the sister group to the other three genera, and so geographically the initial vicariance event took place between *Lovoa* (absent in parts of western Africa where *Entandrophragma* is
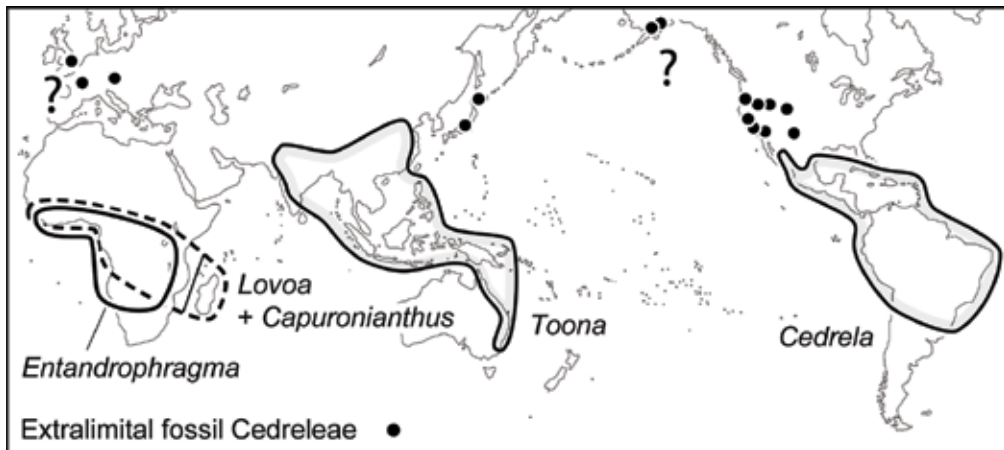
Fig. 6. Distribution of five genera with the phylogeny: *Lovoa* + *Capuronianthus* (*Entandrophragma* (*Toona* + *Cedrela*)).

present) and *Entandrophragma* (absent in parts of East Afria where *Lovoa* is present). The break took place between western and eastern Africa, and occurred before *Lovoa* separated from its sister *Capuronianthus* in Madagascar. (The break between *Lovoa* and *Entandrophragma* also took place before *Entandrophragma* was separated by the Atlantic and Indian Ocean basins from *Toona* + *Cedrela*). Overall, the break corresponds in space and time with activity on the Lebombo monocline (see below), a precursor to the Mozambique Channel rifting. In southern Africa this monocline marks the eastern limit of *Entandrophragma* (and its sisters) and the western limit of *Lovoa* (and its sister).

3. *Lovoa* Harms

Distribution. Two species in Africa. One species is western and one eastern (Fig. 7). In East Africa, the genus is present in several areas where *Entandrophragma* is absent, notably central Kenya, coastal Kenya, eastern Tanzania (Uluguru Mountains) and coastal Tanzamia.

Ecology. Trees, restricted to evergreen rain forest, including riverine forest and lake shore forest where the species can be very common; 180–1525 m.

4. *Capuronianthus* J.-F.Leroy

Distribution. Two species in Madagascar; one species in the far north, one in the far south (Fig. 7; Leroy, 1976).
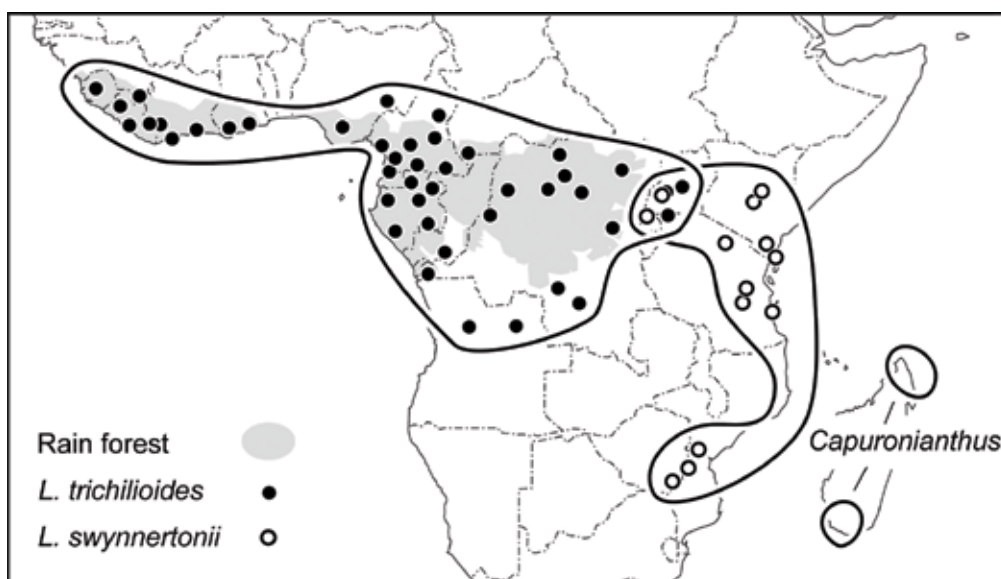
**Fig. 7.** Distribution of *Lovoa* Harms and *Capuronianthus* J.-F.Leroy.

Ecology. Xeromorphic trees in open, xerophilous forest, bush with *Euphorbia* L. and *Didierea* Baill., and coastal and subcoastal forest; on sand and limestone plateaux (Leroy, 1958c).
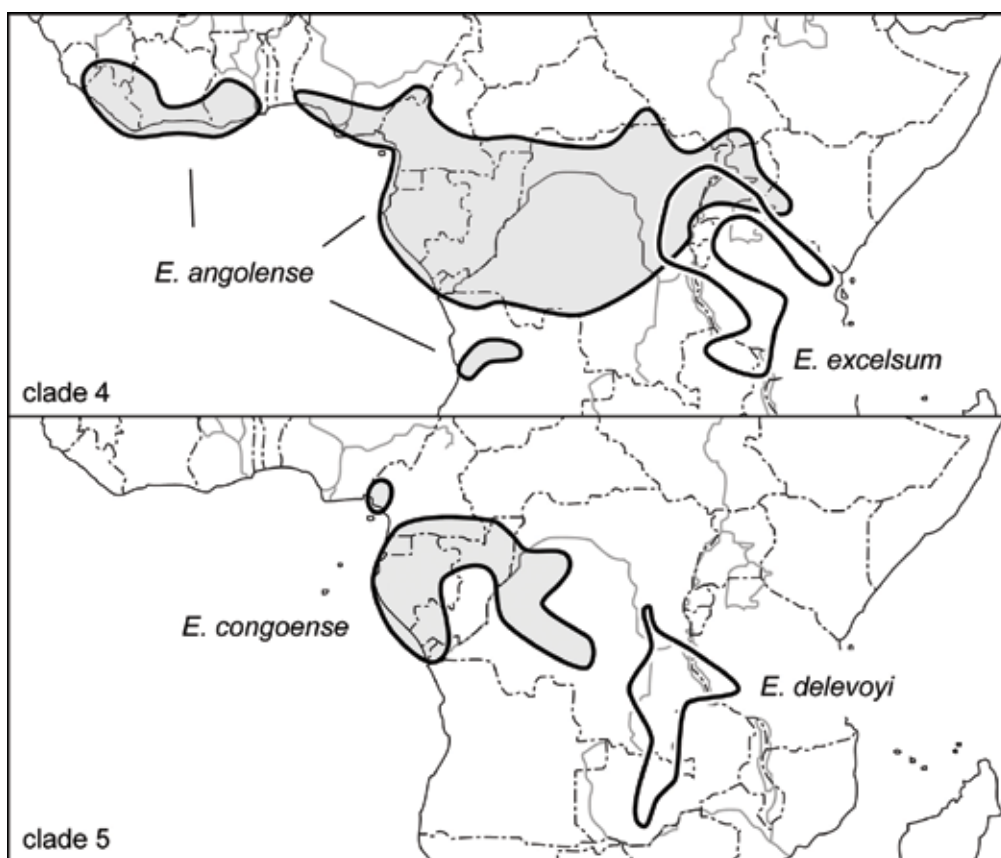
5. *Entandrophragma* C.DC.

Distribution. A genus of 11 species in Africa (Sierra Leone to South Africa) (Fig. 8).

Ecology. Trees of swamp forest, riverine forest, terra firme rain forest, dry, open, semi-deciduous forest, savanna woodland, and deciduous thicket; from the lowlands to 2220 m (*Entandrophragma excelsum* in East Africa). In 2016 a specimen of Entandrophragma excelsum 81.5 m high was discovered on Mt Kilimanjaro, and this is Africa's tallest recorded tree (Hemp et al., 2017).

Notes. A molecular study (Monthe et al., 2019) showed five clades in the genus, and these are mapped here (Fig. 8). The phylogeny of the clades is: 1 (2 (3 (4 + 5))). Clade 1 comprises *Entandrophragma utile* (Dawe & Sprague) Sprague of western and central Africa (in both rain forest and dry forest), and its sister group in eastern and southern Africa. As with the break between the two species of *Lovoa* (Fig. 7), the break in Clade 1 (at a line: SW Angola – Uganda) does not coincide with the boundary between rain forest and savanna woodland. Overall, Clade 1 encircles a large region of eastern Angola, southern DRC, and much of Zambia, where it, *Entandrophragma* as a whole, and in fact the whole subfamily are absent. This area of *absence* is also
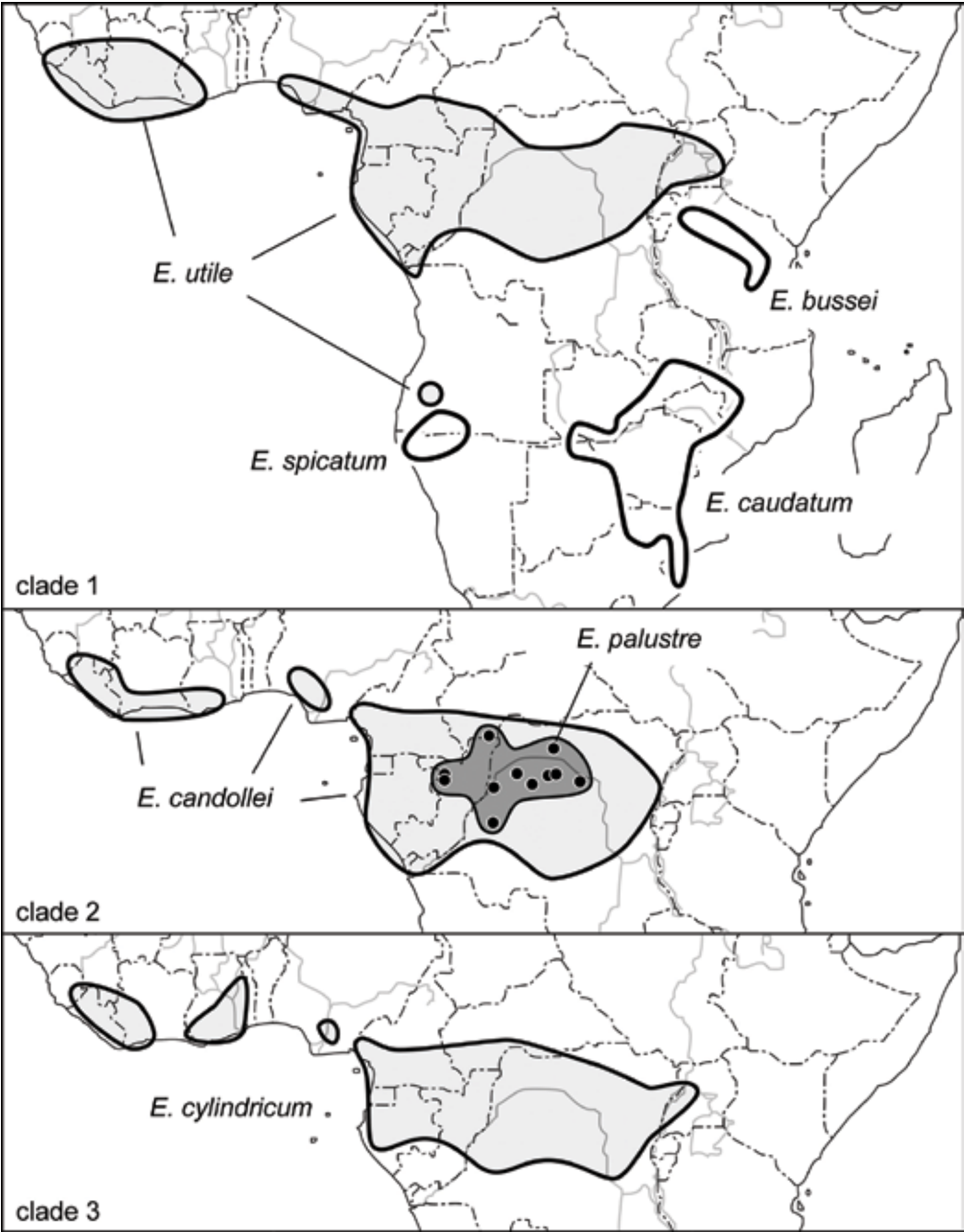
Fig 8. Distribution of *Entandrophragma* C.DC. (Data from Monthe et al., 2019, and African Plant Database, 2019). The five maps (continued on the next page) show the five clades; these have the phylogeny: 1 (2 (3 (4 + 5))).

Fig 8. (Continuation). Distribution of *Entandrophragma* C.DC. (Data from Monthe et al., 2019, and African Plant Database, 2019).

a standard centre of *endemism* for groups in subfam. Melioideae, for example, the rhizomatous subshrub *Trichilia quadrivalvis* C.DC. discussed below; see also *Ekebergia benguelensis* C.DC. The pattern suggests that the absence of Clade 1 is not caused by ecological factors, but is the result of phylogeny; Cedreloideae are replaced there by forms of Melioideae, and this allopatry is a regional trace of the original vicariance between the two subfamilies. Thus while clade 1 *as such* is absent in eastern Angola and neighbouring regions, it is represented there by close relatives, and so the absence is not absolute.

Clade 2 is *Entandrophragma candollei* Harms, widespread in western and central Africa, and its sister, *E. palustre*, restricted to the Congo Cuvette Centrale. Clade 3 is *Entandrophragma cylindricum* (Sprague) Sprague only, with a Guineo-Congolian distribution that duplicates that of *E. utile* and *E. candollei*. Clade 4 is *Entandrophragma angolense* (C.DC.) C.DC. in the west, and *E. excelsum* in the east. The break between the two is in eastern DRC. Yakusu et al. (2018) wrote that *Entandrophragma excelsum* is in both 'Zambezian' and 'Afromontane' phytogeographic regions. Thus it can be

regarded as a 'transgressor species' (of the English authors) or a 'liaison species' (French authors) — the regions are not cut and dried. The underlying idea is that species distribution should conform to regional phytochoria, themselves largely determined by vegetation structure. Physiognomic 'units', such as the 'Guineo-Congolian forest' and 'Amazon forest', often prove not to be biogeographic entities, but composites. Clade 5 is *Entandrophragma congoense* (De Wild.) A.Chev. in west-central Africa and *E. delevoyi* De Wild. in the east, divided at a break in eastern DRC, as in Clade 4.

The main difference between the last two clades is the presence of clade 4 through West Africa, west of Cameroon, where clade 5 is completely absent. Clade 5 has its western boundary at the Cameroon/Nigeria border, an area that corresponds to the Cameroon Volcanic Line (CVL). This originated in the Cretaceous and is one of the main tectonic features in Africa (Fig. 9). Other Cretaceous features shown in Fig. 9 include rifts (the Benue Trough, the Central African Shear Zone, and smaller rifts in Tanzania).

The volcanoes along the CVL do not show a linear age sequence, and so the line is probably controlled structurally rather than by plate movement over a hotspot. It has been active in episodes since the end of the Cretaceous. The CVL abuts a major rift, the Benue Trough, that was active from the early Cretaceous and was associated with the opening of the Atlantic basin. [For more on the geology and biogeography of the CVL/Benue Trough region, see Heads (2015)].

Distributional boundaries and phylogenetic breaks at the CVL occur in several clades of Meliaceae that are discussed in this paper. In addition, at least four species are endemic there: *Trichilia grandifolia* Oliv. on São Tomé Island, and *Heckeldora ledermannii*, *Carapa oreophila* Kenfack and *C. littoralis* Kenfack on the on-land part of the CVL. The CVL also features in many other groups as a centre of endemism, a boundary, and a site of ecological anomalies. For example, *Xylopia africana* (Benth.) Oliv. (Annonaceae) is endemic to the area (Fig. 10), and is unusual in African *Xylopia* species, as it inhabits mossy, montane forest; most species are in the lowlands (Johnson & Murray, 2018).

While the species of *Entandrophragma* in West and central Africa overlap widely, the five species present in southern and East Africa (in clades 1, 4 and 5) are all completely allopatric (Fig. 11). This suggests that the clades were initially allopatric, and that this has been maintained in eastern and southern Africa. In contrast, in the west, the initial allopatry has been obliterated almost entirely by range expansion. Any apparently minor differences among these species may represent traces of the original allopatry. The means of dispersal that facilitated the range expansions in West Africa were the same as those that facilitated in-situ *survival* in the east.

Entandrophragma (Fig. 11) and *Lovoa* (Fig. 7) overlap widely in Africa. However, the former is present in parts of the west (southern Angola and Namibia) where *Lovoa* is absent, and *Lovoa* is present in parts of the east (Kenya and southeastern Tanzania) where *Entandrophragma* is absent.

In the Congo, *Entandrophragma palustre* is restricted to swamp forest in the Cuvette Centrale, while the other species in the genus inhabit dense moist evergreen forest and semi-deciduous forest. *Entandrophragma palustre* is evergreen, the others
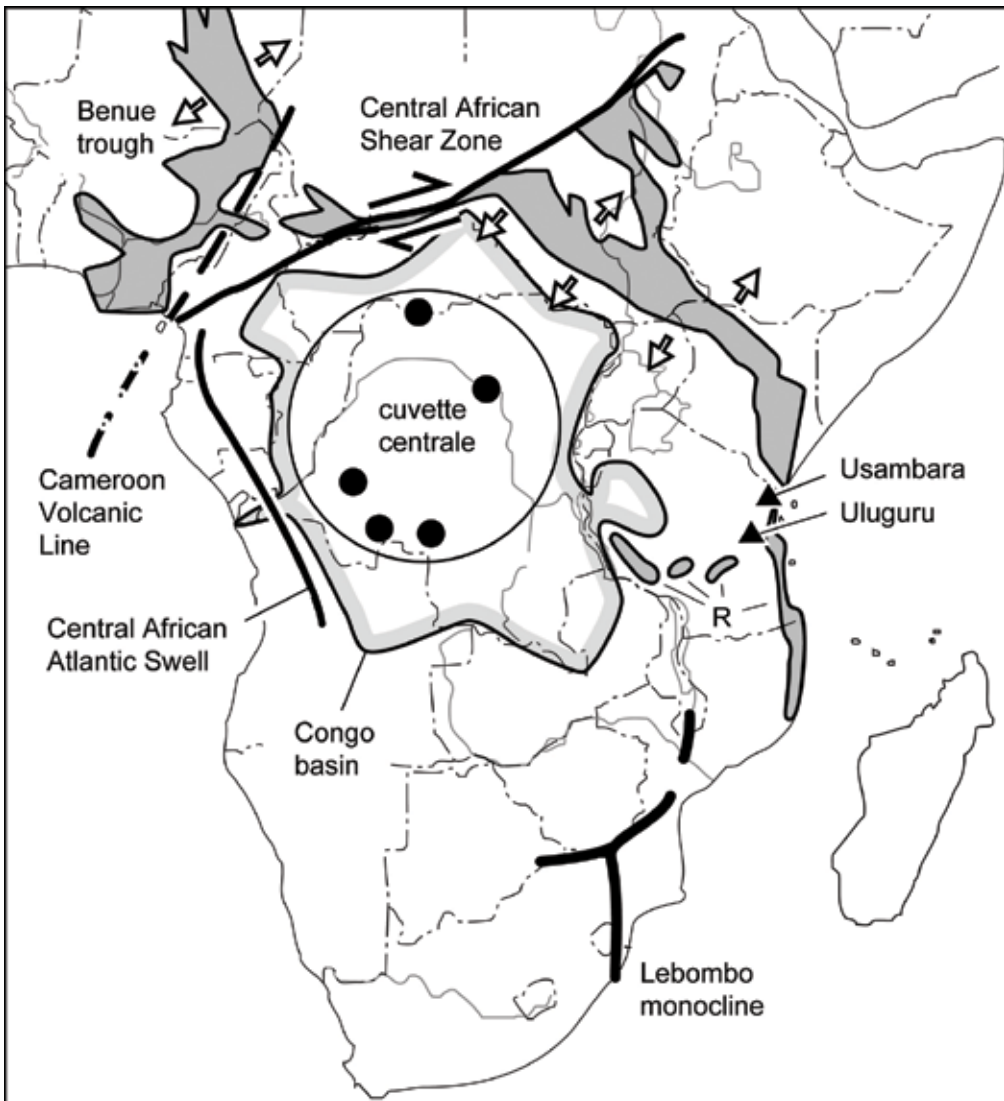
Fig. 9. Some main tectonic features in Africa. Black dots = late Jurassic-Cretaceous fossiliferous marine beds in the Congo basin. R = Rukwa, Usangu, Kilosa and Ruvumal rift basins (Heads, 2012).

deciduous. In the Congo basin, Richards et al. (1996) considered that there are two main types of forest on the hydromorphic (flooded) soils. One is *permanently swampy* forest, and this is dominated by *Entandrophragma palustre* and *Coelocaryon botryoides* Vermoesen (Myristicaceae). The other is *seasonally flooded* forest dominated by *Oubanguia africana* Baill. (Scytopetalaceae) and *Guibourtia demeusei* (Harms Léonard (Leguminosae). The *Entandrophragma–Coelocaryon* forest is comparable to the *igapó* (black water forest) of the Amazon and occupies wet depressions, often covering very large areas. The soil never dries out and contains 50–70% of organic
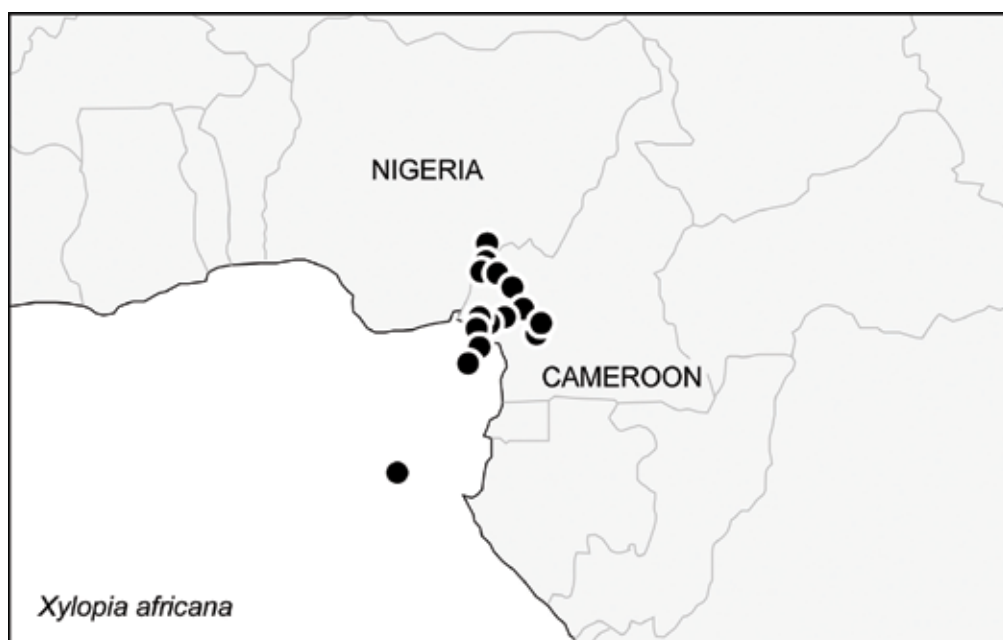
Fig. 10. Distribution of *Xylopia africana* (Benth.) Oliv. (Annonaceae) (Johnson & Murray, 2018).
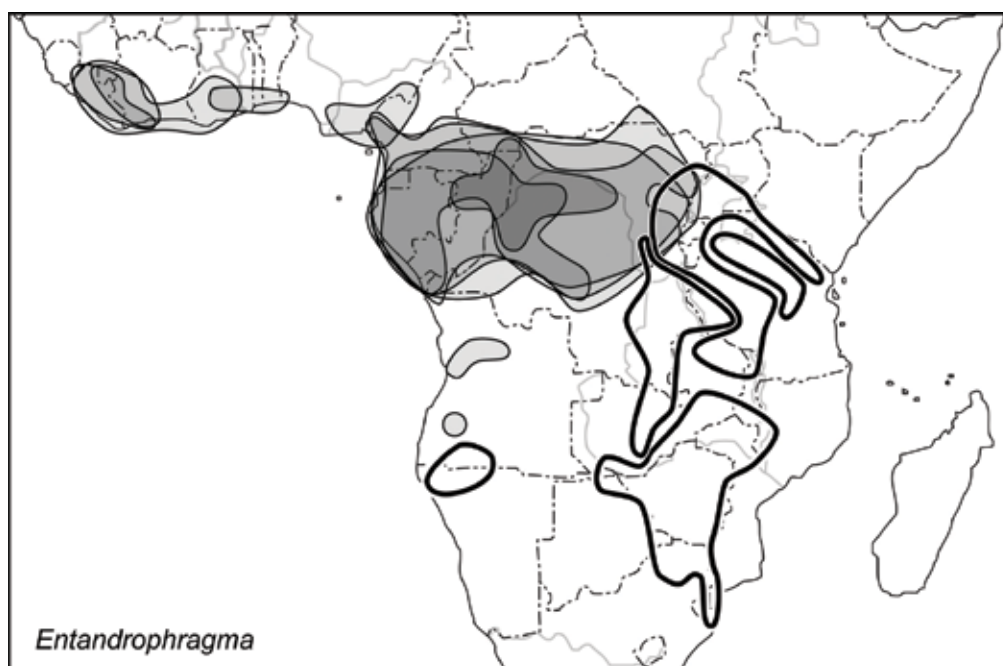
Fig. 11. Distribution of *Entandrophragma* C.DC. Clades show massive overlap from Liberia to eastern DRC, with highest levels of sympatry in the Cuvette Centrale, but east and south of there all species are allopatric.

material. Two subassociations occur, one on peaty soils and one on organic soils with some sand. The *Oubanguia–Guibourtia* association, on the other hand, is comparable to the *várzea* (white water forests) of the Amazon; the soil is sandy to silty in texture and not particularly rich in organic material.

The next two genera, *Toona* and *Cedrela,* make up the tribe Cedreleae (mapped in Fig. 6 with its African sister group, *Entandrophragma)*. Fossil members of Cedreleae from Japan and the contiguous United States do not significantly alter the 'trans-Pacific' nature of the tribe's extant distribution, and the identity of the fossils from Europe and Alaska has been questioned (see above).

In their study of *Cedrela*, Muellner et al. (2010) wrote: "The root node of our data set (i.e., the [most recent common ancestor] of Melioideae and Cedreloideae) was constrained *maximally* to 90 Myr, based on previous estimates (Muellner et al., 2006, 2007, 2008b), and fruit and seed fossils from Senegal 'similar to living Meliaceae' that date back to the Campanian/Maastrichtian boundary [72 Ma]… [T]his date may be regarded as a *minimum* estimate" (italics added). Muellner et al. (2010) proposed that *Toona* and *Cedrela* split at 48 Ma on the basis of "Fossil fruits intermediate between extant *Cedrela* and *Toona*, such as the London Clay [Eocene] *Toona sulcata* (Reid & Chandler, 1933; T.D. Pennington, pers. obs.)…". Nevertheless, the identification of the fossils has been queried (see above). In another study of *Cedrela* (Koecke et al., 2013), "The stem age of the most recent common ancestor (MRCA) of Cedreleae was set to 50 mya based on the minimum age of the oldest known fossils… with a lognormal distribution and a standard deviation of 1.1". But the reason for choosing these priors, including the very low value for the standard deviation, was not explained. Stipulating such a narrow prior means that clade age is assumed to be only a little older than the fossil age, and in this way the traditional belief that the fossil record is accurate is incorporated in the analysis.

Interpretations of the fossil record have suggested that Cedreleae (*Cedrela* and *Toona*) were widespread in the northern hemisphere during the Eocene, with occurrences in Europe, North America and Japan. Fossil material of *Cedrela* is distributed widely through the western United States (Oligocene to Miocene), while there is Pliocene material (and extant populations) in Central America and Peru. Muellner et al. (2010) suggested that these oldest fossils of Cedreleae "support a centre of origin scenario in which the ancestor of Cedreleae moved from Africa to Europe or, alternatively, originated in Europe, and then separated into two lineages, one moving westward into North America (*Cedrela*), the other into Asia (*Toona*)". However, it is difficult to understand why the location of a group's oldest fossils should represent a centre of origin. It is also difficult to see why one lineage would migrate west and the other migrate east, and simple vicariance would explain the pattern more easily.

The complete absence of *Toona a*nd *Cedrela* from Africa would traditionally be explained by extinction there, perhaps caused by aridification. However, while the group *as such* is absent from Africa, it is represented there by its sister group,

Entandrophragma, and so the simplest explanation accounting for both groups is allopatric differentiation of a widespread ancestor by vicariance. This group of three genera is, in turn, absent from Madagascar and parts of East Africa. However, *its* sister group comprises *Capuronianthus*, endemic to Madagascar, and *Lovoa* of mainland Africa.

6. *Toona* (Endl.) M.Roem.

Distribution. Four or five species in eastern Pakistan to China (north to southern Gansu), SE Asia, Malesia, New Britain and eastern Australia (Fig. 6; Muellner et al., 2010).

Ecology. Trees. Primary, secondary, riparian, and disturbed forest. Sea level to 2900 m (*Toona sinensis* (A.Juss.) M.Roem. in China; in Malesia recorded only up to 2000 m). *Toona calcicola* Rueangr. et al. of NE Thailand is apparently restricted to limestone (Rueangruea et al., 2015). *Toona sureni* (Blume) Merr. in Malesia is often present in logged or disturbed areas; both the other species in Malesia are also recorded in disturbed forest. *Toona ciliata* M.Roem. has become extensively naturalised in countries such as Malawi (Styles & White, 1991).

7. *Cedrela* L.

Distribution. Nineteen species (Pennington & Muellner, 2010; Koecke et al., 2013; Köcke et al., 2015; Palacios et al., 2019) throughout tropical America (northern Mexico to Paraguay, including the West Indies) (Fig. 6, from Muellner et al., 2010).

      The genus has its highest species diversity in the northern Andes. As mentioned already, it is thought to have had a North American origin, as the fossil record of the genus there (Oligocene–Miocene) is older than the record in Central and South America (Pliocene) (Muellner et al., 2010; Pennington & Muellner, 2010). Koecke et al. (2013) interpreted this age sequence as an accurate depiction of spatial evolution, referring to "the southward migration of species, as shown by the fossil record". Based on the idea, the authors argued that "the extant South American species are most likely descendants from Central American taxa…". Cavers et al. (2013) reached similar conclusions: "From Europe [the centre of origin], *Cedrela* moved westwards on a boreotropical dispersal path and occurs in North American fossil records from 51 Ma until 15–13 Ma…, finally retreating south in the mid-Miocene… The start of diversification in *Cedrela* is estimated at between 33 and 22 Ma (Muellner et al., 2010) when separate Central and South American clades formed… This suggests that the genus entered South America from North America during the mid-Oligocene (c. 25 Ma), potentially making use of islands... [Following this,] diversification proceeded in the South American branch of *Cedrela* and, from here, recolonisation of Central America and the Antilles occurred…".

However, none of these inferred dispersal events among North, Central and South America would be required if *Cedrela* originated in situ, as an American vicariant of *Toona*. In a vicariance model, the north-to-south geographic sequence in oldest to youngest fossils is an artefact of the record, and there was no centre of origin in North America. Likewise, there is no reason why the centre of *Cedrela* species diversity in the northern Andes should represent the centre of origin of the genus. As discussed below, with the exception of a single, widespread species, the two main clades in *Cedrela* are allopatric around a break in Panama/Costa Rica. This also provides no support for a northern centre of origin.

Ecology. Trees in evergreen rain forest, seasonally dry, deciduous forest, pine-oak forest, *cerrado* savanna in eastern Brazil, and secondary vegetation; on acidic soils on volcanics and alkaline soils on limestone; from the lowlands to 3400 m (Pennington et al., 1981; Muellner et al., 2010). *Cedrela lilloi* C.DC. of SW Peru, NW Argentina, and SE Brazil extends from (800–)1000–3400 m (the upper limit of the family) and is able to withstand considerable frost. *Cedrela montana* (1400–3100 m) is in montane forest, cloud forest and subpáramo. *Cedrela odorata* sensu lato is a strong light demander and appears frequently as a fast-growing pioneer species in secondary forest (Pennington et al., 1981).

Muellner et al. (2010) wrote that: "Most *Cedrela* species have restricted distributions in seasonally dry, deciduous forests… but several species occur in wet rain forest, such as *C. tonduzii* C.DC., which is distributed throughout the mountain ranges of Central America…". Several are in the lowlands, but most species are restricted to montane regions.

Cedrela species are found almost exclusively in well-drained habitats and attain a good size even on the poorest of rocky soils. Most are intolerant of poorly drained situations. *Cedrela 'odorata* I' is often found on limestone, as in Jamaica (Kelly et al., 1988). In Cuba, serpentine and limestone sites are inhabited by *Cedrela cubensis*, whereas *C. odorata* sensu lato occurs at wetter sites (Puentes, 2005).

Cedrela fissilis Vell. is distributed from Colombia to southern Brazil and shows a wide ecological range. In the western part of its distribution it is in lowland, evergreen, seasonal forest (Peru) or evergreen, nonseasonal forest (Ecuador, Colombia), while in the east it occurs in semideciduous forest, gallery forest and *cerrado* vegetation. In southern Brazil (Paraná), it is a component of *Araucaria* forest (Muellner et al., 2010). This variation is consistent with the idea that distribution determines ecology, rather than ecology determining distribution.

Cedrela trees may occur as scattered individuals in undisturbed forest where their crowns are in the canopy, but they are far more numerous in areas of second growth forest (Earle Smith, 1960): "Here, mature trees with their crowns in the canopy and seedlings with their crowns in the understory may occur in groups". *Cedrela odorata* sensu lato is an important invasive species in the Galapagos Islands (Rivas-Torres & Rivas, 2018) and also in South Africa.

Cedrela lilloi is able to regenerate in mature forest stands without large scale disturbances, but is dependent on fine-scale canopy openings (Grau, 2000). The species

has a gap-phase regeneration mode, and its growth rate is rapid compared with many neotropical tree species.

Cedrela occurs in both wet forest and dry forest, and so ecological 'centre of origin' theory suggests that the genus originated in either one or the other. From this, the genus subsequently colonised, at least once, the other forest type. Pennington & Muellner (2010) argued that *Cedrela* originated in seasonal dry forests. However, Muellner et al. (2010) wrote: "On the ML and Bayesian trees, the habitat preferences of the MRCA of *Cedrela* remained ambiguous… The optimisation on the MP strict consensus tree suggested an ancestral preference for a *dry forest* habitat; that on the MP majority rule consensus suggested *wet forest….*". The authors concluded that "… the ancestral habitat preference of *Cedrela* could not be inferred (probably in part because of the crude binary coding of habitats)…". If *Cedrela* originated by vicariance with *Toona*, in situ and over much of America, it is likely that ancestral *Cedrela already* occupied both forest types when it began to differentiate into the modern groups.

Notes. The phylogeny for *Cedrela* presented by Koecke et al. (2013) (and, with slight variants, Cavers et al., 2013) supports two main clades, as follows (distributions from www.tropicos.org). (*Cedrela odorata* L. proved to be polyphyletic, and the different components were referred to as *C. odorata* I, II and III): 1. five species in Mexico to Panama ('Central American 2' of Cavers et al., 2013); and 2. fourteen species in Mexico to Panama, West Indies, and South America.

Clade 1 ranges through Mesoamerica (from Mexico to Panama), while Clade 2 is in Mesoamerica, the West Indies and South America. Thus the only overlap is within Mesoamerica, and in fact most of the species in Clade 2 (11/14) are restricted to South America and the West Indies (where Clade 1 is absent).

The only members of Clade 2 in Mesoamerica are *Cedrela* '*odorata* I' (north to Mexico; this is the only species of clade 2 present from Mexico to Costa Rica), *C.* '*odorata* II' (north to Panama and Costa Rica), and *C. ngobe* Köcke et al. (endemic to Costa Rica and Panama). Thus, with the single exception of the northern populations of one widespread species, *C.* '*odorata* I', the two main clades of *Cedrela* are allopatric: Clade 1 ranges south to Panama, and Clade 2 (apart from *C.* '*odorata* I') ranges north to Costa Rica. The two have a boundary at, and overlap at, Panama and Costa Rica. The northern populations of *Cedrela* '*odorata* I' can be explained as the result of range expansion (dispersal), but the direction of the dispersal (north to south? Pacific to Atlantic versant of Central America?) is unclear.

In the model proposed here, the two main clades of *Cedrela* originated by in situ vicariance around a boundary in Panama–Costa Rica, with range expansion in a single species, *C.* '*odorata* I'. This is much simpler than the 'northern centre of origin/ invasion of South America' model presented in earlier studies.

While Panama and Costa Rica form the main boundary in *Cedrela*, the locality is not simply a boundary. It is also a zone of localised overlap, where the two main *Cedrela* clades occur together. Likewise, the total number of plant species, relative to area, is much higher in Costa Rica and Panama than in any South American country (Prance, 1994). These features could, perhaps, be explained by dispersal into the area

from the north and south. However, the area is also a centre of endemism, with a great many examples, including *Cedrela ngobe* restricted to Panama and southern Costa Rica. (Several other Meliaceae endemic there are discussed below, under *Guarea*). Finally, Panama–Costa Rica is a locality where taxa display large-scale disjunctions and also anomalous absences, and these are difficult to account for in the centre of origin-dispersal models.

In Costa Rica, studies on seedling traits in *Cedrela odorata* sensu lato (Navarro et al., 2002) showed two groups, one in northwestern Costa Rica, including Nicoya Peninsula (*C*. '*odorata* I' of Koecke et al., 2013) and one in eastern Costa Rica (*C*. '*odorata* II'). The Nicoya Peninsula and other areas in Costa Rica and Panama comprise accreted oceanic terranes, including island arcs and ophiolite sequences associated with island arcs (Fig. 12). The area is discussed in more detail below.

Subsequent molecular studies showed that *Cedrela* '*odorata* I' extends from northwestern Costa Rica to Mexico and the West Indies, and also has disjunct populations far to the south, in Ecuador (Cavers et al., 2013; Koecke et al., 2013). The disjunction from Nicoya Peninsula, across Panama and Colombia, to Ecuador, is impressive. However, similar breaks occur in many clades, including several other Meliaceae cited below, and so a general explanation is needed. Climatic or tectonic factors are possibilities.

Cedrela '*odorata* I' populations from the Nicoya Peninsula have similar seedlings to populations from dry Pacific sites, but are located in an area of higher rainfall. Thus while the boundary between *Cedrela* '*odorata* I' and *C*. '*odorata* II' is geographic, it is not related to climate, and Navarro et al. (2002) proposed a vicariance model: "Differentiation may have occurred when the cordilleras Volcanica Central and Guanacaste raised a barrier within the range of the species in Costa Rica…". A tectonic explanation does seem to be the most likely explanation, but uplift on its own does not account for the Nicoya Peninsula–Ecuador disjunction.

The following seven genera form a clade (Koenen et al., 2015; Muellner-Riehl et al., 2016; Guo et al., 2018). The first three break off from the others in sequence: India – Madagascar – Africa, although the statistical support here was not strong.

8. *Soymida* A.Juss.

Distribution. One species in India and Sri Lanka. Widespread in India from Rajasthan in the north-west and the Varanasi region (Uttar Pradesh) in the north-east, through central India (Deccan Plateau, Western Ghats) south to Travancore and the Carnatic (Harms, 1940).

Ecology. Trees in low mountain ranges on laterite, in dry forests, together with *Chloroxylon* (Rutaceae) (Harms, 1940). In Sri Lanka (where it is now thought to be
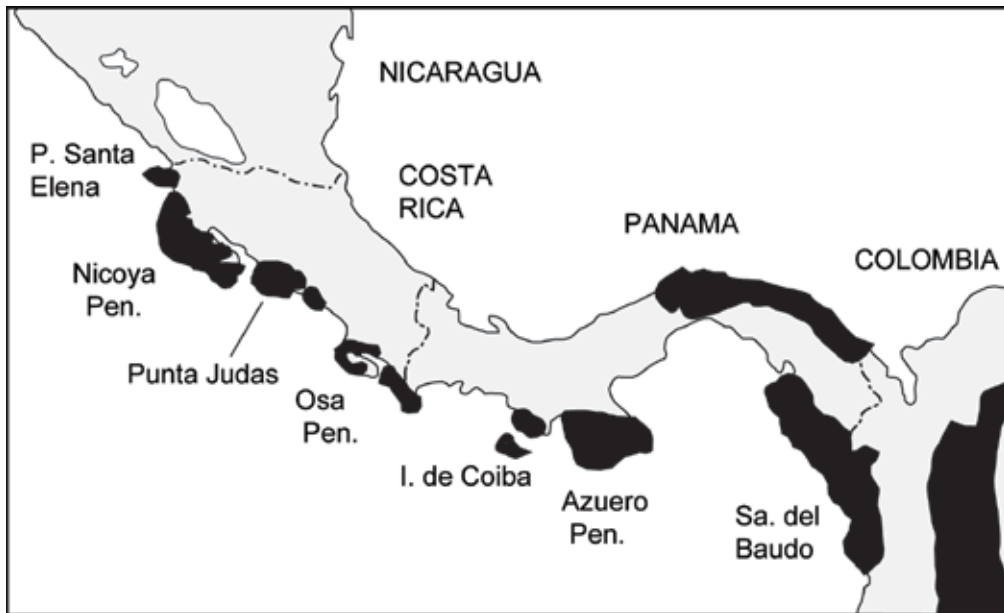
Fig. 12. Locality map of southern Central America (with Nicoya, Osa and Azuero Peninsulas, Punta Santa Elena and Punta Judas, and Serranía del Baudó), showing accreted oceanic terranes (island arcs, ophiolites) in black.

indigenous), *Soymida* inhabits fire-savannas (talawas) in the dry and intermediate zones up to about 1000 ft. [305 m] (Meijer, 1970).

9. *Neobeguea* J.-F.Leroy

Distribution. Three species in Madagascar.

Ecology. Trees in xerophilous vegetation in the west and south (maps in Leroy, 1976). The species inhabit sandy coastal areas and maritime forest, and also present on karst and calcareous plateau. *Neobeguea leandriana* J.-F.Leroy seems restricted to calcareous substrates (Leroy, 1958a, 1970, 1976).

10. *Pseudocedrela* Harms

Distribution. One species in Africa (Senegal to Ethiopia and Uganda) (Fig. 13).

Ecology. Tree, bole often crooked and branched from near the base, often coppicing and regenerating mainly by root-suckers. In gallery forest, savanna woodland, and on terraces along streams, in hollows and on deep sands, often gregarious on moist, heavy soil of valleys or swampy areas; 120–1200 m.
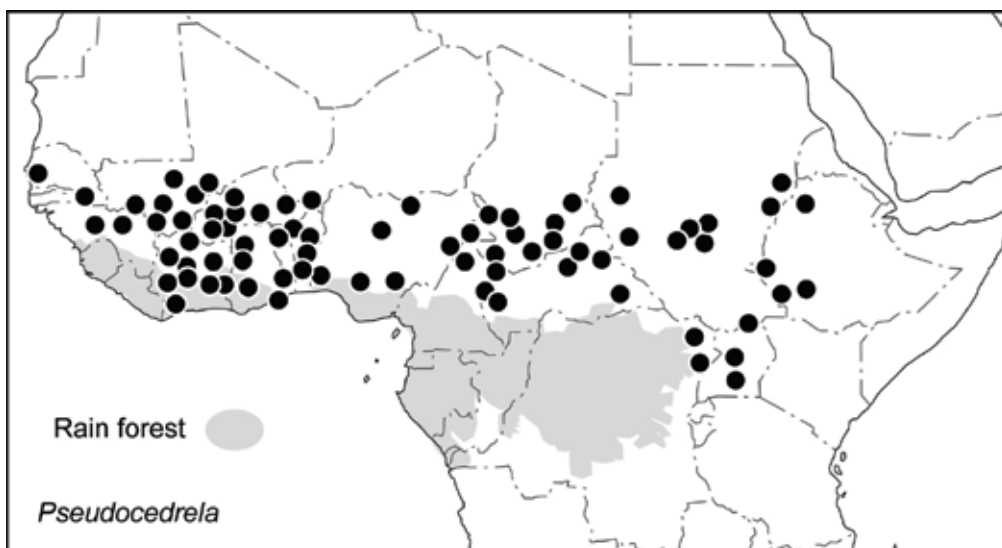
Fig. 13. Distribution of *Pseudocedrela* Harms (African Plant Database, 2019).

11. *Khaya* A.Juss.

Distribution. Eight species in Tropical Africa (7 species), Madagascar and Comoro Islands (1 species) (Fig. 14A). A molecular phylogeny (Monthe et al., 2019) arranged the species in two main clades, and these display a high level of allopatry (Fig. 14A). One is in the north and west, the other lies further south and east, including Bioko and Madagascar. The two clades overlap only in Ivory Coast/Ghana, and in SW Cameroon. Both clades are in rain forest and savanna woodland.

In the northwestern clade, *Khaya senegalensis* (Desr.) A.Juss., *K. grandifoliola* C.DC. and the pair *K. agboensis* A.Chev. + *K. euryphylla* Harms form three, allopatric latitudinal bands, but this is disrupted at the Cameroon Volcanic Line (Fig. 9), where there is a break between *K. agboensis* and *K. euryphylla*.

In the south-eastern clade of *Khaya*, *K. ivorensis* A.Chev. (Ivory Coast to the Congo mouth) is sister to *K. madagascariensis* Jum. & H.Perrier of Madagascar. This disjunction appears to skirt the large area of central Africa occupied by its sister-group, *Khaya anthotheca* (Welw.) C.DC. + *K.* sp. nov., and probably also the area of the unsequenced *K. nyasica* Baker f. (often included in *K. anthotheca*). The disjunct affinity is of special interest, as it repeats a standard west-east disjunction across Africa, but in this case the gap is filled by an allopatric sister group. Thus the disjunction can be explained by simple vicariance, and there is no need to invoke extinction to account for the 'gap'. The break between *Khaya ivorensis* and *K. anthotheca* runs in a north-south line from Gabon to northern Angola, and this corresponds with the belt of uplift at the Central African Atlantic Swell (Fig. 9).
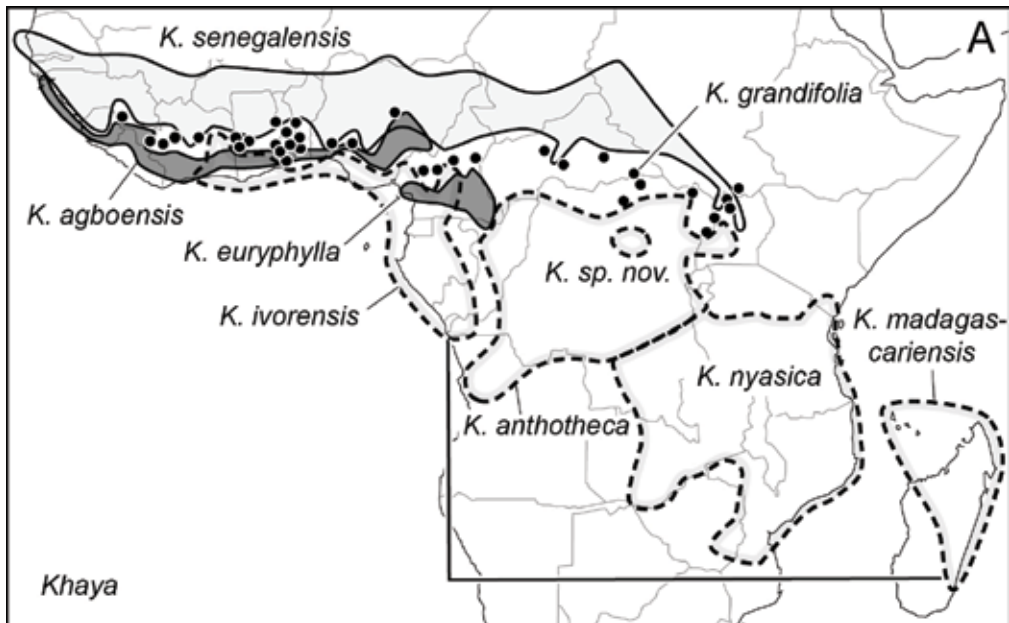
Fig. 14 . Distribution of *Khaya* A.Juss. **A.** One clade in light and dark grey fill and black dots, the other clade in broken lines. (Data from Monthe et al., 2019).

Ecology. Large trees in sandy ground by lagoons (*Khaya ivorensis*), riparian forest, rain forest of lowlands and hills, and savanna woodland, often in rocky places; 10–2000 m. The first main clade of *Khaya*, in the north-west (Fig. 14B), is mainly in savanna, but it also occurs in rain forest in Liberia, Ivory Coast, Ghana and Cameroon. The second clade (Fig. 14C) is mainly in rain forest, but there are savanna-woodland populations in Angola, southern DRC and Madagascar.

12. *Swietenia* Jacq.

Distribution. Three species. Widely cultivated. One species in Mesoamerica, one in the West Indies, and one widespread from Mexico to the Amazon basin (Fig. 15):

    Swietenia humilis Zucc. (Fig. 15A). On the Pacific versant of Mexico and south, mainly on the Pacific side, to Costa Rica. In Mexico it is widespread on the allochthonous terranes (Guerrero terrane etc.); these were accreted in Cretaceous time onto the Pacific margin of the craton. In Guatemala the species occurs along the Motagua fault, almost reaching the Atlantic coast.
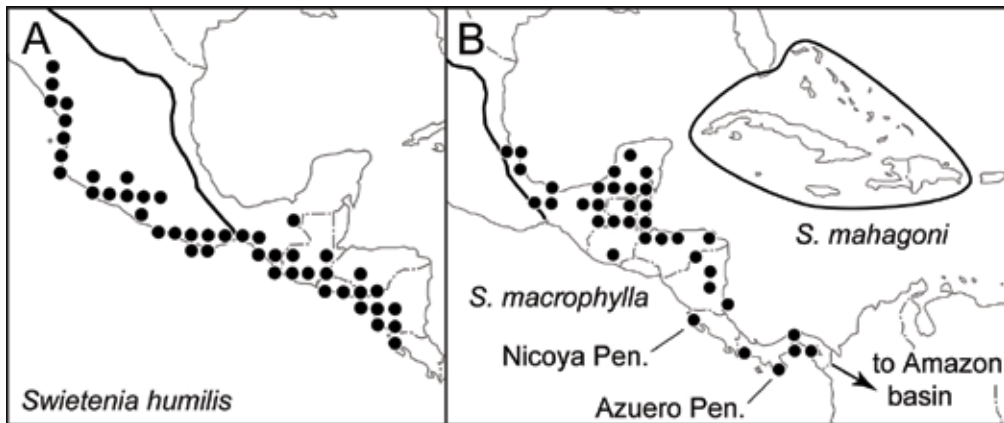
    Swietenia macrophylla King. (Fig. 15B). SE Mexico and through Central America (mainly on the Caribbean side) to the Amazon basin. In Mexico it is absent on the accreted terranes.
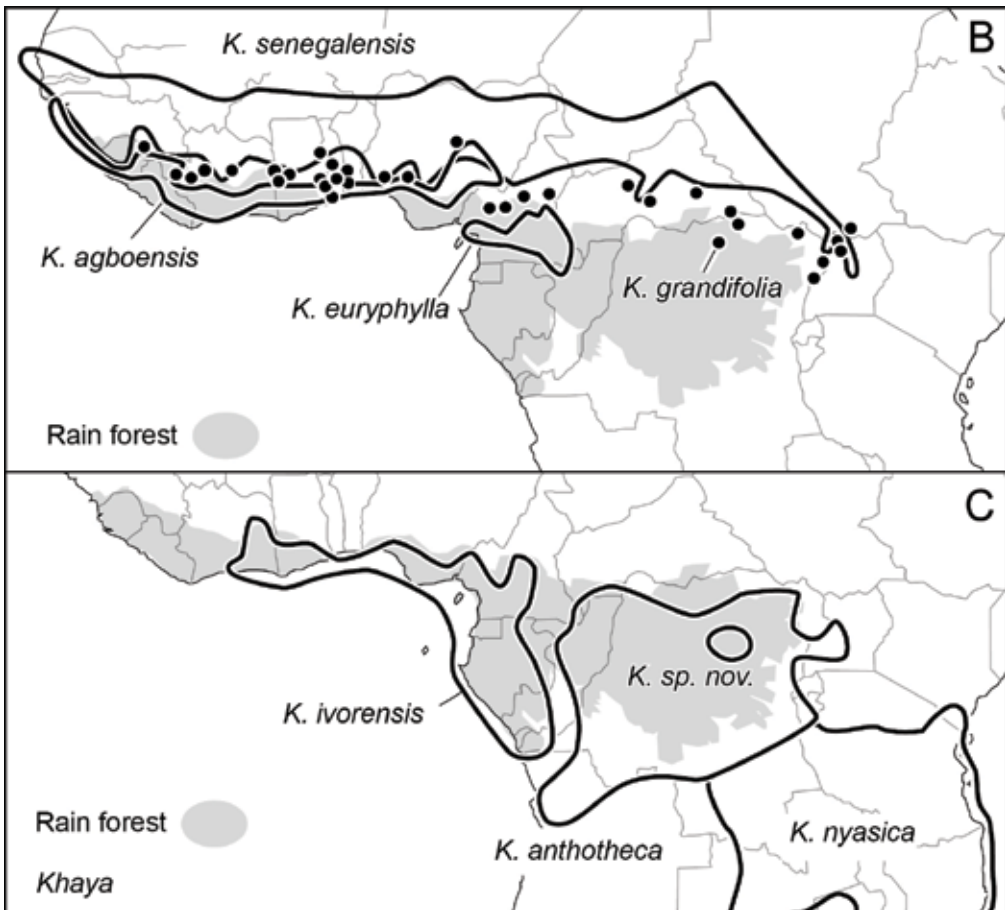
Fig. 14. (Continuation). Distribution of *Khaya* A.Juss. **B.** Distribution of the northern clade in relation to the rain forest. **C.** Distribution of the southern clade in relation to the rain forest. (Data from Monthe et al., 2019).

Swietenia mahagoni (L.) Jacq. (Fig. 15B). West Indies (Cayman Islands, Cuba, Bahamas, Jamaica, Hispaniola) and southern Florida. Often on limestone. It is widely planted and often escaped from cultivation, and so its original area of distribution is difficult to ascertain.

Novick et al. (2003) discussed whether *Swietenia* had a centre of origin in Mesoamerica or in Amazonia. They suggested that "we lack fossil evidence establishing the geographical origin". However, they thought that the northern distribution of all three *Swietenia* species supports an origin of *S. macrophylla* there as well, with later dispersal to the Amazon. Yet the three species are almost completely allopatric, consistent with an origin by simple vicariance, and so there is no need for any range expansion in any of them.

Fig. 15. Distribution of *Swietenia* Jacq. **A.** *Swietenia humilis* Zucc. Solid line = boundary between accreted terranes in the west and craton in the east (Umhoefer, 2003). **B.** *Swietenia macrophylla* King and *Swietenia mahagoni* (L.) Jacq.

Ecology. Trees in moist or dry forest, rocky areas, often on limestone (*Swietenia mahagoni*); sea level–1200 m. *Swietenia mahagoni* regenerates well within unlogged and logged forest, is a good coloniser of abandoned farm land, and "thrives on disturbance…" (Pennington, 2002). On some islands it is regarded as a weed.

Notes. Swietenia macrophylla displays "strong phylogeographic structure" in Mesoamerica, and greater genetic differentiation there than in Amazonian populations (Novick et al., 2003). In Mesoamerica, the two populations on the Pacific coasts of Costa Rica (Santa Rosa, by the Nicoya Peninsula) and Panama (Azuero Peninsula) (see Fig. 12) were genetically distant from all the others. Novick et al. (2003) wrote that the split of these populations from the rest "may have occurred early in the Mesoamerican expansion of mahogany, perhaps prior to the late Miocene development of the Talamanca mountain range".

Novick et al. (2003) pointed out that the pattern in *Swietenia macrophylla*, in which the Nicoya and Azuero populations are distinct from all the others, is similar to that seen in other groups. For example, Perdices et al. (2002) found that vicariance has played a strong role in the diversification of the catfish genus *Rhamdia*, and they identified cis- and trans-Andean clades. One of the species, *Rhamdia guatemalensis*, ranges from southern Mexico to northern Colombia. The basal split within the species is between a population at Cañas, by the Nicoya Peninsula, and all the rest.

The 21 species of *Poeciliopsis* (Poeciliidae) are small topminnows distributed mostly in Pacific-slope drainages from Arizona to western Colombia. The basal break is between subgen. *Aulophallus*, found along the Pacific coast between the Nicoya and Azuero Peninsulas, and the remaining 18 species, making up subgen. *Poeciliopsis* (Mateos et al., 2002).

Other endemics in the region include the mangrove hummingbird, *Amazilia boucardi*, restricted to the sector between the Nicoya and Osa Peninsulas, and the

frog *Craugastor rugosus*, distributed between Punta Judas (= Punta Mala) and the Osa Peninsula and its hinterland. The Osa Peninsula in particular is known for its high diversity and endemism.

The mayfly *Tikuna atramentum* is only known from Santa Elena Peninsula, Nicoya Peninsula, Punta Judas, and Osa Peninsula (Fig. 12; Flowers & Ávila A., 2006). In another mayfly genus, *Choroterpes*, both the Costa Rican species show a similar pattern to that of *Tikuna*, with *C. maireana* restricted to Santa Elena Peninsula, and *C. gregoryi* at Nicoya Peninsula, Punta Judas and opposite Osa Peninsula (Ávila A. & Flowers, 2006). Flowers & Ávila A. (2006) made the critical observation that the localities of *Tikuna atramentum* show a 'tight spatial correlation with ophiolitic terranes' in the 'Nicoya Complex' in the broad sense. Ávila A. & Flowers (2006) mapped a similar correlation in *Choroterpes*. The Nicoya Complex includes a Jurassic–Paleogene ophiolite sequence, comprising ultramafic rocks, epiclastic material indicating a Cretaceous volcanic island arc, and a Campanian–Eocene arc-related complex. Flowers & Ávila A. (2006) noted that a similar, close association of hemipterans, plants, and birds with ophiolite terranes has been reported in New Guinea. They wrote that these taxa seem to have arrived in New Guinea by accretion of the terranes on which they occur, and that a similar accretion process may be responsible for the distribution of *Tikuna atramentum* in Costa Rica.

Many marine rocks on land were deposited as sediments during marine transgressions. However, ophiolite suites, like those in the Nicoya Complex, are of special interest as they did not form in situ, but have been tectonically emplaced from elsewhere. They represent slices of oceanic crust and upper mantle that have been ramped up onto land during obduction (the opposite of subduction), a process that occurs at plate margins when an island arc collides with a continent.

Ophiolites often include ultramafic rocks, and botanists have inferred that the endemism typical of them is due to soil chemistry. However, this is unlikely to be the real explanation, as there is usually striking endemism in animals as well as plants, and ophiolite terranes can harbour both ultramafic and non-ultramafic endemics. Thus ophiolites are probably so significant for biogeography, not because of their chemistry, but because they are arc terrane markers. The most mature phase of arc collision is seen in old arc fragments now deeply embedded in modern mainlands, as in Borneo, the Philippines, New Guinea, and New Zealand. The remnants of these Mesozoic arc systems have been crushed between arcs or continents, but they have left a biological signature in the distributions of living taxa.

The biogeographic problem in Costa Rica and Panama requires several features to be explained together: endemism on the Nicoya, Osa and Azuero peninsulas in *Swietenia* and others; endemism along the rest of the Costa Rica–Panama biogeographic centre; anomalous absences in the same area; and major disjunctions in the area (such as the Nicoya–Ecuador disjunction in *Cedrela* 'odorata I').

These phenomena can all be explained, not as the result of dispersal from north to south or from south to north, but with reference to the Nicoya Complex of island arcs, seamounts, and associated ocean floor that formed in the Pacific, and were translated eastward. Parts ended up being 'smeared' onto the west coast of America

and are now embedded in the mainland of Costa Rica (at the peninsulas discussed above), Panama (Azuero Península and the Serranía del Sapo) and Colombian Chocó (Serranía de Baudó, continuous with the Serranía del Sapo; see Fig. 12).

As North and South America moved apart, the Caribbean trench and its associated active island arc moved east into the Caribbean (Fig. 16). The process resulted in the accretion of oceanic terranes, including arcs and seamounts, onto the mainland (Fig. 17). Movement of the trench into the Caribbean took place on strike slip faults to the north (Motagua fault system) and south (Romeral fault system). The process explains the geometry of distribution patterns seen in several Meliaceae described below, and also in parrots (Fig. 18), passerines (Fig. 19), and frogs (Fig. 20) (for other examples, see Heads, 2016).

Savage et al. (2005) wrote that "Theories about the origin of the biota of Costa Rica have generally assumed dispersal across a Central American land bridge that was formed by volcanic and tectonic activity sometime during the Pliocene". Biota are thought to have crossed the bridge from the north and from the south in a great 'interchange'. However, Savage et al. (2005) noted that the correlation of mayfly distributions with the Nicoya Complex suggested "the intriguing possibility that Costa Rica acquired some of its biodiversity eons before the Great American Interchange". Accretion of Cretaceous–Cenozoic island arc/s in the region would account for many aspects of the diversity there, including both endemism and disjunction.

The idea of a Great American Biotic Interchange was derived from a literal reading of the mammalian fossil record, and it remains a central tenet of dispersal biogeography. Nevertheless, it would seem unlikely that the only groups arriving in southern Central America/Chocó on island arcs formed in the Pacific were the mayflies described by the authors cited above; probably entire rain forest communities were involved.

An 'interchange' across a Costa Rica–Panama landbridge might explain the overlap of distributions and the high diversity there, but it does not account for the abrupt boundaries in the area, the high endemism, the strange absences, the large-scale disjunctions, or the precise correlations of distributions with allochthonous terranes. These, together with the diversity, can all be explained if a large part of the regional biota, rather than forming in situ, instead represents tectonic introduction from the Pacific plate. The Costa Rica-Panama region is an important biogeographic centre in its own right, with its own endemics and anomalous absences; it is not simply a 'bridge' (or a 'barrier' or 'filter') between North and South America.

13. *Carapa* Aubl.

Distribution. Four, 12 or 27 species have been recognised in different treatments. America, São Tomé Island, mainland Africa (Fig. 21A, B). The genus was earlier treated with four species (three in America and one in Africa). Kenfack (2011a) carried out morphometric and molecular analyses, and referred to numbered morphospecies. Nine of these were later named as new species (Kenfack, 2011b), and overall Kenfack
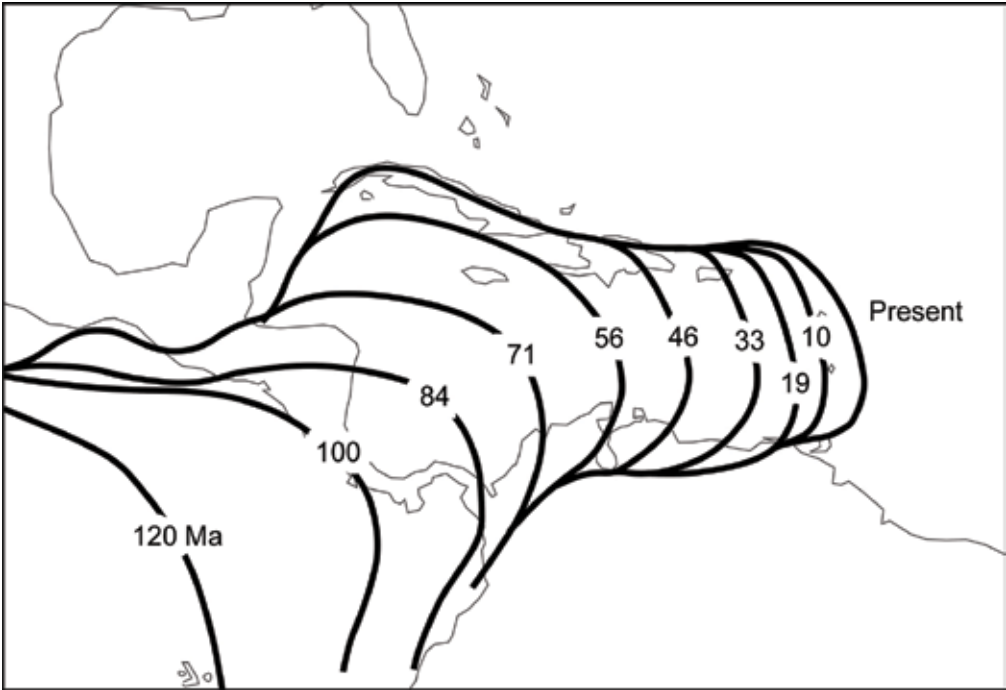
Fig. 16. Former relative positions of the Caribbean Trench from 120 Ma to the Present (Pindell & Kennan, 2009). The base map has no palaeogeographical significance; over the time period shown, North and South America have drifted apart.
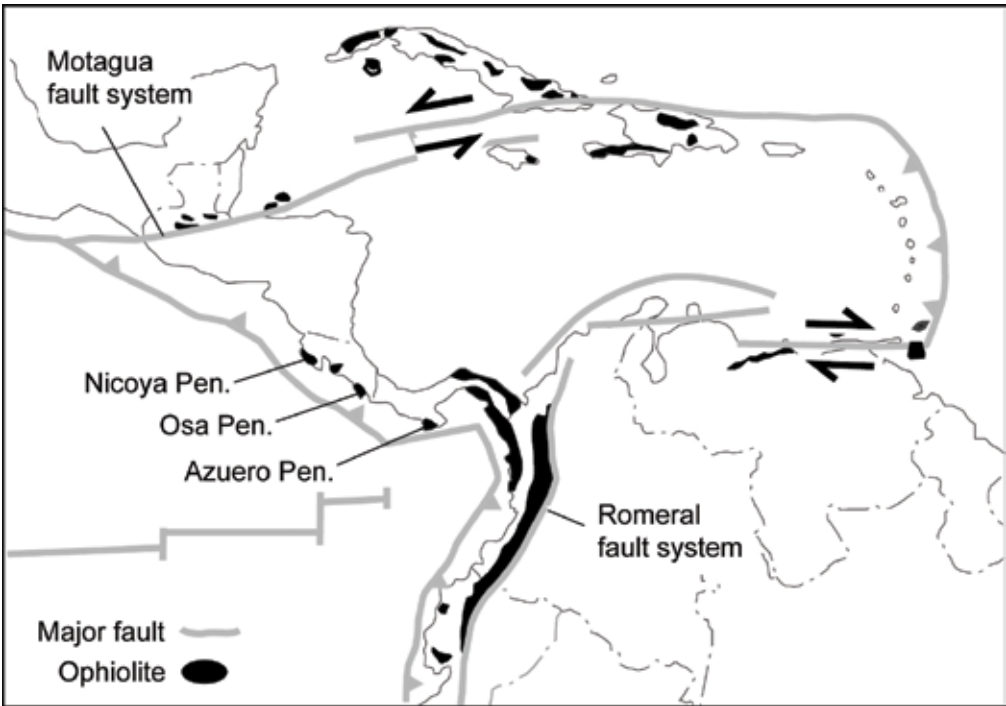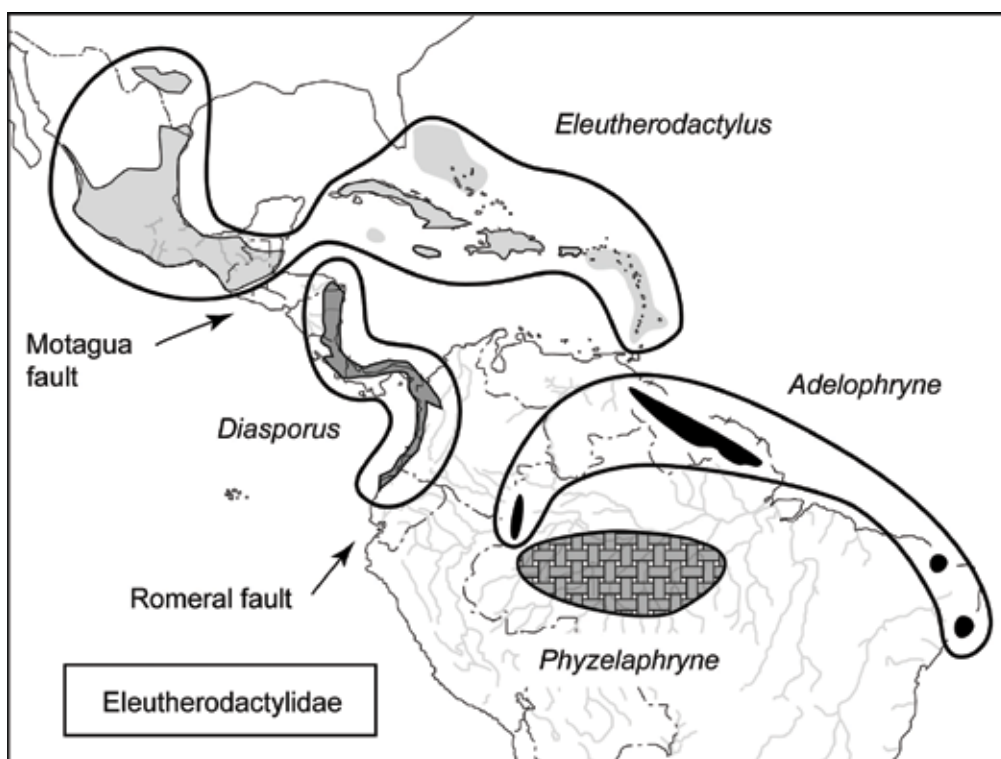

Fig. 17. Outline of Caribbean tectonics (Denyer & Baumgartner, 2006; Weber et al., 2009).
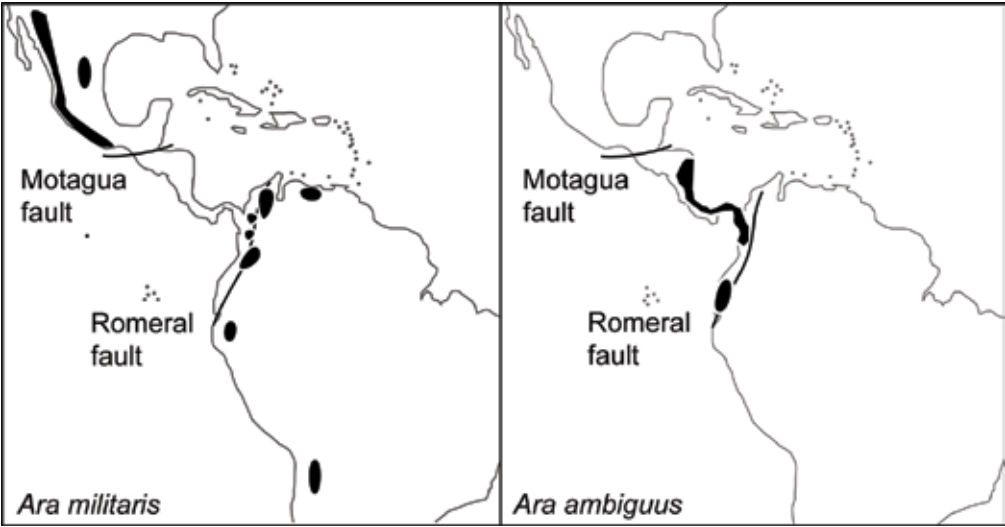
Fig. 18. Distribution of the parrots *Ara militaris* (L.) and *Ara ambiguus* (Bechstein) (Psittacidae) (Heads, 2016).
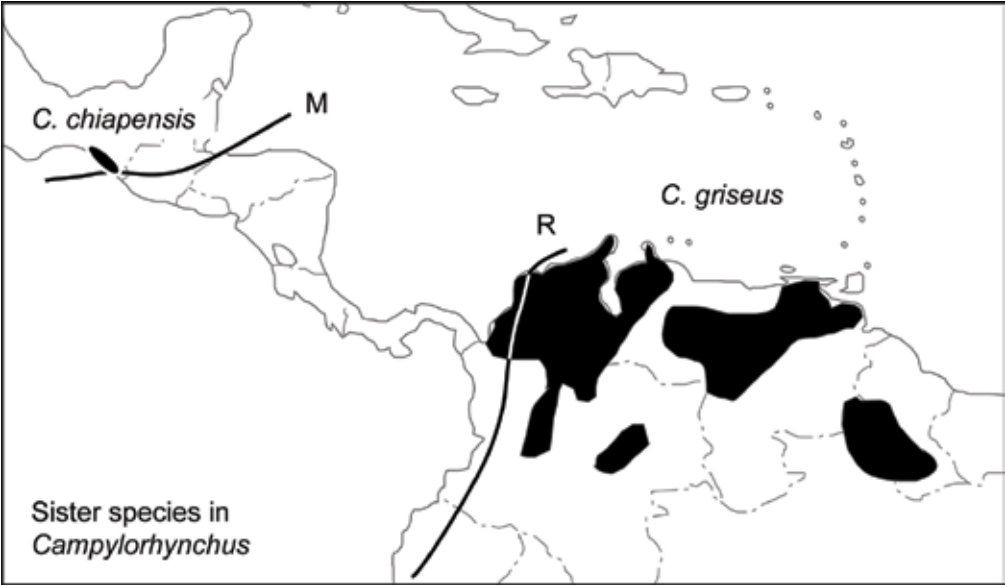
Fig. 19. Distribution of two sister species in the passerine bird *Campylorhynchus* Spix (Troglodytidae) (Heads, 2016).

Fig. 20. Distribution of the frog family Eleutherodactylidae (Heads, 2016).

recognised 27 species (11 in America and 16 in Africa). Koenen et al. (2015) accepted 12 species (two in America, 10 in Africa).

Ecology. Trees present at the inland limits of mangroves (in Gabon and Panama) and often in saline soil, flood plains and marshy conditions, periodically inundated forest, streams in wet forests, lowland rain forest, gallery forest in savannas, disturbed forest, and montane forest; gregarious in rocky mountains in Ivory Coast (Aubréville, 1936); up to 2300 m in America and 2500 m in Africa. The sister pair *Xylocarpus* and *Carapa* shows the transition from mangrove (*Xylocarpus*, some *Carapa* species) to higher montane forest (some *Carapa*).

In America, *Carapa* ranges from the mangrove up to 2300 m. In Clade I, the widespread *Carapa guianensis* sensu stricto is of special interest. Throughout most of its range it grows in flood plains and marshy conditions (Kenfack, 2011a). In the north of Guyana, for example, it is a small, basally branched tree that grows in forest that is subject to tidal inundation. However, further inland, in the Brazilian Amazon and in Peru, it grows in terra firme forest and is a large tree to 40 m tall (Kenfack, 2011b). It generally occurs between sea level and 300 m altitude but reaches 400 m in the Dominican Republic and 500 m in Venezuela.
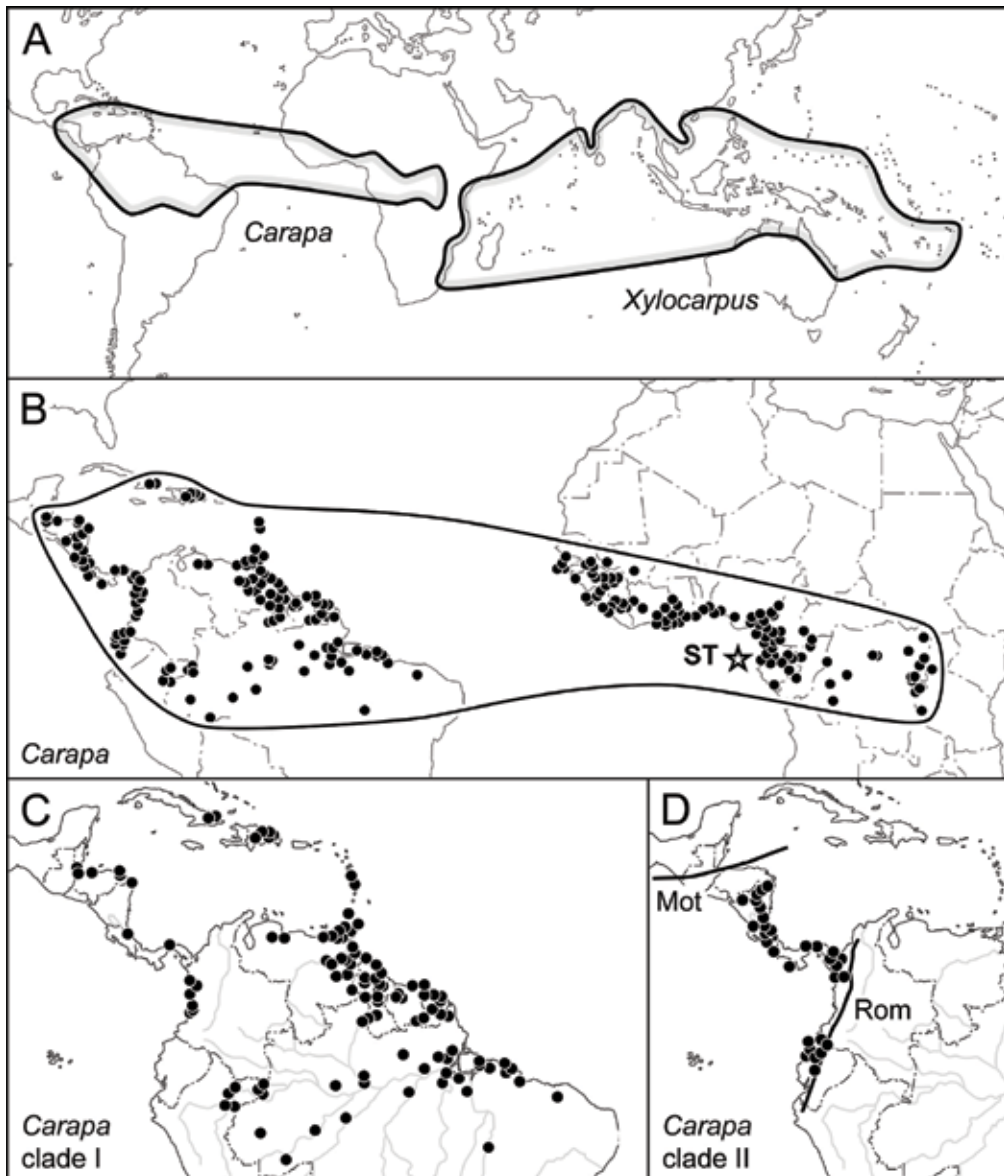
Fig. 21. A. Distribution of *Xylocarpus* J.Koenig and *Carapa* Aubl. **B.** Distribution of *Carapa*. ST = *Carapa gogo* Kenfack (possibly not a distinct species) on São Tomé Island. **C.** Distribution of *Carapa* clade I. **D.** Distribution of *Carapa* clade II. Mot = Motagua fault system, Rom = Romeral fault system.

In the floodplain forests (*várzea*) of the Amazon estuary, at 5 m elevation, Londres et al. (2017) studied the population structure of *Carapa guianensis* sensu lato in three types of *várzea* differentiated by tidal influence, species dominance and composition, and edaphic conditions. In all three, densities of *Carapa guianensis* were much higher than in terra firme forests

Carapa nicaraguensis C.DC. (morphospecies 4 in Kenfack, 2011a) is recorded from periodically inundated forest and, on Coiba Island off the south coast of Panama, from riverbanks in an area of mangrove.

In mainland Africa, *Carapa* inhabits mangrove, coastal and lowland forest, including gallery forest in savanna, and extends up to montane forest at 2500 m (*C. grandiflora* Sprague in East Africa and *C. oreophila* in SW Cameroon and SE Nigeria). In West Africa, *Carapa procera* DC. sensu lato has been reported as "Forest tree; habit varies from a sprawling tree with arching branches up to about 50' high in swamp forest to a tall tree with clear bole in lowland rain forest" (Keay, 1958).

Asuk et al. (2018) recorded *Carapa procera* sensu lato from mangrove swamp at Calabar, Nigeria. In East Africa, *Carapa procera* sensu lato is recorded "in lake-shore, riparian and mid-altitude forest (especially where drainage is impeded); 1140–1830 m" (Styles & White, 1991). The mangrove associates recognised by Kenfack (2011b) in African *Carapa* are as follows: *Carapa dinklagei* Harms (= morphospecies 17 of Kenfack, 2011a) in SW Nigeria to Gabon, edge of mangrove swamp (Rio del Rey, SW Cameroon), low depressions in coastal forest, wet valleys along rivers and streams; sea level to 800 m; *Carapa mangarevensis* Kenfack & Issembe (= morphospecies 24 of Kenfack, 2011a) in Gabon, mostly along the inland edge of mangroves, often under saline conditions; *Carapa littoralis* (= morphospecies 22 of Kenfack, 2011a) in Cameroon, coastal sites, sometimes more or less associated with mangrove forests. These species record an ecophyletic transition between mangrove and dry ground. Another species of special interest is *Carapa microcarpa* A.Chev. (= morphospecies 13 of Kenfack, 2011a). It occurs from Ivory Coast to Benin in periodically inundated terrains and along streams in wet forests, in contrast to morphospecies 12 [*Carapa procera*] and 14 [*C. velutina* C.DC.], which grow in gallery forest in savanna or dry forest. In Ghana, *Carapa microcarpa* grows along streams in montane rain forest, with branches that arch downwards and occasionally take root where they touch the ground (pers. obs., Atewa Range).

Notes. The trans-Atlantic *Carapa* and the trans-Indian Ocean mangrove *Xylocarpus* were long thought to be sisters. The phylogeny in Koenen et al. (2015) instead proposed a phylogeny: *Soymida* (*Neobeguea* (*Pseudocedrela* (*Swietenia* (*Xylocarpus* (*Khaya* + *Carapa*))))), but without strong support. However, recent studies support the traditional status of *Carapa* and *Xylocarpus* as sisters. Muellner-Riehl et al. (2016) presented a phylogeny mainly similar to that of Koenen et al. (2015), but with a clade: (*Khaya* of Africa + *Swietenia* of America) (*Carapa* + *Xylocarpus*). Guo et al. (2018) proposed the arrangement used here: *Khaya* (*Swietenia* (*Carapa* + *Xylocarpus*)).

The American species of *Carapa* fell in two molecular clades showing distinct allopatry (Fig. 21C, D) (Kenfack, 2011a). In Clade I, the northern limit corresponds closely with the Motagua fault system. Clade I includes the most widespread species in the genus, *Carapa guianensis* Aubl. sensu stricto (morphospecies 1 of Kenfack, 2011a). In Central America *Carapa guianensis* is present only on the Caribbean coast, while in the West Indies (where it is the only *Carapa* present), it occurs in Cuba (Oriente only), Hispaniola, and the central Lesser Antilles (Grenada, Dominica, and

Martinique) (Kenfack, 2011b). The species (and genus) is notably absent from Puerto Rico and Jamaica, and is disjunct between Dominica/Martinique and Hispaniola/eastern Cuba.

Carapa clade II is restricted to the area between the Motagua and Romeral fault systems, consistent with its accretion, with the oceanic terranes, to the mainland. It displays a notable gap in Chocó, and this is filled by members of Clade I. In Central America, Clade I is restricted to the Caribbean coast, while clade II is widespread.

Carapa gogo Kenfack (= morphospecies 18 in Kenfack, 2011a) was treated as endemic to the island of São Tomé (Kenfack, 2011b) but is probably not a distinct species (Koenen et al., 2015). Whatever the exact taxonomic status of the population might be, the locality is significant.

14. *Xylocarpus* J.Koenig

Distribution. Two species in East Africa (Somalia to Mozambique), Madagascar, Mascarene Islands, India and east to Tonga and Samoa (Fig. 21A). *Xylocarpus* is distributed in East Africa and around the Indian Ocean, and it is allopatric with its sister group, the trans-Atlantic *Carapa* of America and West and Central Africa. The two genera are "geographic vicariants with different ecology" (Mabberley, 1988); *Xylocarpus* is usually in mangrove and other maritime sites, while *Carapa* usually occurs in forest on dry land.

Ecology. Xylocarpus granatum J.Koenig is in mangrove, usually estuarine and often associated with *Nypa* palm and *Sonneratia* (Lythraceae). *Xylocarpus moluccensis* (Lam.) M.Roem. sensu lato is also in mangrove, but usually in the upper reaches and often in only slightly brackish water; it also occurs ('*X. rumphii*'-type populations) above high water mark in scrub, woodland and forest, on cliffs, rocks (including limestone) and sandy substrates, often near surf, up to 20 m alt.

Notes. Three species of *Xylocarpus* have often been recognised, but a molecular study did not support the traditional distinction between *X. moluccensis* and *X. rumphii* (Kostel.) Mabb. (Guo et al., 2018), and these are treated here as a single species (*moluccensis* is the earlier epithet). Guo et al. (2018) proposed the following phylogeny: *Xylocarpus granatum* (*X. moluccensis* [samples BG1, MW4] (*X. moluccensis* [all other samples] + *X. rumphii*)). The two samples of *Xylocarpus moluccensis* sensu stricto from the Indian Ocean that were sequenced (BG1 from Bangladesh and MW4 from the western Malay Peninsula) form the sister to the rest of *X. moluccensis* sensu lato.

Despite the overall sympatry of the two species from East Africa to Tonga, allopatry does occur at more local scales. For example, around East Africa and around New Caledonia the distributions differ as follows (White & Styles, 1963; Styles & White, 1991; Mabberley 1988):

Xylocarpus granatum is present in Somalia and India, in the north, but not in the Mascarenes, and is present *in* New Caledonia on Grande Terre only.

Xylocarpus moluccensis sensu lato (incl. *X. rumphii*) is absent from Somalia and India, but present in the Mascarenes, and is present *i*n New Caledonia on the Loyalty Islands only.

In the New Caledonian archipelago, the break between Grande Terre (*Xylocarpus granatum)* and the Loyalty Islands (*X. moluccensis* sensu lato) is a standard biogeographic division (Heads, 2012). The break has been attributed to the late Cretaceous opening of the South Loyalty basin (at 85 Ma); subsequently, in the Paleocene, the basin closed, almost completely.

With respect to their morphology, the two species differ as follows: *Xylocarpus granatum* has buttresses extended, flattened and ribbon-like, spreading across the mud, pneumatophores absent; *Xylocarpus moluccensis* sensu lato has buttresses not extended or ribbon-like, pneumatophores present, peg-like and erect, pointed. (*Xylocarpus rumphii*-type populations of *X. moluccensis* occur above the mangrove and have neither buttresses nor pneumatophores).

The morphological distinction between 'pneumatophores' and 'ribbon-like buttresses' may not be as great as it appears, but the Grande Terre–Loyalty Islands break between the species suggests it is an old one.

The next three genera form a trans-Indian Ocean clade that is sister to the rest of subfam. Melioideae. In the phylogeny of Koenen et al. (2015) the three genera formed an unresolved tritomy; *Melia* has usually been placed close to *Azadirachta*.
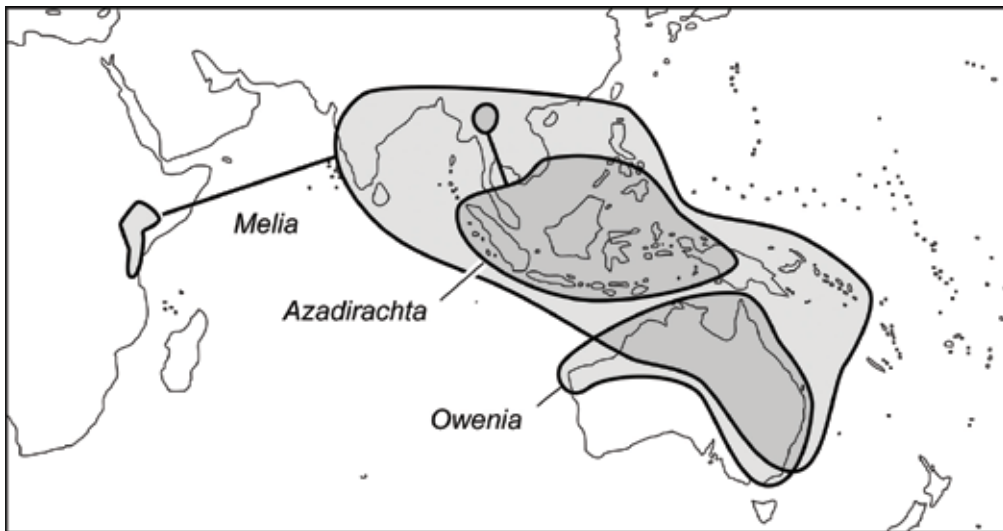
15. *Owenia* F.Muell.

Distribution. Five species in Northern Australia (north of a line: Carnavon–Alice Springs–Sydney) (Fig. 22). The genus is allopatric with *Azadirachta*. Within *Owenia* the distributions of the species scarcely overlap. *Owenia cepiodora* F.Muell. is locally endemic at the McPherson-Macleay Overlap, an important area of endemism located where the border of Queensland and New South Wales meets the coast (Heads, 2012)

Ecology. Trees in dry rain forest, woodland, grassland, disturbed vegetation, and on sandy plains, often locally dominant. Sucker shoots can develop in *Owenia venosa* F.Muell. and *O. acidula* F.Muell.

16. *Melia* L.

Distribution. Two species. Tropical East Africa (*Melia volkensii* Gürke); India to Australia and the Solomon Islands (*M. azedarach* L.). (Fig. 22). *Melia azedarach* is widely naturalised. In Australia it is widespread, but the original distribution, somewhere north-east of a line: Kimberley–Alice Springs–southern New South Wales, is completely obscured by cultivated and naturalised forms (Mabberley, 2013).

Fig. 22. Distribution of *Owenia* F.Muell., *Melia* L., and *Azadirachta* A.Juss.

Ecology. Both species are trees. *Melia volkensii* is in deciduous bushland, sometimes fringing seasonal watercourses and on rock outcrops, in reddish soils over limestone; 350–1675 m. *Melia azedarach* inhabits rain forest, seasonal forest, bamboo thickets, woodland and savanna, where it may coppice; recorded on limestone; up to 1800 m (in the Himalayas). In Australia it is in "subtropical and dry rain forest and in *Eucalyptus-Acacia* forest where smaller, often in regrowth" (Mabberley, 2013). *Melia azedarach* is widely cultivated and often invasive (Tilney et al., 2018). In parts of South Africa, "… it is naturalised and has become a pest. As early as 1906 it was established near Barberton, and now, in the Transvaal, it is the most widespread and aggressive of the invasive introduced trees" (White & Styles, 1986).

17. *Azadirachta* A.Juss.

Distribution. Two species. *Azadirachta indica* A.Juss., the Neem tree, is now widespread globally but is probably native in Burma. *Azadirachta excelsa* Jacobs ranges from Sumatra to New Guinea (Fig. 22).

Ecology. Both species are trees. *Azadirachta excelsa* is in rain forest, to 350 m altitude, *A. indica* is naturalised in savanna and thicket, up to 225 m. It is considered a weed in parts of the Middle East and sub-Saharan Africa where it dominates large areas of savanna. In West Africa it is one of the main sources of fuel (as charcoal). In the Northern Territory, Australia, it is invasive along waterways and is classified as a class B and C weed (https://nt.gov.au/environment/weeds).

The following three genera form a trans-Indian Ocean group disjunct between Madagascar and Sumatra.

18. *Sandoricum* Cav.

Distribution. Five species in Sumatra, Thailand and Malay Peninsula to the Philippines and New Guinea (East Sepik, Madang and Morobe; www.IUCNredlist.org; W. Takeuchi pers. comm. 12 May 2019) (Fig. 23). All five species occur in Borneo, and three are endemic there, including *Sandoricum caudatum* Mabb. restricted to the Kuching area.

Ecology. The species are all trees. Their respective habitats form a sequence from tidal level up to 1200 m altitude, consistent with an interpretation of the group as a series of uplifted mangrove associates: 1. *Sandoricum borneense*. Riverbank forest subject to inundation down to just above tidal influence; 2. *Sandoricum beccarianum*. Peat swamp forest, codominant locally, up to 30 m; 3. *Sandoricum caudatum*. Dipterocarp forest and kerangas, up to 350 m; 4. *Sandoricum dasyneuron* . Dipterocarp forest and ecotone to kerangas, also *Agathis* forest on acid sands, 50–600 m; 5. *Sandoricum koetjape* (Burm.f.) Merr. Periodically inundated swamp forest (W. Takeuchi pers. comm., 12 May 2019) and primary and secondary forest, 40–1200 m.

19. *Quivisianthe* Baill.

Distribution. Two species in Madagascar (Fig. 23).

Ecology. Trees in dry deciduous forest, *Acacia* scrub forest, and gallery forest.

20. *Ekebergia* Sparrm.

Distribution. Three species in Africa (Senegal to South Africa) (Fig. 23).

Ecology. Trees in rain forest, riparian forest, montane forest, savanna woodland, savanna, rocky places; near sea level to 2650 m (*Ekebergia capensis* Sparrm. in East Africa).

Notes. Ekebergia capensis is widespread through much of sub-Saharan Africa, and largely overlaps the range of *E. benguelensis* (southern central Africa) and *E. pterophylla* (C.DC.) Hofmeyr (South Africa). From West Africa to Uganda *Ekebergia capensis* occurs in savanna woodland and drier parts of the rain forest region, while in east and southern Africa it is mostly in montane forest, riparian forest, and temperate forest (as at Knysna in South Africa). White (1986) wrote: "Because it occurs in more
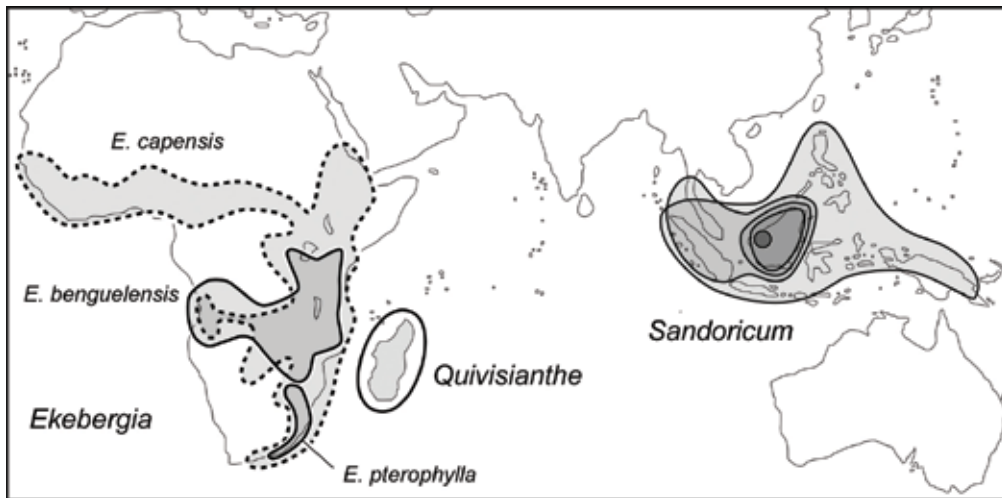
Fig. 23. Distribution of *Ekebergia* Sparrm., *Quivisianthe* Baill. and *Sandoricum* Cav.

than one major vegetation type and more than one regional phytochorion, it is an ecological and chorological transgressor…",

The neat allopatry among *Ekebergia*, *Quivisianthe* and *Sandoricum* (Fig. 23) suggests that none of the genera have spread very far. In contrast, the overlap between *Ekebergia capensis* and each of the two other species, which are themselves neatly allopatric, can be explained by vicariance of the three followed by range expansion of *E. capensis*. In this model the original area of *Ekebergia capensis*, the area that does not overlap with either of the other species, is still very large and would likely have included both closed rain forest and open savanna. Thus there is no need for the species itself to have ever migrated from one to the other.

The following two genera, *Walsura* and *Heynea*, range from India to New Guinea and form the sister group to a large, pantropical clade (Fig. 3). The pair is mapped here (Fig. 24) with *Vavaea*, but the three genera do not form a clade; instead, *Walsura* + *Heynea* broke off first from a pantropical clade, then *Vavaea* separated from the remainder of the pantropical clade. The distributions of *Walsura* + *Heynea* and of *Vavaea* thus represent the approximate locations of two successive breaks in a widespread ancestor.

21. *Walsura* Roxb.

Distribution. Sixteen species in NE India (Assam), Sri Lanka, Andaman Islands to western New Guinea (Vogelkop Peninsula); not naturally in Sumatra or Java (Clark, 1994; Mabberley, 2003). Borneo is a major centre of diversity, with seven species, six endemic (cf. *Sandoricum*).
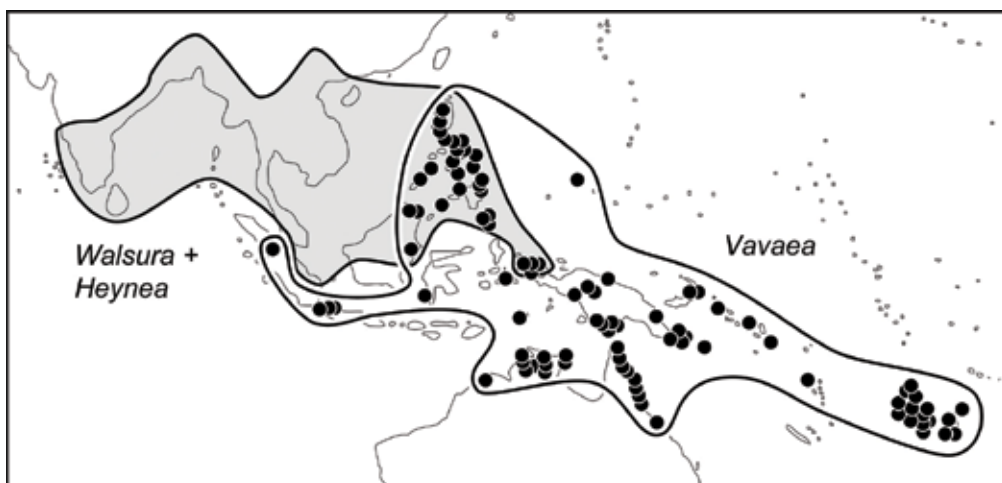
Fig. 24. Distribution of *Walsura* Roxb. + *Heynea* Roxb. (Clark, 1990, 1994) and *Vavaea* Benth. (Van Balgooy, 1966; Mabberley, 2013).

Ecology. Trees. In Malesia usually in wet evergreen forest, in China usually in sparse or dense forests in hilly regions. *Walsura monophylla* Merr. of Palawan (Philippines) is largely restricted to ultrabasic soils, while *W. grandifolia* Ridl. of Kuching (Borneo) is only known from limestone (Mabberley, 2003). From 5 m up to 2500 m (highest records in Thailand).

22. *Heynea* Roxb.

Distribution. Two species in Southern India (not Sri Lanka), Sikkim to Nicobars, southern China, Indochina, Malay Peninsula, Sumatra, Borneo and the Philippines (map in Clark, 1990: 283).

Ecology. Trees. In Malesia in rain forest, especially at forest edges, in regenerating clearings and along roadsides. In China in forests, sparse forests and thickets at low elevations and in hilly regions. Up to 1600 m (in Thailand).

23. *Vavaea* Benth.

Distribution. Four species from Sumatra to Tonga, including Yap in Micronesia (Fig. 24). One widespread species, *Vavaea amicorum* Benth., has the range of the genus. Two other species are endemic to Papua New Guinea, and one is endemic to Fiji.

Ecology. Trees with *Terminalia*-branching. Inner edge of mangrove swamps, beach thickets, primary and secondary forests, often on limestone (throughout the generic range), including limestone just above high tide level (*Vavaea amicorum* in Fiji; Heads, 2006) and limestone cliffs; up to 1250 m.

Notes. The previous two genera, *Heynea + Walsura*, range from India to western New Guinea, and are largely allopatric with *Vavaea*, ranging from Sumatra to Tonga. Overlap is restricted to north-eastern Borneo, the Philippines, and Vogelkop Peninsula of New Guinea. This suggests that three clades, *Heynea + Walsura*, *Vavaea*, and the pantropical sister of *Vavaea*, formed in allopatry, and that the third clade later underwent large-scale range expansion. The allopatry between the first two has remained largely intact, although local overlap has developed in eastern Borneo, Philippines and Vogelkop Peninsula. The single Sumatra record of *Vavaea* is based on a Junghuhn collection discussed by Van Steenis (1950).

   The eastern boundary of *Vavaea* at Tonga corresponds with the eastern limit of the mangrove *Xylocarpus* (Fig. 21A) and also the mutual boundary of the Australia and Pacific plates. Smith (1985) wrote: "It is of some significance, in a biogeographical consideration, that *Vavaea*, an abundant component of forest vegetation in Fiji and Tonga, has apparently been unable to cross the water barriers to the Horne and Wallis Islands or Samoa; this fact does not suggest ease of dispersibility…".

   In the widespread *Vavaea amicorum*, Pennington (1969) recognised four main centres of variation: Philippines, New Guinea, Solomon Islands and Fiji. (Specimens with a spreading indumentum, i.e. '*V. pilosa* Merr.', occur in the Philippines, New Guinea, and the Solomon Islands). These localities mark a common distribution and also the south-western margin of the Philippine and Pacific plates. *Vavaea* is sister to a large pantropical complex (the following two genera and the diverse TT and GA clades) that comprises more than half the family, and so its close distributional alignment with the plate margins is of special interest.

The next two genera, *Lepidotrichilia + Astrotrichilia*, form an East Africa-Madagascar pair that is sister to the pantropical group: TT clade + GA clade.

24. **Lepidotrichilia** T.D.Penn. & Styles, sensu stricto

Distribution. One species, *Lepidotrichilia volkensii* (Gürke) J.-F.Leroy, in East Africa (Ethiopia to Malawi) (Fig. 25). In mountains around the East African Rift, and almost reaching the coastline in southernmost Kenya. The other species currently placed in this genus are treated here under *Lepidotrichilia*2 of Madagascar.

Ecology. A tree of mid-altitude and montane forest; 1050–3300 m. *(*African Plant Database, 2019).
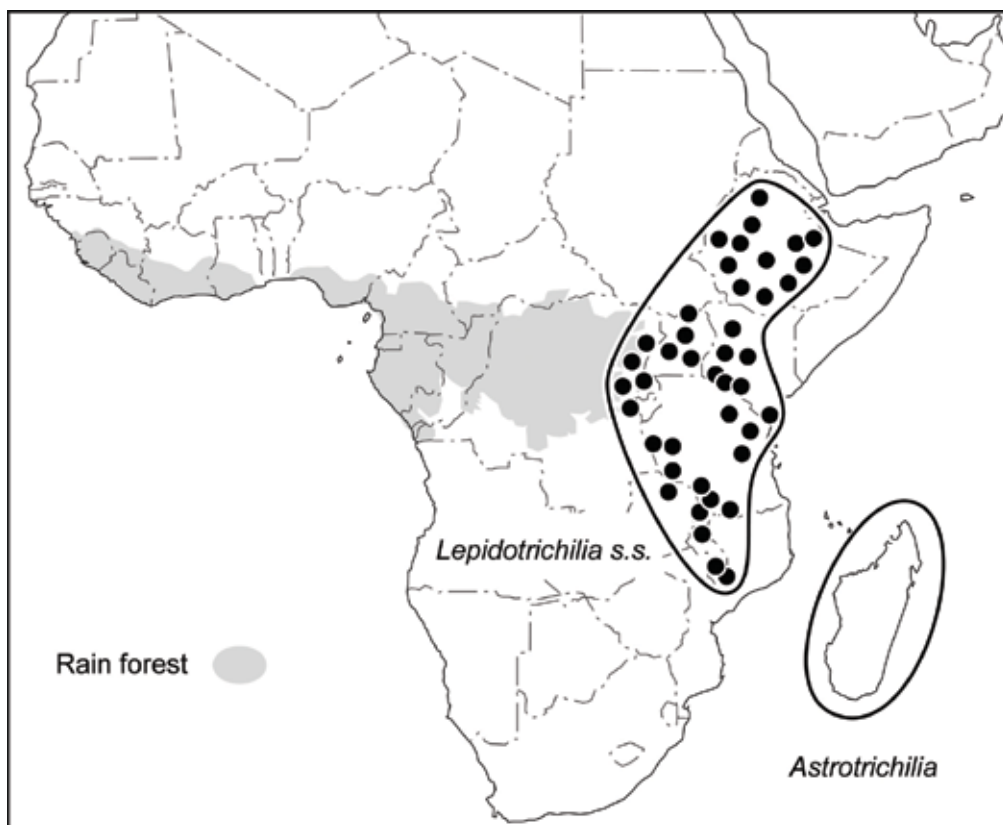
Fig. 25. Distribution of *Lepidotrichilia* T.D.Penn. & Styles sensu stricto and *Astrotrichilia* T.D.Penn. & Styles.

25. *Astrotrichilia* T.D.Penn. & Styles

Distribution. Twelve species in Madagascar. Ten of the species were described by Leroy & Lescot (1996).

Ecology. Trees and shrubs in littoral forest, damp depressions on sandy soil (*Astrotrichilia voamatata* J.-F.Leroy), dense forest, xerophilous bush and montane forest; sea level–2000 m (Leroy, 1958d; Leroy & Lescot, 1996).

The remaining genera of Meliaceae make up a large, pantropical group comprising the TT (*Trichilia–Turraea*) clade and its sister the GA (*Guarea–Aglaia*) clade (Fig. 26). The group as a whole includes all seven Meliaceae genera with more than 20 species, three in the TT clade (*Trichilia, Turraea and Malleastrum*), and four in the GA clade (*Aglaia, Guarea, Dysoxylum and Chisocheton*). *Trichilia* (America, Africa, Madagascar) and *Aglaia* (Asia, Pacific) are the only genera in the family with more than 100 species.
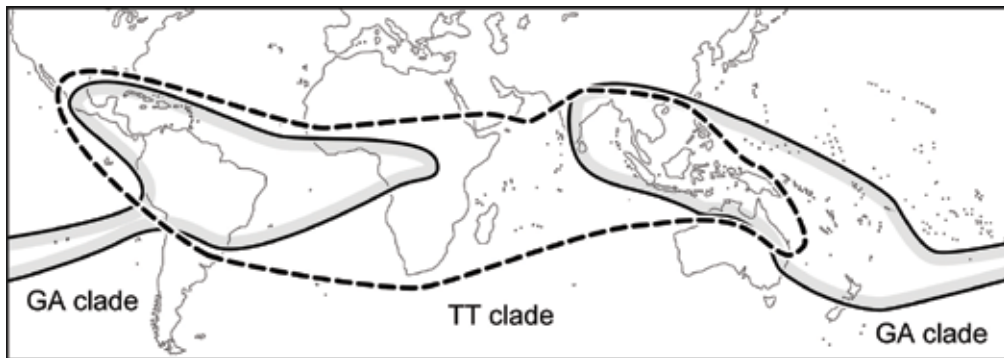
Fig. 26. Distribution of the *Trichilia–Turraea* clade and the *Guarea–Aglaia* clade.

The TT clade is diverse in southern Africa and East Africa, and reaches Yemen. It is also widespread on the islands in the western Indian Ocean: Socotra, Aldabra, Madagascar, and the Mascarenes. It is absent east of Australia and New Guinea, and while the TT clade displays trans-Atlantic affinities (in *Trichilia*) and trans-Indian Ocean affinities (in *Turraea* and *Naregamia*), there is no direct trans-Pacific affinity.

The GA clade, in contrast with the TT clade, is absent from southern Africa, East Africa (except for a single possible record of *Leplaea* Vermoesen from Tanzania), Yemen and the islands in the western Indian Ocean. It is diverse in Australia and New Guinea, and present in the Pacific islands east to Tonga. While there are no direct trans-Indian Ocean connections, there is a trans-Pacific affinity in *Cabralea* sensu lato.

The TT and GA clades overlap only in America–West Africa, and in India–New Guinea; in much of the western Indian Ocean region the TT clade occurs alone, and in much of the west Pacific only the GA clade is present. This allopatry can be interpreted as a trace of the original allopatry, and the areas of overlap as secondary developments.

26. *Munronia* Wight

Distribution. Five species (incl. the long misunderstood *'Turraea' breviflora* Ridl., now *Munronia breviflora* (Ridl.) Mabb. & Muellner; Muellner & Mabberley, 2008; Cuong et al., 2014). India and Sri Lanka, east to Timor. In the widespread *Munronia pinnata* (Wall.) W.Theob. (India to Timor), some specimens from Java "resemble the Indian plants…", (Mabberley et al., 1995), suggesting possible disjunctions across the Bay of Bengal.

Ecology. Shrublets, sometimes suckering with apparently short-lived shoots. Just behind the mangrove, drier, open and seasonal forest, bamboo forest thicket; sea level to 1800 m (in China). *Munronia pinnata* occupies the whole generic range from mangrove to 1800 m. Four of the five species are recorded from limestone rocks, cliffs, and crevices.

The next two genera, *Cipadessa* and *Pseudoclausena*, are sisters and together range from India to Timor and New Guinea (Fig. 27), repeating the India–New Guinea pattern of *Walsura + Heynea*, and the India–Timor distribution of *Munronia*. There is a high level of allopatry between *Cipadessa*, which is western, and *Pseudoclausena*, which is eastern. The two overlap only in a small part of eastern Sumatra, Sulawesi, and SW Philippines (Mindanao etc.). In the Malay Peninsula the two appear to be neatly allopatric, with *Cipadessa* present in Kedah only (Mabberley et al., 1995), while *Pseudoclausena* occurs east of there and through the rest of the Peninsula (Clark, 1994).

27. *Cipadessa* Blume

Distribution. One species in India and Sri Lanka, to Timor (Fig. 27).

Ecology. Small trees or shrubs, sometimes subscandent, in sparse forests, forest edge, thicket, early successional forest, ravines and crevices in rocks, hilly regions on limestone; 200–2250 m (in Thailand).
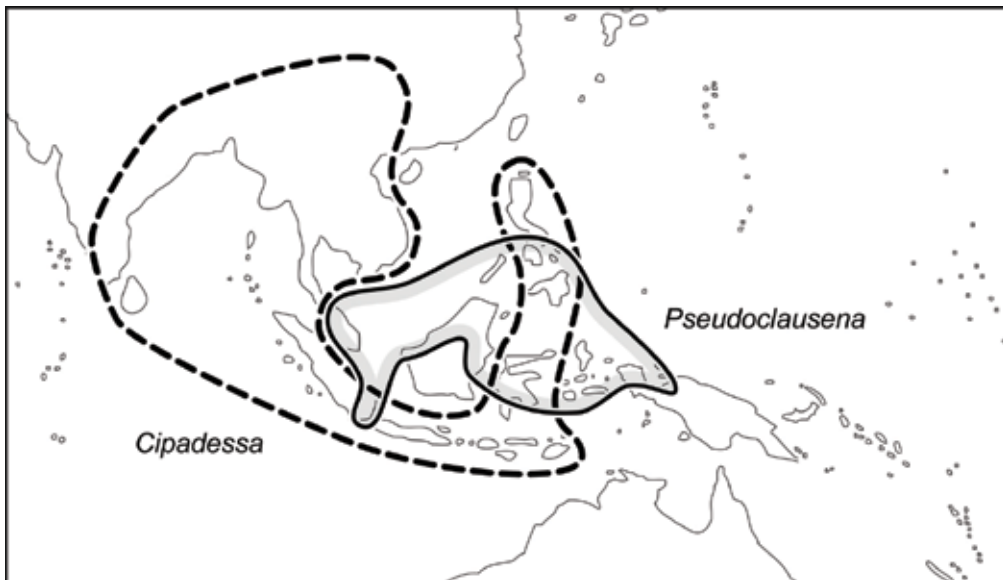
28. *Pseudoclausena* T.P.Clark

Distribution. One species in the Malay Peninsula, Sumatra, Borneo, Philippines, Sulawesi, Moluccas, western New Guinea (Fig. 27; Clark, 1994).

Ecology. A tree of wet forest; 500–1650 m (in Thailand).

The next six genera form a clade (making up the rest of the TT clade), and their overall distribution is mapped in Fig. 28. *Trichilia* and allies form a trans-Atlantic clade, while *Turraea* and allies form a trans-Indian Ocean group, and the two overlap only in Africa and Madagascar. The high level of allopatry suggests original vicariance at a break somewhere in Africa, followed by widespread overlap there (although not in SW Africa, where the *Turraea* group occurs alone).

     The next three genera make up the distinctive *Turraea* group, part of the TT clade. The plants are small trees or shrubs, sometimes scrambling or climbing, and the leaves are nearly always simple (pinnate only in *Turraea streyi* F.White & Styles of SE South Africa).

**Fig. 27.** Distribution of *Cipadessa* Blume and *Pseudoclausena* T.P.Clark.
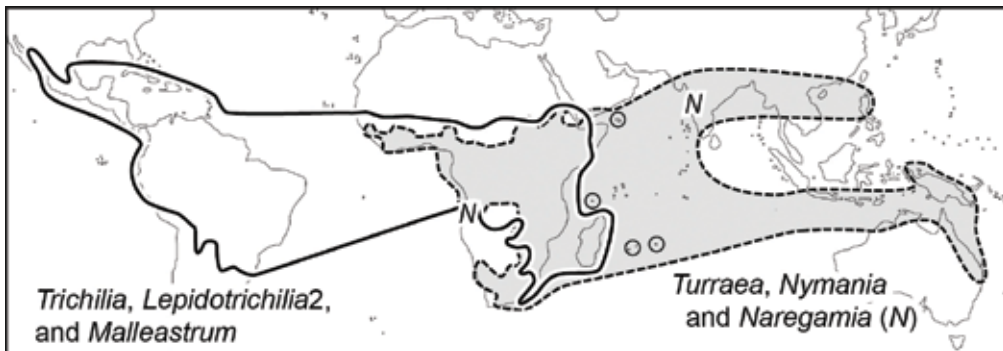
Fig. 28. Distribution of the *Trichilia* group (*Trichilia* P.Browne, *Lepidotrichilia*2 and *Malleastrum* (Baill.) J.-F.Leroy) and the *Turraea* group (*Nymania* Lindb., *Turraea* L., and *Naregamia* Wight & Arn.).

29. *Nymania* Lindb.

Distribution. One species in South Africa and Namibia (Fig. 29, from White, 1986). Semi-desert areas in the Karoo-Namib region, also in the Cape Floristic Region in enclaves of karoid vegetation (absent from typical Cape vegetation) (White, 1986). There is significant local differentiation in the species, and different catchments contain genetically distinct lineages (Potts, 2017).

　　Nymania capensis (Thunb.) Lindb. is located west of the Lebombo monocline (Fig. 9), an important biogeographic boundary (Heads, 2012). In the eastern part of its
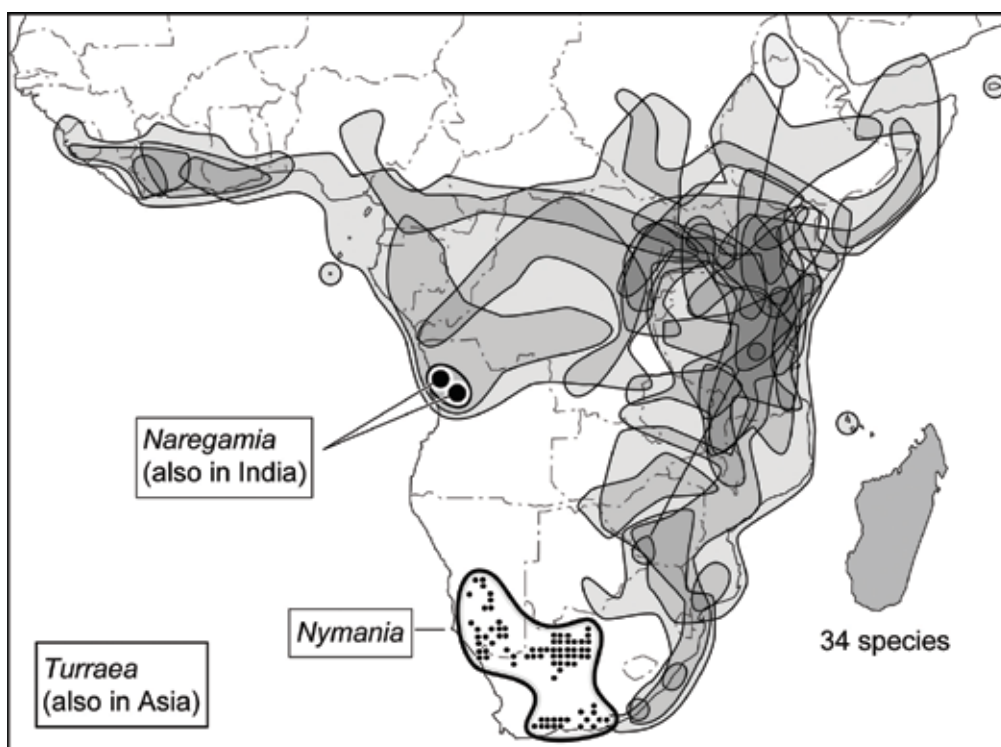
Fig. 29. Distribution of *Nymania* Lindb., and the African species of *Turraea* L. and *Naregamia* Wight & Arn.

range, its distribution overlaps that of *Ekebergia capensis* (Fig. 23), but in the western part of its area, *Nymania* is the only Meliaceae present. It is allopatric with its sister clade, *Turraea* + *Naregamia*, with the two meeting at the Albany node (where the mountain ranges of the Cape Fold Belt intersect the coast).

Ecology. Shrub in semi-desert, karoid vegetation (dense, woody, and thorny thicket, often with succulents), and in bushland peripheral to the main area of the Karoo desert (Potts, 2017; White & Styles, 1986). Not in true desert or in the fynbos heathland of south-western South Africa.

Notes. The present paper does not consider the architecture of Meliaceae in any detail (notes on rhizomes were given above, in the section 'Mangrove and associated vegetation'). However, *Nymania* is so unusual that it warrants some brief discussion. The morphology of a plant helps determine its ecology, and the following paragraphs propose a mechanism of generating small-leaved plants, such as *Nymania*, that can survive in arid areas.

In most Meliaceae, shoot growth conforms to the architectural models of Corner, Aubréville, Champagnat, Rauh and Attims (Mabberley et al., 1995; African

Plant Database, 2019). Even Meliaceae found in drier, open vegetation, such as *Pseudocedrela* and *Ekebergia*, are more or less 'normal', large-leaved members of the family. However, architecture in *Nymania* is radically different, and the plant has been described as "un-meliaceous-looking" (Penningon & Styles, 1975). The architecture (Fig. 30; see also the many photographs at www.GBIF.org), together with its distinctive flower and fruit, has meant that the genus has been placed in as many as six families, including its own.

Nymania capensis is a shrub 1–5 m high, and the shoots are differentiated into brachyblasts (short shoots) with abortive internodes, and long shoots with abortive apices. The leaves are small, just 1–2(–4) cm × 3–5 mm, and form tufts or fascicles on the brachyblasts. The same shoot differentiation seen in *Nymania* also occurs in many other plants of southern and eastern Africa, Madagascar, Australia, New Zealand and warmer parts of America. The species are often described as 'divaricate' *or* 'divaricately branched', as in, for example, *Melicope simplex* A.Cunn. (Rutaceae) of New Zealand (Allan, 1961) and *Boronia acanthoclada* Paul G.Wilson (Rutaceae) of south-western Australia (Duretto et al., 2013). However, many other plants described with 'divaricate' branching (such as *Aglaia odoratissima* Blume in Mabberley et al., 1995) do not have the distinctive shoot differentiation discussed here.

In their epochal treatment of tree architecture, Hallé et al. (1978: 59) did not consider 'divaricate' growth, as they treated brachyblasts as "ephemeral units equivalent to leaves". However, 'divaricate' architecture (long shoots with abortive apices, short shoots with abortive internodes) was described accurately by Philipson (1978), and so it is referred to here as Philipson's model. Apart from *Nymania*, other Meliaceae with shoot architecture conforming to Philipson's model include species of northeast Africa species such as *Turraea parvifolia* Deflers and *T. retusa* Styles & F.White, discussed below, and Malagasy species such as *Turraea rhombifolia* Baker.

Interpreting the morphology of plants with Philipson's model is challenging. The brachyblasts, abortive long shoots, and several other features mean that the plants are not simply small versions of typical Meliaceae. The latter have large, compound leaves (up to 240 cm long in *Chisocheton macrophyllus* King), large, branched inflorescences (up to 7 m long in *Chisocheton penduliflorus* Hiern), and bracts that are small (two or three orders of magnitude smaller than the leaves), simple and linear. In contrast, the leaves in *Nymania* are small, simple, and linear, the flowers are solitary, and there are no inflorescence bracts — the flowers are borne in the axils of leaves.

If the vegetative shoot system of a normal, large-leaved Meliaceae were suppressed, leaving only the inflorescence, and if most of the flowers in the inflorescence were then also suppressed, leaving bracts as the only foliage, the result would be something like *Nymania*. In this interpretation, the *Nymania* shoot system is not homologous with a *Chisocheton* plant, but with its inflorescence, largely sterilised. The foliage in *Nymania* is made up, not of reduced leaves, but of sterilised inflorescence bracts. There appear to be no bracts because *all* the leaves are bracts, and the flowers appear to be solitary because the whole plant is an inflorescence.

The morphogenetic changes required to produce Philipson's model in a 'normal' plant are quite simple and may require only a small number of minor genetic changes;

Fig. 30. *Nymania capensis* (Thunb.) Lindb. **A & B**. Flowering twigs (×0.7). **C.** Flower (× 3). **D.** Calyx lobe (× 3). **E.** Lateral petal (× 1). **F.** Cross section of fruit (× 1). **G.** Fruiting twigs (× 0.7); **H.** Seed (× 2.7). **I.** Seed in longitudinal section (× 2.7). (Drawing by Rosemary Wise, reproduced with permission from the South African National Biodiversity Institute.)

no new structures are required, only reduction and sterilisation of parts already present. Other plants with shoot systems interpreted as largely sterilised inflorescences are discussed elsewhere (Heads, 2012: 16, 79, 250, 257; 2017: 440).

30. *Naregamia* Wight & Arn.

Distribution. Two species. *Naregamia alata* Wight & Arn. is in India (Western Ghats, from Konkan southwards to Travancore), and *N. africana* is in Angola (Figs. 27 and 28). Cheek (1996) sank *Naregamia* in *Turraea*; Koenen et al. (2015) sequenced *N. alata* only, and so the composition of the genus still requires testing. The disjunction between southern Africa and India displayed in *Naregamia* is also seen in other groups. Jeffrey (1988) noted the "astonishing geographical disjunction" of *Dactyliandra welwitschii* Hook.f. (Cucurbitaceae), found in deserts of the Namib (SW Africa) and Rajasthan (India).

Ecology. Small, barely woody, rhizomatous shrublets or herbs with a woody rootstock. The ecology is poorly known. The type of *Naregamia africana* (Welw.) Exell is recorded from thin woods at forest edges with Leguminosae at stream bank; 300 m.

31. *Turraea* L. sensu lato
(Incl. *Humbertioturraea* J.-F.Leroy and *Calodecaryia* J.-F.Leroy, both of Madagascar; Koenen et al., 2015).

Distribution. 73 species (*Turraea* sensu stricto with 66 spp., *Humbertioturraea* with five, and *Calodecaryia* with two) in Africa, Socotra, and Yemen (30 species), Madagascar and Mascarenes (c. 43 species), and Asia-Australasia (1 species) (Fig. 28).

Turraea *species* are concentrated in tropical East Africa, Madagascar, and the Mascarenes (Fig. 29). Species numbers rapidly diminish to the east and to the west: the Zambesi region has nine species, DRC seven, west tropical Africa five or six, southern Africa four. *Turraea* ranges east to mainland New Guinea and north-eastern Australia, but it is notably absent from Sumatra, Borneo, Sulawesi and the Moluccas, and along the chain: Bismarck Archipelago, Solomon Islands, Vanuatu, New Caledonia, Fiji, and Tonga.

Although *Turraea* is widespread through most of sub-Saharan Africa, including all the islands in the Gulf of Guinea, it is absent in the southwest (Angola, Namibia, western South Africa). This is precisely the region where its allies, *Naregamia* and *Nymania*, are concentrated (*Naregamia* is also in India). In north-eastern Africa, *Turraea parvifolia* is in northern Kenya, Ethiopia, Djibouti, Somalia and Yemen, often on limestone. The only other Meliaceae in the Arabian Peninsula is *Trichilia emetica* Vahl, which also extends from mainland Africa to Yemen. Disjunction across *the* Gulf of Aden also occurs in other groups, such as *Rhigozum somalense* Hallier f.

(Bignoniaceae; Philipson's model), and Kilian et al. (2004) mapped several other trans-Gulf of Aden endemics. During the early Miocene (c. 25 Ma), Arabia and Africa were rifted apart when the Red Sea and Gulf of Aden were formed by seafloor spreading. This process would explain the disjunction evident in the Meliaceae, Bignoniaceae, and many others that straddle the plate boundary.

Turraea socotrana Styles & F.White is endemic to Socotra, where it is the only member of Meliaceae. It inhabits limestone cliffs at medium elevations and also granite in the mountains (Brown & Mies, 2012: 211).

In *Turraea mombassana* C.DC. (Ethiopia to Malawi) and *T. robusta* Gürke (Uganda and Kenya to Malawi and Zambia) the distributions intersect the current coastline near the Tanzania/Kenya border. This repeats the pattern seen in *Lovoa swynnertonii* Baker f. (Fig. 7), *Melia volkensii* (Fig. 22) and *Lepidotrichilia volkensii* (Fig. 25).

In Madagascar, 31 species of *Turraea* sensu stricto were accepted in an unpublished manuscript by Leroy, but 16 of these remain undescribed (Callmander et al., 2012). Callmander et al. (2012) described two new species from Madagascar, and Randrianarivony et al. (2017) described another.

In the Mascarenes, *Turraea* is the only genus of Meliaceae present. It is notably diverse on the islands, with nine species, all endemic (Baider & Florens, 2016). Mauritius and Réunion have two species each, four others are shared between Mauritius and Réunion, and Rodrigues has one.

The single Asian species of *Turraea*, *T. pubescens* Hell., is closely related to some of the East African species (Mabberley et al., 1995). A similar transoceanic distribution is seen in the allied *Naregamia* (the previous genus), in Angola and India.

Ecology. Small trees, shrubs (sometimes scrambling or climbing), subshrubs, possibly rhizomatous (*Turraea streyi* F.White & Styles of South Africa), and one liane (*T. laurentii* De Wild. of the Congo basin). Behind mangrove, in forest and thicket on coastal dunes, wet, swampy and riverine rain forest, drier and deciduous forest, savanna woodland, bushland, thicket, banks of wadis (dry, gently sloping valleys or depressions in desert that are periodically flooded), secondary forest and areas of abandoned cultivation, on and around rocks, including limestone. From sea level to 2500 m altitude (*Turraea holstii* Gürke in the East African mountains). *Turraea pellegriniana* Keay and *T. vogelii* Benth. each occur in both rain forest and savanna.

Termitaria create an important heterogeneity in the landscape, soil and vegetation of African forest and savanna woodland (Craw et al., 1999), and comprise mounds often 10 m across and several metres high. They are composed of soils with a higher pH and higher levels of clay, nutrients (N, P, K, Ca and Na), and water retention than the surrounding acidic, sandy soils. Not surprisingly, they host a distinctive flora and fauna. *Turraea robusta*, *Turraea nilotica* Kotschy & Peyr., *Trichilia emetica* and *Trichilia capitata* Klotzsch are all recorded on termite mounds.

In southern tropical Africa, a lower altitude flora of basic soils (dominated by the legumes *Colophospermum* J.Léonard and *Acacia* Mill.) can be distinguished from a flora of acidic soils at higher altitude (dominated by another legume, *Brachystegia*

Benth.). However, in some ways the former is always present in the latter, for example in the flora of termite mounds. On the plateaux of southern and eastern Africa, a high proportion of the angiosperm species found on termitaria (e.g. Capparaceae) are important components of deciduous woodlands at lower altitudes. It is suggested that the basic soils of the termitaria have allowed many coastal elements to survive uplift, more or less in situ.

The nine species of *Turraea* in the Mascarenes extend from dry coastal areas to about 800 m elevation in the wet vegetation of the highest mountain peaks (Baider & Florens, 2016).

The single species of *Turraea* in Asia–Australasia is *Turraea pubescens*, a deciduous shrub found behind mangrove and in other coastal vegetation, in semi-evergreen forest, deciduous forest, thicket, savanna, secondary vegetation at forest edges, on dunes and rocks including limestone and basalt; sea level–1000 m.

Notes. *Turraea* has one main concentration of diversity in Madagascar (34 species) and another in Tanzania, Kenya, and Uganda (18 species). In the latter area the plants range from sea level (*Turraea nilotica, T. mombassana, T. wakefieldii* Oliv.) up to 2500 m (*T. holstii*) (Styles & White, 1991). In a key to the species of the region, the first couplet separates 'species with leaves, flowers and fruits borne on short lateral shoots of slow and limited growth' from 'species with leaves borne mostly on long shoots, usually widely spaced' (Styles & White, 1991). The two groups may well not be clades, but they provide a useful summary of architecture in the genus. In the first group, both long and short shoots are present. One example is *Turraea parvifolia*, cited above with reference to its presence in Yemen. The species is a rigidly branched shrub or small tree to 4 m tall. The short shoots have very short internodes, and so the leaves are borne in fascicles, while the long shoots undergo apical abortion. Thus the growth in these plants conforms to Philipson's model, as in *Nymania*. One of the synonyms of *Turraea parvifolia* is *T. lycioides* Baill., and *Lycium* L. (Solanaceae) does have very similar architecture.

Another *Turraea* with Philipson's model is *T. retusa* (syn. *T. pevelingii* Cheek) of Somalia (outside the East African region covered by Styles & White, 1991). The species is a shrub 1–2.5 m tall, bearing 'spur shoots' (brachyblasts) with numerous, very short internodes, and 'extension shoots' (long shoots), the latter 'sometimes with spiny tips developing from main axes when leafless' (Cheek, 1991). Leaves are extremely variable in size and shape. Cheek (1991) wrote that the species displays a tendency to spininess that has not been observed previously in the genus, although apical abortion of long shoots is also seen in *Turraea parvifolia,* described above. Whether the aborted apex is simply parenchymatised (as in most New Zealand 'divaricates') or indurated as a spine (as in most African 'divaricates') is a secondary aspect of the morphology. *Turraea retusa* grows in *Acacia-Commiphora* bushland, usually on stabilised sand dunes, sometimes on limestone, and often in areas of heavy agricultural disturbance.

There are close architectural and ecological parallels between *Turraea* and other plants, such as *Terminalia* (Combretaceae). The last revision of African *Terminalia* recognised two main groups (Griffiths, 1959). In Group 1, the 'spinosa' group, leaves

are borne in fascicles on short spur shoots of very slow growth, while branchlets and branches (long shoots) often abort apically. Growth thus conforms to Philipson's model. The species in Group 1 include *Terminalia fatraea* DC., known from shore thicket and closed bush on coral rocks and sandbanks in mangrove (coastal Kenya to Mozambique and Madagascar). Members of Group 2 are non-divaricates. They grow in savanna woodland, sometimes by the coast, in seasonally saturated soils and by the edge of *dambos* (seasonally flooded, grassy depressions), some on Kalahari Sand. The group includes *Terminalia scutifera* M.A.Lawson (Guinea to Sierra Leone), found in the "mangrove zone" or "knotted and gnarled by seashore", or in freshwater swamp forest (Griffiths, 1959). It is "extremely closely related" to *Terminalia nyssifolia* Britton of the Americas, a species that inhabits similar vegetation.

If a plant's stems are not strong enough to form an erect trunk a decumbent or climbing habit can result, as seen in several *Turraea* species recorded as sometimes scrambling: *Turraea mombassana* subsp. *mombassana, T. robusta, T. wakefieldii, T. floribunda* Hochst. and *T. obtusifolia* Hochst. *Turraea vogelii* ranges from Ghana to Uganda and Angola, including Bioko ('near the sea'; Keay, 1958), Príncipe, and São Tomé. The species is a climbing shrub 5–12 m tall, rarely an erect shrub to 2 m. It inhabits forest and savanna at the edge of gallery forest, from 10–1375 m. In contrast, its close ally *Turraea vogelioides* Bagsh. & Baker f. (eastern DRC to Kenya) is an erect shrub; it inhabits the understorey of riparian forest and well-drained and swampy rain forest, from 1150–1800 m. Of special interest is *Turraea laurentii* of rain forest and forest edge in DRC and Republic of Congo, recorded as a "sarmentous shrub or large liane" (African Plant Database, 2019). This seems to be the only known liane in the family.

The two *Turraea* species endemic in South Africa are distinctive through their architecture. *Turraea streyi* (SE coast of Natal, South Africa, from 50–200 m) is a subshrub or suffrutex up to 0.75 m high. It occurs in grassland, and inside and at the edges of scrub forest. *Turraea pulchella* T.D.Penn. (SE coast of Transkei, South Africa; 305–365 m) is a second suffrutex. The plant is up to 0.2 m high with tufted, herbaceous stems arising from a short (50 mm), branched, woody base, and with a strong, woody, possibly rhizomatous rootstock. Cheek (1991) grouped this species with *Turraea streyi*.

The next three genera, *Trichilia* and allies, form a trans-Atlantic clade that, overall, shows a high level of allopatry with the last three genera, a trans-Indian Ocean group (Fig. 28).

32. *Lepidotrichilia2*

Distribution. Three species in Madagascar. Leroy (1958b) and Leroy & Lescot (1996) placed the species in *Lepidotrichilia* of East Africa, but molecular evidence indicates

that they form a new genus, sister to *Malleastrum* (Koenen et al., 2015). Pending further revision, the new genus is referred to here as *Lepidotrichilia*2.

Ecology. Small trees in forest; 800–1000 m (Leroy & Lescot, 1996).

33. *Malleastrum* (Baill.) J.-F.Leroy

Distribution. A genus of 23 species in Madagascar, Comoro Islands, and Seychelles (Aldabra). Leroy (1964) treated 11 species (with maps), Leroy (1989) described three new species, and Leroy & Lescot (1996) described six more. Fosberg (1974) described *Malleastrum leroyi* Fosberg from Aldabra.

Ecology. Small trees. Beach forest on maritime dune sand, evergreen forest, dry forest, gallery forest, on limestone, coastal sand and sandy-gritty terrain, dry ravines; sea level to 2000 m (Leroy, 1964, 1989; Leroy & Lescot, 1996).

34. *Trichilia*
P.Browne
(Incl. *Pterorhachis* Harms and *Pseudobersama* Verdc.; Koenen et al., 2015).

Distribution. A genus of 107 species in Tropical America (81 species), Africa (20 species) and Madagascar (4 species).

Ecology. In America most species are trees of lowland rain forest, but a significant number are in seasonally dry deciduous forest and montane rain forest. Overall, the ecological range is: behind mangrove, flooded freshwater forest (including permanently and periodically inundated forest, *várzea*, *igapó*, rocks among cataracts; 16 species), dry seasonal forest, deciduous forest, secondary forest, savanna woodland, *cerrado*, limestone (12 species), montane forest (11 species); sea level to 3300 m.

The only record of the genus associated with mangrove is *Trichilia* sp., inhabiting backswamp behind mangrove and also dry forest on San Andrés Island off Nicaragua (González et al., 2010). (The only *Trichilia* recorded on the island by Pennington, 2016, is *T. martiana* C.DC.).

Eleven species of American *Trichilia* inhabit montane forest. *Trichilia multifoliola* of Bolivia reaches a very high altitude for Meliaceae, 3300 m (Pennington, 2016: 44; although on p. 42 the upper limit was given as 3200 m). The species occurs in high montane rain forest and cloud forest, including secondary formations. *Trichilia pallida* Sw. has a wide ecological range; it is usually in lowland rain forest, but in the Andes it inhabits montane forest and reaches 2000 m elevation.

In Africa, *Trichilia* ranges from sea level, on both west and east coasts, to 2100 m (*T. dregeana*) in Uganda**.** Most of the species (14 out of 18) are mainly confined to the Guineo-Congolian rain forest region, where they occupy rain forest (de Wilde, 1968). Two of the rain forest species are recorded from littoral forest:

Trichilia prieureana A.Juss. Littoral forest (Ivory Coast), riparian forest, rain forest, moist semi-deciduous rain forest, deciduous forest, savanna woodland; coastal to 1500 m; gregarious in forest, solitary in savanna; in Uganda it was formerly regarded as a weed tree and was poisoned locally by the Forest Department (White, 1986).

Trichilia monadelpha. Littoral forest (Audoin, Ivory Coast), often on river banks in evergreen and semi-deciduous forest, including gallery forest, common in secondary forest and sometimes abundant in very old secondary forest; 0–650 m.

Four other rain forest species are recorded in swamp forest or periodically inundated forest. Three of these are also in drier and secondary forest, and one of these, *Trichilia rubescens*, is another weed species, poisoned in managed forest. De Wilde (1968) wrote that "Many of the rain forest species favour secondary vegetation, and due to this habit, to some extent, their survival is enhanced by human interference in the original vegetation".

Two of the 'Guineo-Congolian' species of *Trichilia* species are recorded from both forest and savannah woodland: *T. prieureana* (also in littoral forest, see above; Senegal to Zambia) and *T. retusa* (Nigeria to eastern DRC).

Four other species of African *Trichilia* are unusual, as they mainly occur outside the 'Guineo-Congolian' rain forest region. The first, *Trichilia dregeana*, occurs in drier rain forest up to 2100 m. On the coast of SE Africa it also occurs in seasonal swamp forest (near Maputo), and on sand flats behind mangrove (at Inhaca Island and at Isipingo, south of Durban). In West Africa it is found from 800–1600 m, but near the mouth of the Congo River it occurs near sea level, a feature which is "hard to explain" (de Wilde, 1968) and "puzzling" (White, 1986). However, White noted that *Nuxia congesta* Fresen. (Stilbaceae), an Afromontane near-endemic, also has small, local populations at low altitudes, including one near the mouth of the Congo River.

Of the three other species outside the Guineo-Congolian region, *Trichilia emetica* is recorded on coral limestone and the leeward side of dunes. *Trichilia capitata*, a scrambling shrub, is also recorded from sea level, and extends up to 300 m. *Trichilia quadrivalvis* is unlike the others as it is restricted to inland sites (in southcentral Africa) and also has a distinctive architecture. It is a rhizomatous suffrutex, 10–40 cm high, that forms spreading clumps and carpets on the ground, with long, flexible rhizomes just below or on the soil surface. All other African species of *Trichilia* are erect trees or shrubs. *Trichilia quadrivalvis* is only known from *miombo* woodland with *Brachystegia* and *Julbernardia (Leguminosae)*, on Kalahari Sands and from 1200–1250 m altitude. Evidence suggesting the origin of *miombo* as a back-mangrove community that has been stranded inland is discussed elsewhere (Craw et al., 1999).

Notes. An initial molecular phylogeny indicated that *Trichilia* sensu lato comprises three main clades (Clarkson et al., 2016): with a phylogeny *Trichilia havanensis* of America (35 American *Trichilia* species (6 African *Trichilia* species, *Pseudobersama* + *Pterorrhachis*, both from Africa, and *T. trifolia* of America)).

The phylogeny is: New World (New World (New World and Old World)), and so Clarkson et al. (2016) wrote that: "The African species of *Trichilia* are nested within the neotropical clade". However, strictly speaking, they are nested in an African +

Neotropical clade. The paraphyletic basal grade in America would usually be taken as evidence of a centre of origin there, but as stressed above (Fig. 1), this is not necessarily correct.

In their study of *Trichilia* phylogeny, Clarkson et al. (2016) wrote that: "within the monophyletic crown group (sect. *Moschoxylum*) the majority of the species are on short branches with low sequence divergence between species, suggesting recent speciation… The causes of these recent rapid radiations within this seemingly stable and unchanging tropical environment are not immediately straightforward to understand". The reason for this problem could be that evolution in the group did not proceed by recent radiations, but by old divergences and juxtapositions.

The first clade in *Trichilia* comprises the American *T. havanensis* Jacq. This is widespread from Mexico (Sinaloa and Tamaulipas), through Central America to Colombia and northern Venezuela, also Cuba, Jamaica and Hispaniola (Pennington, 2016). (Absent from Puerto Rico, the Lesser Antilles and eastern Venezuela). The species inhabits a wide ecological range: lowland rain forest, wet montane forest, deciduous forest, and, often, disturbed areas; up to 2000 m elevation.

The 'American' clade of *Trichilia* includes all the sequenced American species except *Trichilia havanensis* (last section) and *T. trifolia* L. (in the African clade, below). It occurs throughout tropical America, from northern Mexico to northern Argentina, including the West Indies (Pennington, 2016).

In the American clade, *Trichilia americana* (Sessé & Moc.) T.D.Penn. ranges from NW Mexico south, on the Pacific seaboard, to Panama (Fig. 31A). In Mexico, north of the Motagua fault, the distribution is restricted to the western terranes that were accreted from the Pacific side in the Cretaceous (cf. *Swietenia humilis*, Fig. 15A). The southern boundary is at Panama. As discussed already (see *Swietenia*), the 'landbridge' theory of Costa Rica-Panama biogeography would account for the high diversity in the region, but it does not explain the boundaries, endemism or disjunctions there.

Several *Trichilia* species show significant disjunctions. *Trichilia moschata* Sw. subsp. *moschata* (Fig. 31B) is disjunct across most of Central America, between the Motagua fault zone and the Romeral fault zone. This suggests that it was never present on the main Caribbean arc (Fig. 16), which would have had its own endemics. Several other species are disjunct across Panama and Chocó. *Trichilia pittieri* C.DC. (Fig. 31C) is disjunct across Panama and Colombia, and *T. adolfi* Harms, of Costa Rica, Colombia, Ecuador, and Peru, is disjunct across most of Panama (present in the far west). *Trichilia poeppigii* C.DC. (Fig. 31D) is disjunct across most of Chocó.

Trichilia quadrijuga Kunth subsp. *quadrijuga* (Fig. 32) is distributed from Panama to SE Brazil, but is disjunct across much of Panama and Chocó. The gap is filled by the other member of the species, *Trichilia quadrijuga* subsp. *cinerascens* (C.DC.) T.D.Penn., found west of the Romeral fault zone. *Trichilia erythrocarpa* Lundell (Fig. 32) is a close relative of *T. quadrijuga* (Pennington, 2016) and has a southern boundary at the Motagua fault zone. Another species with a southern boundary there is *Trichilia minutiflora* Standl.

Of the 15 *Trichilia* species in the West Indies, eight are also more or less widespread on mainland America but have restricted distributions in the West Indies,
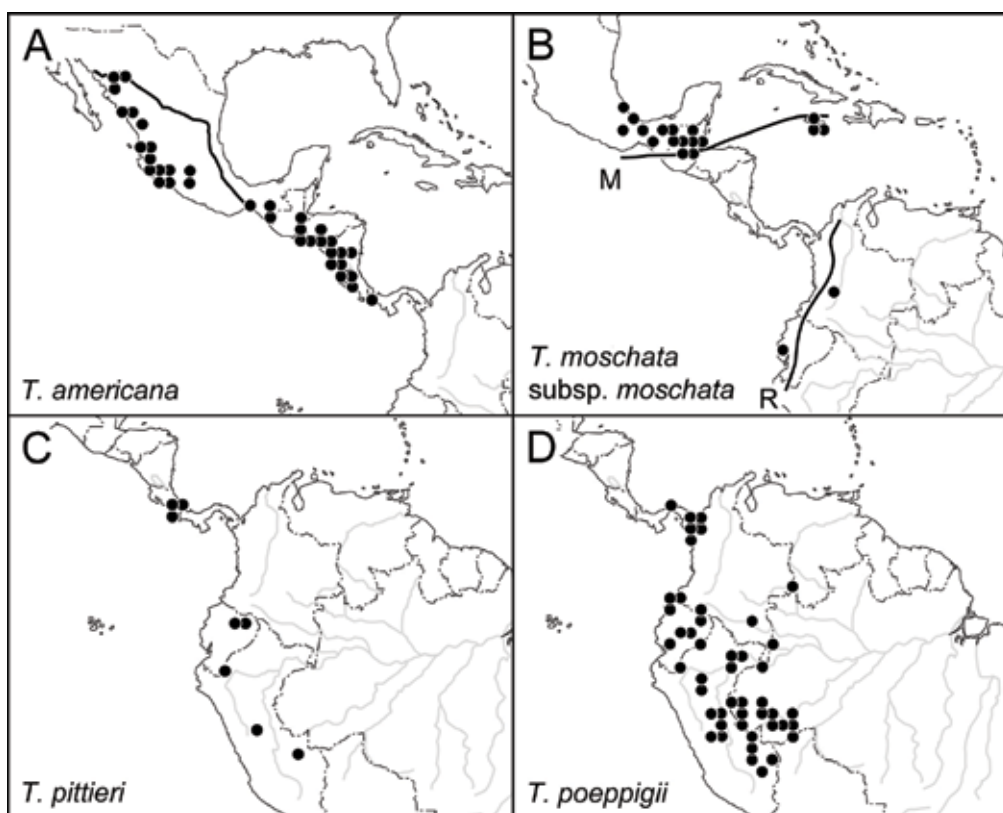
Fig. 31. Distribution of four *Trichilia* species. **A.** *Trichilia americana* (Sessé & Moc.) T.D.Penn. Solid line = boundary between accreted terranes in the west and craton in the east of Mexico. **B.** *Trichilia moschata* Sw. subsp. *moschata*. M = Motagua fault system; R = Romeral fault system. **C.** *Trichilia pittieri* C.DC. **D.** *Trichilia poeppigii* C.DC.

where they show a significant level of allopatry. The remaining seven species in the West Indies are endemic to the Greater Antilles and are all allopatric, apart from the overlap of two species in eastern Cuba: 1. *Trichilia reticulata* P.Wilson. Jamaica; 2. *Trichilia trachyantha* (Griesb.) C.DC. Cuba (widespread); 3. *Trichilia pungens* Urb. Eastern Cuba; 4. *Trichilia stenophylla* Urb. & Ekman. NW tip of Haiti (Mole St. Nicolas); 5. *Trichilia aquifolia* P. Wilson. Northern Haiti (but not the NW tip) and southern Dominican Republic; 6. *Trichilia monacantha* Urb. Northern Dominican Republic; and 7. *Trichilia triacantha* Urb. Puerto Rico.

The seven species all inhabit drier forest and woodland on limestone. *Trichilia reticulata* and *T. trachyantha* have normal, non-spiny leaves, but the five other species all have distinctive, spiny leaves. The spiny-leaved species were regarded as a related group, but the molecular study by Clarkson et al. (2016) sampled two of the species, *Trichilia aquifolia* and *T. triacantha*, and these did not form a clade. (The non-spiny-leaved species were not sampled). The relatives of the seven West Indian endemics
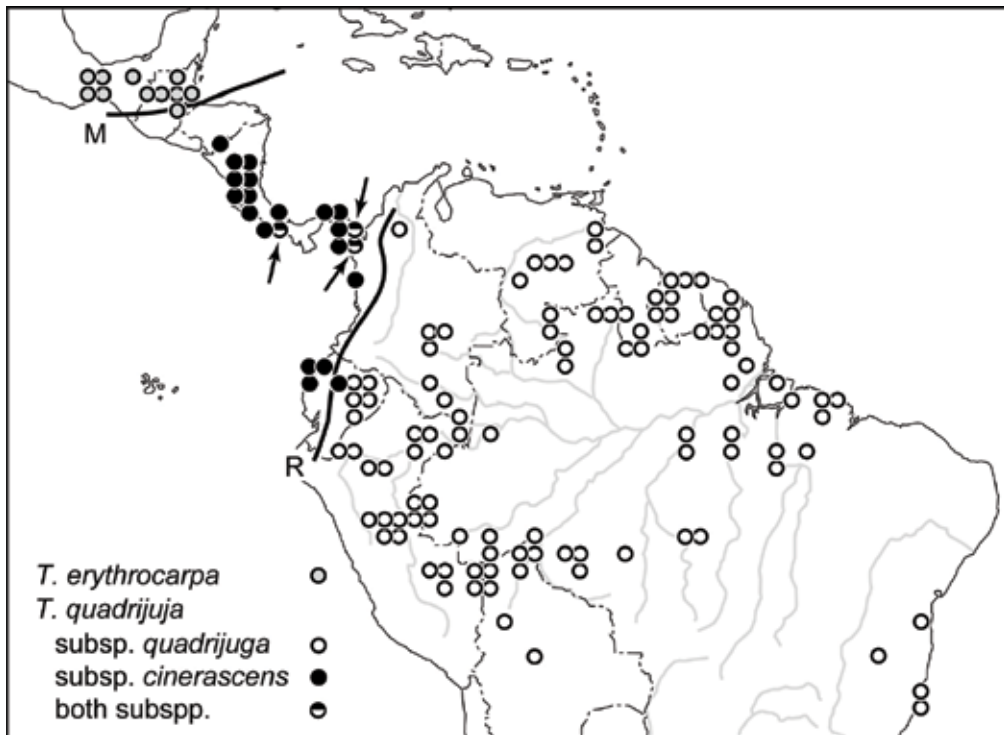
Fig. 32. Distribution of *Trichilia quadrijuga* Kunth and *Trichilia erythrocarpa* Lundell. M = Motagua fault system; R = Romeral fault system.

are unknown. Nevertheless, the striking allopatry among the seven can be explained by vicariance among their respective clades. If the phylogeny is clarified, any overlap among the other members of their respective clades would be explicable by subsequent range expansion.

The south-eastern seaboard of Brazil represents the other main centre of localised endemism in American *Trichilia.* Six of the endemics there form a molecular clade (Clarkson et al., 2016 Fig. 2): *Trichilia congesta* T.D.Penn., *T. tetrapetala* C.DC., *T. magnifoliola* T.D.Penn., *T. florbranca* T.D.Penn.*, T. blanchetii* C.DC., and *T. pseudostipularis* (A.Juss.) C.DC. in part (the species in the broad sense, as mapped here, is polyphyletic) (Fig. 33). Five of the six species are in rain forest (up to 500 m), while *Trichilia blanchetii* is in in the transition zone between wet rain forest and *restinga*, at 50–450 m altitude.

Endemism in SE Brazil can be accounted for by the uplift that took place there as the Atlantic opened. Subsidence along a rift, as in the Atlantic, can cause elastic rebound along its margins, or 'shoulders' (Ribeiro, 2006; Heads, 2012: 172). This same process of 'rift shoulder uplift' also occurred along the Atlantic coast of Africa (see the 'Atlantic Swell' in Fig. 9), and explains the high levels of endemism in the belt SW Cameroon–Gabon–Angola.
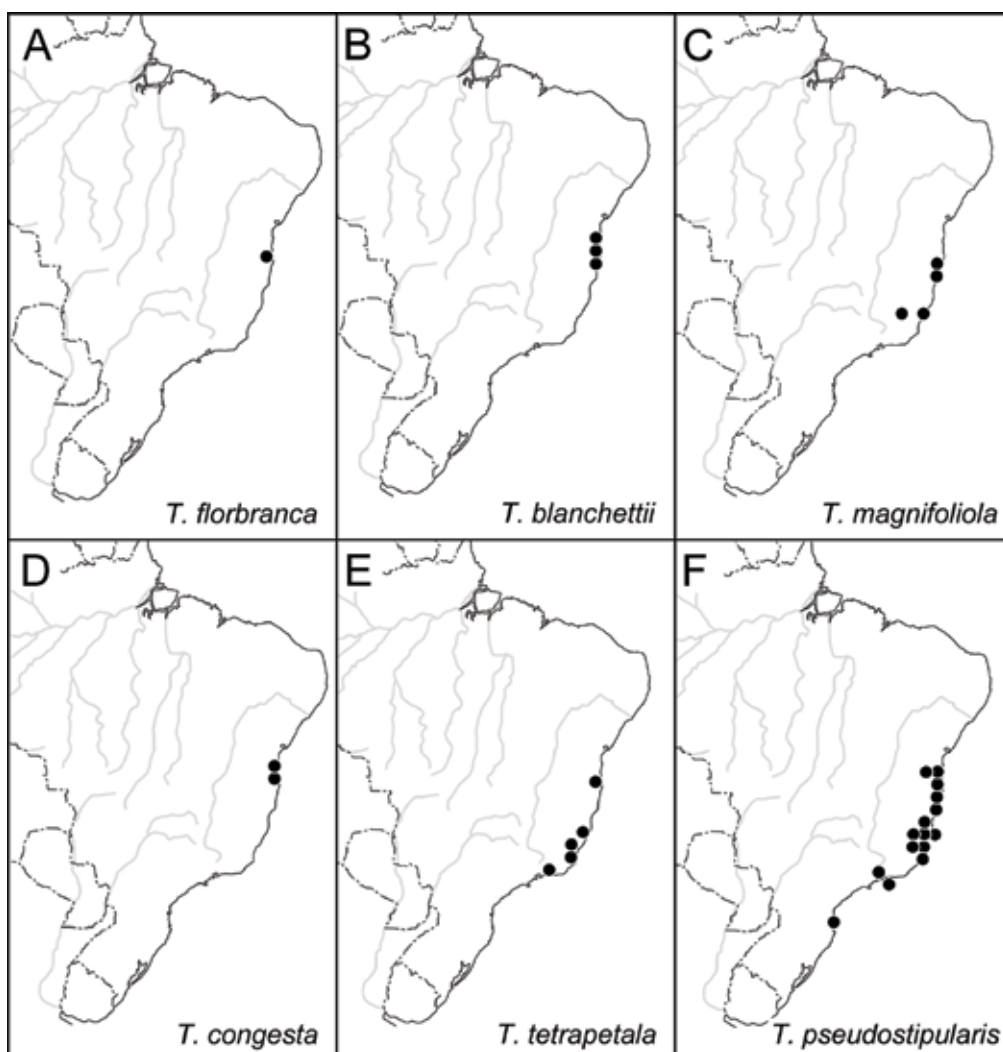
Fig. 33. Distribution of six *Trichilia* species endemic in SE Brazil. **A.** *Trichilia florbranca* T.D.Penn. **B.** *Trichilia blanchetii* C.DC. **C.** *Trichilia magnifoliola* T.D.Penn. **D.** *Trichilia congesta* T.D.Penn. **E.** *Trichilia tetrapetala* C.DC. **F.** *Trichilia pseudostipularis* (A.Juss.) C.DC.

Western Amazonia is well known as a centre of endemism and diversity, and 15 *Trichilia* taxa are endemic there: *T. multifoliola*, *T. trimera* T.D.Penn., *T. hispida* T.D.Penn., *T. stipitata* T.D.Penn., *T. obovata* W.Palacios, *T. pachypoda* (Rusby) C.DC., *T. elsae* Harms, *T. ulei* C.DC., *T. tuberculata* subsp. *lanceolata* (C.DC.) T.D. Penn., *T. laxipaniculata* Cuatrec., *T. reynelii* T.D.Penn., *T. schomburgkii* subsp. *javariensis* T.D. Penn., *T. deminuta* T.D.Penn., *T. minima* T.D.Penn., and *T. vestigialis* T.D.Penn.

In another common pattern, the Amazon river, which follows a Cretaceous rift, forms an important distributional break. It is displayed in members of *Trichilia* such as: *Trichilia euneura* C.DC., *T. tenuifructa* T.D.Penn. and *T. surumuensis* C.DC. along the

Amazon River and north of there; and *T. hispida*, *T. bullata* T.D.Penn., *T. fasciculata* T.D.Penn., *T. solitudinis* Harms*, and *T. elegans* subsp. *richardiana* (A.Juss.) T.D.Penn. along the Amazon River and south of there.

In the last revision, de Wilde (1968) recognised 18 species of *Trichilia* in mainland Africa, and there are also about four species in Madagascar. In a molecular phylogeny (Clarkson et al., 2016), the 'African clade' includes all six of the African species sampled so far, as well as *Pterorhachis* (2 species) and *Pseudobersama* (one species) of Africa, and a single American species, *Trichilia trifolia* L. The last species is known from Mexico to Venezuela, also Cuba, and, massively disjunct, on the coast of SE Brazil (Pennington, 2016).

In *Trichilia* there is a strong concentration of African species in the west (and the immediate allies, *Malleastrum* and *Lepidotrichilia*2, are in Madagascar) (Fig. 34). This is quite different from the arrangement in *Turraea*, in which the African species are concentrated in the east (and the allied plants, *Naregamia* and *Nymania*, are in the south-west) (Fig. 29). *Trichilia* is abundant in rain forest, but is not diverse in most of the Congo Cuvette Centrale. Instead, highest species diversity lies north and west of the Cuvette. Thus maximum diversity in the genus occurs around the *margins* of the Congo basin and also around the margins of the Atlantic basin, in West Africa and Brazil.

In Africa, *Trichilia* has disjunct centres of diversity in West Africa (western Ivory Coast: eight species), and in a central African belt that runs parallel with the Atlantic coast from central Gabon (10 species) to the Congo mouth region (nine species). Many other rain forest groups, such as *Xylopia* (Annonaceae), also show maximum levels of diversity along this Atlantic belt (Fig. 35; data from Johnson & Murray, 2018). *Xylopia* has 45 species in tropical Africa, and maximum species diversity occurs in a zone extending from SW Cameroon to SW Republic of Congo (10–11 species per degree square). The diversity can be accounted for evolution mediated by uplift in the region.

The South Atlantic coast of Africa has three main relief elements: the South African Plateau, the Angola Mountains, and the Congo-Cameroon Atlantic Swell (Fig. 9). The belt, which corresponds with uplift in SE Brazil, reaches its maximum elevation of 1,575 m in south-central Gabon (Guillocheau et al., 2015). Geological data suggest two main uplift periods along the Atlantic Swell as a whole, one in the Late Cretaceous and one in the Oligo-Miocene (Colli et al., 2014). Late Cretaceous uplifts are documented by apatite fission track data in South Africa, Namibia, Gabon, and Equatorial Guinea. Significant vertical displacement is also confirmed by numerous lowstand wedges along the margins.

The Gulf of Guinea islands are located on the oceanic part of the Cameroon Volcanic Line. *Trichilia* is represented on the islands by the widespread *T. rubescens* Oliv. and *T. monadelpha* (Thonn.) J.J.de Wilde on Bioko, and *T. grandifolia* endemic to São Tomé Island (allopatric with the rest of the genus). Another Meliaceae on São Tomé is *Carapa gogo* (Fig. 21B) (perhaps not a distinct species), and it is interesting that both populations occur in trans-Atlantic genera. *Trichilia grandifolia* has beaked fruit, which are known elsewhere in African *Trichilia* only in *T. zewaldae* J.J.de Wilde of Cameroon and Gabon. This feature and the distribution "suggest that *Trichilia*
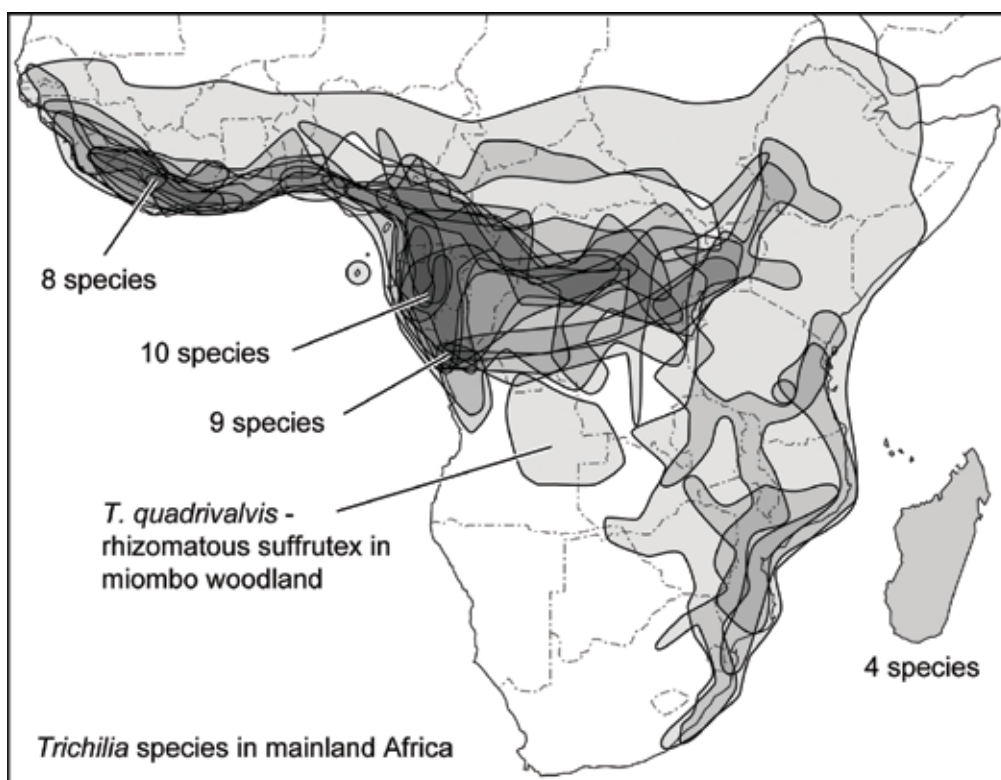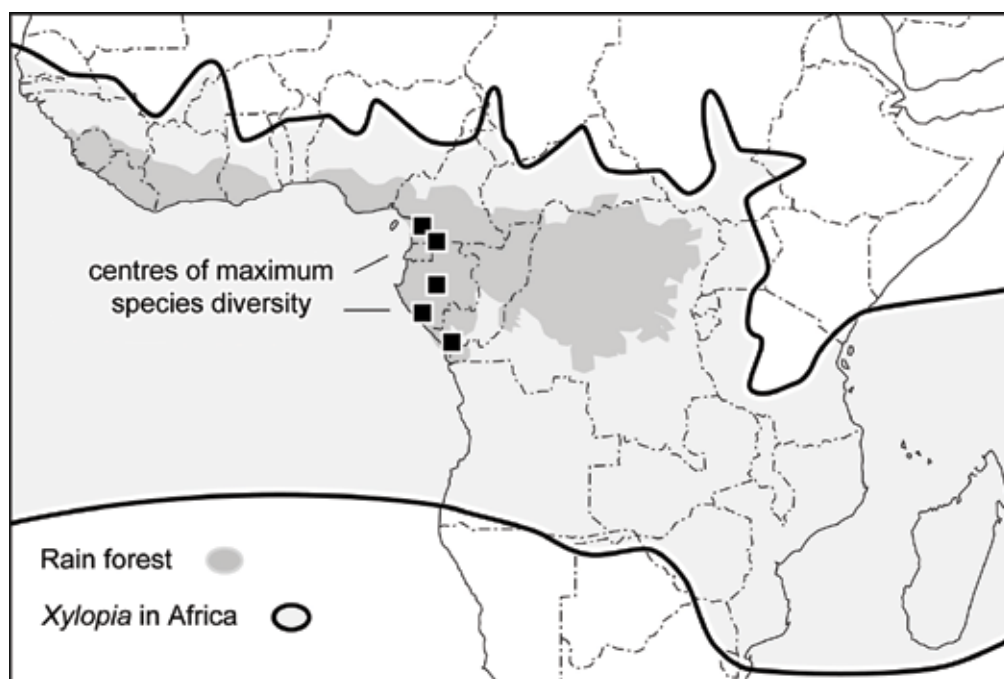
Fig. 34. Distribution of *Trichilia* species in Africa and Madagascar (individual species in Madagascar not shown).

zewaldae and *T. grandifolia* are descendants of a common ancestor" (de Wilde, 1968). This is more likely than one being derived from the other. The portion of the Cameroon Volcanic Line on the mainland is also important for *Trichilia*; a typical central African endemic, *T. gilgiana* Harms (Fig. 36), extends from the Benue Trough/CVL at the SE Nigeria/Cameroon border to eastern DRC.

'*Pterorhachis*' (two species, Cameroon and Gabon) and '*Pseudobersama*' (one species, East African coast) form a sister pair within *Trichilia* (Clarkson et al., 2016) and show a massive disjunction across central Africa (Fig. 37). *Trichilia dregeana* shows a similar disjunction, with a gap of c. 1500 km between both areas (Fig. 38). The disjunction also occurs in *Khaya* (Fig. 13), and it can be attributed to connections skirting central Africa somewhere to the south.

Similar east–west disjunctions occur in many groups. For example, *Sirdavidia* Couvreur & Sauquet (Annonaceae) of Gabon (Ivindo, Crystal Mountains) is sister to *Mwasumbia* Couvreur & D.M. Johnson, of Tanzania, by the Uluguru Mountains (200 km west of Dar es Salaam), 2800 km away (Fig. 38). Couvreur et al. (2015) *described* the gap as *"An incredible disjunction"*. However, they also observed that "East West/ Central disjunctions between rain forest restricted species are a common feature in African plants…".

Fig. 35. Distribution of *Xylopia* L. (Annonaceae) in Africa, with areas of maximum species diversity (data from Johnson & Murray, 2018).
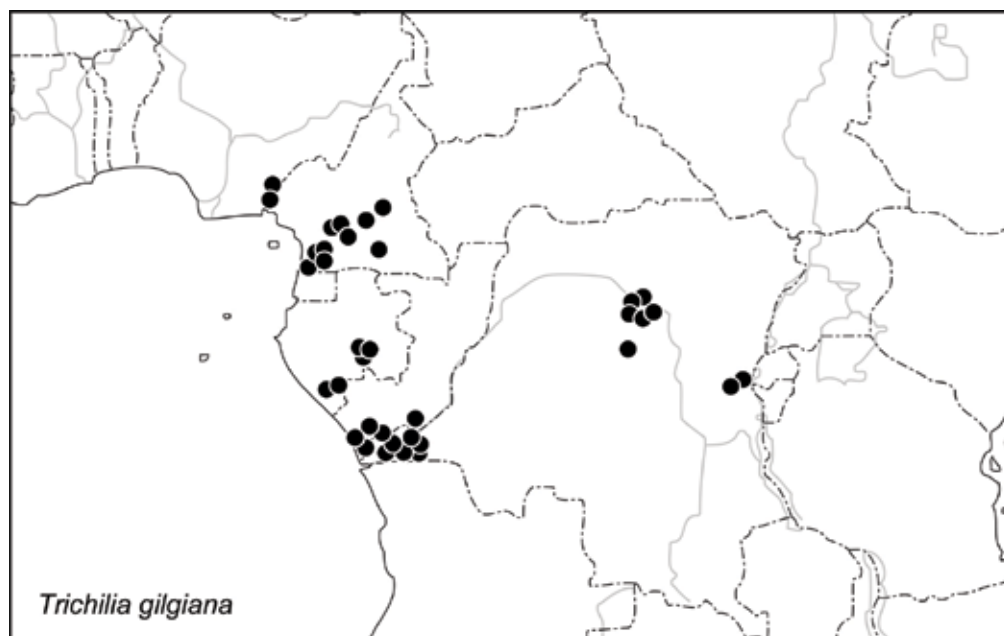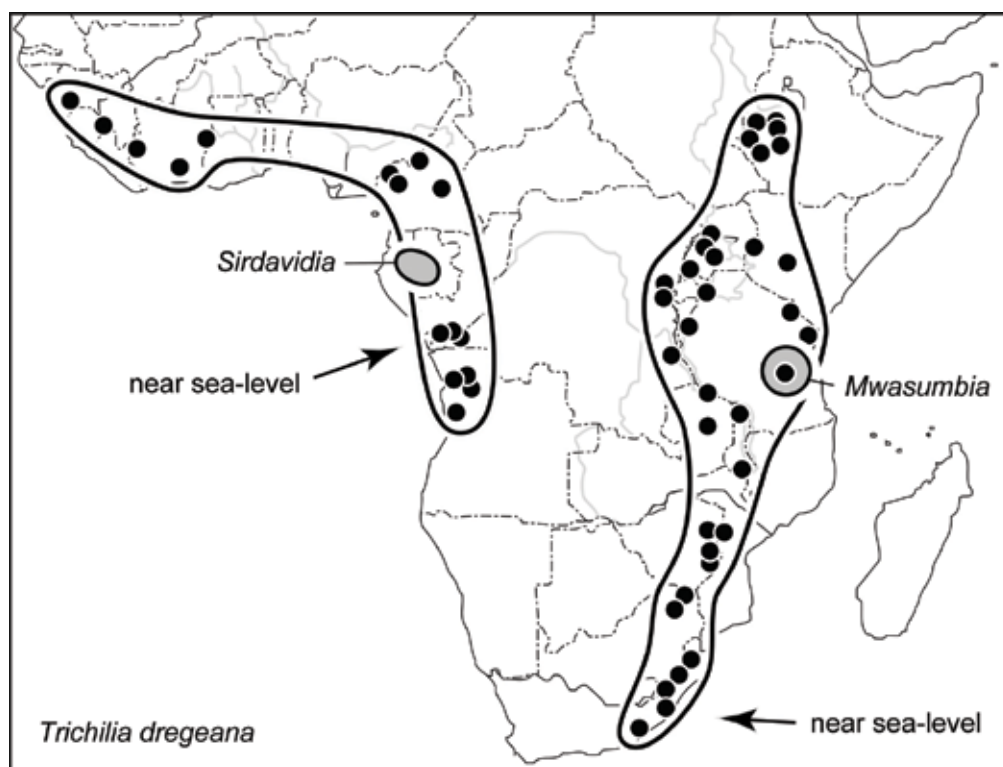

Fig. 36. Distribution of *Trichilia gilgiana* Harms.
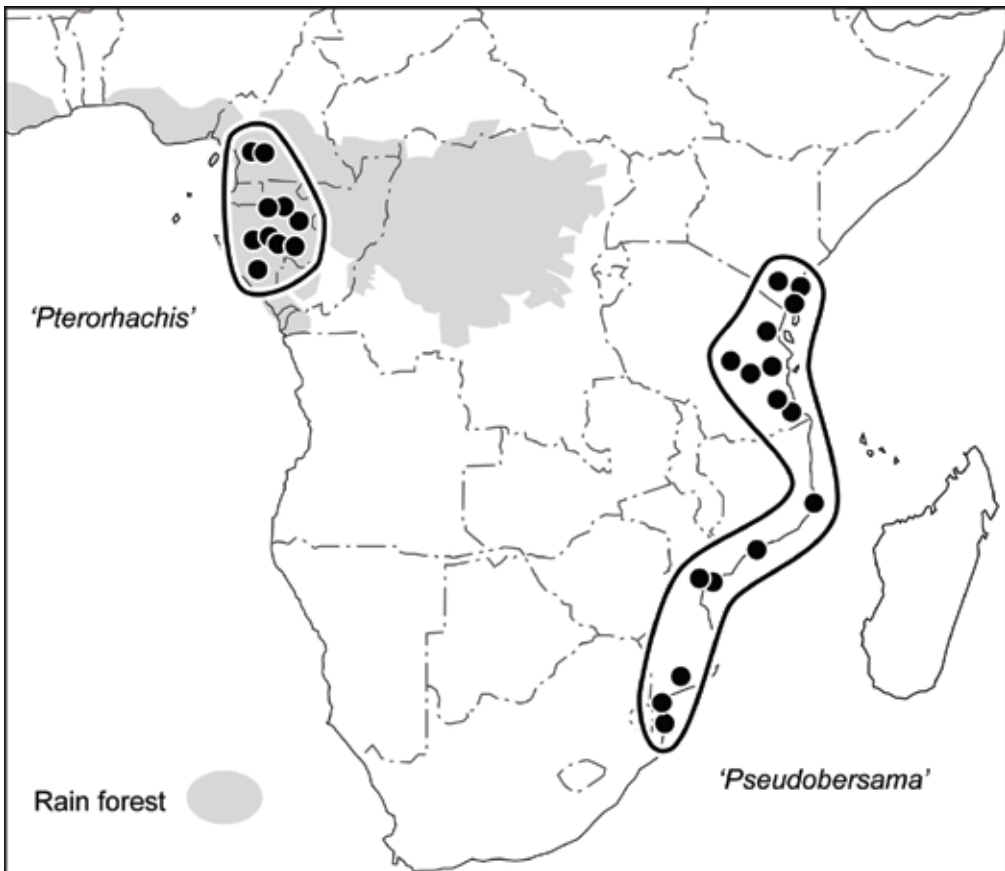
Fig. 37. Distribution of '*Pterorhachis*' Harms and '*Pseudobersama*' Verd., both treated here in *Trichilia*.

The 'eastern arc' mountain ranges of Tanzania are uplifted parts of the old African shield. They lie east of the East African Rift, which is a more recent structure. The ranges are well known for their biodiversity, and this reaches maximum levels in the Usambara and Uluguru Mountains (Fig. 9). These last ranges, as well as being a centre of diversity, also comprise an important centre of endemism, a biogeographic boundary (as in *Lovoa*; Fig. 7), a centre of disjunction (for example, to Madagascar), and a site of altitudinal anomalies in many groups (such as the low altitude giant lobelia, *Lobelia longisepala* Engl.) (WWF, 2019).

The uplift of the current 'eastern arc' mountains began in the Miocene, but the faults, and therefore perhaps also the biogeography, are considerably older than this — the fault blocks of the Usambara and Uluguru Mountains developed along reactivated Mesozoic (Karoo) faults (Griffiths, 1993; Heads, 2012).

Fig. 38. Distribution of *Trichilia dregeana* Harv. & Sond., and of two sister genera in Annonaceae, *Sirdavidia* Couvreur & Sauquet in Gabon, and *Mwasumbia* Couvreur & D.M.Johnson, by the Uluguru Mountains (Couvreur et al., 2015).

The African Plant Database (2019) accepted four species of *Trichilia* in Madagascar: *T. tsaratanensis* Lescot (forest at mid-altitude) and *T. cauliflora* J.-F. Leroy & Lescot (both described in Leroy & Lescot, 1996), *T. mucronata* (Cav.) Harms, and *T. sambiranensis* Callm. & Philipson.

The remaining groups of Meliaceae comprise the diverse *Guarea–Aglaia* clade.

Dysoxylum Blume sensu lato

Dysoxylum, in the sense used by all modern authors, comprises about 80 species. However, a molecular phylogeny (Fig. 3; Koenen et al., 2015) indicates that it is polyphyletic, as suspected by Mabberley (1979: 313). In the molecular study, the eight sequenced species of *Dysoxylum* were dispersed among five clades that also include other accepted genera. These five clades are considered individually in more detail below, but it is difficult to assign most of the unsequenced *Dysoxylum* species

to any one of the five clades. The delimitation of these clades is the most pressing phylogenetic problem in the family. The following notes concern *Dysoxylum* in the broad, polyphyletic sense, but see '35. *Dysoxylum* sensu stricto' below.

Distribution. Dysoxylum in the traditional, wide sense is distributed from India and Sri Lanka (three species) to southern China, through Indochina and Malesia (including Christmas Island) (50 species), south to the Solomon Islands (13), Australia (14), Lord Howe Island (1), Norfolk Island (1), New Caledonia (9), New Zealand (1), and east to Vanuatu (4), Fiji (9), Tonga (2), Samoa (3) and Niue (1) (Mabberley et al., 1995).

   Dysoxylum sensu lato has its highest levels of endemism in New Caledonia (8 species of 9 total, = 89%), Fiji (7 of 9, 78%) and New Guinea (16 of 28, 57%). Further west, endemism is much lower (Borneo has 2 of 22 species, or 9%, endemic, the Malay Peninsula has 2 of 17, or 11%). Thus the genus demonstrates "a distinctly austral richness" by comparison with its allies *Chisocheton* and *Aglaia*; "Unlike those... *Dysoxylum* cannot be said to be essentially Malesian and has to be understood in a Pacific context" (Mabberley et al., 1995).

Ecology. In Malesia, *Dysoxylum* sensu lato is recorded from edges of mangrove swamps, back mangrove, freshwater (including tidal) swamp forest, peat swamp forest, riverine forest, primary forest, semi-deciduous forest, thicket (one species, *Dysoxylum latifolium* of "Rain forest and semi-deciduous thicket, Port Moresby region" (Mabberley et al., 1995), kerangas (heath forest), and secondary forest; substrates include ultramafics, limestone, coral, and sand. Sea level to 3000 m.

   Among the nine *Dysoxylum* species in New Caledonia, *D. rufescens* Sebert & Pancher and *D. minutiflorum* are in *maquis* shrubland, where they are stunted and bushy with polymorphic foliage; *D. minutiflorum* is only on serpentine (Mabberley, 1988). In Fiji, the nine species range from sea level to 1150 m. Two species are recorded on limestone, including *Dysoxylum richii* (A.Gray) C.DC. This last species inhabits the edges of mangrove swamps, forest and thickets, from near sea level to 1000 m (Smith, 1985). On Vanua Mbalavu Island it is restricted to the northern limestone section.

   In Malesia, *Dysoxylum* sensu lato is well documented up to 2580 m (the highest altitudes are occupied by *D. setosum* (Span.) Miq. of Timor, New Guinea and Queensland). However, there is also an unidentifiable (juvenile) *Dysoxylum* specimen from 3000 m in the Wichmann Mountains, SW New Guinea (it is cited in Mabberley et al., 1995, under *D. annae* Mabb., to which it is possibly related).

   Dysoxylum inopinatum of northern and central New Guinea occurs in forest, from just behind mangrove to mossy fagaceous forest at 1500 m; it can be very common at low altitudes. The ecological range is consistent with that of a weedy form of back-mangrove, in which some populations have survived rapid uplift into the montane zone.

Notes. Several aspects of species biogeography in *Dysoxylum* sensu lato are of particular interest, and are not affected by the problems in delimiting the genus. The first involves the famous biogeographic break at Wallace's line.

Wallace's line, between Borneo–Bali and Sulawesi–Flores, represents a classic problem in biogeography as there is no obvious ecological explanation for it; there is no apparent environmental difference either side of the line. Despite this, the biogeographic breaks in clades there are often very precise. A good example is *Dysoxylum mollissimum*, widespread from NE India to the SW Pacific. In this species, variation in the fruit wall is associated with geography "in that, uncannily following Wallace's Line, plants to the west [India to Bali; subsp. *mollissimum*] have smooth fruits, while those to the east [Sulawesi, Flores, Timor to Niue; subsp. *molle* (Miq.) Mabb.] have pustular lenticellate ones" (Mabberley et al., 1995).

Mabberley et al. (1995) pointed out several other examples in which related *Dysoxylum* taxa occur on each side of Wallace's Line: 1. *Dysoxylum cyrtobotryum* of SE Asia to the Andamans, Nicobars, Sumatra, Java, and Bali, and *D. latifolium* Benth. in New Guinea, northern Australia, and Solomon Islands. 2. *Dysoxylum cauliflorum* Hiern in Burma, Thailand, Cambodia, Malay Peninsula, Vietnam, Sumatra, Bangka, Borneo, and the Philippines (Palawan only), and *D. cumingianum* C.DC. in the Philippines (not Palawan), Taiwan (Lan Yu), Sulawesi, Bali, and the Moluccas. 3. *Dysoxylum grande* Hiern from continental Asia to Borneo, and *D. oppositifolium* F.Muell. from the Philippines to Queensland. 4. *Dysoxylum pachyrhache* Merr. in Borneo, and *D. kaniense* Harms in New Guinea. 5. *Dysoxylum magnificum* Mabb. in SE Sumatra and Sarawak, and *D. brassii* Merr. & L.M.Perry in New Guinea. 6. *Dysoxylum crassum* in Borneo, and *D. inopinatum* (Harms) Mabb. in New Guinea (northern and central).

Lan Yu (or Lanyu) Island, also known as Orchid Island or Botel Tobago, lies off the southeastern coast of Taiwan. Despite its small size it is important for its endemism, and it is also a biogeographic-tectonic boundary (Heads, 2014: 375). Three species of *Dysoxylum*, *Aglaia lawii,* and the genus *Aphanamixis* Blume have northern limits there, and two *Aglaia* species have limits on the nearby Hengchun Peninsula (Mabberley et al., 1995; Peng et al., 2008): 1. *Dysoxylum arborescens* (Blume) Miq. Andaman and Nicobar Islands, Taiwan (Lan Yu), throughout Malesia, Solomon Islands, Queensland, and Vanuatu; 2. *Dysoxylum parasiticum* (Osbeck) Kosterm.: Taiwan (Lan Yu), Malesia, northern Queensland and Solomon Islands; 3. *Dysoxylum cumingianum*. Taiwan (Lan Yu), Philippines (but not in Palawan), Sulawesi, Bali, Moluccas; 4. *Aphanamixis polystachya* (Wall.) R.Parker (and the genus *Aphanamixis*). India, Indochina, Taiwan (Lan Yu) and through Malesia to the Solomon Islands; 5. *Aglaia lawii* Ramamoorthy. India to mainland China, Taiwan (Lan Yu), Indochina and Malesia to the Solomon Islands; 6. *Aglaia rimosa* (Blanco) Merr. Southernmost Taiwan (Hengchun Peninsula) and nearby islands including Lan Yu, Philippines, Sulawesi, Moluccas, New Guinea, New Britain and New Ireland; and 7. *Aglaia elaeagnoidea* (A.Juss.) Benth. India, Sri Lanka, Indochina, southernmost Taiwan (Hengchun Peninsula), Philippines and widespread through Malesia to Australia and Tonga. (The three species of *Aglaia* listed here are the only members of the genus in Taiwan).

Dysoxylum excelsum Blume ranges from India and Sri Lanka to the Solomon Islands, but so far it is unrecorded from the Bismarck Archipelago. A similar, anomalous absence there is recorded in a large number of other groups, such as birds

of paradise and *Aglaia elaeagnoidea*, and a tectonic rather than ecological explanation seems most likely. In Fiji, *Dysoxylum tenuiflorum* A.C.Sm. is absent from the main islands (where it is replaced by other species) and is restricted to islands of Kandavu, Taveuni, Lakemba, and Kambara (on limestone).

　　　In New Caledonia, *Dysoxylum minutiflorum* displays a classic case of disjunction along the West Caledonian fault zone (Fig. 39A, from Mabberley, 1988), a major strike-slip feature. This pattern is repeated in many groups (two examples are shown in Fig. 39B and C) and is discussed elsewhere (Heads, 2014).

　　　The eight sequenced species of *Dysoxylum* are dispersed among five clades in the molecular phylogeny presented by Koenen et al. (2015). These five clades also include *Chisocheton*, *Cabralea*, and *Aphanamixis* (incl. *Sphaerosacme*). The five clades form a paraphyletic, basal grade in a clade that also includes *Aglaia* (incl. *Lansium* Corr. Serr. and *Reinwardtiodendron* Koord.). As yet the sampling is not sufficient to indicate the precise composition of the five clades. In the meantime they are treated here as five genera, *Dysoxylum* sensu stricto, *Chisocheton* sensu lato, '*Cyrtochiton*' (= *Dysoxlum* sect. *Cyrtochiton*), *Cabralea* sensu lato and *Aphanamixis* sensu lato

35. *Dysoxylum* Blume sensu stricto

Distribution. Number of species unknown. ?India and Sri Lanka to the Solomon Islands (?Niue).

Ecology. Coastal forest behind mangrove (*Dysoxylum mollissimum*, sometimes viviparous), freshwater swamp forest, riverine forest, primary rain forest, montane forest, secondary forest; limestone; sea level to 1900 m.

Notes. Dysoxylum alliaceum (Blume) Blume is widespread from the Andaman Islands to the Solomon Islands and is the type species of the genus. In the molecular phylogeny (Koenen et al., 2015) it appears in a clade of its own. It is distinct in *Dysoxylum* sensu lato through its overpowering garlic smell, but it is "intimately allied" with *D. excelsum* (NE India, Sri Lanka to Solomon Islands) (Mabberley et al., 1995). Both species are variable, but appear to have more or less distinct 'satellite taxa', namely *Dysoxylum klanderi* F.Muell. of Queensland and *D. hongkongense* (Tutcher) Merr. of China. Finally, *Dysoxylum mollissimum*, of India to Niue, has a slash in which the smell "is similar to that of *D. alliaceum*" (Mabberley et al., 1995), and it might also belong here.

36. *Chisocheton* Blume sensu lato

Distribution. Possibly 56 species (53 species in *Chisocheton* sensu stricto, plus three(?) in *Dysoxylum* (*Didymocheton*)) in NE India and tropical China through Malesia (46 species in *Chisocheton* sensu stricto) to NE Queensland and Vanuatu (*Chisocheton* sensu stricto) and Samoa.
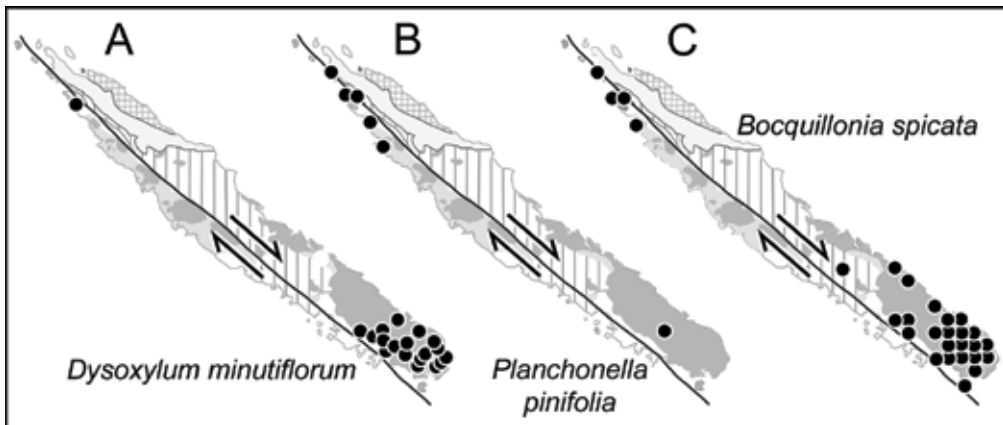
Fig. 39. Distribution of three species showing a dextral disjunction along the West Caledonian fault (solid line). Main terranes also shown (ultramafic terrane as dark grey). **A.** *Dysoxylum minutiflorum* C.DC. (Mabberley, 1988). **B.** *Planchonella pinifolia* (Baill.) Dubard (Sapotaceae) (www.endemia.nc). **C.** *Bocquillonia spicata* Baill. (Euphorbiaceae) (www.endemia.nc).

Ecology. Trees and treelets, often pachycaul. Stilt roots are recorded in *Chisocheton tomentosus* and *C. polyandrus*, both of which grow in lowland and hill dipterocarp forest. In *Chisocheton macrophyllus* the leaves are up to 240 cm long when shed and are the largest in the family (the leaves of *Guarea cartaguenya* Cuatrec. were described as 3 m long in Pennington, 1981, but this is probably a mistake. Apart from this record, the largest leaves that Pennington et al. (1981) and Pennington & Clarkson (2013) documented in the genus are those of *G. grandifolia* DC., which are 140 cm long and were described by Pennington et al. (1981) as "enormous"). Mabberley (1979) listed seven other *Chisocheton* species in which leaves are at least 2 m long. The leaves in *Chisocheton* have a terminal bud and show indeterminate growth, as in many *Guarea* species. In *Chisocheton pohlianus* Harms and *C. tenuis* P.F.Stevens of New Guinea the leaves also bear epiphyllous inflorescences. Corner (1954) discussed the leaves in *Chisocheton* and argued that the indeterminate growth is more archaic than the determinate. One of the ways a modern seed plant leaf can be derived from a shoot is by suppression of both vegetative and reproductive buds.

    Chisocheton sensu lato is recorded in Malesia from primary rain forest, riparian forest, freshwater and peat swamp forest, disturbed and secondary forest, montane forest, forest on limestone and ultramafics; from sea level to 1850 m (*C. montanus* P.F.Stevens in New Guinea). Five species are recorded on limestone, including *Chisocheton ruber*, restricted to limestone, '*Dysoxylum*' *nutans*, on both limestone and ultramafics, and *C. amabilis*, restricted to peat swamp forest and riparian forest.

Notes. In the molecular phylogeny (Koenen et al., 2015), *Chisocheton* sensu lato includes a monophyletic *Chisocheton* sensu stricto, as well as *Dysoxylum gaudichaudianum* Miq. (Java to Samoa). The last species is allied morphologically with *Dysoxylum sessile* Miq. (Moluccas) and *D. nutans* (Java to Moluccas). (*Dysoxylum nutans* is the

type species of *Didymocheton* Blume). These three species are distinct in Malesian *Dysoxylum* through their sepaloid bracteoles (see the key in Mabberley et al., 1995), and together they range from Java to Samoa. The placement of *Dysoxylum nutans*, at least, with *Chisocheton* makes some morphological sense, as it has "the appearance of a species of *Chisocheton* sect. *Clemensia"* (Mabberley et al., 1995).

The western limit of *Chisocheton*, in both narrow and wide senses, follows a line: Darjeeling and Rajabhatkhawa (West Bengal), Khasi Hills and Garo Hills (Meghalaya), and Cox's Bazar (Bangladesh, near the border with Burma) (these are localities for *Chisocheton cumingianus* Harms, as listed by Mabberley, 1979). Thus *Chisocheton* is present in India, but only in the northeast; its western distribution boundary follows the margin of the Indian plate.

In *Chisocheton*, the greatest concentrations of both endemic species and total number of species are in Borneo and New Guinea (Mabberley, 1979). Borneo has eight endemics out of 18 total, while New Guinea has nine endemics out of 13 total. Both islands are geological composites formed from many different terranes with independent histories.

Chisocheton ruber is a local endemic in Borneo, known only from limestone near Kuching (cf. *Chukrasia*, Fig. 5, *Sandoricum caudatum*, and *Walsura grandifolia*). As many as 57 species of dipterocarp have a distributional boundary at the Lupar River by Kuching (Corner, 1978), and the region is also significant in geology (Hall, 2017). The 'Lupar Line' of the geologists is a major strike-slip fault that was active during the latest Cretaceous and early Cenozoic. *Chisocheton ruber*, just south of the Lupar line, is keyed out in Mabberley et al. (1995) with the Borneo representative of *C. cumingianus*, subsp. *kinabaluensis* Mabb., which is found only in the north, in the Mount Kinabalu region.

Palawan in the SW Philippines is distinct biogeographically from the rest of the archipelago (Heads, 2014), and this is evident in two taxa of *Chisocheton* as well as six other Meliaceae: 1. *Chisocheton pentandrus* Merr. subsp. *paucijugus Mabb*. Peninsular Thailand, Malay Peninsula, Sumatra to Borneo and Philippines (Palawan); 2. *Chisocheton pentandrus* subsp. *medius* Mabb. Northern Borneo and Palawan; 3. *Walsura monophylla*. Palawan, restricted to ultramafics; 4. *Dysoxylum cauliflorum*. Burma, Indochina, Malay Peninsula, Vietnam, Sumatra, Bangka, Borneo, and Palawan (distinguished by its cauliflory, but closely allied to D. *cumingianum* of Taiwan (Lan Yu), Philippines (not Palawan), Sulawesi, Bali, and the Moluccas); 5. *Dysoxylum acutangulum*. ?Peninsular Thailand, Malay Peninsula, Sumatra, Java, Lesser Sunda Islands, Borneo, Palawan, Moluccas, New Guinea, Australia, Solomon Islands (not in Sulawesi); 6. *Aphanamixis borneensis* (Miq.) Harms. Borneo, Palawan, Moluccas (not in Sulawesi); 7. *Aglaia macrocarpa* (Miq.) Pannell. Vietnam, Peninsular Malaysia, Sumatra, Java, Borneo, Palawan, Sulawesi, ?Moluccas; and 8. *Aglaia smithii* Koord. Philippines (Palawan and Basilan), Lesser Sunda Islands, Moluccas and New Guinea (Adi I. off the south coast of the Vogelkop).

Dysoxylum gaudichaudianum, treated here in *Chisocheton* sensu lato*, ranges from the Philippines, Java and Christmas Island to Australia, New Guinea, Bismarcks, Solomons, Vanuatu and Samoa. The species is one of the most widely distributed in

the genus, "though its absence from Fiji is not readily explained" (Mabberley et al., 1995). The absence is all the more striking as *Dysoxylum* sensu lato is otherwise so diverse in Fiji, with nine species there, seven endemic (the only sequenced member belongs to *Cabralea* sensu lato).

37. '*Cyrtochiton*'
(≡ *Dysoxylum* sect. *Cyrtochiton* Miq.)

Distribution. Possibly 14 species in India to Australia and Santa Cruz Island.

Ecology. Primary rain forest, riparian forest, peat swamp forest, secondary forest, semi-deciduous thicket; two of the four known species occur on limestone; up to 2900 m (New Guinea).

Notes. In the molecular phylogeny of Koenen et al. (2015), this clade comprises *Dysoxylum binectariferum* Hook.f. (India to Vietnam) and *D. cyrtobotryum* (Nicobars to Bali). The latter is the only sequenced member of *Dysoxylum* sect. *Cyrtochiton* (species 34–46 in Mabberley et al., 1995). In the molecular phylogeny, *Dysoxylum* sect. *Dysoxylum* is evidently polyphyletic, while the only other section in the genus, *Dysoxylum* sect. *Cyrtochiton*, may or may not be monophyletic. '*Cyrtochiton*' may have a total range: India, southern China, Hainan, Vietnam, Thailand, Nicobars, Andamans, through Malesia to NE Australia, ?Bismarck Archipelago, and Solomon Islands (including the Santa Cruz Group).
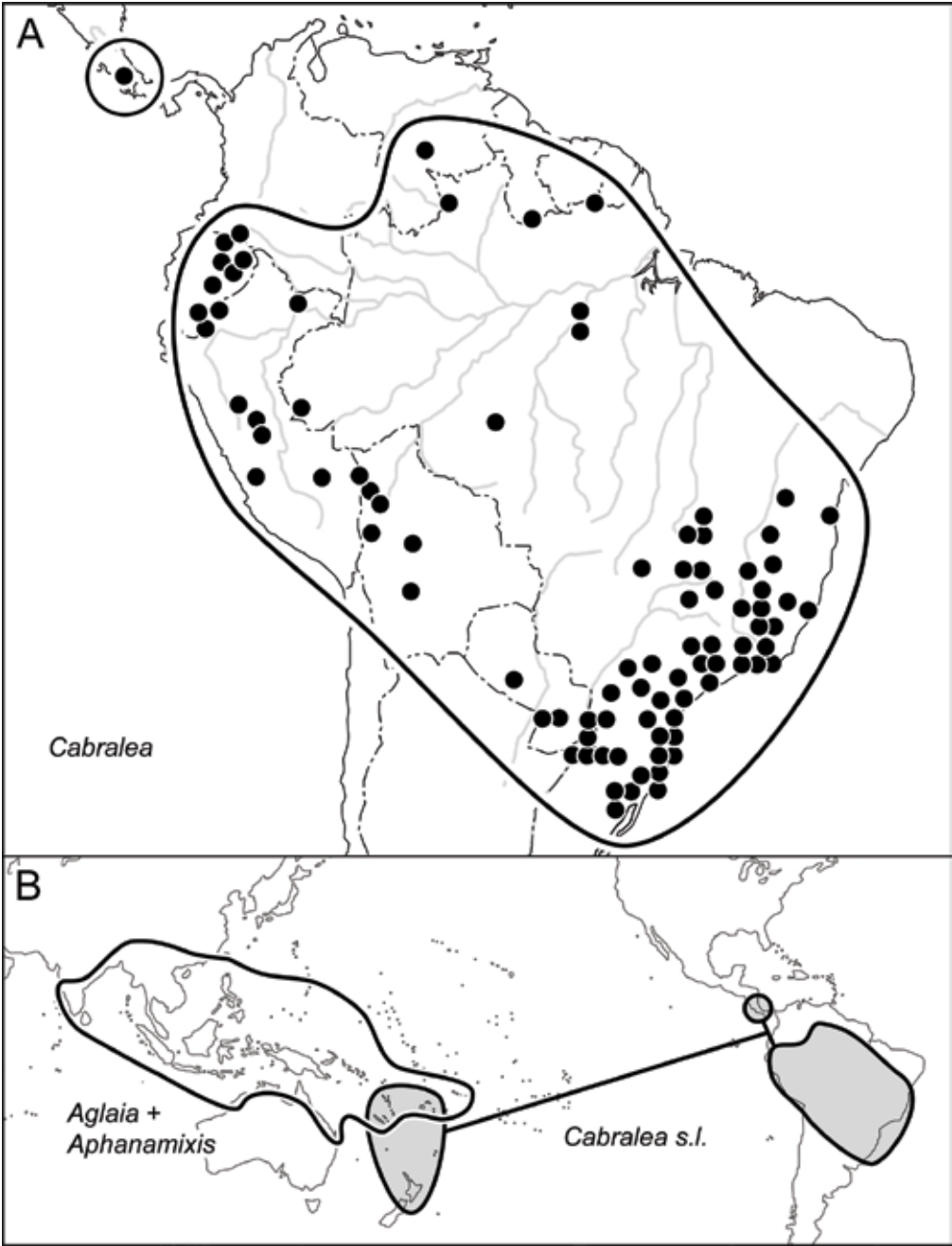
38. *Cabralea* A.Juss. sensu lato

Distribution. Four to nine species in New Zealand, Norfolk Island, New Caledonia, Vanuatu, Fiji; Costa Rica to SE Brazil (Fig. 40A).

Notes. In the molecular phylogeny of Koenen et al. (2015), this group comprises *Cabralea* sensu stricto of America (Pennington et al., 1981), *Dysoxylum rufescens* of New Caledonia, *D. bijugum* (Labill.) Seem. of Norfolk Island, New Caledonia, Vanuatu, and Fiji (Mabberley, 1988), and *D. spectabile* of New Zealand. The clade has good statistical support (PP = 1), but further sampling is needed to determine its precise composition.

     Cabralea sensu stricto has a single, variable species recorded from Ecuador and southern Venezuela to SE Brazil (sparse records in the Amazon) and also, disjunct across Chocó and Panama, in Costa Rica (Cartago, near Turrialba) (Pennington, 1981). The disjunction between Ecuador and Costa Rica repeats the pattern seen in *Cedrela* '*odorata* I' and *Trichilia pittieri* (Fig. 31C). The same disjunction often occurs in groups from the páramo, above the tree line, and so is attributed to the lack of suitable highlands in most of Panama. However, the members of Meliaceae cited here cannot

Fig. 40. A. Distribution of *Cabralea* A.Juss. sensu stricto (Pennington, 1981; www.tropicos. org). **B.** Distribution of *Cabralea* sensu lato and its sister group, *Aglaia* Lour. + *Aphanamixis* Blume.

be explained in this way, and a general explanation for the pattern would be preferable.

Koenen (2011) suggested that "dispersal to South America across the Pacific Ocean has also occurred as is evident from a sister-relationship between the Neotropical monotypic genus *Cabralea* and *Dysoxylum spectabile* native to New Zealand… [The affinity] suggests that New Zealand may have been the ancestral area of this clade". Instead, in the alternative model suggested here, *Cabralea* sensu lato originated by vicariance with its sister group. This is straightforward, as the two show a large degree of allopatry (Fig. 40B): *Cabralea* sensu lato ranges from New Zealand, north and east to New Caledonia, Vanuatu and Fiji, while its sister group, *Aglaia + Aphanamixis*, ranges *south* to the same three localities, which form the only area of overlap between the two clades.

Ecology. Trees and treelets. *Dysoxylum spectabile* (treated here in *Cabralea* sensu lato) is the only member of Meliaceae in New Zealand, where it inhabits "coastal forests… often in pure stands" (Moore & Irwin, 1978: 90). In areas that are free of the introduced Australian possum, regeneration of *Dysoxylum spectabile* takes place even under a closed canopy, in microsites with deep leaf litter (Court & Mitchell, 1988, 1989). As in other shade-tolerant species, the juveniles are slow-growing but can respond rapidly to an increase in available light.

In New Caledonia, *Dysoxylum bijugum* (Labill.) Seem. is recorded in back-mangrove and littoral forests, and up to 400 m. It is also very common in calcareous soil and sand.

In South America, the monotypic *Cabralea* sensu stricto is usually in lowland and coastal non-flooded, evergreen forest and lower montane rain forest. However, in eastern Brazil (Minas Gerais and Goiás) it inhabits areas with drier, strongly seasonal climate and is confined to gallery forest (Pennington et al., 1981).

39. *Aphanamixis* Blume sensu lato
(incl. *Sphaerosacme decandra* (Wall.) T.D.Penn. and *Dysoxylum arborescens*).

Distribution. Possibly five species in India, Sri Lanka, Nepal, tropical China, Indochina, throughout Malesia to the Solomon Islands (Peng et al., 2008).

Ecology. Trees of seasonally flooded forest, swamp forest (in Thailand), riverbanks, primary rain forest, heath forest, secondary forest, forest on limestone; up to 1800 m (Himalayas and Malesia).

Notes. In the molecular phylogeny (Koenen et al., 2015) this clade comprises *Aphanamixis* sensu stricto (3 species), *Sphaerosacme* (monotypic), and *Dysoxylum arborescens*. The distribution overlaps that of its sister, *Aglaia*, in the north, but *Aglaia* is the only member of the pair present in Australia, New Caledonia, Vanuatu, Fiji, Tonga and Samoa.

40. *Aglaia* Lour. sensu lato
(incl. *Lansium* Corr. Serr. + *Reinwardtiodendron* Koord. as a clade)

Distribution. A genus of 127 species (including the 10 species of *Lansium* and *Reinwardtiodendron*), 95 in Malesia. *Aglaia* ranges from India (including the Western Ghats) and Sri Lanka to the central east coast of Australia (Gympie, 120 km north of Brisbane), Tonga and Samoa, including the Mariana Islands (Saipan, Roti and Guam) and Caroline Islands (Palau and Ponape). (It has also been introduced to Niue and the Cook Islands). The distribution encloses that of its sister, *Apahanamixis* (India to the Solomon Islands) (Fig. 40B).

Ecology. Aglaia species are trees and treelets. Habitats include mangrove, back-mangrove, beach forest (including *Barringtonia* formation on sand), rocky seashore, tidal estuaries, *Nypa* palm swamp, freshwater swamp forest (including peat swamp forest), periodically inundated forest, riverine forest, primary terra firme forest, kerangas heath forest, deciduous forest, monsoon forest, thicket, and secondary forest.

The species inhabit various substrates, including limestone or coral (41 species), and ultramafics (two species), and range from sea level to 2570 m (*Aglaia subcuprea* Merr. & L.M.Perry in New Guinea). [*Aglaia sapindina* Harms is recorded from 3800 m in Mabberley et al., 1995, and Pannell, 1992, but this is an error (Pannell, pers. comm. 22 April 2019)].

The following are recorded in, or associated with, mangrove and illustrate the ecophyletic series away from this habitat into dry land forest: 1. *Aglaia cucullata* (Roxb.) Pellegr. From the Ganges delta in Bangladesh to New Guinea. Tree with plank buttresses to 3 m high, sometimes with pneumatophores up to 7 m away from the bole and up to 60 cm high, mangrove, back-mangrove, tidal estuaries, *Nypa* palm swamp, riverine forest, lowland evergreen forest, 0–50 m (in Thailand). *Aglaia cucullata* is the only member of the genus with pneumatophores and the only species that grows in mangrove swamps; 2. *Aglaia luzoniensis* Merr. & Rolfe. Borneo, Philippines, Sulawesi. Primary forest, secondary forest, near mangrove, on sand, sandy alluvium, sandstone, clay, volcanic clayey sand, limestone, 10–1400 m; 3. *Aglaia brownii* Pannell. New Guinea and Northern Territory of Australia. Semi-deciduous forest at edge of beach close to mangroves, on rocks and dunes near the sea, monsoon forest on coastal dunes, fringing coastal woods, *Eucalyptus* forest; 4. *Aglaia rubiginosa.* Sumatra, Peninsular Malaysia. Borneo. Upper reaches of mangrove (Mabberley, 2007: 18), peat swamp forest (often emergent), kerangas, and less frequently in primary lowland and hill forest, secondary forest and along roadsides; on granitic sand; 2–300 m.

Eight species of *Aglaia* sensu lato are recorded from seashore habitats other than mangrove, including beach forest (such as the *Barringtonia* formation), on sand, dunes, and rocks. All eight species are also recorded in secondary or disturbed forest, and four are on limestone or coral.

Eighteen species of *Aglaia* sensu lato are recorded in freshwater swamp forest

of which 16 of these are also in primary (non-swampy) forest, 11 are also in secondary forest, and eight are also on limestone. Four species of *Aglaia* sensu lato are recorded in peat swamp forest. All of these sometimes occur in primary dryland forest, three are also in kerangas, three are also in secondary forest, and two are recorded on limestone.

Nine species in *Aglaia* sensu lato are recorded in forest that is periodically (but not tidally) flooded with freshwater. All nine occur at sea level (two are recorded down to 5 m elevation only), and from there extend to higher elevations, varying from 450–2570 m. Eight of the nine species also occur in secondary forest, and six of the nine are also recorded on limestone or coral. In addition 25 *Aglaia* species are recorded from riverine forest, including three specialist rheophytes. Eight of the species are also recorded in periodically inundated forest.

Fourteen species of *Aglaia* sensu lato are recorded from kerangas (heath forest) or semi-kerangas. Six of these are also in freshwater swamp forest (including peat swamp) and three are also in riverine forest.

Forty-four out of 127 (35%) species of *Aglaia* sensu lato are recorded on limestone or coral, of which 20 of the limestone species are also found in secondary forest, five near mangrove or from other seashore habitat, five from swamp forest or periodically inundated forest, and two (*A. grandis* Korth. and *A. elaeagnoidea*) are also on ultramafics. Three of the species are found above 1500 m; for example, *Aglaia eximia* Miq. ranges from sea level to 2000 m, sometimes on limestone, consistent with uplift of a maritime ancestral population.

Of the 105 species of *Aglaia* sensu stricto accepted in the revision by Pannell (1992), 51 are recorded in secondary forest (Pannell, 1992; Mabberley et al., 1995). [Records from secondary forest are not given in Pannell (2007), so the status of nine of the ten new species there is not clear, but *Aglaia stellatopilosa* is recorded from secondary forest in Pannell (2004)]. None of the ten species of *Lansium* or *Reinwardtiodendron* are cited from secondary forest. Thus at least 52 species of 127 total in *Aglaia* sensu lato, or 41%, are present in secondary forest.

The close ties of *Aglaia* with secondary vegetation, limestone, peat swamp forest and mangrove are explained here as relictual features. In this model, the ecology has been inherited from Mesozoic weeds that were associated with mangrove and coral reefs. These ancestral forms would have expanded their range inland with marine transgressions and survived uplift to different degrees in different areas.

Notes. Pannell (1992) accepted 105 species in *Aglaia* sensu stricto. Pannell (2004, 2007) reinstated six species from Borneo that were earlier treated as straight synonyms (Pannell, 1992) (*Aglaia glabriflora*, *A. meliosmoides* Craib, *A. neotenica* Kosterm., *A. sterculioides* Kosterm., *A. lancifolia*, and *A. beccarii* C.DC.), and also accepted three new species from Borneo: *Aglaia bullata* Pannell, *A. sessilifolia* Pannell and *A. stellatopilosa* Pannell. Other new species described after Pannell's (1992) revision are *A. mackiana* Pannell, *A. soepadmoi* Pannell, and *A. pannelliana* W.N.Takeuchi.

None of the three sections previously recognised in *Aglaia* (Sectt. *Aglaia*, *Amoora* and *Neoaglaia*) were recovered as monophyletic in molecular studies (Grudinski et al., 2014b). In addition, several widespread, variable species (e.g. *Aglaia elaeagnoidea*: India to Samoa; *A. lawii*: India to Solomon Islands; *A. tomentosa* Teijsm. & Binn.:

India to New Guinea) were not recovered as monophyletic. Despite the impressive revision by Pannell (1992), there is still much work needed on the systematics of *Aglaia*, at all levels.

The most diverse region for *Aglaia* is Borneo; there are 60 species there and often as many as 12 at a single forest site (Pannell, 2005). However, *endemism* in Borneo is less impressive. Instead, a maximum proportion of endemic species is found in Fiji, where 80% (8/10) of the species are endemic. Figures for other areas are: New Guinea 39% (13/33), India 30% (3/10), Australia 25% (3/12), Borneo 20% (12/60) and the Philippines 9% (3/35). It is notable that New Caledonia has only one, non-endemic species of *Aglaia*, namely, the widespread, eastern component of *A. elaeagnoidea* (the species itself appears to be polyphyletic).

Muellner et al. (2008a) studied ITS sequences in *Aglaia* (incl. *Lansium* and *Reinwardtiodendron*) and its small sister clade, *Aphanamixis* (incl. *Sphaerosacme*). Fossil-calibrated dates were treated as maximum ages for clades. The authors wrote: "The root node of our data set (i.e. the most recent common ancestor of Melioideae and Swietenioideae [= Cedreloideae]) was constrained to maximally 137 Ma, based on the onset of angiosperm radiation". However, this proposed date for the onset of angiosperm radiation is fossil-based and, logically, a minimum age. There are many reasons to think that the actual onset of angiosperm diversification was much earlier (Heads, 2014). The fossil-calibrated study by Li et al. (2019) found a Triassic age (about 209 Ma) for crown-group angiosperms, and this is probably a more realistic minimum age.

Muellner et al. (2008a) found that "The crown group of the tribe Aglaieae [*Aglaia* + *Aphanamixis*] dates back *at least* to the Late Eocene", and this treatment of the fossil-calibrated date as a *minimum* age is justified. However, in their discussion they treated the date as a *maximum* age: "…the group is *not old enough* for major tectonic events to have influenced current distribution by vicariance. On the contrary, our data *clearly indicate* that long-distance dispersal has played a major role in the distribution and divergence of taxa within the Aglaieae… Divergence of living taxa from their closest living relatives took place *during* both the Miocene and the Pliocene, and peaked *in* the Pliocene. The present-day distribution of many species in the tribe *must* therefore have arisen as a result of dispersal rather than vicariance events" (italics added). Muellner et al. (2008a) concluded that "Our fossil calibrations would have to be at least 40–50 Myr older to make divergence events consistent with continental break-up scenarios…". The 40–50 Myr gap may be a more or less accurate estimate of the gap between the *age of fossilisation* of the clade used for calibration and its *age of origin*.

In another fossil-calibrated study, Grudinski et al (2014a) wrote that the crown group of *Aglaia* "dates back to the Oligocene/Miocene boundary…". But again, this is a minimum age. The authors used S-DIVA and DEC algorithms and located a centre of origin (in Sunda). Following its origin, the group started to disperse eastwards: "The directionality of dispersal events to or across Wallacea was predominantly eastwards… However, several reversal dispersal events occurred as well… there were long-distance dispersal events from the western Pacific islands back to Sundaland or the Philippines, which might have been facilitated by birds".

Grudinski et al. (2014a) wrote that: "Only a few biogeographical studies employing phylogenetic methods are available for [Malesian] plants, most of them revealing a predominant west to east dispersal with diversification after the late Miocene...". However, this revelation is simply an artefact of the algorithms used — these will guarantee a centre of origin at the location of a basal paraphyletic grade, even if this is not a centre of origin (Fig. 1). Grudinski et al. continued: "With at least 46 dispersal events across Wallace's and/or Lydekker's Line, our results *clearly* indicate that in the case of *Aglaia*, Wallacea acted as a transition zone…" (italics added). However, an alternative model explains the facts more simply, including several that are difficult to account for using chance, overseas dispersal. As stressed already, the pair *Aglaia* + *Aphanamixis* and its sister group, *Cabralea* sensu lato, display a high level of allopatry (Fig. 40B). The former pair ranges from India south to New Caledonia, Vanuatu and Fiji, while *Cabralea* sensu lato extends from New Zealand north to the same localities, which form a narrow belt of overlap. This is consistent with the origin of the two clades by vicariance, with local overlap subsequently developing around the break zone. This would account for the strange fact that *Aglaia* is represented in New Caledonia only by a single, widespread species. *Cabralea* sensu lato has at least one endemic there (*Dysoxylum rufescens*). Of the nine *Dysoxylum* species on New Caledonia, the only other species sequenced was *D. bijugum*, also on Norfolk Island, Vanuatu, and Fiji, and also in the *Cabralea* sensu lato clade.

In molecular studies of *Aglaia* (Grudinski et al., 2014b), the three main clades in the genus are: 1. *Aglaia pannelliana* of New Guinea; 2. *Aglaia* 'Clade 10', comprising 5 species of India, Sulawesi, and Moluccas; 3. All other *Aglaia* species. The three main clades form an unresolved tritomy. *Aglaia pannelliana* is easily distinguished by its large fruits and flowers, and has a special phylogenetic significance. It is known only from forest on limestone karst in the Strickland basin, in wet forest at 240 m (Fig. 41; Takeuchi, 2009a). The site is in a hydrocarbon production area, and hydrocarbon reserves often coincide with areas of high biodiversity as in this case. The eastern foothills of the Andes in Peru and Ecuador are another good example. In these areas both the hydrocarbons and the biodiversity can be explained by the peculiar tectonic history and distinctive styles of faulting (e.g. 'flower structures') (Heads, 2012).

The same area inhabited by *Aglaia pannelliana* (the square in Fig. 41) hosts several other local endemics, including *Harpullia mabberleyana* W.N.Takeuchi (Sapindaceae), *Fittingia paniculata* W.N.Takeuchi (Myrsinaceae), *F. headsiana* W.N.Takeuchi, *Hypserpa calcicola* W.N.Takeuchi (Menispermaceae), *Kairoa endressiana* W.N.Takeuchi & S.S.Renner (Monimiaceae) and *Dysoxylum middletonianum* W.N.Takeuchi (Takeuchi, 2007, 2008, 2009a, 2009b, 2010, 2011). The last species, from 1430 m in moss forest, is the smallest *Dysoxylum* in eastern Malesia and is one of only two species with whip infructescences.

The species cited here all lie in the Papuan fold belt (Fig. 41), on the margin of the Australian craton that has been caught up in the New Guinea orogeny. The evolution of the species can be attributed to the dynamic tectonism of the region, rather than the stratigraphy. The species could predate the limestone, and would have colonised the strata as soon as these emerged from the sea, from other strata in the region.
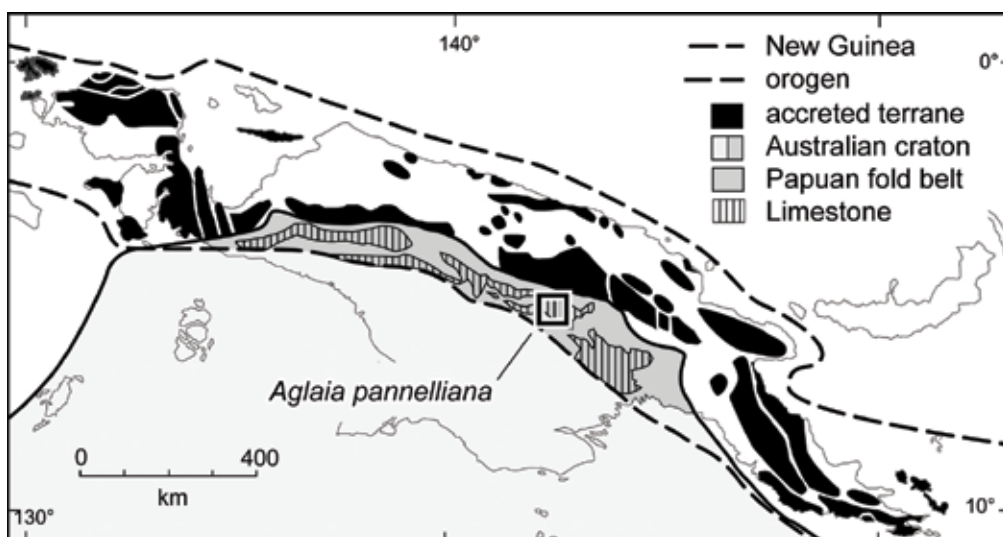
Fig. 41. Tectonic structure of New Guinea (Davies, 2012), with the location of *Aglaia pannelliana* W.N.Takeuchi and other endemics on the limestone of the Papuan fold belt.

In New Guinea, *Aglaia* species have their main diversity on the part of the island formed from accreted, allochthonous terranes, north of the part formed on the Australian craton (Fig. 42; Heads, 2001). In contrast, *Aglaia pannelliana* is located in southern New Guinea, on the deformed margin of the Australian craton. The boundary between the craton and the accreted terranes has been proposed as a major phylogenetic break in New Guinea (Heads, 2001, 2014).

Aglaia elaeagnoidea is distributed widely from India and Sri Lanka to Australia, New Caledonia, Vanuatu, and Samoa. Populations from Sulawesi to New Caledonia have been sampled and form a clade (Grudinski et al., 2014b). However, the species is not recorded in most of mainland New Guinea (apart from records near Port Moresby and Lae), the Bismarck Archipelago, the Solomon Islands and Fiji. This conspicuous gap in the range of the species corresponds with an area of endemism in other groups, including many species on mainland New Guinea, and *Aglaia parksii* A.C.Sm. of the Solomon Islands (including Bougainville) and Fiji.

Similar absences are seen in other groups. For example, *Aglaia samoensis* A.Gray is present on mainland Papua New Guinea, New Britain, New Ireland, Bougainville, Solomon Islands, Santa Cruz Islands, Vanuatu, Wallis Islands, and Samoa — but not Fiji. While the absence from Fiji seems as strange here as it does in *Dysoxylum gaudichaudianum* (cited above under *Chisocheton*), other species of *Aglaia* are endemic there, and so it is probably a case of simple vicariance.

Another disjunction in the SW Pacific is seen in the clade comprising *Aglaia saltatorum* A.C.Sm. and allies (Grudinski et al., 2014b). The group is recorded in the Philippines (*Aglaia macrocarpa* and *A. costata* Merr.), and, 5000 km away, in Santa Cruz Islands (between the main Solomon Islands and Vanuatu), Vanuatu, Fiji, Wallis
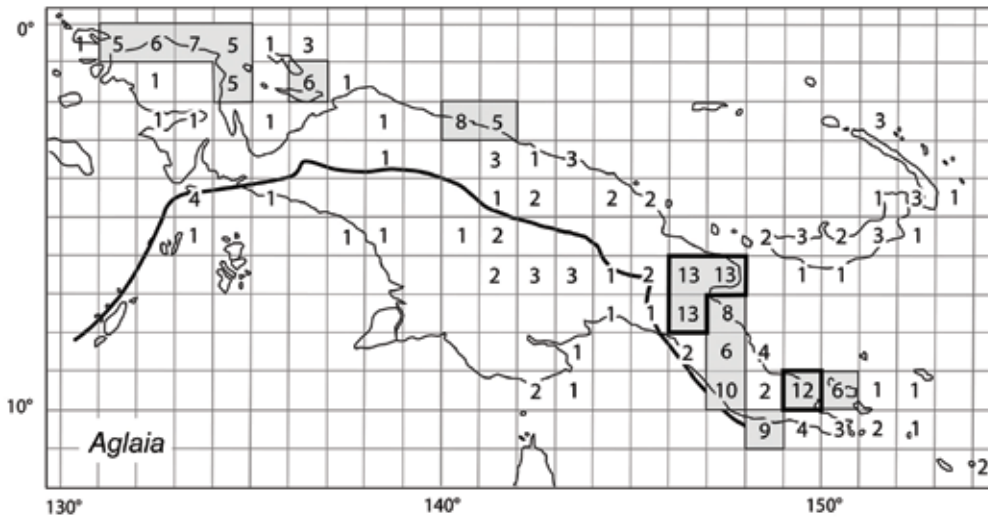
Fig. 42. Species density of *Aglaia* Lour. in New Guinea, with numbers of species in each 1° latitude × 1° longitude square (Heads, 2001). Solid line = margin of Australian craton.

Island, and (possibly introduced) Tonga. The great gap between the Philippines and the Santa Cruz islands is filled by a related clade made up of *Aglaia parviflora* C.DC. and allies in the Moluccas, New Guinea, New Britain, and Solomon Islands. The allopatry is very precise ["*A. parviflora* is not recorded from the Santa Cruz Islands, while this is the only part of the Solomon Islands where *A. saltatorum* occurs" (Mabberley et al., 1995)], and this is consistent with an origin of both groups by vicariance.

The next four genera comprise an Australasian group and its sister trans-Atlantic clade, connecting either across the Indian Ocean or Pacific Ocean basins. The whole complex is pantropical.

41. *Synoum* A.Juss.

Distribution. One species on the eastern seaboard of Australia (Cairns to the New South Wales/Victoria border).

Ecology. Trees inhabiting most kinds of rain forests, especially at margins and near the sea; up to 1300 m.

42. *Anthocarapa* Pierre

Distribution. One or two species in the Philippines (Luzon), Sulawesi, Flores, Sumba, New Guinea, Queensland Solomon Islands, New Caledonia, Vanuatu, and northern Fiji (Rotuma Island; Mabberley, 2013). In NE Australia the species range from Cape York south to Rockingham Bay, and, disjunctly, from SE Queensland to Richmond River, NE New South Wales. *Anthocarapa* and its sister, *Synoum*, overlap in eastern Australia around Cairns and Brisbane. The gap in the distribution of *Anthocarapa* in central Queensland is filled by populations of *Synoum*.

Ecology. Trees of rain forest, monsoon forest and hill forest; up to 1400 m.

43. *Ruagea* H.Karst.

Distribution. Seven species from Guatemala to Peru, mainly in the Andes. Pennington et al. (1981) recognised five species and cited several doubtful ones, and Palacios (1994) described two new species.

Ecology. Trees and treelets. Lowland tropical rain forest (Peru), montane forest, cloud forest; sea level (rarely, in Amazonian Peru) to 3200 m.

44. *Guarea* F.Allam.

Distribution. A genus of 69 species in tropical America, northwestern Mexico to northern Argentina, including the West Indies (Pennington & Clarkson, 2013).

Ecology. Nearly all species of *Guarea* are trees and treelets recorded, at least sometimes, in lowland rain forest below 1000 m altitude (some exceptions are listed below). Eight species are recorded either in mangrove or other flooded forest. Sixteen species are recorded only in non-flooded, lowland forest, and not on riverbanks. A few are also known in drier areas and at higher altitudes (see below).

 Guarea glabra subsp. *excelsa* of western Mexico to Costa Rica is the only member of the genus recorded from mangrove. It also occurs in tropical deciduous forest (in wet places such as riversides and damp ravines) and in poorly drained savanna.

 Eight *Guarea* taxa occur in periodically flooded forest (Pennington & Clarkson, 2013, did not record any species from 'swamp forest', but this term is used more in the Old World).

 Four species occur in periodically flooded forest and on riverbanks. Of these, *Guarea pubescens* subsp. *pubiflora* (A.Juss.) T.D.Penn. has a close relative (*G. pubescens* (Rich.) A.Juss. subsp. *pubescens*) in non-flooded forest, while *G. fissicalyx* Harms is closely related to a species of lower montane forest (*G. persistens*

W.Palacios). Five species occur in both periodically flooded and non-flooded forest. Three species are not in flooded forest but occur by rivers (on riverbanks or in gallery forest).

In areas with a strongly seasonal climate, as on the Pacific coast of Central America, *Guarea* species are confined to shady canyons, riversides and other situations with a plentiful supply of ground water. At least eight taxa inhabit drier areas. First, Pennington & Clarkson (2013) wrote: "In the West Indies a few, such as *G. jamaicensis* and *G. sphenophylla*, are found in seasonally dry forest". The other six taxa are in damp ravines and along water courses in drier deciduous and semi-deciduous forest, *brejo* forest, and *cerrado.*

Three species are recorded on limestone: *Guarea mexicana* of Chiapas, Mexico, *G. jamaicensis* of Jamaica, and *G. sphenophylla* of Hispaniola (the last two are found in seasonally dry forest).

Guarea cristata T.D.Penn. of western Amazonia is mostly recorded in lowland rain forest on infertile white sand. This is an analogue of the kerangas forest of Malesia. (For notes on the biogeography and evolution of Amazonian flora and fauna on white sand, see Heads, 2012: 194).

Only two species are recorded from secondary vegetation: 1. *Guarea silvatica*: "Mostly a component of primary lowland rain forest on non-flooded land. Its ability to sucker from cut trunks enables it to persist in secondary regrowth" (Pennington & Clarkson, 2013); 2. *Guarea chiricana*: primary and old secondary rain forest, lowland to 1500 m.

Six *Guarea* species reach 2000 m altitude. Five of these occur in Central America, and only one is restricted to South America. The upper limit of the genus is represented by *Guarea bijuga* (Mexico to Ecuador), which ranges from sea level to 2700 m. *Guarea luxii* (Mexico to El Salvador), at (900–)1800–2600 m, is very similar to *G. glabra* subsp. *excelsa* of deciduous forest at low elevations.

Notes. The African species that were formerly placed in *Guarea* have been transferred to *Leplaea*, *Neoguarea* (Harms) E.J.M.Koenen & J.J. de Wilde and *Heckeldora* Pierre (Koenen & de Wilde, 2012; Koenen et al., 2015). Most species of *Guarea* occur in Amazonia, but a substantial number are in Central America, the West Indies and coastal Brazil.

With respect to the overall phylogeny, Pennington & Clarkson (2013) proposed three main clades: 1. *Guarea silvatica* C.DC. of the Amazon basin + *G. anomala* T.D. Penn. of SE Brazil; 2. The *G. glabra* Vahl complex (15 species and subspecies), found mainly in Mexico, Central America and Chocó, with two widespread subspecies extending to the Amazon. This is sister to Clade 1; 3. A large group (57 species), found mainly in South America.

Both species in Clade 1 (Fig. 43) inhabit lowland rain forest. Pennington & Clarkson (2013) described the two as "ancestral South American species", but clade 1 and 2 are sister to the main South American clade, not ancestral to it. Clades 1 and 2 themselves are largely allopatric (apart from the widespread *G. glabra* subsp. *glabra* and *G. glabra* subsp. *microcarpa* (C.DC.) T.D.Penn. in Clade 2), consistent with their origin by vicariance.
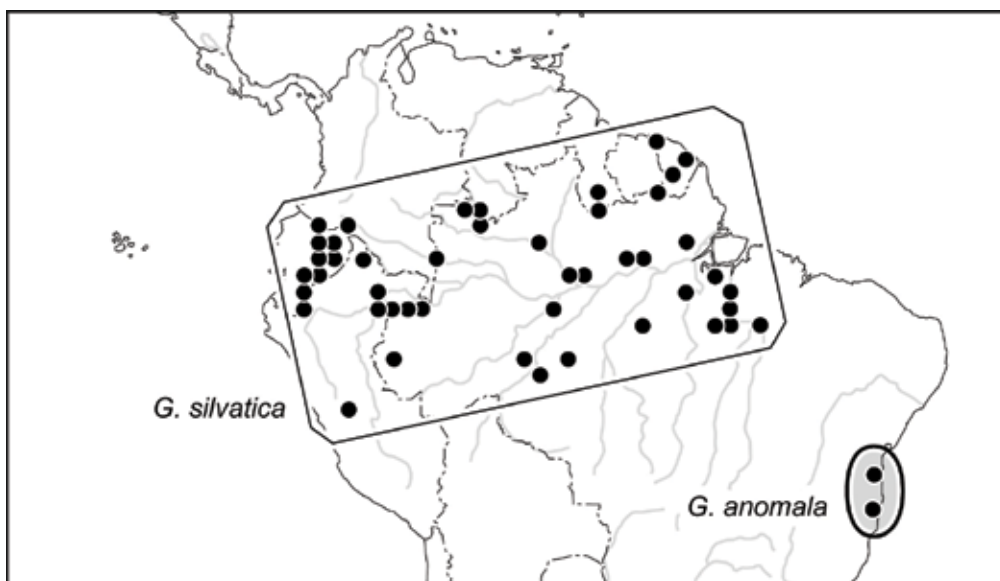
Fig. 43. Distribution of *Guarea* F.Allam. 'clade 1': *Guarea silvatica* C.DC. and its sister *Guarea anomala* T.D.Penn.

The 15 putative members of Clade 2 are mapped in Fig. 44. They comprise six subspecies of *Guarea glabra*, six other sequenced species, and three species that have not been sequenced, but which are linked with the group morphologically (*G. donnell-smithii* C.DC., *G. constricta* Al.Rodr. and *G. subsessilifolia* Al.Rodr.). The two sequenced subspecies of *Guarea glabra* did not form a group in the molecular phylogeny, suggesting that the the species is polyphyletic. The *Guarea glabra* complex as a whole is widespread from Mexico to Brazil, but the taxa show a strong concentration in Mesoamerica (Fig. 44). Only *Guarea glabra* subsp. *glabra* (Fig. 44A), the most widespread taxon in *Guarea*, occurs in Brazil. *Guarea glabra* susbsp. *microcarpa* (Fig. 44M) occurs south to Peru. The remaining 13 members are all located west of the Romeral fault system, the boundary in western Colombia between the accreted terranes in the west and continental terrane in the east (Fig. 17). In Cretaceous time, this boundary was the north-western coast of South America. In the *Guarea glabra* complex, twelve of the 15 taxa, or 80%, occur in Costa Rica/Panama. Of these species, three (*Guarea subsessilifolia*, *G. tonduzii* C.DC., *G. constricta*) are endemic there, and one (*G. chiricana*) is almost endemic. As discussed already (under *Swietenia* and *Trichilia*), the 'landbridge' theory for the biogeography of Costa Rica—Panama might explain diversity there (as the result of overlap), but it does not account for endemism, absence or disjunction.

Pennington & Clarkson (2013: 202) wrote that within the *Guarea glabra* complex "There is little genetic or morphological variation between the component species, and their placement at the end of a long branch suggests an *ancestral dispersal into Central America* and a recent species radiation" (italics added). Nevertheless, the
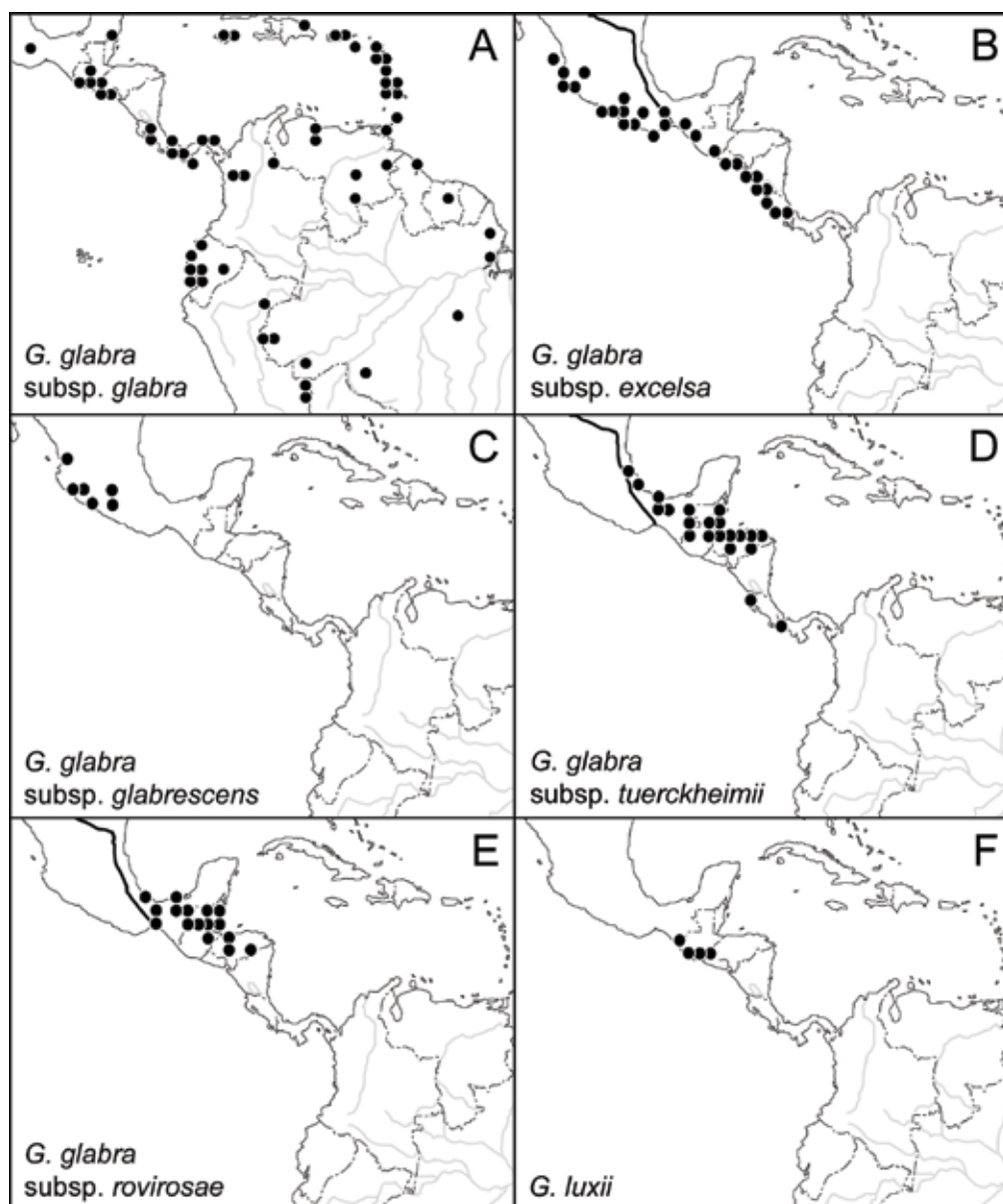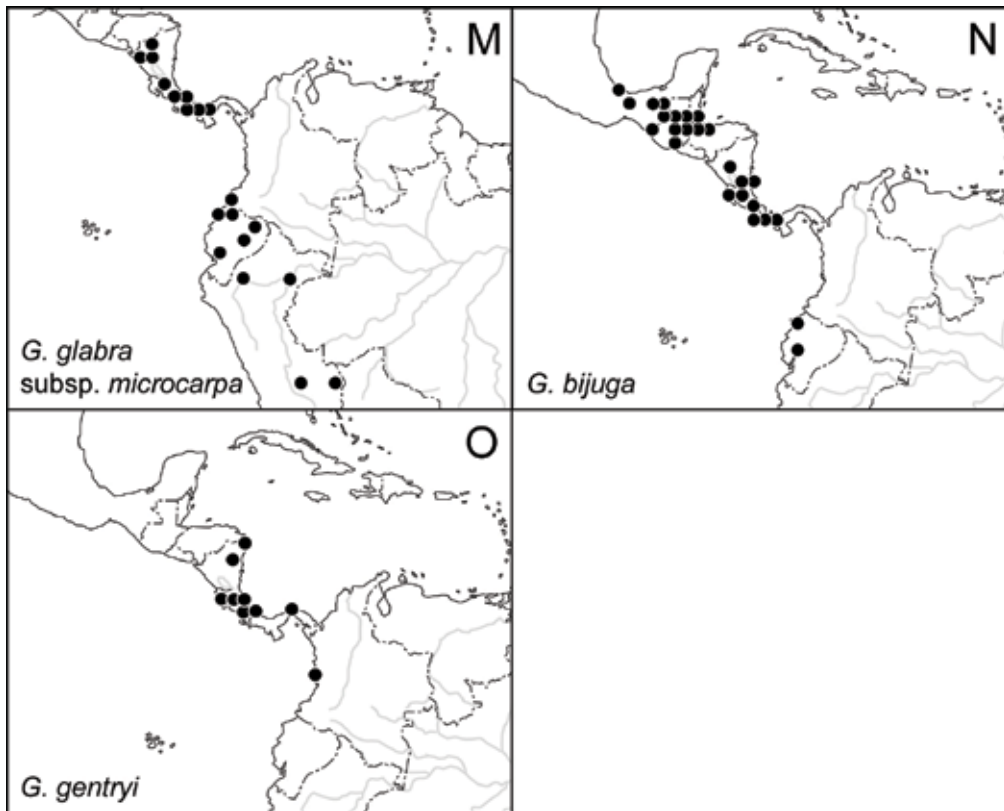
Fig. 44. Distribution of the *Guarea glabra* complex. Solid line in B, D and E = boundary between accreted terranes in the west and craton in the east. **A.** *Guarea glabra* Vahl subsp. *glabra*. **B.** *Guarea glabra* subsp. *excelsa* (Kunth) T.D.Penn. **C.** *Guarea glabra* subsp. *glabrescens* (Hook. & Arn.) T.D.Penn. **D.** *Guarea glabra* subsp. *tuerckheimii* (Donn.Sm.) T.D.Penn. **E.** *Guarea glabra* subsp. *rovirosae* (C.DC.) T.D.Penn. **F.** *Guarea luxii* C.DC.
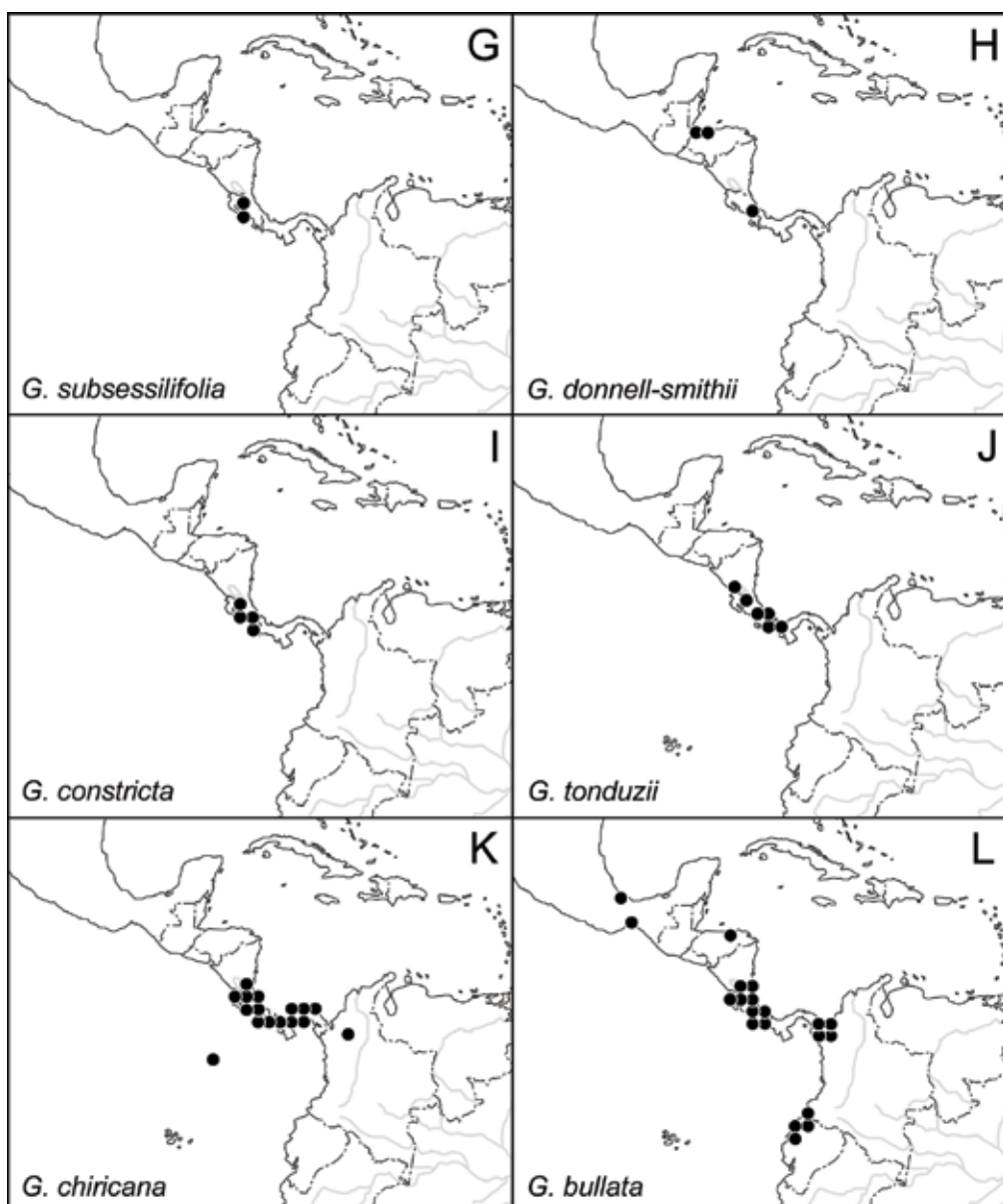
Fig. 44. (Continuation). Distribution of the *Guarea glabra* complex. **G.** *Guarea subsessilifolia* Al.Rodr. **H.** *Guarea donnell-smithii* C.DC. **I.** *Guarea constricta* Al.Rodr. **J.** *Guarea tonduzii* C.DC. **K.** *Guarea chiricana* Standl. **L.** *Guarea bullata* Radlk.

Fig. 44. (Continuation). Distribution of the *Guarea glabra* complex. **M.** *Guarea glabra* subsp. *microcarpa* (C.DC.) T.D.Penn. **N.** *Guarea bijuga* C.DC. **O.** *Guarea gentryi* Coronado.

long branch is equally consistent with vicariance. The high level of allopatry between the *Guarea glabra* complex, mainly in Central America–Chocó, west of the Romeral fault system, and its sister group (*G. anomala* + *G. silvatica*, Fig. 43), east of the fault system, also suggests that both groups originated by vicariance, with some subsequent overlap. Most of the overlap involves a single, widespread form of the *Guarea glabra* complex, *C. glabra* subsp. *glabra*, which has probably undergone secondary range expansion. In Mexico two members of the *Guarea glabra* complex are restricted to the western, accreted terranes (*G. glabra* subsp. *excelsa* (Kunth) T.D.Penn., Fig. 44B; and *G. glabra* subsp. *glabrescens* (Hook. & Arn.) T.D.Penn., Fig. 44C) (cf. *Swietenia humilis*, Fig. 15, and *Trichilia americana*, Fig. 30A), while three others are restricted to the eastern, cratonic side (*G. glabra* subsp. *tuerckheimii* (Donn.Sm.) T.D.Penn., Fig. 44D; *G. glabra* subsp. *rovirosae* (C.DC.) T.D.Penn., Fig. 44E; and *G. bijuga* C.DC., Fig. 44N).

Guarea subsessilifolia (Fig. 44G), *G. constricta* (Fig. 44I) and *G. tonduzii* C.DC. (Fig.44J) are restricted to the Costa Rica–Panama sector. *Guarea tonduzii* forms a clade with *Guarea chiricana* Standl. (Fig. 44K) and *G. bullata* Radlk. (Fig. 44L). The last species is widespread from Mexico to Ecuador, but is disjunct between

northwestern and southwestern Colombia, across much of Chocó. Similar disjunctions occur in *Guarea glabra* subsp. *microcarpa* (Fig. 44M), *G. bijuga* (Fig. 44N) and, possibly, *G. gentryi* Coronado (Fig. 44O).

The *Guarea glabra* complex has a wide ecological range, from mangrove forest (*G. glabra* subsp. *excelsa*; Fig. 44B) high into the montane zone. *Guarea luxii* C.DC. (Fig. 44F) is in high altitude, evergreen cloud forest, at 1800–2600 m., but is very similar to *G. glabra* subsp. *excelsa* of tropical deciduous forest at low elevations. *Guarea bijuga* (Fig. 44N) inhabits wet lowland rain forest, wet montane forest and cloud forest, from sea level to 2700 m. These wide ranges are consistent with rapid, passive uplift of populations during orogeny.
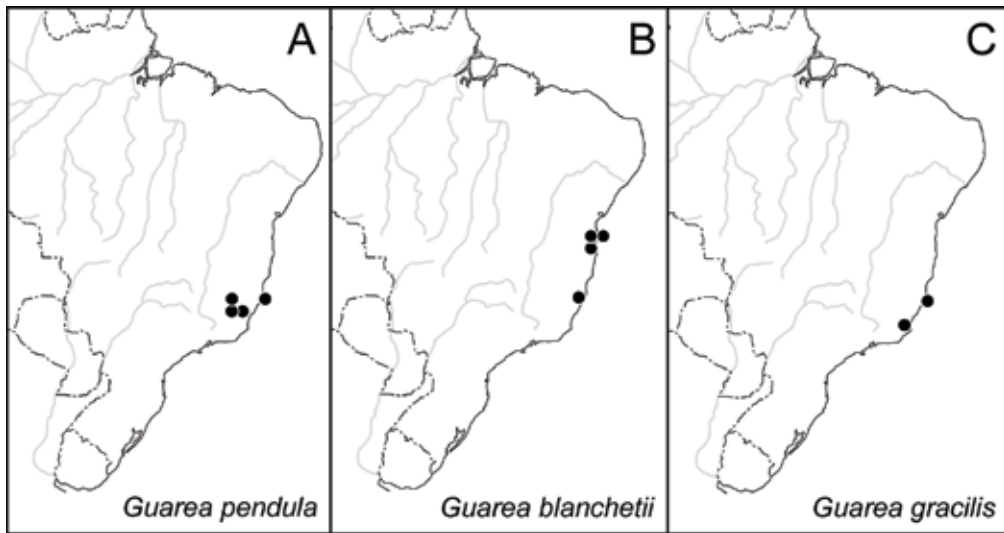
Clade 3, the 'South American' clade of *Guarea*, consists of 57 species and is predominantly Amazonian, but there are important exceptions. The first is a clade of three species endemic to coastal SE Brazil, between Rio de Janeiro and Bahia: *Guarea blanchetii* C.DC., *G. gracilis* T.D.Penn. and *G. pendula* R.S.Ramalho et al. (Fig. 45). The same centre of endemism was illustrated above in *Guarea anomala* (Fig. 43) and *Trichilia* species (Fig. 32).

Another group of non-Amazonian *Guarea* species in the 'South American clade' is a clade of three species confined to Costa Rica: *G. zarceroensis* Coronado, *G. macrocalyx* Al.Rodr. and *G. tafae-malekui* Al.Rodr. (Fig. 46A, B, C) (*Guarea tafae-malekui* has 3–4 ovules in each ovary locule; this is unique in the subfamily Melioideae but occurs in Cedreloideae).

Pennington & Clarkson (2013) wrote that the Costa Rican clade "appears to be recently descended from the South American group (according to the short branch lengths) and its ancestors must have dispersed to Central America and then speciated into the three extant species". However, the sister group (Bayesian analysis) of the Costa Rican clade is *Guarea subandina* W.Palacios of Ecuador and Peru, in wet montane and cloud forest between 2000 and 2400 m altitude (Fig. 44D). This gives a disjunction from Costa Rica to Ecuador, across Panama and Chocó, repeating the pattern seen in *Trichilia pittieri* (Fig. 31C). The repetition suggests the disjunction is not the result of individual events of chance dispersal, but has a common cause. This could, in theory, be ecological, but there is no obvious environmental factor. The other explanation is that it reflects tectonic history, and the accretion of oceanic terranes (including island arcs) west of the Romeral fault system could explain the pattern.

Other members of the 'South American clade' that are present in Costa Rica–Panama include as many as seven species that are endemic there (Fig. 47). *Guarea talamancana* Gómez-Laur. & M.Valerio (Fig. 47A) and *G. grossa* T.D.Penn. (Fig. 47B) are in Costa Rica on the Caribbean slopes; *G. inesiana* Al.Rodr. (Fig. 47C), *G. aguilarii* Al.Rodr. (Fig. 47D) and *G. corticosa* Al.Rodr. (Fig. 47E) are in Costa Rica on Pacific slopes, and *G. hoffmanniana* C.DC. (Fig. 47F) and *G. rhopalocarpa* Radlk. (Fig. 47G) are in Costa Rica and Panama.

Two species in the 'South American clade' are confined to southern Central America and Chocó: *Guarea pyriformis* T.D.Penn. (Fig. 48A) and *G. caulobotrys* Cuatrec. (Fig. 48B). Rather than being simply nested in, say, Colombian groups, as dispersal theory might suggest, both have diverse, widespread sisters.
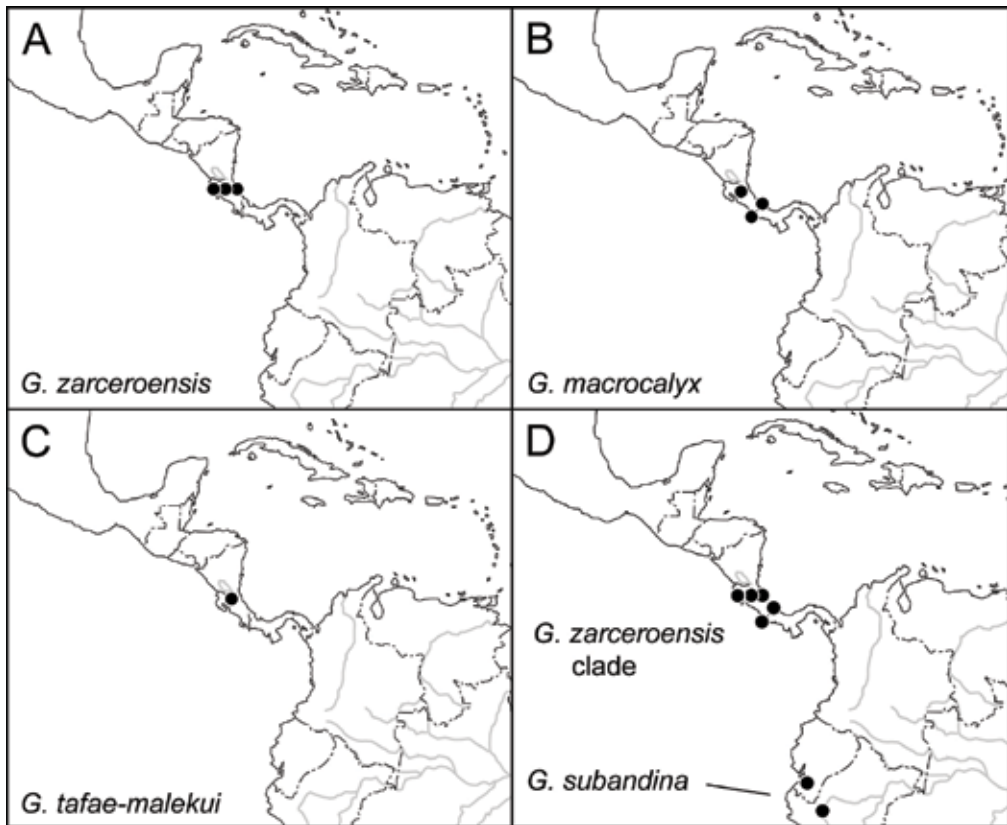
Fig. 45. Distribution of three species of *Guarea* endemic to SE Brazil. **A.** *Guarea pendula* R.S.Ramalho et al. **B.** *Guarea blanchetii* C.DC. **C.** *Guarea gracilis* T.D.Penn.

Guarea caulobotrys is sister to the rest of the entire South American clade except *G. pterorhachis* Harms, and *G. pyriformis* is sister to a widespread clade of five species found from Mexico to SE Brazil.

Four species are endemic to Chocó (Fig. 49): *Guarea corrugata* Cuatrec., *G. reticulatovenosa* T.D.Penn., *G. polymera* Little, and *G. cartaguenya.* In contrast, two taxa are disjunct between Panama and Ecuador, across Chocó (cf. *Trichilia* species; Figs. 31 and 32). One is *Guarea fistulosa* W.Palacios (Fig. 50A), sister to a widespread clade. The other is *Guarea pterorhachis* subsp. *pterorhachis* (Figs. 50B), in which the gap is filled by the only other subspecies in the species, subsp. *submarginalis* T.D.Penn., endemic to Chocó. (*Guarea pterorhachis* as a whole is sister to the rest of the 'South American' clade). The pattern could, perhaps, be explained by chance 'leapfrog dispersal' from Ecuador to Panama (~1000 km), or by chance extinction of subsp. *pterorhachis* in the gap. An alternative, tectonic explanation attributes the pattern to the north-eastward translation of terranes and populations west of the Romeral fault system. Before this process ruptured the populations of subsp. *pterorhachis* they were adjacent to each other, and subsp. *marginalis* lay to the south.

Finally, Pennington & Clarkson (2013) referred to several 'Amazonian' species of *Guarea* that "now extend into" Panama and Costa Rica (e.g. *G. macrophylla* Vahl, *G. guidonia* (L.) Sleumer, and *G. grandifolia*). However, there is no real reason to consider these as essentially 'Amazonian' species, or that their presence in Panama–Costa Rica is secondary.

Six members of *Guarea* are present in the West Indies. The first is *Guarea glabra* subsp. *glabra*. (Fig. 44A), which is widespread on the mainland, and is also widespread in the Greater Antilles (except Cuba) and Lesser Antilles. In contrast with the other five West Indian forms of *Guarea*, which are mainly allopatric, this is widespread

Fig. 46. Distribution of the *Guarea zarceroensis* group (three species) and its sister, *Guarea subandina* W.Palacios. **A.** *Guarea zarceroensis* Coronado. **B.** *Guarea macrocalyx* Al.Rodr. **C.** *Guarea tafae-malekui* Al.Rodr. **D.** The *Guarea zarceroensis* clade as a whole and *Guarea subandina*.

in the West Indies and overlaps widely with all the other forms there. This can be explained by range expansion of subsp. *glabra*. *Guarea glabra* subsp. *glabra* is also the only member of the '*glabra* complex' that overlaps in Amazonia with the 'South American' clade, again suggesting that it has expanded its range. The five other taxa of *Guarea* in the West Indies are all allopatric there (except for overlap on Dominica and Martinique); three are also represented on the mainland. This arrangement is consistent with an origin of the distributions by vicariance, followed by overlap on the mainland. The five species are: 1. *Guarea kunthiana* A.Juss. Widespread on the mainland, also on Dominica and Martinique; 2. *Guarea amaicensis* Proctor. Endemic to Jamaica (this and the last species form the sister to the the rest of the South American clade); 3. *Guarea guidonia*. Widespread on the mainland and also in Cuba, Hispaniola (not southwest), and Puerto Rico; 4. *Guarea sphenophylla* Urb. Endemic to SW Hispaniola; the locality is separated from the rest of Hispaniola and *G. guidonia* by the Enriquillo fault (movement on this fault caused the 2010 Haiti earthquake); 5. *Guarea macrophylla* subsp. *macrophylla*. This has a single record in northern Venezuela (in Yaraquy), and
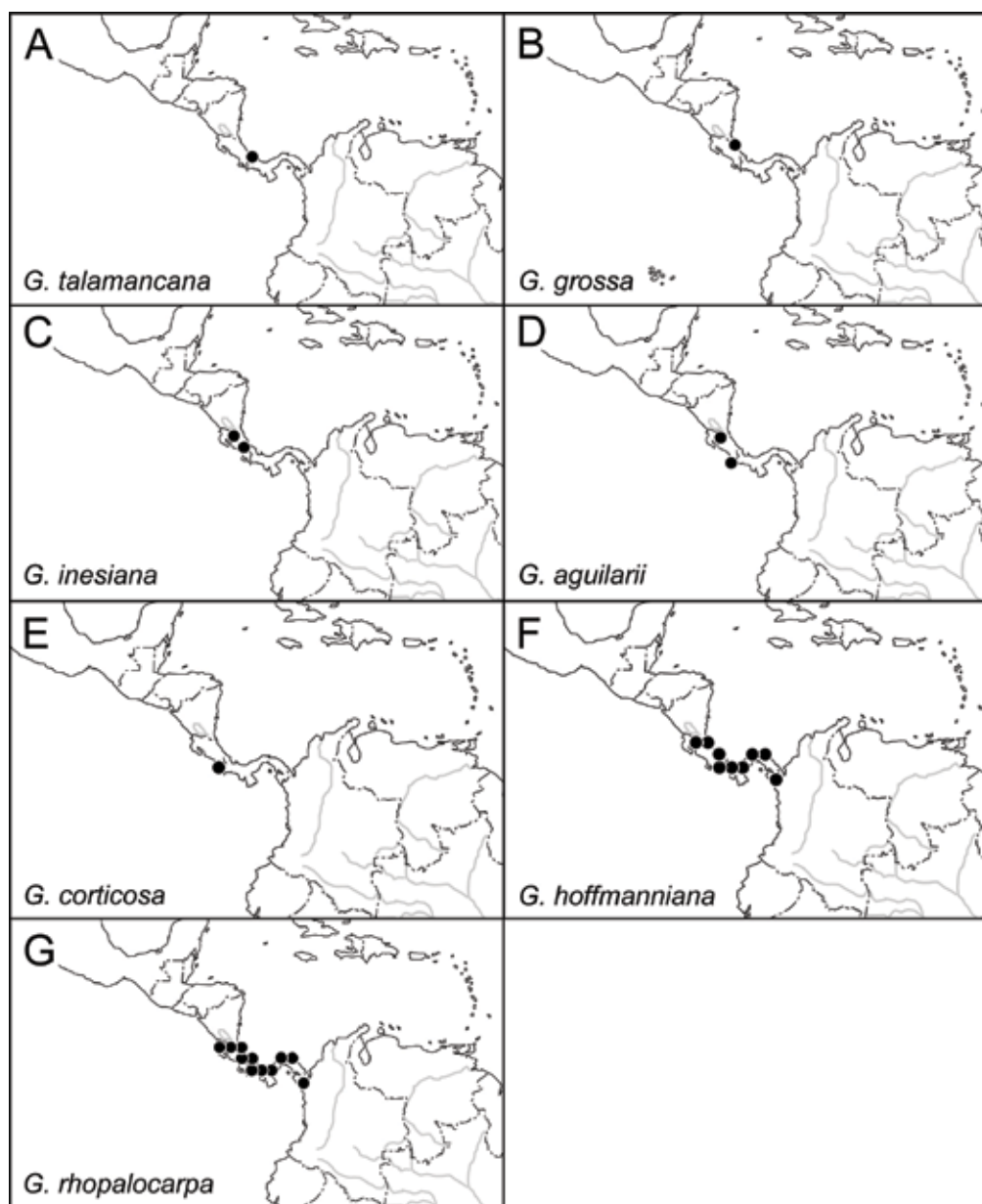
Fig. 47. Distribution of seven *Guarea* species in the 'South American' clade that are endemic to Costa Rica–Panama. **A.** *Guarea talamancana* Gómez-Laur. & M.Valerio. **B**. *Guarea grossa* T.D.Penn. **C.** *Guarea inesiana* Al.Rodr. **D.** *Guarea aguilarii* Al.Rodr. **E.** *Guarea corticosa* Al.Rodr. **F.** *Guarea hoffmanniana* C.DC. **G.** *Guarea rhopalocarpa* Radlk.
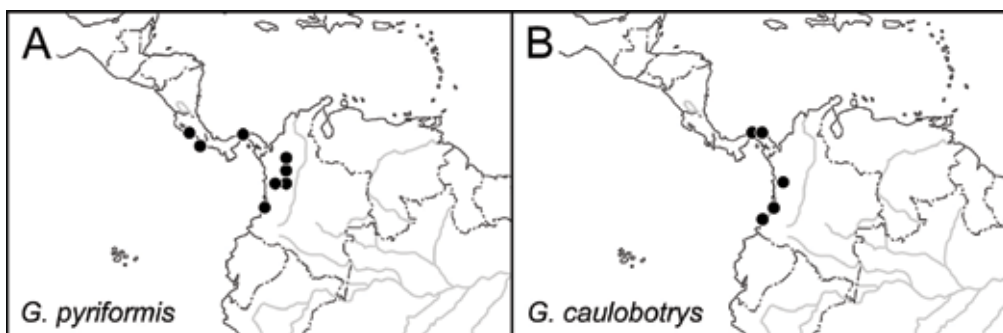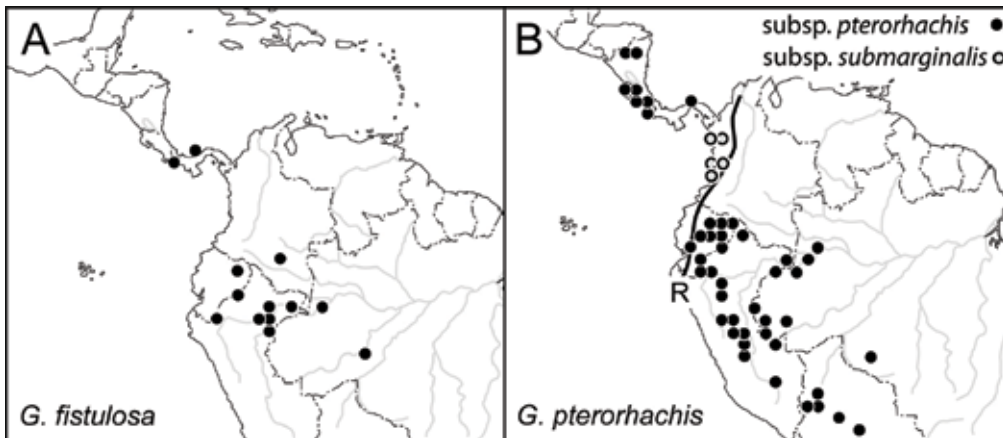
Fig. 48. Distribution of *Guarea* species endemic to southern Central America and Chocó. **A.** *Guarea pyriformis* T.D.Penn. **B.** *Guarea caulobotrys* Cuatrec.
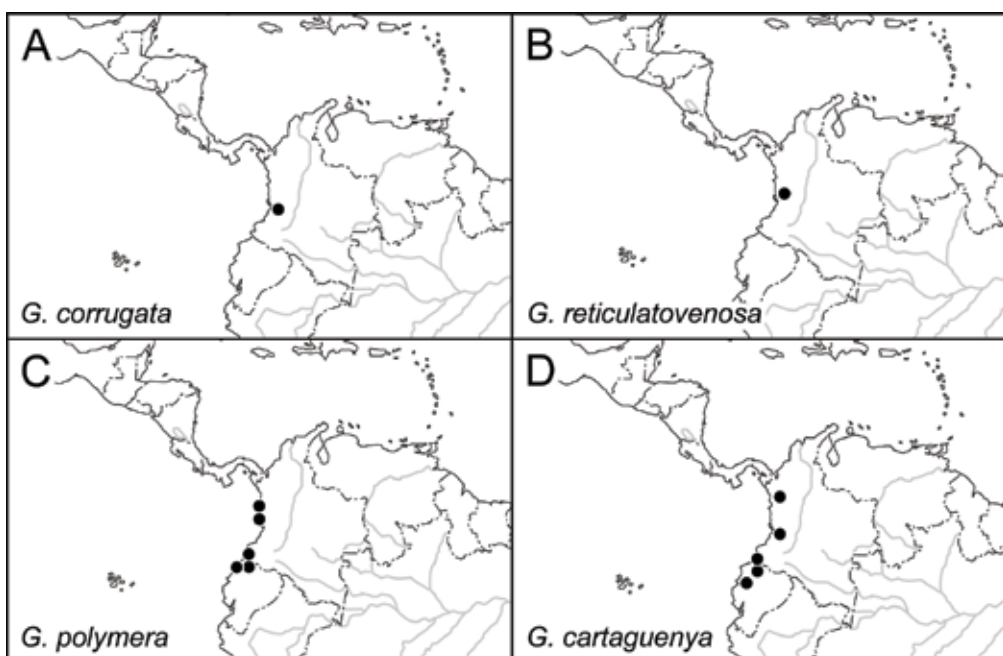
Fig. 49. Distribution of four *Guarea* species endemic to Chocó, **A.** *Guarea corrugata* Cuatrec. **B.** *Guarea reticulatovenosa* T.D.Penn. **C.** *Guarea polymera* Little. **D.** *Guarea cartaguenya* Cuatrec.

Fig. 50. A. Distribution of *Guarea fistulosa* W.Palacios. **B.** Distribution of *Guarea pterorhachis* Harms.

is also widespread in the Lesser Antilles. The disjunction between Yaracuy and the Lesser Antilles can be explained by strike-slip displacement along the southern margin of the Caribbean (Fig. 17). The species overlaps with *Guarea kunthiana* on Dominica and Martinique.

The next four genera form a clade (Koenen et al., 2015), although the exact affinities of *Neoguarea* within the group are not clear.

45. *Neoguarea* (Harms) E.J.M.Koenen & J.J. de Wilde

Distribution. One species (*Neoguarea glomerulata* (Harms) E.J.M.Koenen & J.J. de Wilde*,* formerly placed in *Guarea*) in central Africa (Fig. 51; Koenen & de Wilde, 2012). The genus ranges from the Benue trough region to the Cuvette Centrale of DRC. Koenen & de Wilde (2012) observed that it is present on both Bioko and Mount Cameroon, where the related genus *Leplaea* is notably absent.

Ecology. Treelet or shrub in primary forest and older secondary forest; sea level to 1750 m.

Notes. Different analyses present *Neoguarea* as sister to *Turraeanthus* of West and central Africa (Koenen et al., 2015, fig. 1) or to two American genera, *Guarea* and *Ruagea* (Koenen & de Wilde, 2012, figs. S1 & S2). The latter would not be anomalous, as there is a standard connection between the Gulf of Guinea islands (*Neoguarea* is on Bioko) and America (Heads, 2015).
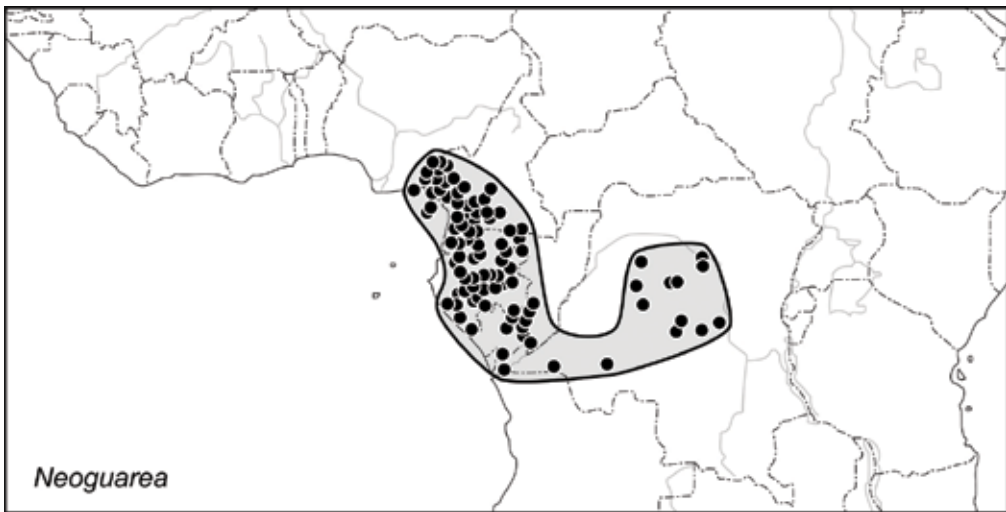
**Fig. 51**. Distribution of *Neoguarea* (Harms) E.J.M.Koenen & J.J. de Wilde.

46. *Turraeanthus* Baill.

Distribution. Three species from West Africa to central Africa (Sierra Leone to Angola and Uganda) (Fig. 52).

Ecology. Trees and treelets in forest. The widespread *Turraeanthus africanus* (C.DC.) Pellegr. is a tree of evergreen rain forest and deciduous forest, in riparian and poorly drained areas (30–1700 m). It is often gregarious, especially in moist places. The more localised *Turraeanthus longipes* Baill. (30–700 m) and *T. mannii* Baill. are both small trees or treelets in forest (African Plant Database, 2019). The last two species are divided at the Cameroon Volcanic Line, with some local overlap in SW Cameroon.

47. *Leplaea* Vermoesen

Distribution. Seven species (Koenen & de Wilde, 2012) (Fig. 53) (six of the seven species were formerly placed in *Guarea*) in West and central Africa: Sierra Leone to Uganda. A sterile collection from Tanzania (Morogoro, Uluguru Mountains) is of doubtful identity; Koenen & de Wilde (2012) treated it under *Leplaea cedrata* (A.Chev.) E.J.M.Koenen & J.J. de Wilde. The record needs to be confirmed, but a boundary here, at the Uluguru Mountains, would be standard (see the note under *Trichilia*). Despite its wide range, *Leplaea* is absent from Bioko and Mount Cameroon, on the Cameroon Volcanic Line. This area of absence corresponds with a region that, for other groups, is a centre of endemism (see *Neoguarea*). *Leplaea cauliflora* E.J.M.Koenen & J.J. de Wilde and *L. mayombensis* (Pellegr.) Staner have western limits at the Cameroon Volcanic Line. The major centre of diversity for the genus is in eastern Gabon.
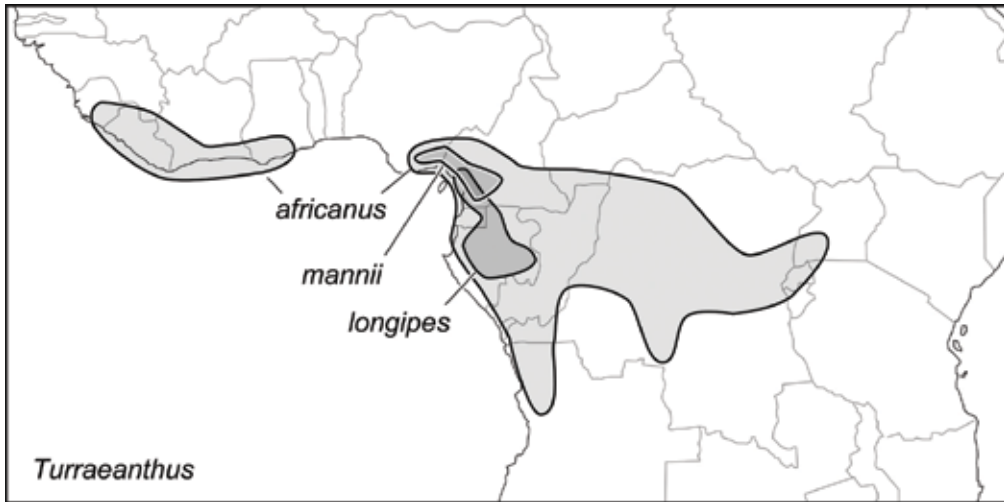
Fig. 52. Distribution of *Turraeanthus* Baill.

Ecology. Trees, treelets and shrubs. Evergreen rain forest and semi-deciduous forest. *Leplaea mangenotiana* (Aké Assi & Lorougnon) E.J.M.Koenen & J.J. de Wilde is known only from riparian forest. Sea level to 2000 m (*Leplaea mayombensis* near the DRC/Uganda border).

48. *Heckeldora* Pierre

Distribution. Seven species in West and central Africa (Fig. 54, based on de Wilde, 2007; Koenen & de Wilde, 2012). Most diverse in SW Cameroon (4 species) and W Gabon (3 species).

    Heckeldora leonensis (Hutch. & Dalziel) E.J.M.Koenen is sister to the rest of the genus (Koenen et al., 2015), implying a primary break in or around Liberia. There is a large gap in the records between SW Ivory Coast and SE Nigeria, and similar large-scale disjunctions across the Gulf of Guinea occur in many groups. Holmgren et al. (2004: 75–76) mapped 21 woody plant species disjunct between upper and lower Guinea ('continental disjunct' groups), and similar examples from the fauna are discussed elsewhere (Heads, 2015). The disjunction is seen within species and also in many affinities above species level, as in *Heckeldora*. The gap is usually explained by Pleistocene extirpation in the gap, but it occurs in both high-altitude and low-altitude forms. It is more likely to be related to the disjunction between the Cameroon Volcanic Line and America, and the disjunction in America between the Caribbean part of Venezuela and SE Brazil. It is probably not coincidence that this last disjunction occurs in the only American member of the African clade of *Trichilia*, *T. trifolia* (Pennington, 2016).
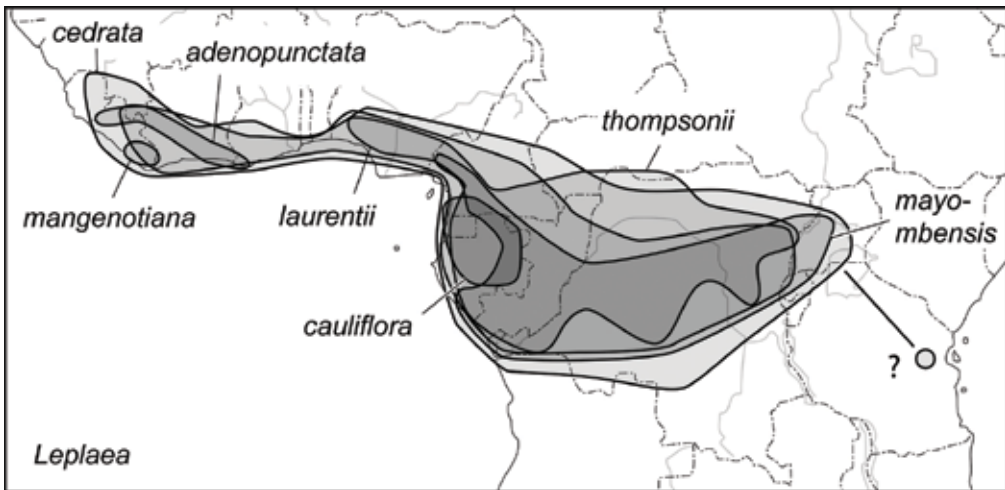
Fig. 53. Distribution of *Leplaea* Vermoesen.
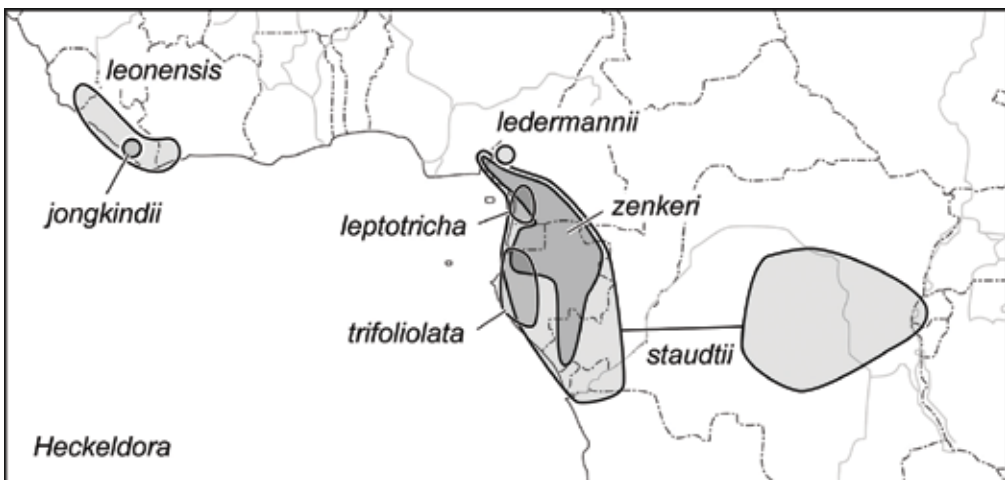
Fig. 54. Distribution of *Heckeldora* Pierre.

Ecology. Small trees in lowland rain forest, semi-deciduous, riparian, secondary and disturbed forest; on fertile volcanic soil, sand and rocky outcrops; sea level to 1500 m (*Heckeldora ledermannii* (Harms) J.J. de Wilde).

Discussion

Biogeography by revelation
In *Entandrophragma,* Monthe et al. (2019) wrote that the phylogenetic relationships "reveal multiple rain/dry forest transitions" (italics added). However, this is an

inference, not an observation, and is based on the questionable assumption that paraphyletic basal grades occupy ecological centres of origin. Likewise, in their study on *Aglaia*, Grudinski et al. (2014a) wrote, as quoted above, "Only a few biogeographical studies employing phylogenetic methods are available for [Malesian] plants, most of them *revealing* a predominant west to east dispersal with diversification after the late Miocene..." (italics added). But, again, the studies reached this conclusion only because there were basal, paraphyletic grades in the west, and the claim that biogeographic analyses simply 'reveal' processes that occurred millions of years ago is misleading.

The idea that progress in biogeography is made by 'revelation', rather than the continual proposing and testing of ideas, is becoming popular. Authors are even starting to use the word 'reveal' in the title of their papers (e.g. Yu et al., 2017; Johnson et al., 2017; Lim & Marshall, 2017; Andersen et al., 2018; Louchart et al., 2018; Kalkman et al., 2018; Appelhans et al., 2018; Price & Wagner, 2018; Labiszak et al., 2019; Jiang et al., 2019). The idea that the results are revelations indicates how uncritically the authors have accepted the infallibility of the programmes they ran — the ichthyologist Lynne Parenti (pers. comm.) has termed this approach 'plug and play' biogeography. The studies use the same or similar programmes, and so it is not surprising that they 'reveal' the same truth; as Church (1919: 9) wrote a century ago: "The ultra-orthodox botanist may have much in common with an orthodox theologist".

The general model proposed here is presented, not as a revelation, but as a working hypothesis to account for many aspects of biogeography and ecology, including those considered to be anomalous. The standard model of recent radiation does not provide reasoned explanations for many of the patterns in Meliaceae, such as the breaks and disjunctions at the Motagua and Romeral fault systems, at the Cameroon Volcanic Line/Benue Trough, across the tropical Pacific, between the cratonic and accreted parts of New Guinea, at the West Caledonian fault, and many others.

Chronology
A survey of molecular clock studies on Malesian plants, including the work on *Aglaia* by Muellner et al. (2008a), stressed that: "All of the studies included used fossils to calibrate molecular evolutionary rates (either directly or secondarily) and thus the inferred ages were minima" (Crayn et al., 2015). However, in practice, fossil-calibrated, minimum clade ages are often treated as maximum ages. This can be done either informally, or in formal Bayesian analyses by imposing suitable priors, stipulating that a clade cannot be much older than its oldest fossil.

By treating the data in this way, molecular clock studies have concluded that the tribes and genera of Meliaceae all originated in (not 'in or before') the Cenozoic, too late to have been affected by the rifting of Gondwana (Koenen et al., 2015). Thus the trans-oceanic affinities must all be explained by chance, trans-oceanic dispersal. Nevertheless, the result depends on interpreting minimum ages as maximum ages, and the accepted clade ages are probably too young. If the fossil-calibrated clade ages are instead treated as minimum ages, as Crayn et al. (2015) argued they should be, the many disjunctions across ocean basins, for example, are consistent with the fossil record, and can be interpreted as the normal results of plate tectonics rather than chance events.

The standard view on evolutionary chronology was expressed in a recent study: "fossils know best" (Aghová et al., 2018). But it is only possible to know whether or not fossil-based methods are 'best' by comparing them with others. One other method utilises the geography of clades.

The importance of geography is a recurring theme in current molecular studies. Many authors are finding clades that are incongruent with earlier ideas on morphological homologies and classification, but instead show distinct geographic structure, often much more so than in the earlier arrangements (review in Heads, 2014: 56). Geographic distribution has turned out to be the 'character of characters' for molecular phylogeny in general.

This close relationship between geography and phylogeny can be exploited in dating evolution. Since the 19th century, phylogenies have been calibrated with fossils, but an alternative method calibrates the trees with tectonic events that coincide spatially with the molecular clades (Heads, 2012, 2014; De Baets et al., 2016; Landis, 2017). This methodology incorporates fossils and uses these to give minimum clade ages.

Earlier work correlating distributions with tectonics suggested that many groups thought to be Pleistocene are actually Mesozoic (Craw et al., 1999). This was controversial, but fossil-calibrated clock studies continue to push species dates further back. Working on *Cedrela*, Cavers et al. (2013) wrote: "the once widely supported Pleistocene refuge theory… , has now been modified by models suggesting much older, Neogene (23–2.5 Ma) origins for diversity at the species level and below… The consequence of this shift in perspective is that palaeogeographical drivers such as Andean uplift, Amazonian marine incursions and the formation of the Isthmus of Panama may have played an equal or stronger role in driving diversification than Pleistocene climate fluctuations…". As mentioned above ('Previous models of Meliaceae biogeography'), recent molecular studies have proposed that plant species (such as *Gunnera herteri*) and animal species (such as petalurid dragonflies and the frog *Leiopelma hochstetteri*) originated in the Cretaceous. These are fossil-calibrated, minimum ages.

Evolution in form: ancestral polymorphism, and evolution by recombination of ancestral characters

Throughout the 20th century, the ancestor of any group was accepted as a Platonic ideal — a pure, undifferentiated species (or even parent pair) with a very localised distribution and a single habitat type. From this beginning, the group evolved by radiating out into new morphological, geographical, and ecological space.

However, this model fails to account for many aspects of genetics and biogeography. It now appears more likely that the ancestor of a group was already widespread and diverse before the group itself originated and differentiated into its modern components. Inheritance of ancestral polymorphism is now accepted by many geneticists and is termed 'incomplete lineage sorting' (Heads, 2014: 27). Its effects mimic those of hybridism, but the polymorphism dates back to before, not after, the appearance of the modern groups. The existence of ancestral polymorphism means that extant groups may have no new characters, only new combinations of characters; the characters existed in the ancestors and are older than the groups themselves.

This new model helps explain the situation in many Meliaceae. For example, in *Guarea*, Pennington & Clarkson (2013) noted "an absence of unique characters which could be used to define species groups". In their treatment, "All species were defined on the basis of unique combinations of often quantitative characters, without distinct character states". For Meliaceae as a whole, Pennington & Styles (1975) wrote: "Many of the structures vary independently and because of this, well-defined sets of characters which can be used to delimit genera clearly, are difficult to find… [Uncertainty in generic and tribal delimitation] has been due to the diffuse and often reticulate nature of the variation… Parallel evolutionary trends are numerous… Some genera and most tribes can only be diagnosed by using a combination of several 'differential' characters… There are no absolutely diagnostic characters that can be used to distinguish *Chisocheton* from *Guarea…*".

It is suggested here that the ancestors of the main Meliaceae clades were widespread entities that were highly variable in morphology, based in and around mangrove, and able to survive at least a degree of uplift onto dry land. A modern analogue might be *Xylocarpus moluccensis* sensu lato: a variable form ranging from East Africa to Tonga in mangrove, and also (*X. rumphii*-type populations) immediately above the mangrove.

'Basal' vs ancestral character states, and the ancestral ecology of Meliaceae in back-mangrove

It was once thought that 'common is primitive', and so the ancestral Meliaceae would be located in Malesian rain forest. Later, it became accepted that the characters in a 'basal group' were primitive, and so members of subfamily Cedreloideae would be regarded as primitive. However, a basal group is simply a small sister group, and there is no reason why it should be more primitive than its sister. More recently, it has been assumed that the location, morphology or ecology of a paraphyletic basal grade is ancestral. But a phylogeny: a (b (c (d))) does not imply that clade d evolved from a + b + c; it is just as likely that a, b, c and d all evolved from common ancestor (Fig. 1). For example, it would usually be assumed that the only true mangrove in Meliaceae, *Xylocarpus*, must be derived from a dry land ancestor, such as its sister genus *Carapa*. Instead, it is suggested here that both are derived from a third habitat, the back-mangrove. In this habitat, trees typical of mangrove, freshwater swamp forest, terra firme rain forest, and secondary forest can often be found growing together in different micro-habitats.

An origin of Meliaceae by the shore explains many aspects of the biogeography, such as the great overlap of clades. It is also consistent with the ecology of its sister group, Simaroubaceae, which includes the following Malesian species (Nooteboom, 1960): 1. *Eurycoma longifolia* Jack. Beach forest on sandy soil, primary and secondary forest, heath forest, and kerangas – a characteristic silicicolous species frequent at low altitudes; 2. *Quassia indica* (Gaertn.) Noot. Wet places in lowland forest below 150 m, sometimes in localities that are periodically inundated by fresh or by salt water, for example, on the edge of the mangrove; it is common in north-eastern Borneo in young swamp forest behind the mangrove.

The significance of secondary, weedy ecology

The old idea of 'undisturbed tropical forest' is oversimplistic (Willis et al., 2004), and the 'weediness' of many rain forest groups has been underestimated. For example, Mabberley (1992: 241) wrote that "Where large gaps are formed in Ugandan rain forests, such light-demanders as the mahoganies (Meliaceae) become conspicuous, so that it has been suggested that the mahogany-rich forests of West Africa are truly secondary".

In America, work on *Swietenia macrophylla* (Fig. 15B) showed that "under natural conditions this species regenerates in essentially even-aged stands after catastrophic disturbances destroy many or most trees, and, in the case of fires and flooding, saplings and seedlings as well. Adult mahoganies tend to survive these events, and regenerate by shedding seed onto the resulting gaps or clearings" (Snook, 1996).

A study on *Swietenia humilis* (Fig. 15A) concluded: "Distances of pollen flow more than 10 times greater than previously reported were detected. Our results show that some tropical angiosperm tree species may be much more adaptable and resilient to habitat destruction and fragmentation than previously considered. … Despite the high level of fragmentation and small size of the subpopulations there was an extensive network of gene exchange over the spatial scale of the study site" (White et al., 2002).

The 'weediness' of many Meliaceae does not imply that their distribution is the result of chance dispersal. Many groups with a weedy, pioneer ecology are local endemics (Heads, 2006). However, this ecology means that they are able to survive, more or less in situ, even under relatively high levels of disturbance.

Does ecology determine distribution, or does distribution determine ecology?

Species survive (or not) in the area they inherit, not in their optimum environment. Niche models are especially valuable, as they show that species distributions do not simply track suitable environment (Heads, 2015). Climate and other environmental factors may affect the physiognomy of the vegetation, but they do not determine the clades that are present, except on a very small scale. For example, very few species (and no Meliaceae) are shared among the lowland tropical rain forests of America, Africa and Asia. Ecological 'anomalies', such as the populations of *Trichilia dregeana* near sea level at the mouth of the Congo (Fig. 38), *Cedrela* in subpáramo, or the highest populations of *Munronia pinnata* at higher, rather than lower, latitudes (in China), all have heuristic value, as they indicate that factors other than current ecology are in play.

Conclusions

A biogeographic model for Meliaceae must account for the high level of overlap among the clades, which include four, separate pantropical groups, two in each subfamily. Of the 48 genera in Meliaceae, 11 have been recorded in mangrove or back-mangrove, 10 in swamp forest (either periodically or permanently flooded), 22 on limestone, and 22

in secondary vegetation. Several species are actively invasive weeds. It is suggested that these features occurred in early members of the group, enabling them to undergo massive range expansion (and overlap) during the last great marine transgressions, in the mid-Cretaceous. The dispersal and range expansion that led to the overlap can thus be explained, not by chance, but by geological events. With the regression of the epicontinental seas, many groups were left stranded in the Amazon basin, the Congo basin, central Australia, and elsewhere.

Along with the great overlap, there is also extensive allopatry within the main clades of Meliaceae. Many of the main boundaries coincide with tectonic structures that were active in the Cretaceous. Many of the most important examples occur in Guatemala (Motagua fault system), western Colombia (Romeral fault system), between Pacific and Caribbean Mexico (at the margin between the craton and the terranes accreted in the Cretaceous), in Amazonia (Cretaceous seas), at the Atlantic Ocean basin (rifting), in SE Brazil and Gabon–Angola (rift shoulder uplift), at the Cameroon Volcanic Line and the adjacent Benue Trough in Nigeria, in the Congo basin (Cretaceous seas), in NE India (at the eastern margin of the Indian plate), in New Guinea (at the boundary between the cratonic and allochthonous sectors), between Solomon Islands–Fiji–New Zealand, and Australia–New Guinea (eastward migration of the Pacific arc from Australia into the Pacific), and across the Pacific (subaerial igneous plateaux that formed in the West Pacific and drifted to America).

Boundaries at the Mozambique Channel coincide with a belt of earlier, Jurassic rifting. In three cases, a Madagascar group is sister to (not nested in) a widespread African group. In two cases, a Madagascar group separates before the African and American components in its sister group do.

Aspects of distribution in Costa Rica–Panama (and Colombian Chocó) were examined above in more detail. A 'Great American Biotic Interchange' across a landbridge there might explain the overlap of distributions and the high diversity, but it does not account for the abrupt boundaries, the high endemism, the strange absences, the large-scale disjunctions, the precise correlations of distributions with allochthonous terranes, or the repetition of all of these in many groups with different ecology. These different phenomena, together with the diversity, can all be explained if a large part of the regional biota, rather than forming in situ, was tectonically introduced with the island arcs and other structures that encroached from the Pacific. The Costa Rica–Panama region is an important biogeographic centre in its own right; it is not simply a 'bridge' (or a 'barrier' or 'filter') between North and South America.

Although all the genera of Meliaceae (except *Schmardaea*) are present in the lowlands, five occur at or above 3000 m altitude, 12 others at or above 2000 m, and 12 others above 1500 m. These records can be explained most simply by continuous, passive uplift of lowland populations through the Cenozoic in the rapidly rising mountains of the Andes and other ranges. The uplift has also led to the differentiation of many upland species and at least one upland genus, *Schmardaea* of the northern Andes (Fig. 5).

When the distribution of Meliaceae is analysed into its separate parts, which is a main task of biogeography, it is seen to be made up of completely recognisable, ordinary components. For example, Meliaceae include three trans-Atlantic, five trans-Indian and three trans-Pacific clades. All three types of distribution also occur in the family's sister group, the Simaroubaceae (see the section 'Global distribution of Meliaceae and allied families'). In fact, all the patterns discussed in this paper are repeated in many other groups, and this indicates that they are not the result of chance events occurring in individual clades, but have a common cause. In theory this could be tectonic or ecological, but it is difficult to see an ecological explanation for most of the patterns described here.

Future work

Despite groundbreaking studies on the phylogeny of Meliaceae by Koenen et al. (2015) and others, in several clades the topology is still not well resolved. This is true especially in *Dysoxylum* sensu lato, but also in the position of *Soymida* and of *Neoguarea*, and in the phylogeny of the *Carapa–Xylocarpus* group. In addition, the species delimitation in many genera, even well-studied ones such as *Cedrela* and *Aglaia*, is still far from clear.

  Ecological information is often very scanty, and for many species (and even genera, such as *Naregami*a) there is practically no published data. Good altitudinal information (including both upper and lower limits) is often lacking in what are otherwise excellent treatments. For many taxa there is more published information on their phytochemistry than on the most basic aspects of their distribution and ecology. The data tabulated in Fig. 4 is very incomplete, but hopefully it will stimulate further observations in the field and herbarium. Especially desirable would be treatments of the Meliaceae of Madagascar (also India and Angola) with maps, good illustrations and ecological notes. The *Dysoxylum* problem has been stressed already and needs resolving, and a revision of *Turraea* would also be of great interest — some of the forms are remarkable.

References

African Plant Database. (2019). (version 3.4.0). Conservatoire et Jardin botaniques de la Ville de Genève, and South African National Biodiversity Institute, Pretoria. http://www.ville-ge.ch/musinfo/bd/cjb/africa/.

Aghová, T., Kimura, Y., Bryja, J., Dobigny, G., Granjon, L. & Kergoat, G.J. (2018). Fossils know it best: using a new set of fossil calibrations to improve the temporal phylogenetic framework of murid rodents (Rodentia: Muridae). *Molec. Phylogen. Evol.* 128: 98–111.

Allan, H.H. (1961). *Flora of New Zealand*, vol. 1. Wellington: Government Printer.

Andersen, M.J., McCullough, J.M., Mauck III, W.M., Smith, B.T. & Moyle, R.G. (2018). A phylogeny of kingfishers reveals an Indomalayan origin and elevated rates of diversification on oceanic islands. *J. Biogeogr.* 45: 269–281.

Anderson, C.L., Bremer, K. & Friis, E.M. (2005). Dating phylogenetically basal eudicots using *rbcL* sequences and multiple fossil reference points. *Amer. J. Bot.* 92: 1737–48.

Appelhans, M.S., Reichelt, N., Groppo, M., Paetzold, C. & Wen, J. (2018). Phylogeny and biogeography of the pantropical genus *Zanthoxylum* and its closest relatives in the proto-Rutaceae group (Rutaceae). *Molec. Phylogen.* Evol. 126: 31–44.

Asuk, S.A., Offiong, E.E., Ifebueme, N.M. & Akpaso, E.O. (2018). Species composition and diversity of mangrove swamp forest in southern Nigeria. *Int. J. Avian Wildlife Biol.* 3: 166–171.

Aubréville, A. (1936). *La flore forestière de la Côte d'Ivoire.* Paris: Larose.

Ávila A., S. & Flowers, R.W. (2006). Two new species of *Choroterpes* Eaton (Ephemeroptera: Leptophlebiidae) from Costa Rica. *Zootaxa* 1245: 59–68.

Bacon, C.D., Velásquez-Puentes, F.J., Hinojosa, L.F., Schwartz, T., Oxelman, B., Pfeil, B., Arroyo, M.T., Wanntorp, L. & Antonelli, A. (2018). Evolutionary persistence in *Gunnera* and the contribution of southern plant groups to the tropical Andes biodiversity hotspot. *PeerJ* 6: e4388.

Baider, C. & Florens, F.V. (2016). A new and critically endangered species of *Turraea* (Meliaceae) endemic to the island of Mauritius. *Phytotaxa* 247: 219–228.

Backer, C.A. & Van Steenis, C.G.G.J. (1951). Sonneratiaceae. In: Backer, C.A. & Van Steenis *Flora Malesiana*, ser. 1, Seed Plants, vol. 4, pp. 280–289. Djakarta: Noordhoff-Kolff N.V.

Banks, H., Feist-Burkhart, S. & Klitgaard, B. (2006). The unique pollen morphology of *Duparquetia* (Leguminosae: Caesalpinioideae): developmental evidence of aperture orientation using confocal microscopy. *Ann. Bot.* 98: 107–115.

Beaulieu, J.M., Tank, D.C., & Donoghue, M.J. (2013). Southern Hemisphere origin for campanulid angiosperms, with traces of the breakup of Gondwana. *BMC Evol. Biol.* 13: 80.

Bromham, L. (2015). Macroevolutionary patterns of salt tolerance in angiosperms. *Ann. Bot.* 115: 333–341.

Bromham, L. (2019). Six impossible things before breakfast: assumptions, models, and belief in molecular dating. *Trends Ecol. Evol.* 34: 474–486.

Brown, G. & Mies, B. (2012). *Vegetation ecology of Socotra*. Dordrecht: Springer.

Buchs, D.M., Kerr, A.C., Brims, J.C., Zapata-Villada, J.P., Correa-Restrepo, T. & Rodríguez, G. (2018). Evidence for subaerial development of the Caribbean oceanic plateau in the Late Cretaceous and palaeo-environmental implications. *Earth Planetary Sci. Lett.* 499: 62–73.

Callmander, M.W., Phillipson, P.B. & Lowry, P.P. (2012). Novelties from the northern mountains complex of Madagascar. III. Two new species of *Turraea* L. (Meliaceae). *Adansonia* 34: 93–102.

Carr, L.M., McLenachan, P.A., Waddell, P.J., Gemmell, N.J. & Penny, D. (2015). Analyses of the mitochondrial genome of *Leiopelma hochstetteri* argues against the full drowning of New Zealand. *J. Biogeogr.* 42: 1066–1076.

Cavers, S., Telford, A., Arenal Cruz, F., Pérez Castañeda, A.J., Valencia, R., Navarro, C., Buonamici, A., Lowe, A.J. & Vendramin, G.G. (2013). Cryptic species and phylogeographical structure in the tree *Cedrela odorata* L. throughout the Neotropics. *J. Biogeogr.* 40: 732–746.

Chapman, V.J. (1976). *Mangrove vegetation*. Vaduz: Cramer.

Cheek, M. (1991). A new species of *Turraea* (Meliaceae) from Somalia and a note on the species in continental Africa. *Kew Bull.* 46: 683–690.

Cheek, M. (1996). The identity of *Naregamia* Wight & Arn. (Meliaceae). *Kew Bull.* 51: 716.

Church, A.H. (1919). *Thalassiophyta and the subaerial migration.* London: Oxford University Press.

Clark, T.P (1990). Studies in the *Trichilia-Walsura* complex (Meliaceae). Doctoral thesis, University of Oxford.

Clark, T.P. (1994). The species of *Walsura* and *Pseudoclausena* genus novum (Meliaceae). *Blumea* 38: 247–302.

Clarkson, J.J., Pennington, T.D., Chase, M.W., Haynes, G., Engstrand, R., Kaye, M., Michalak, I. & Muellner-Riehl, A. (2016). Phylogenetic relationships in *Trichilia* (Meliaceae) based on ribosomal ITS sequences. *Phytotaxa* 259: 6–17.

Clayton, J.W., Soltis, P.S. & Soltis, D.E. (2009). Recent long-distance dispersal overshadows ancient biogeographical patterns in a pantropical angiosperm family (Simaroubaceae, Sapindales). *Syst. Biol.* 58: 395–410.

Colli, L., Stotz, I., Bunge, H.-P., Smethurst, M., Clark, S., Iaffaldano, G., Tassara, A., Guillocheau, F. & Bianchi, M.C. (2014). Rapid South Atlantic spreading changes and coeval vertical motion in surrounding continents: Evidence for temporal changes of pressure-driven upper mantle flow. *Tectonics* 32: 1304–1321.

Collinson, M.E. (1983). *Fossil plants of the London Clay*. London: The Palaeontological Association.

Corner, E.J.H. (1952). Durians and dogma. *Indonesian J. Nat. Sci.* 5–6: 141–145.

Corner, E.J.H. (1954). The Durian Theory extended — II. The arillate fruit and the compound leaf. *Phytomorphology* 4: 263–274.

Corner, E.J.H. (1978). *The freshwater swamp-forest of south Johore and Singapore*. Singapore: Botanic Gardens, Parks and Recreation Department.

Cota-Sánchez, J.H., Reyes-Olivas, A. & Abreu, D.D. (2011). Vivipary in the cactus family: a reply to Ortega-Baes' et al. evaluation of 25 species from northwestern Argentina. *J. Arid Environ.* 75: 878–880.

Court, A.J. & Mitchell, N.D. (1988). The germination ecology of *Dysoxylum spectabile* (Meliaceae). *New Zealand J. Bot.* 26: 1–6.

Court, A.J. & Mitchell, N.D. (1989). The growth responses of *Dysoxylum spectabile* (Meliaceae) to a shaded environment. *New Zealand J. Bot.* 27: 353–357.

Couvreur, T.L., Niangadouma, R., Sonké, B. & Sauquet, H. (2015). *Sirdavidia*, an extraordinary new genus of Annonaceae from Gabon. *PhytoKeys* 46: 1–19.

Craw, R.C., Grehan, J.R. & Heads, M.J. (1999). *Panbiogeography: Tracking the history of life.* New York: Oxford University Press.

Crayn, D.M., Costion, C. & Harrington, M.G. (2015). The Sahul–Sunda floristic exchange: dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *J. Biogeogr.* 42: 11–24.

Cuong, N.T., Hoan, D.T. & Mabberley, D.J. (2014). *Munronia petiolata* (*Meliaceae*), a new species from Vietnam. *Blumea* 59: 139–141.

Czekanski-Moir, J.E. & Rundell, R.J. (2019). The ecology of nonecological speciation and nonadaptive radiations. *Trends Ecol. Evol.* 34: 400–415.

Dargie, G.C., Lewis, S.L., Lawson, I.T., Mitchard, E.T.A., Page, S.E., Bocko, Y.E. & Ifo, S.A. (2017). Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature* 542: 86–89.

Davies, H.L. (2012). The geology of New Guinea — the cordilleran margin of the Australian continent. *Episodes* 35: 87–102.

De Baets, K., Antonelli, A. & Donoghue, P.C.J. (2016). Tectonic blocks and molecular clocks. *Philos. Trans., Ser. B.* 371: 20160098.

De Wilde, J.J.F.E. (1968). A revision of the species of *Trichilia* P. Browne (Meliaceae) on the African continent. *Meded. Landbouwhogeschool Wageningen* 68 (2): 1–207.

De Wilde, J.J.F.E. (2007). A revision of the African genus *Heckeldora* (Meliaceae). *Blumea* 52: 179–199.

Denyer, P. & Baumgartner, P.O. (2006). Emplacement of Jurassic–Lower Cretaceous radiolarites of the Nicoya Complex (Costa Rica). *Geol. Acta* 4: 203–218.

Ding Hou (1958). Rhizophoraceae. In: Van Steenis, C.G.G.J. (ed.) *Flora Malesiana*, ser. 1, Seed Plants, vol. 5, pp. 429–493. Djakarta: Noordhoff-Kolff N.V.

Dowling, R.M. & McDonald, T.J. (1982). Mangrove communities of Queensland. In: Clough, B.F. (ed.) *Mangrove ecosystems in Australia: structure, function and* management, pp. 79–93. Canberra: Australian Institute of Marine Science/Australian National University Press.

Duretto, M.F., Wilson, P.G. & Ladiges, P.Y. (2013). *Boronia*. In: Wilson, A.J.G. (ed.) *Flora of Australia*, vol. 26, pp. 124–282. Canberra: Australian Biological Resources Study, and Melbourne: CSIRO Publishing.

Earle Smith, C. (1960). A revision of *Cedrela* (Meliaceae). *Fieldiana*, *Bot.* 29: 295–341.

Farnsworth, E. (2000). The ecology and physiology of viviparous and recalcitrant seeds. *Annual Rev. Ecol. Syst.* 31: 107–138.

Flowers, R.W. & Ávila A., S. (2006). Biogeographical and ecological notes on the genus *Tikuna* Savage, Flowers, and Porras (Ephemeroptera: Leptophlebiidae) from Central and South America. *Entomol. News* 117: 133–138.

Fosberg, F.R. (1974). Miscellaneous notes on the flora of Aldabra and neighbouring islands: III. *Kew Bull.* 29: 253–266.

Givnish, T.J. (2015). Adaptive radiation versus 'radiation' and 'explosive diversification': why conceptual distinctions are fundamental to understanding evolution. *New Phytol.* 207: 297–303.

González, C., Urrego, L.E., Martínez, J.I., Polanía, J. & Yokoyama, Y. (2010). Mangrove dynamics in the southwestern Caribbean since the 'Little Ice Age': a history of human and natural disturbances. *The Holocene* 20: 849–861.

Grande, L. (2016). Donn Rosen and the perils of paleontology. In: Crother, B.I. & Parenti, L.R. (eds) *Assumptions inhibiting progress in comparative biology,* pp. 159–168. Boca Raton, FL: Taylor & Francis.

Grau, H.R. (2000). Regeneration patterns of *Cedrela lilloi* (Meliaceae) in northwestern Argentina subtropical montane forests. *J. Trop. Ecol.* 16: 227–242.

Griffiths, C.J. (1993). The geological evolution of East Africa. In: Lovett, J.C. & Wasser, S.K. (eds) *Biogeography and ecology of the rain forests of eastern Africa*, pp, 9–21. Cambridge: Cambridge University Press.

Griffiths, M.E. (1959). A revision of the African species of *Terminalia. Bot. J. Linn. Soc.* 55: 818–907.

Grudinski, M., Wanntorp, L., Pannell, C.M. & Muellner-Riehl, A.N. (2014a). West to east dispersal in a widespread animal-dispersed woody angiosperm genus (*Aglaia*, Meliaceae) across the Indo-Australian Archipelago. *J. Biogeogr.* 41: 1149–1159.

Grudinski, M., Pannell, C.M., Chase, M.W., Ahmad, J.A. & Muellner-Riehl, A.N. (2014b). An evaluation of taxonomic concepts of the widespread plant genus *Aglaia* and its allies across Wallace's Line (tribe Aglaieae, Meliaceae). *Molec. Phylogen. Evol.* 73: 65–76.

Guillocheau, F., Chelalou, R., Linol, B., Dauteuil, O., Robin, C., Mvondo, F., Callec, Y. & Colin, J.P. (2015). Cenozoic landscape evolution in and around the Congo Basin: constraints from sediments and planation surfaces. In: De Wit, M.J., Guillocheau, F. & De Wit, M.C. (eds) *Geology and resource potential of the Congo Basin*, pp. 271–313. Berlin: Springer.

Guo, Z., Guo, W., Wu, H., Fang, X., Ng, W.L., Shi, X., Liu, Y., Huang, Z., Li, W., Gan, L. et al. (2018). Differing phylogeographic patterns within the Indo-West Pacific mangrove genus *Xylocarpus* (Meliaceae). *J. Biogeogr.* 45: 676–689.

Guppy, H.B. (1906). *Observations of a naturalist in the Pacific between 1896 and 1899, vol. II. Plant-dispersal*. London: Macmillan.

Hall, R. (2017). Southeast Asia: new views of the geology of the Malay Archipelago. *Ann. Rev. Earh Planet. Sci.* 45: 331-358.

Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978). *Tropical trees and forests: An architectural analysis*. New York: Springer.

Harms, H. (1940). Meliaceae. In: Engler, A. & Prantl, K. (eds) *Die natürlichen pflanzenfamilien*, 2nd edition, vol. 19b, pt. 1, pp. 1–172. Leipzig: W. Engelmann.

Hauenschild, F., Favre, A., Michalak, I. & Muellner-Riehl, A.N. (2018). The influence of the Gondwanan breakup on the biogeographic history of the ziziphoids (Rhamnaceae). *J. Biogeogr.* 45: 2669–2677.

Hay, A. (1998). The genus *Alocasia* (Araceae—Colocasieae) in West. Malesia and Sulawesi. *Gard. Bull. Singapore* 50: 221–334.

Hay, A. & Mabberley, D.J. (1991). 'Transference of function' and the origin of aroids: their significance in early angiosperm evolution. *Bot. Jahrb. Syst*. 113: 339–428.

Heads, M. (2001). Regional patterns of biodiversity in New Guinea plants. *Bot. J. Linn. Soc.* 136: 67–73.

Heads, M. (2003). Ericaceae in Malesia: vicariance biogeography, terrane tectonics and ecology. *Telopea* 10: 311–449.

Heads, M. (2006). Seed plants of Fiji: an ecological analysis. *Biol. J. Linn. Soc.* 89: 407–431.

Heads, M. (2012). *Molecular panbiogeography of the tropics*. Berkeley, California: University of California Press.

Heads, M. (2014). *Biogeography of Australasia: A molecular analysis*. Cambridge, UK: Cambridge University Press.

Heads, M. (2015). Biogeography by revelation: investigating a world shaped by miracles. *Austral. Syst. Bot.* 27: 282–304.

Heads, M. (2016). Pan-biogeografia da América do Sul. In: de Carvalho, C.J.B. & Almeida, E.A.B. (eds) *Biogeografia da América do Sul: Análise de tempo, espaço e forma*, pp. 57–103. Rio de Janeiro: Roca.

Heads, M. (2017). *Biogeography and evolution in New Zealand*. Boca Raton, FL: Taylor & Francis.

Heads, M. (2019). Passive uplift of plant and animal populations during mountain-building. *Cladistics. https://doi.org/10.1111/cla.12368*.

Hemp, A., Zimmermann, R., Remmele, S., Pommer, U., Berauer, B., Hemp, C. & Fischer, M. (2017). Africa's highest mountain harbours Africa's tallest trees. *Biodivers. & Conservation* 26: 103–113.

Hetherington, A.M. (2015). Special issue: Evolutionary plant radiations. *New Phytol*. 207: 249–479.

Hochmuth, K. & Gohl, K. (2017). Collision of Manihiki Plateau fragments to accretional margins of northern Andes and Antarctic Peninsula. *Tectonics* 36: 229–240.

Hochmuth, K., Gohl, K., Uenzelmann-Neben, G. & Werner, R. (2019) Multiphase magmatic and tectonic evolution of a large igneous plateau: evidence from the crustal structure of the Manihiki Plateau, western Pacific. *Tectonophysics* 750: 434-457.

Holland, S.M. (2016). The non-uniformity of fossil preservation. *Philos. Trans., Soc. B* 371 (1699): p.20150130.

Holmgren, M., Poorter, L., & Siepel, A. (2004). What explains the distribution of rare and endemic West African plants? In: Poorter, L., Bongers, F., Kouamé, F.N. & Hawthorne, W.D. (eds) *Biodiversity of West African forests: an ecological atlas of woody plant species*, pp. 73–86. Wallingford, UK: CABI.

Jeffrey, C. (1988). [Review of] The Plant Book. *Kew Bull.* 43: 722–724.

Jestrow, B., Gutiérrez Amaro, J. & Francisco-Ortega, J. (2012). Islands within islands: a molecular phylogenetic study of the *Leucocroton* alliance (Euphorbiaceae) across the Caribbean Islands and within the serpentinite archipelago of Cuba. *J. Biogeogr.* 39: 452–464.

Jiang, Y., Gao, M, Meng, Y., Wen, J., Ge, X.-J., & Nie, Z.-L. (2019). The importance of the North Atlantic landbridges and eastern Asia in the post-Boreotropical biogeography of the Northern hemisphere as revealed from the poson ivy genus (*Toxicodendron*, Anacardiaceae). *Molec. Phylogen. Evol.* Doi.org/10.1016/j.ympev.2019.106561

Johnson, D.M. & Murray, N.A. (2018). A revision of *Xylopia* L. (Annonaceae): the species of tropical Africa. *PhytoKeys* 97: 1–252.

Johnson, M.A., Clark, J.R., Wagner, W.L. & Mcdade, L.A. (2017). A molecular phylogeny of the Pacific clade of *Cyrtandra* (Gesneriaceae) reveals a Fijian origin, recent diversification, and the importance of founder events. *Molec. Phylogen. Evol.* 116: 30–48.

Kalinganire, A., & Pinyopusarerk, K. (2000). *Chukrasia: biology, cultivation and utilisation.* ACIAR Technical Reports [Canberra] No. 49. Canberra: Australian Centre for International Research.

Kalinganire, A., Pinyopusarerk, K. & Williams, E.R. (2002). Geographic variation in seedling morphology of *Chukrasia* species. *Austral. J. Bot.* 50: 319–330.

Kalkman, V.J., Dijkstra, K.-D. B., Dow, R.A., Stokvis, F.R. & Van Tol, J. (2018). Out of Australia: the Argiolestidae reveal the Melanesian Arc System and East Papua Composite Terrane as possible ancient dispersal routes to the Indo-Australian Archipelago (Odonata: Argiolestidae). *Int. J. Odonatol.* 21: 114.

Keay, R.W.J. (1958). Meliaceae. In: Hutchinson, J. & Dalziel, J.M. (eds) *Flora of West Tropical Africa*, 2nd edition, vol. 1, pp. 697–709. London: Crown Agents for Overseas Governments and Administrations.

Kelly, D.L., Tanner, E.V.J., Kapos, V., Dickinson, T.A., Goodfriend, G.A. & Fairbairn, P. (1988). Jamaican limestone forests: floristics, structure and environment of three examples along a rainfall gradient. *J. Trop. Ecol.* 4: 121–156.

Kenfack, D. (2011a). Resurrection in *Carapa* (Meliaceae): a reassessment of morphological variation and species boundaries using multivariate methods in a phylogenetic context. *Bot. J. Linn. Soc.* 165: 186–221.

Kenfack, D. (2011b). A synoptic revision of *Carapa* (Meliaceae). *Harvard Pap. Bot.* 16: 171–231.

Kilian, N., Hein, P. & Hubaishan, M.A. (2004). Further notes on the flora of the southern coastal mountains of Yemen. *Willdenowia* 34: 159–183.

Koecke, A.V., Muellner-Riehl, A.N., Pennington, T.D., Schorr, G. & Schnitzler, J. (2013). Niche evolution through time and across continents: the story of Neotropical *Cedrela* (Meliaceae). *Amer. J. Bot.* 100: 1800–1810.

Köcke, A.V., Muellner-Riehl, A.N., Cáceres, O. & Pennington, T.D. (2015). *Cedrela ngobe* (Meliaceae), a new species from Panama and Costa Rica. *Edinburgh J. Bot.* 72: 225–233.

Koenen, E. (2011). *Phylogenetic and biogeographic studies in Guareeae (Meliaceae: Melioideae)*. Thesis, Wageningen University.

Koenen, E.J. & de Wilde, J.J. (2012). A taxonomic revision of the reinstated genus *Leplaea* and the newly recognized genus *Neoguarea* (Meliaceae, Sapindales): the exclusion of *Guarea* from Africa. *Plant Ecol. Evol.* 145: 209–241.

Koenen, E.J., Clarkson, J.J., Pennington, T.D. & Chatrou, L.W. (2015). Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. *New Phytol.* 207: 327–339.

Łabiszak, B., Zaborowska, J. & Wachowiak, W. (2019). Patterns of mtDNA variation reveal complex evolutionary history of relict and endangered peat bog pine (*Pinus uliginosa*). *AoB PLANTS* 11: plz015.

Landis, M.J. (2017). Biogeographic dating of speciation times using paleogeographically informed processes. *Syst. Biol.* 66: 128–144.

Leroy, J.-F. (1958a). Les Acajous de Madagascar (*Khaya* et *Neobeguea*). *Compt. Rend. Acad. Sci. Paris* 246: 2638–2641. [= Leroy, J.-F. (1958). Contributions à l'étude des forêts de Madagascar. *J. Agric. Trop. Bot. Appl.* 5: 593–595].

Leroy, J.-F. (1958b). Recherches sur les Meliaceae: sur un genre africano-malgache, le *Lepidotrichilia* (Harms) J. F. Leroy. *Compt. Rend. Acad. Sci. Paris* 247: 1025–1027. [= Leroy, J.F. (1958). Contributions à l'étude des forêts de Madagascar II.-Sur un genre africano-malgache: le *Lepidotrichilia* (Harms)]. *J. Agric. Trop. Bot. Appl.* 5: 673–675].

Leroy, J.-F. (1958c). Recherches sur les Meliaceae: le *Capuronianthus*, genre nouveau endémique à Madagascar, type de la tribu des Capuroniantheae trib. nov., sousfamille des Carapoideae subf. nov. *Compt. Rend. Acad. Sci. Paris* 247: 1374–1376.

Leroy, J.-F. (1958d). Recherches sur les Meliaceae: sur un genre endémique à Madagascar, l'*Astrotrichilia* (Harms) J. F. Leroy (14 especes). *Compt. Rend. Acad. Sci. Paris* 247: 1889–1891. [= Leroy, J.-F. (1958). Contributions à l'étude des forêts de Madagascar. IV. Sur un genre endémique de Madagascar: l'*Astrotrichilia*. *J. Agric. Trop. Bot. Appl.* 5: 861–862].

Leroy, J.-F. (1964). Contributions à l'étude des forêts de Madagascar. VII. Recherches sur les Meliaceae: le *Malleastrum* (Baill.) J. F. Ler., genre nouveau endémique de la Grande Ile et des Comores. *J. Agric. Trop. Bot. Appl.* 11: 127–149.

Leroy, J.-F. (1970). Le genre *Neobeguea* (Méliacée). *J. Agric. Trop. Bot. Appl.* 17: 232–233.

Leroy, J.-F. (1976). Essais de taxonomie syncretique. 1. Etude sur les *Meliaceae* de Madagascar. *Adansonia* sér. 2, 16: 167–203.

Leroy, J.-F. (1989). Taxonomie des Meliaceae malgaches: espèces nouvelles du genre *Malleastrum* (Baillon) J.-F. Leroy. *Bull. Mus. Nat.. Hist. Nat., B, 4è sér., Adansonia 11:* 397–402.

Leroy, J.-F., & Lescot, M. (1996). Taxons nouveaux de Trichilieae (Meliaceae-Melioideae) de Madagascar. *Bull. Mus. Natl. Hist. Nat., B*, 4è série, *Adansonia* 18: 3–34.

Li, H.T., Yi, T.-S., Gao, L.-M., Ma, P.-F., Zhang, T., Yang, J.-B., Gitzendanner, M.A., Fritsch, P.W., Cai, J. et al. (2019). Origin of angiosperms and the puzzle of the Jurassic gap. *Nature Plants* 5: 461–470.

Lian, L., Xiang, K.-L., Ortiz, R. del C. & Wang, W. (2019). A multi-locus phylogeny for the Neotropical Anomospermeae (Menispermaceae): Implications for taxonomy and biogeography. *Molec. Phylogen. Evol.* 136: 44–52.

Lim, J.Y. & Marshall, C.R. (2017). The true tempo of evolutionary radiation and decline revealed on the Hawaiian archipelago. *Nature* 543: 710–713.

Lloyd, F.E. (1902). Vivipary in *Podocarpus. Torreya* 2: 113–117.

Lomolino, M.V. & Brown, J.H. (2009). The reticulating phylogeny of island biogeography theory. *Quart. Rev. Biol.* 84: 357–390.

Londres, M., Schulze, M., Staudhammer, C.L. & Kainer, K.A. (2017). Population structure and fruit production of *Carapa guianensis* (Andiroba) in Amazonian floodplain forests: implications for community-based management. *Trop. Conservation Sci.* 10: p.1940082917718835.

Louchart, A., Bastian, F., Baptista, M., Guarino-Vignon, P., Hume, J.P., Jacot-des-Combes, C., Mourer-Chauviré, C., Hänni, C. & Ollivier, M. (2018). Ancient DNA reveals the origins, colonization histories, and evolutionary pathways of two recently extinct species of giant scops owl from Mauritius and Rodrigues Islands (Mascarene Islands, south-western Indian Ocean). *J. Biogeogr.* 45: 2678–2689.

Mabberley, D.J. (1979). The species of *Chisocheton* (Meliaceae). *Bull. Brit. Mus. (Nat. Hist.) Bot.* 6: 301–386.

Mabberley, D.J. (1988). Meliaceae. In: Morat, P. & Mackee, H.S. (eds) *Flore de la Nouvelle-Calédonie et Dépendances*, vol. 15, pp. 17–89. Paris: Muséum National d'Histoire Naturelle.

Mabberley, D.J. (1992). *Tropical rain forest ecology*. 2nd edition. New York: Chapman & Hall.

Mabberley, D.J. (1995). Meliaceae. (*Aglaia* by C.M. Pannell). In: Dassanayake, M.D., Fosberg, F.R. & Clayton W.A. (eds) *A revised handbook to the Flora of Ceylon*, vol. 9, pp. 228–300. New Delhi: Amerind Publishing.

Mabberley, D.J. (2003). New species of, and other notes on, *Chisocheton* and *Walsura* (Meliaceae). *Gard. Bull. Singapore* 55: 189–200.

Mabberley, D.J. (2007). Meliaceae. In: Soepadmo, E., Saw, L.G., Chung, R.C.K. & Kiew, R. (eds) *Tree flora of Sabah and Sarawak*, pp. 17–218. Kuala Lumpur: Forest Research Institute Malaysia, Sabah Forestry Department and Sarawak Forestry Department.

Mabberley, D.J. (2011). Meliaceae. In: Kubitzki, K. (ed.) *Flowering Plants. Eudicots*, *vol. 10*, *Sapindales, Cucurbitales, Myrtaceae*, pp. 185–211. Berlin: Springer.

Mabberley, D.J. (2013). Meliaceae [*Aglaia* by C.M. Pannell]. In: Wilson, A. (ed.) *Flora of Australia*, vol. 26, pp. 1–42. Canberra: CSIRO Publishing.

Mabberley, D.J. (2017). *Mabberley's plant-book: A portable dictionary of plants*, 4th edition. Cambridge, UK: Cambridge University Press.

Mabberley, D.J., Pannell, C.M. & Sing, A.M. (eds) (1995). *Meliaceae. Flora Malesiana*, ser. 1, Seed Plants, vol. 12, pt. 1. Leiden: Foundation Flora Malesiana.

Mateos, M., Sanjur, O.I. & Vrijenhoek, R.C. (2002). Historical biogeography of the livebearing fish genus *Poeciliopsis* (Poeciliidae: Cyprinodontiformes). *Evolution* 56: 972–984.

Meijer, W. (1970). Botanical notes on Ceylon trees. I. *Soymida febrifuga* (Roxb.) Juss. (Meliaceae) indigenous in Ceylon. *Ceylon Forest*. 9: 95–97.

Monteillet, J. & Lappartient, J.-R. (1981). Fruits et graines du Crétacé Supérieur des Carrieres de Paki (Senegal). *Rev. Palaeobot. Palynol.* 34: 331–344.

Monthe, F.K., Migliore, J., Duminil, J., Bouka, G., Demenou, B.B., Doumenge, C., Blanc-Jolivet, C., Ekué, M.R.M. & Hardy, O.J. (2019). Phylogenetic relationships in two African Cedreloideae tree genera (Meliaceae) reveal multiple rain/dry forest transitions. *Perspect. Pl. Ecol. Evol. Syst.* 37: 1–10.

Moore, L.B. & Irwin, J.B. (1978). *Oxford book of New Zealand Plants. Auckland:* Oxford University Press.

Muellner, A.N. & Mabberley, D.J. (2008). Phylogenetic position and taxonomic disposition of *Turraea breviflora* (Meliaceae), a hitherto enigmatic species. *Blumea* 53: 607–616.

Muellner, A.N., Savolainen, V., Samuel, R. & Chase, M.W. (2006). The mahogany family 'out-of-Africa': divergence time estimation, global biogeographic patterns inferred from *rbcL* DNA sequences, extant, and fossil distribution of diversity. *Molec. Phylogen. Evol.* 40: 236–250.

Muellner, A.N., Vassiliades, D.D. & Renner, S.S. (2007). Placing Biebersteiniaceae, a herbaceous clade of Sapindales, in a temporal and geographic context. *Pl. Syst. Evol.* 266: 233–252.

Muellner, A.N., Pannell, C.M., Coleman, A. & Chase, M.W. (2008a). The origin and evolution of Indomalesian, Australasian and Pacific island biotas: insights from Aglaieae (Meliaceae, Sapindales). *J. Biogeogr.* 35: 1769–1789.

Muellner, A.N., Samuel, R., Chase, M.W., Coleman, A. & Stuessy, T.F. (2008b). An evaluation of the tribes and of generic relationships in Melioideae (Meliaceae) based on nuclear ITS ribosomal DNA. *Taxon* 57: 98–106.

Muellner, A.N., Pennington, T.D., Koecke, A.V. & Renner, S.S. (2010). Biogeography of *Cedrela* (Meliaceae, Sapindales) in Central and South America. *Amer. J. Bot.* 97: 511–518.

Muellner-Riehl, A.N., Weeks, A., Clayton, J.W., Buerki, S., Nauheimer, L., Chiang, Y.C., Cody, S. & Pell, S.K. (2016). Molecular phylogenetics and molecular clock dating of Sapindales based on plastid *rbcL*, *atpB* and *trnL-trnF* DNA sequences. *Taxon* 65: 1019–1036.

Nadkarni, N.M. (1981). Canopy roots: convergent evolution in rainforest nutrient cycles. *Science* 214: 1023–1024.

Navalón, G., Bright, J.A., Marugán-Lobón, J., & Rayfield, E.J. (2019). The evolutionary relationship between beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution* 73: 422-435.

Navarro, C., Ward, S. & Hernández, M. (2002). The tree *Cedrela odorata* (Meliaceae): a morphologically subdivided species in Costa Rica. *Revista Biol. Trop.* 50: 21–29.

Nei, M. (2013). *Mutation-driven evolution*. New York: Oxford University Press.

Nooteboom, H.P. (1960). Simaroubaceae. In: Van Steenis, C.G.G.J. (ed.) *Flora Malesiana*, ser. 1, Seed Plants, vol. 6, pp.193–226. Groningen: Wolters-Noordhoff.

Novick, R.R., Dick, C.W., Lemes, M.R., Navarro, C., Caccone, A. & Bermingham, E. (2003). Genetic structure of Mesoamerican populations of Big-leaf mahogany (*Swietenia macrophylla*) inferred from microsatellite analysis. *Molec. Ecol.* 12: 2885–2893.

Pagel, M.D. & Meade, A. (2007). *BayesTraits*. http://www.evolution.reading.ac.uk/BayesTraits.html.

Palacios, W.A. (1994). Especies nuevas de Meliaceae del Ecuador y areas adyacentes. *Novon* 4: 155–163.

Palacios, W.A., Santiana, J. & Iglesias, J. (2019). A new species of *Cedrela* (Meliaceae) from the eastern flanks of Ecuador. *Phytotaxa* 393: 84–88.

Pannell, C.M. (1992). A taxonomic monograph of the genus *Aglaia* Lour. (Meliaceae). *Kew Bull. Add. Series* 16. London: HMSO.

Pannell, C.M. (2004). Three new species, two new subspecies and five new combinations at the subspecific level in *Aglaia* Lour. (Meliaceae). *Kew Bull.* 59: 87–94.

Pannell, C.M. (2005). *Aglaia soepadmoi* Pannell (Meliaceae), a new species for Borneo. *Gard. Bull. Singapore* 57: 183–185.

Pannell, C.M. (2007). *Aglaia* Lour. In: Soepadmo, E., Saw, L.G., Chung, R.C.K., & Kiew, R. (eds) *Tree flora of Sabah and Sarawak*, vol. 6, pp. 24–107. Kuala Lumpur: Forest Research Institute Malaysia, Sabah Forestry Department and Sarawak Forestry Department.

Peng, H., Mabberley, D.J., Pannell, C.M., Edmonds, J.M. & Bartholomew, B. (2008). Meliaceae. In: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds) *Flora of China*, vol. 11, pp. 98–131. Beijing: Science Press; and St. Louis: Missouri Botanical Garden.

Pennington, T.D. (1969). Materials for a monograph of the Meliaceae. I. A revision of the genus *Vavaea*. *Blumea* 17: 351–366.

Pennington, T.D. (2002). Mahogany carving a future. *Biologist* [London] 49: 204–208.

Pennington, T.D. (2016). Systematic treatment of American *Trichilia* (Meliaceae). *Phytotaxa* 259: 18–162.

Pennington, T.D. & Clarkson, J.J. (2013). A revision of *Guarea* (Meliaceae). *Edinburgh J. Bot.* 70: 179–362.

Pennington, T.D. & Muellner, A.N. (2010). *A monograph of Cedrela (Meliaceae)*. Sherborne, UK: DH Books.

Pennington, T.D. & Styles, B.T. (1975). A generic monograph of the Meliaceae. *Blumea* 22: 419–540.

Pennington, T.D., Styles B.T. & Taylor, D.A.H. (1981). Meliaceae. *Flora Neotropica*, vol. 28. New York: NYBG Press.

Perdices, A., Bermingham, E., Montilla, A. & Doadrio, I. (2002). Evolutionary history of the genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Molec. Phylogen. Evol.* 25: 172–189.

Pfeil, B.E. & Crisp, M.D. (2008). The age and biogeography of *Citrus* and the orange subfamily (Rutaceae: Aurantioideae) in Australasia and New Caledonia. *Amer. J. Bot.* 95: 1621–1631.

Philipson, W.R. (1978). Araliaceae: growth forms and shoot morphology. In: Tomlinson, P.B. & Zimmerman, M. (eds) *Tropical trees as living systems,* pp. 269–284. Cambridge, UK: Cambridge University Press.

Pigg, K.B., DeVore, M.D., Benedict, J.C. & Creekmore, R.M. (2014). Fruits of *Melia* (Meliaceae, Melioideae) from the Middle Miocene Yakima Canyon flora of central Washington State, USA. In: Stevens, W.D., Montiel, O.M., & Raven P. (eds) *Paleobotany and biogeography: A festschrift for Alan Graham in his 80th year*, pp. 326–337. Chicago: University of Chicago Press.

Pindell, J.L. & Kennan, L. (2009). Tectonic evolution of the Gulf of Mexico, Caribbean and northern South America in the mantle reference frame: an update. *Geol. Soc. London Special Publ.* 328: 1–55.

Potts, A.J. (2017). Catchments catch all in South African coastal lowlands: topography and palaeoclimate restricted gene flow in *Nymania capensis* (Meliaceae) — a multilocus phylogeographic and distribution modelling approach. *PeerJ* 5: e2965.

Prance, G. (1994). A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. *Phil. Trans., Ser. B* 345: 89–99.

Price, J.P. & Wagner, W.L. (2018). Origins of the Hawaiian flora: phylogenies and biogeography reveal patterns of long-distance dispersal. *J. Syst. Evol.* 56: 600–620.

Puentes, D.A. (2005). *Flora de la Republica de Cuba*. Liechtenstein: A.R. Ganther.

Randrianarivony, T.N., Randriatsivery, M.F., Andriamihajarivo, T.H. & Callmander, M.W. (2017). Une nouvelle espèce de *Turraea* (Meliaceae) du Sud-Ouest de Madagascar. *Candollea* 72: 283–288.

Reid, E.M. & Chandler, M.E.J. (1933). *The London Clay flora*. London: British Museum (Natural History).

Ribeiro, A.C. (2006). Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotrop. Ichthyol*. 4: 225–246.

Richards, P.W., with contributions by Walsh, R.P.D., Baillie, I.C. & Grieg-Smith, P. (1996). *The tropical rainforest*. 2nd edition. Cambridge, UK: Cambridge University Press.

Rivas-Torres, G. & Rivas, M.G. (2018). Allelopathic impacts of the invasive tree *Cedrela odorata* L. (Meliaceae, Sapindales: Magnoliidae) in the Galapagos flora. In: de Lourdes Torres, M. & Mena, C.F. (eds) *Understanding invasive species in the Galapagos Islands: From the molecular to the landscape*, pp. 77–93. Cham, Switzerland: Springer.

Rueangruea, S., Tagane, S., Suddee, S., Tetsana, N., Poopath, M., Nagamasu, H. & Naiki, A. (2015). *Toona calcicola*, a new species and *Reinwardtiodendron humile*, a new record to Thailand. *Thai Forest Bull., Bot.* 43: 79–86.

Savage, H.M., Flowers, R.W. & Porras, V. W. (2005) Rediscovery of *Choroterpes atramentum* in Costa Rica, type species of *Tikuna* new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the 'Great American Interchange'. *Zootaxa* 932: 1–14.

Simpson, G.G. (1953). *The major features of evolution*. New York: Columbia University Press.

Slavenko, A., Feldman, A., Allison, A, Bauer, A.M., Böhm, M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., LeBreton, M. et al. (2019). Global patterns of body size evolution in squamate reptiles are not driven by climate. *Global Ecol. Biogeogr*. 28: 471-483.

Smith, A.C. (1985). Meliaceae. In: Smith, A.C. (ed.) *Flora Vitiensis nova: a new flora of Fiji (spermatophytes only)*, vol. 3, pp. 527–578. Lawai, Kauai: Pacific Tropical Botanical Garden.

Smith, S.A., Beaulieu, J.M. & Donoghue, M.J. (2010). An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. *Proc. Natl. Acad. Sci. U.S.A.* 107: 5897–5902.

Snook, L.K. (1996). Catastrophic disturbance, logging and the ecology of mahogany (*Swietenia macrophylla* King): grounds for listing a major tropical timber species in CITES. *Bot. J. Linn. Soc.* 122: 35–46.

Soepadmo, E. (1972). Fagaceae. In: Van Steenis, C.G.G.J. (ed.) *Flora Malesiana*, ser. 1, Seed Plants, vol. 7, pp. 265–403. Leyden: Noordhoff.

Soepadmo, E., Saw, L.G., Chung, R.C.K., Wong, K.M. & Kiew, R. (eds) (1995–2014) *Tree flora of Sabah and Sarawak*, vols. 1–8. Kuala Lumpur: Forest Research Institute of Malaysia, Sabah Forestry Department and Sarawak Forestry Department.

Soulebeau, A., Aubriot, X., Gaudeul, M., Rouhan, G., Hennequin, S., Haevermans, T., Dubuisson, J.Y. & Jabbour, F. (2015). The hypothesis of adaptive radiation in evolutionary biology: hard facts about a hazy concept. *Organisms Diversity Evol*. 15: 747–761.

Staner, P. & Gilbert, G. (1958). Meliaceae. In: Robyns, W. (ed.) *Flore du Congo Belge et du Ruanda-Urundi*, vol. 7, pp. 147–213. Bruxelles: Institut National pour l'Étude Agronomique du Congo Belge.

Stevens, P.F. (2001 onwards). Angiosperm phylogeny website. Version 14, July 2017. www. mobot.org/mobot/research/apweb/welcome.html. Accessed 20 Mar. 2019.

Styles, B.T. & Bennett, S.T. (1992). Notes on the morphology, chemistry, ecology, conservation status and cytology of *Schmardaea microphylla* (Meliaceae). *Bot. J. Linn. Soc.* 108: 359–373.

Styles, B.T. & White, F. (1991). Meliaceae. In: Polhill, R.M. (ed.) *Flora of Tropical East Africa.* 68 pp. Rotterdam: Balkema.

Sun, G., Dilcher, D.L., Wang, H. & Chen, Z. (2011). A eudicot from the Early Cretaceous of China. *Nature* 471: 625–628.

Takeuchi, W. (2007). Additions to the flora of the Strickland Basin, Papua New Guinea: *Hypserpa calcicola* (Menispermaceae), a new species from the southern limestone. *Harvard Papers Bot.* 13: 277–283.

Takeuchi, W. (2008). Additions to the flora of the Strickland Basin, Papua New Guinea: *Fittingia paniculata* (Myrsinaceae), a new calciphilous species from the southern limestone. *Harvard Papers Bot.* 13: 267–271.

Takeuchi, W. (2009a). Occurrence records in Papuasian *Aglaia* (Meliaceae): *A. pannelliana* and *A. puberulanthera* from the Southern Karst of Papua New Guinea. *Harvard Papers Bot.* 14: 31–38.

Takeuchi, W. (2009b). *Dysoxylum middletonianum* (Meliaceae), a distinctive new species from the Southern Fold Mountains of Papua New Guinea. *Edinburgh J. Bot. 66: 347–353.*

Takeuchi, W. (2010). A new addition to the endemic genus *Fittingia* (Myrsinaceae) of New Guinea: *F. headsiana* from the southern limestone, with a synoptical key to the species. *Harvard Papers Bot.* 15: 37–40.

Takeuchi, W. (2011). Notes on Papuasian Sapindaceae: *Harpullia mabberleyana* sp. nov., *Harpullia rhachiptera* and *Lepisanthes mixta*. *Edinburgh J. Bot.* 68: 1–9.

Tilney, P.M., Nel, M. & van Wyk, A.E. (2018). Foliar secretory structures in *Melia azedarach* (Meliaceae), a widely cultivated and often invasive tree. *New Zealand J. Bot.* 56: 198-215.

Tomlinson, P.B. (1986). *The botany of mangroves*. Cambridge: Cambridge University Press.

Umhoefer, P.J. (2003). A model for the North America Cordillera in the early Cretaceous: tectonic escape related to arc collion of the Guerrero terrane and a change in North America plate motion. In: Johnson, S.E. Paterson, S.R. Fletcher, J.M. Girty, G.H. Kimbrough, D.L. & Martín-Barajas, A. (eds) *Tectonic evolution of northwestern México and the southwestern USA. Geol. Soc. America Special Paper*, vol. 374, pp. 117–134. The Geological Society of America.

Van Balgooy, M.M.J. (1966). *Vavaea* Bth. *Pacific Plant Areas* 2. *Blumea* Suppl. 5: 92–93.

Van Balgooy, M.M.J. (1971). Plant genera of the Pacific as based on a census of phanaerogam genera. *Blumea* Suppl. 6: 1–222.

Van Steenis, C.G.G.J. (1950). *Contributions to the history of botany and exploration in Malaysia. Bull. Jard. Bot. Buitenzorg*, ser. 3, vol. 18: 463–471.

Van Steenis, C.G.G.J. (1958). Rhizophoraceae: ecology. In: Van Steenis, C.G.G.J. (ed.) *Flora Malesiana*, ser. 1, Seed Plants, vol. 5, pp. 429–444. Djakarta: Noordhoff-Kolff N.V.

Van Steenis, C.G.G.J. (1981). *Rheophytes of the world: an account of the flood-resistant flowering plants and ferns and the theory of autonomous evolution.* Rockville, MD: Sijthoff and Noordhoff.

Ware, J.L., Beatty, C.D., Sánchez Herrera, M., Valley, S.A., Johnson, J.T., Kerst, C., May, M.L. & Theischinger, G. (2014). The petaltail dragonflies (Odonata: Petaluridae): Mesozoic

habitat specialists that survive to the modern day. *J. Biogeogr.* 41: 1291–1300.

Weber, M.B.I., Cardona, A., Paniagua, F., Cordani, U., Sepúlveda, L. & Wilson, R. (2009). The Cabo de la Vela Mafic-Ultramafic Complex, Northeastern Colombian Caribbean region: a record of multistage evolution of a Late Cretaceous intra-oceanic arc. *Geol. Soc. London Special Publ.* 328: 549–568.

White, F. (1986). The taxonomy, chorology and reproductive biology of southern African Meliaceae and Ptaeroxylaceae. *Bothalia* 16: 143–168.

White, F. & Styles, B.T. (1963). Meliaceae. In: Exell, A.W., Fernandes, A. & Wild, H. (eds) *Flora Zambesiaca*, vol. 2, pp. 285–319. London, UK: Crown Agents.

White, F. & Styles, B.T. (1986). Meliaceae. In: Leistner, O.A. (ed.) *Flora of Southern Africa*, vol. 18, pp. 39–61. Pretoria, South Africa: Botanical Research Institute, Department of Ariculture and Water Supply.

White, G.M., Boshier, D.H. & Powell, W. (2002). Increased pollen flow counteracts fragmentation in a tropical dry forest: an example from *Swietenia humilis* Zuccarini. *Proc. Natl. Acad. Sci. U.S.A.* 99: 2038–2042.

Whitmore, T.C. (1984). *The tropical rain forests of the Far East*, 2nd edition. Oxford: Oxford University Press.

Willis, K.J., Gillson, L. & Brncic, T.M. (2004). How "virgin" is virgin rainforest? S*cience* 304: 402–403.

Wongprasert, T., Phengklai, C. & Boonthavikoon, T. (2011). Synoptic account of the Meliaceae of Thailand. *Thai Forest Bull., Bot.* 39: 210–266.

WWF (World Wildlife Fund) (2019). Eastern Africa: central Tanzania extending into Kenya. https://www.worldwildlife.org/ecoregions/at0109.

Yakusu, E.K., Monthe, F.S., Bourland, N., Hardy, O.J., Louppe, D., Lokanda, F.B.M., Hubau, W., Muhongya, J.-M.K., Bulcke, J.V. van, Acker, J. van et. al. (2018). Le genre *Entandrophragma* (Meliaceae): taxonomie et écologie d'arbres africains d'intérêt économique (synthèse bibliographique). *Biotechnol. Agron. Soc. Environm.* 22: 113–127.

Yu, X.Q., Gao, L.M., Soltis, D.E., Soltis, P.S., Yang, J.B., Fang, L., Yang, S.X. & Li, D.Z. (2017). Insights into the historical assembly of East Asian subtropical evergreen broadleaved forests revealed by the temporal history of the tea family. *New Phytol.* 215: 1235–1248.