The endemic plant families and the palms of New Caledonia: a biogeographical analysis

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ABSTRACT

This paper provides a panbiogeographical analysis of the endemic plant families and the palms of New Caledonia. There are three endemic plant families in New Caledonia and several genera that were previously recognized as endemic families. Of these taxa, some are sister to widespread Northern Hemisphere or global groups (Canacomycyrca, Austrotaxus, Amborella). The others belong to trans-Indian Ocean groups (Strasburgeria), trans-tropical Pacific groups (Oncotheca) or Tasman Sea/Coral Sea groups (Phelline, Paracyphia) that are sister to widespread Northern Hemisphere or global groups. In palms, the four clades show allopatric regional connections in, respectively: (1) western Indonesia, Malaysia and Thailand; (2) Vanuatu/Fiji and the southern Ryukyu Islands near Taiwan; (3) the western Tasman/Coral Sea (eastern Australia, New Guinea and the Solomon Islands); and (4) the eastern Tasman/Coral Sea (Lord Howe and Norfolk Islands, New Zealand, Vanuatu, Fiji and the Solomon Islands). The four clades thus belong to different centres of endemism that overlap in New Caledonia. The patterns are attributed not to chance dispersal and adaptive radiation but to the different histories of the eight terranes that fused to produce modern New Caledonia. Trans-tropical Pacific connections can be related to the Cretaceous igneous plateaus that formed in the central Pacific and were carried, with plate movement, west to the Solomon Islands and New Zealand, and east to Colombia and the Caribbean.

Keywords
Ecology, limestone, New Caledonia, panbiogeography, rain forest, tectonics, ultramafic, vicariance.

INTRODUCTION

The flora and fauna of New Caledonia are of special interest through their high levels of diversity, their endemism and their far-flung geographical affinities. In seed-plants, for example, there is probably no other region of comparable area in the world with such a rich and peculiar flora, one which ‘has good claim to be considered the most remarkable in the world’ (Thorne, 1965, p. 1; cf. Good, 1974). Apart from the endemic families, discussed below, 105 of the 711 genera (15%) and 2324 of the 3004 indigenous species (77%) are endemic (Jaffré et al., 2001). It must also be one of the smallest areas in the world with an endemic bird family (Rhynochetidae) and there is also an endemic liverwort family (Perssoniellaceae) (Crandall-Stotler et al., 2009).

Distribution patterns of plant and animal taxa within New Caledonia and the tectonic development of the region are discussed elsewhere (Heads, 2008a,b, 2009a). This paper provides an analysis of various plant groups and their global affinities. The patterns are related to the tectonic history of the region but, as indicated in the next section, this does not mean simply interpreting biological patterns in the light of geological reconstructions. Many aspects of the geology are still unclear, and data from biogeography constitute a separate source of evidence that may help resolve tectonic problems. A good example is the West Caledonian fault. Some geologists deny that it exists, while others regard it as a major structure. Biogeographical evidence supports the latter view (Heads, 2008b).

The panbiogeographical approach used in this paper involves an analysis of distribution patterns and a synthesis of biogeography and geology. In particular, this method assumes that phylogenetic and geographical breaks are caused by vicariance, not by the physical movement (dispersal) of taxa (Heads, 2009b). Physical movement may lead to subsequent
overlap but invoking long-distance dispersal and founder effect speciation to explain phylogenesis is unnecessary. The New Caledonian groups studied in this paper were selected as they include some of the most distinctive clades in the country. Analyses of their distributions have revealed shared patterns and these are attributed to common tectonic and phylogenetic causes rather than to independent dispersal events.

TECTONIC HISTORY

New Caledonia is not simply a fragment of Gondwana but is a complex mosaic of eight allochthonous terranes—fault-bounded crustal blocks with independent histories (Heads, 2008a). The four New Caledonian basement terranes formed from island arc–derived and arc-associated material which accumulated in the pre-Pacific Ocean, not in Gondwana. They amalgamated and were accreted to Gondwana (eastern Australia) in the Late Jurassic/Early Cretaceous, but in the Late Cretaceous they separated from Australia with the opening of the Tasman Sea and the break-up of Gondwana. A convergent margin with associated subduction developed near the island and an Eocene collision of the basement terranes with an island arc arriving from the north-east—possibly the Loyalty Ridge—is of special biogeographical interest in connection with New Caledonia–central Pacific affinities. Thus New Caledonia is a geological composite formed from Gondwanan and Pacific components, a similar pattern to that seen in New Guinea and New Zealand.

Many authors have attributed New Caledonian endemism to the long isolation of the island and the variety of habitat types present. These factors may account for the survival of an archaic biota but they do not, on their own, explain its origin. This is more likely to be related to the different histories of the terranes that make up modern New Caledonia (Heads, 2008a). For example, New Caledonia is exceptionally rich in marine molluscs (Marshall, 2001; Bouchet et al., 2002) and the country is the world centre of diversity for families such as the Volutomitridae (Bouchet & Kantor, 2003). Marshall (2001, p. 41) proposed that ‘Since the Melanesian arc [including New Caledonia] is situated at current or former [convergent] boundaries of the Australian and Pacific lithospheric plates, species richness there is probably due at least partly to progressive accumulation of taxa transported on the plates’. This process, with taxa being ‘scraped off’ at a subduction zone, would account for many biogeographical phenomena in and around New Caledonia. The strata that the current endemics originally occupied may have disappeared. Large structures in the region, such as the South Loyalty Basin (between Grande Terre – the New Caledonian mainland – and the Loyalty Islands), have been largely destroyed by subduction but were probably among the prior areas of endemism that have left traces in the extant flora and fauna.

Oceanic sediments deposited in the Palaeogene are widespread in New Caledonia. Authors such as Pole (1994) have accepted the idea that New Caledonia was completely submerged by Palaeogene marine transgressions and so have supported an ‘entirely long-distance dispersal’ explanation for the biota of the island. Nevertheless, without a stratum of a single age completely covering the island, total submergence is difficult to prove from geological data and in such a dynamic region tectonic uplift and subsidence can be very local. With respect to biogeography, the Australian eucalypts are represented in New Caledonia by Arillastrum, and Ladiges et al. (2003) noted that long-distance dispersal is unlikely, due to the limited dispersal capacity of the seeds. Ladiges et al. (2003, quoting Russell-Smith et al., 1993) concluded that the presence in New Caledonia of ancient angiosperms, such as Amborella and Winteraceae, and the high levels of endemism there also imply that ‘emergent land existed in the vicinity of New Caledonia throughout its rifted Late Cretaceous and Cainozoic history’. Authors such as Morat et al. (1984), de Laubenfels (1996), Lowry (1998), Jolivet (2008) and Jolivet & Verma (2008a,b) have agreed that complete submergence is unlikely, based on biogeographical evidence. Very small tropical islands can preserve diverse biotas and so could have provided effective microrefugia.

Murienne (2009, p. 1433) argued that phylogenies and molecular dating provide the ‘necessary framework’ for analysing New Caledonian biodiversity. He concluded that the different hypotheses (island refugia during flooding, long-distance dispersal after flooding) cannot be separated on the basis of the phylogenies alone and so he relied on molecular dating studies. These have indicated that most New Caledonian groups are of Cenozoic age (cf. Figure 2 in Grandcolas et al., 2008) and Murienne (2009) argued that for these groups the ‘only valid interpretation’ is long-distance dispersal. Nevertheless, the two methods employed in the dating studies (treating the oldest fossils and clock dates derived from these—minimum ages—as maximum ages; using the age of the young islands currently emergent on the old Loyalty Ridge to date the taxa there) will both give systematic underestimates of clade age (Heads, 2008a). Murienne (2009) concluded that ‘the presence of numerous relict groups in New Caledonia remains puzzling’ (p. 1434), but this is only because the clades were assumed to be so young. Likewise, while Grandcolas et al. (2008) accepted that the New Caledonian biota was wiped out by ‘total submergence’ during Palaeogene flooding and is the result of long-distance dispersal since 37 Ma, they concluded that the ‘Phylogenetic relics remain puzzlingly enigmatic…’ (p. 3312). Neither Murienne (2009) nor Grandcolas et al. (2008) mentioned the New Caledonian terranes or their history, although this may provide a simple explanation for what are otherwise enigmas in the biota.

THE ENDEMIC PLANT FAMILIES

The New Caledonian flora is well known for its endemic families of angiosperms and, until recently, four or five were often cited. Molecular studies have clarified their relationships and now only three are accepted (Amborellaceae, Oncothecaceae and Phellinaceae; Stevens, 2009), but this is still an unprecedented number for such a small area. Whatever rank the groups are given, the endemic families and the other
endemics sometimes regarded as families are well-documented and their affinities can be used to illustrate some of the main biogeographical connections of the island’s biota.

The plant groups concerned are all woody, and Jaffré (1995) noted that three of them, Paracryphia, Phellinaceae and Strasburgeria, are well represented in dense, evergreen, montane forest found above c. 1000 m elevation. *Izerba*, related to *Strasburgeria*, inhabits similar higher-elevation forest in northern New Zealand. *Amborella*, recorded from 200–1000 m a.s.l. in New Caledonia, is also absent from the lowest-elevation rain forest.

1. Amborellaceae. This family comprises one species, *Amborella trichopoda*, endemic to New Caledonia. It is the sister-group (or with Nymphaeales the sister-group) of all other angiosperms (Brown, 1999; Soltis & Soltis, 2004; Müller et al., 2006; Qiu et al., 2006). The biogeographical pattern is similar in both the two alternative relationships, as Nymphaeales are almost cosmopolitan (but are absent in New Zealand and New Caledonia). Bergerthorsson et al. (2004) reported massive horizontal transfer of mitochondrial genes into *Amborella* from other land plants (including three mosses).

2. Strasburgeria (Crossosomatales) (Fig. 1). The genus comprises one species, *Strasburgeria robusta*, endemic to New Caledonia. The affinities of this plant were formerly unclear and it was treated as the monotypic Strasburgeriaceae, but it is now known to be sister to another monotype, *Izerba* of northern North Island, New Zealand (Cameron, 2003). The two species form a clade in Crossosomatales with Geissolomataceae (monotypic) of South Africa and Aphloiacae (monotypic) of south-eastern Africa, Madagascar, the Mascarenes and the Seychelles (Stevens, 2009). This group, based around the Indian Ocean is sister to a neatly vicariant group centred around the northern Pacific: Crossosomataceae, Stachyuraceae, Guamatelaceae and Staphyleaceae.

As well as the genetic sequences that link *Strasburgeria* and *Izerba*, Cameron (2003) also noted the strikingly similar wood, the persistent sepals and the clawed petals of the two genera. In addition, personal observations made on material in the herbarium of the Institut de Recherche pour le Développement (IRD), Nouméa (January 2002), showed that the gynoecia are similar. The style in both is truncate, persistent and not clearly demarcated from the ovary, while the ovary in both has five longitudinal flanges and is star-shaped in cross section. The style of *Strasburgeria* is also sometimes more or less twisted, as in *Izerba*, although it shows no sign of the deflected apex seen in that genus. The gynoecium of the Cape endemic *Geissoloma* (Geissolomataceae) is similar and shows comparable torsion (Figure 31 in Dahlgren & Rao, 1969). In both *Strasburgeria* and *Izerba* the ovules are anatropous and descending, with the micropyles upwards and outwards (epitropous). Matthews & Endress (2005) also noted the presence of an aril (at least in the ovule) and other features which ally the two families, as well as features that link the two with *Geissoloma* (e.g. similar unicellular, T-shaped perianth hairs). There are differences between *Strasburgeria* and *Izerba*; for example, the fruit is indihiscent in the former and dehiscent in the latter, and *Strasburgeria* has a very high chromosome number, $2n = 500$, compared with $2n = 50$ in *Izerba* (Oginuma et al., 2006). Nevertheless, the two genera can easily be accommodated in one family. Xeronemataceae (Asparagales) is another plant family restricted to New Caledonia and New Zealand.

Fossil pollen (*Bluffopolis scabratus*) from the Cenozoic of New Caledonia, western and southern Australia, Tasmania and New Zealand is ‘directly comparable’ to *Strasburgeria* pollen (Cameron, 2003), although it is only half the size (Jarzen & Pocknall, 1993). As Cameron (2003, p. 428) concluded, this indicates that ‘the common ancestor of *Strasburgeria* and

![Figure 1](https://example.com/figure1.png) Distribution of Crossosomatales (from Stevens, 2009). Cro, Crossosomataceae; Gua, Guamatelaceae. Fossil pollen (*Bluffopolis scabratus*) attributed to *Strasburgeria* extends the range to western Australia, southern Australia, Tasmania and southern New Zealand.
Ixerba most likely evolved prior to the break-up of Gondwana’. Miocene leaf material from southern New Zealand shows a ‘good match’ with Strasburgeria (Pole, 2008), but was not compared with Ixerba.

3. Oncothecaceae (Fig. 2). This family, with Oncotheca balansae and Oncotheca humboldtiana in New Caledonia, and the Metteniusaceae of Costa Rica to Ecuador, form the first and second basal branches in the cosmopolitan clade Lamiales, Solanales and Gentianales (Fig. 2; González & Rudall, 2007; González et al., 2007). This topology indicates a trans-tropical Pacific sequence of initial differentiation events in a global ancestor: (i) New Caledonia versus the rest, and (ii) Colombia/Panama versus the rest. However, the statistical support is weak and the two groups may instead be sisters, giving a trans-tropical Pacific clade basal in a large group of asterids. Although the pattern is seldom discussed, trans-tropical Pacific affinities are common (e.g. Polygalaceae tribe Moutabeae, comprising Balgoya of New Caledonia, Eriandra of New Guinea and the Solomon Islands and three other genera of northern South America). The Pacific pattern in Oncotheca–Metteniusa contrasts with the Indian Ocean (Gondwana) affinity in Strasburgeriaceae and relatives.

The localities of Oncothecaeae and Metteniusaceae may reflect the Cretaceous emplacement of large igneous plateaus in the central Pacific and their subsequent dispersal to the west (the Hikurangi plateau of New Zealand, the Ontong Java plateau of the Solomon Islands, etc.) and to the east (plateaus of Colombia and the Caribbean) (Heads, 2009a). Many of the localities of Metteniusaceae occur west of the Romeral fault zone (running through Cali and Medellin), the boundary between autochthonous crust of the South American plate, to the east, and accreted terranes, to the west.

4. Phellinaceae (Asterales). This family comprises the genus Phelline, with 12 extant species in New Caledonia and records of fossil leaf cuticle in Miocene strata of southern New Zealand (Pole, 2010) (Fig. 3). The family is sister to Argophyllaceae (Argophyllum and Corokia), distributed in Queensland south to the ‘McPherson–Macleay Overlap’ (Heads, 2009a), Lord Howe Island, New Zealand, Chatham Islands and Rapa Island (van Balgooy, 1966). The two families are sister to the Alseuosmiaceae, of eastern Australia, New Guinea, New Caledonia and New Zealand (van Balgooy, 1993; Tirel, 1996; Kârehed, 2002).

Alseuosmiaceae and Argophyllaceae overlap in north-eastern Queensland, New Caledonia and New Zealand, but Alseuosmiaceae has a ‘centre of gravity’ to the west of Argophyllaceae, with records in western New Guinea and south-eastern Australia, and in New Zealand it only occurs west of the Alpine Fault (south to Mount Ellery, Jackson’s Bay; pers. obs.). The partial allopatry of the two families probably reflects initial vicariance. All three families of this Tasman/Antarctic clade are sister to each other (van Balgooy, 1966; van Balgooy & Fedorovitch, 1985), and both the Alseuosmiaceae and Argophyllaceae are sister clades to the Monimiaceae (van Balgooy & Fedorovitch, 1985; van Balgooy, 1993; 2000; van Balgooy & Hickey, 2002; van Balgooy & Craven, 2003; Zardini et al., 2010).
Coral Sea ‘Phelline complex’ occur together only in New Caledonia and, including the fossil material, in New Zealand.

In contrast, the related Stylidiaceae sensu lato comprises three genera, *Stylidium*, *Forstera* and *Donatia*, which all overlap in Tasmania and New Zealand (Fig. 4). This group shows significant allopatry with the *Phelline* complex as it is absent from New Caledonia, central New Guinea and central Polynesia, but does occur in Southeast Asia, Tasmania, the far south of New Zealand (Stewart Island and the sub-Antarctic islands) and Patagonia, where the *Phelline* complex is unknown.

The bulk of the Asterales comprises a clade with three subclades: (*Phelline* complex (Stylidiaceae sensu lato (Asteraeae + Goodeniaceae + Calyceraceae + Menyanthaceae))). The third subclade forms a very diverse, global group. (The phylogeny as indicated is from Kärhehed et al., 1999; Stevens, 2009, shows the three subclades as an unresolved trichotomy.) Thus the phylogeny of the whole group involved a world-wide ancestor that underwent: (i) a split between the *Phelline* complex, centred on New Caledonia/New Zealand terranes, and the remaining groups; (ii) a split between Stylidiaceae, centred on Tasmania/South Island terranes, and the remaining groups; (iii) subsequent regional overlap of the three clades; and (iv) differentiation within the groups. The high diversity of the *Phelline* complex in New Caledonia is correlated with the anomalous low diversity of Asteraceae there (only eight endemic species) and this pattern may be the direct result of phylogeny rather than ecology.

Other New Caledonian taxa that were formerly treated as endemic families include the following listed below.

5. *Paracryphia*. This genus comprises *Paracryphia alticola* endemic to New Caledonia; there are also records of fossil cuticle from the New Zealand Miocene (Pole, 2010) (Fig. 5). Until recently *Paracryphia* was regarded as the only member of Paracryphiales (Paracryphiaceae) but the family is now taken to include *Quintinia* of New Zealand, New Caledonia, eastern Australia, New Guinea and the Philippines. *Sphenostemon* of New Caledonia, north-eastern Queensland, New Guinea and Sulawesi is also closely related to, or part of, this clade (Bremer et al., 2004; Winkworth et al., 2008; Stevens, 2009). This south-west Pacific trio (Paracryphiaceae) is sister to the large clade Dipsacales (Dipsacaceae, Caprifoliaceae, Adoxaceae, Valerianaceae). Dipsacales are more or less cosmopolitan but
are notably absent in the indigenous floras of New Zealand, New Caledonia, the Bismarck Archipelago/Solomon Islands and the central Pacific. As Winkworth et al. (2008) suggested, a simple geographical split between the Paracryphiales and the Dipsacales seems likely. This implies a break between an eastern group centred around New Caledonia and a group with its diversity further west, a similar pattern to that seen in the break between the Phelline complex and the Stylidiaceae (Figs 3 & 4). Early divisions within the Dipsacales also took place in this general region; for example, *Viburnum* (160 species; Northern Hemisphere, South America, Asia) is one of the largest genera in the order and has its basal species (*Viburnum clemensae*) in Borneo (Winkworth & Donoghue, 2005). This does not mean that the species was ‘the first diverging clade’ in the genus (Jacobs et al., 2008, p. 428) – it is the same age as the clade it diverged from – but does indicate that the first division within the genus occurred around here.

6. *Canacomyrica.* This monotypic New Caledonian endemic genus has been treated in its own family (Doweld, 2000), but most authors place it in Myricaceae (Macdonald, 1989; Kubitzki, 1993; Carlquist, 2002). Recent molecular studies have retrieved it as sister to the rest of the family (Herbert et al., 2006). *Canacomyrica* is extant only in New Caledonia, but Eocene to Miocene pollen from New Zealand has been identified as belonging to this genus (Lee et al., 2001). The only other member of the family, *Myrica,* is widespread globally but is notably absent from New Caledonia, Australia, eastern New Guinea, New Zealand and southern South America.

7. The conifer *Austrotaxus* is another monotypic genus endemic to New Caledonia and is sometimes treated in its own family (Bobrov et al., 2004). Recent studies (Cheng et al., 2000; Price, 2003) showed it to be sister of the other Taxaceae *sensu stricto,* comprising *Pseudotaxus* (China) and *Taxus* (north temperate zone, south to the Philippines, Sulawesi and Mexico).

To summarize, the New Caledonian endemics cited here are either sister to widespread Northern Hemisphere or even global groups (*Amborella, Canacomyrica, Austrotaxus*), or form parts of Indian Ocean (*Strasburgeria*), Pacific Ocean (*Onoclea*) or Tasman/Coral Sea (*Phelline, Paracyphia*) groups that are sister to widespread Northern Hemisphere or global groups.

*Amborella,* the basal angiosperm, shows a ‘globally basal’ pattern. A similar case occurs in the orchid *Pachyplectron,* endemic to New Caledonia and basal in the virtually cosmopolitan subtribe Goodyerinae (Cribb et al., 2003). This does not mean that *Amborella* and *Pachyplectron* are the same age; the two genera are distributed on different terranes on Grande Terre (Aubréville et al., 1967–present; Heads, 2008a,b) and the island is a geological and biological composite.

A basal group is just a small sister-group and so its location does not indicate a centre of origin. The fact that the New Caledonia endemics have diverse sister-groups that are widespread globally but not on New Caledonia does not mean, as might be inferred, that New Caledonia is a centre of origin from which the widespread groups have migrated. But sister-group relationships do indicate that the endemics did not migrate recently to New Caledonia. These patterns also explain why so many familiar groups that are more or less cosmopolitan are strangely absent in New Caledonia – they are represented there by other, locally endemic taxa.

The direct relationship of many New Caledonian taxa with trans-tropical Pacific groups could be due to some New Caledonian terranes having originated in the central Pacific and subsequently colliding with New Caledonia. The Bismarck Archipelago is a similar case. Its biota is quite different from that of nearby mainland New Guinea, although the two land masses are now almost joined and probably will be in the near geological future. The biological differences can be attributed to the history of the Bismarck Archipelago basement, which formed thousands of kilometres away from mainland New Guinea in the central Pacific.

**THE NEW CALEDONIAN PALMS**

Palms are a conspicuous, well-studied group and the New Caledonian members are especially diverse, with 10 genera represented. The group is thus a good example for showing differentiation around New Caledonia in the south-west Pacific region. The molecular phylogeny presented by Baker et al. (2009, their Fig. 2) is followed here, along with the classification of Pintaud & Baker (2008).

The fan palm *Pritchardia* (subfamily Coryphoideae; Fig. 6a) is perhaps the rarest palm in the world, with just a few individual plants in southern Grande Terre (the three other lineages of New Caledonian palms, discussed below, are all widespread in Grande Terre). *Pritchardia* is sister to *Johannesteijsmannia* and *Pholidocarpus,* both in western Malesia.

The other New Caledonian palms make up a remarkable assemblage of nine genera (eight endemic) in the tribe Areceae (subfamily Arecoideae). Areceae range from Pemba Island, 50 km off mainland Tanzania, to the Pacific islands (Samoa). The distinctive western limit so close to the African mainland is seen in many widespread Indo-Pacific taxa (plant, bird and mammal examples are cited in Heads, 2006). The tribe Areceae comprises an ‘Indian Ocean clade’ which extends east to the Solomon Islands and Fiji but is not in New Caledonia, and a ‘Western Pacific’ clade which is very diverse in New Caledonia and other Pacific islands, and extends west to eastern Australia, Indonesia and Sri Lanka (Norup et al., 2006). The Indian Ocean and the Western Pacific clades are mainly vicariant, with secondary overlap around the margin of the Pacific plate. The basal group in the Western Pacific clade is *Loxococcus* of Sri Lanka, but this does not require the eastward dispersal that Norup et al. (2006) proposed, only an eastward sequence of differentiation. The New Caledonian genera have ‘invaded’ the region by evolving there, not as the result of nuts being blown or carried there from Sri Lanka.

The New Caledonian Areceae belong to three separate groups of the Western Pacific clade. (Baker et al., 2009): (1)
the "Clinosperma" clade is in New Caledonia, Vanuatu/Fiji and the southern Ryukyu Islands near Taiwan (Fig. 6b); (2) the "Archontophoenix" clade is in New Caledonia, eastern Australia, New Guinea, the Bismarck and Louisiade Archipelagos and Bougainville Island (northern Solomon Islands) (Fig. 6c); and (3) the "Basselinia" clade is in New Caledonia, Lord Howe and Norfolk Islands, New Zealand, Vanuatu, Fiji, the Solomon Islands and New Britain (Fig. 6d). Thus the four clades of palms in New Caledonia have relatives in different places: western Malesia ("Pritchardiopsis" clade), Ryukyu Islands ("Clinosperma" clade), western Tasman/Coral Sea ("Archontophoenix" clade) and eastern Tasman/Coral Sea ("Basselinia" clade). The simplest explanation for this allopatry is an origin of the groups by vicariance, followed by overlap caused by tectonic juxtaposition of terranes in New Caledonia, local range expansion, or both.

This process of vicariance is reflected in aspects of the morphology. Norup et al. (2006) stressed that several genera in Areceae have no unique characters but are distinguished instead by different 'combinations of widespread character states'. This phenomenon is common in all groups – Reinert et al. (2006) described it in mosquito genera, to cite just one detailed study – although it is seldom acknowledged as a general principle. This may be because it is incompatible with the idea of hierarchical phylogeny and the idea that taxa are defined by 'uniquely derived characters'. Recombination of characters would not be expected if every new mutation, form or taxon arose at a centre of origin and spread from there by

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**Figure 6** Affinities of the New Caledonian palms. (a) Distribution of the "Pritchardiopsis" clade. (b) Distribution of the "Clinosperma" clade ("Clinosperma" includes Lavoixia and Brongniartikentia, "Cyphokentia" includes Moratia). (c) Distribution of the "Archontophoenix" clade ("Kentiposis" includes Mackee). (d) Distribution of the "Basselinia" clade ("Basselinia" includes Aloschmidia). Taxonomy from Pintaud & Baker (2008), distributions from Uhl & Dransfield (1987), Dowe (1989), Dowe et al. (1996), Fuller (1999) and Pintaud et al. (2001).
physical movement. It would be expected if vicariant groups evolved as recombinations of widespread ancestral characters already distributed over different, broad sectors of the ancestral range before the evolution of the modern groups (cf. Heads, 2009c). It is well known that parallel evolution is ubiquitous and recombination of characters probably takes place by parallel evolution in the populations of a given biogeographical sector.

In the New Caledonian palms, the distributions of the Pritchardiopsis and Clinosperma clades are notable for their large disjunctions to the north-west. Another palm, Clinostigma, has a similar pattern: Samoa/Fiji, Vanuatu, Solomon Islands, New Ireland, Caroline and Bonin islands, skirting mainland New Guinea to the north. Uhl & Dransfield (1987, p. 437) described this as a 'great arc...a most interesting distribution'. In dispersal interpretations, the arcs would be regarded as routes of migration, perhaps along 'stepping-stone' islands. But the arcs are interpreted here instead as allopatric sectors and fragments of formerly widespread ancestral ranges, with central Pacific taxa having survived as metapopulations on ephemeral volcanic islands. Pritchardiopsis, for example, is represented in neighbouring Vanuatu by Licuala, in eastern Australia by Livistona, and in the central Pacific by Pritchardia (Fig. 7). Pritchardia has its sister-group, Copernicia, in Cuba (20 species), Hispaniola (two species) and South America (three species). These genera belong to tribe Trachycarpeae (18 genera) which is itself largely allopatric with Phoeniceae (the date palms), its sister-group. Thus the evolution of the two tribes has involved the allopatric break-up of a more or less global ancestor into Phoeniceae, based around the Atlantic and Indian oceans, and Trachycarpeae based around the Pacific, with subsequent secondary overlap along the Tethys sector. Within the tribes, differentiation of the genera (cf. Pritchardia, Pritchardiopsis, etc.) has also been allopatric. The central Pacific representative, Pritchardia, indicates evolution on and around the large igneous plateaus emplaced in the Cretaceous. These include many flat-topped seamounts that originally formed high islands. Other Cretaceous volcanics that Pritchardia may have occupied include the Line Islands, an archipelago 4000 km long (between south-eastern Polynesia and Hawaii) in which all the islands are now reduced to atolls (Heads, 2009a).

In Australia, Crisp et al. (2010) tested whether Livistona was a Gondwana relict or a Miocene immigrant and relied on fossil-calibrated dates. These are minimum ages and can only eliminate later events as relevant, not earlier ones. Despite this, the minimum dates were illogically transmogrified into maximum ages, used to rule out early vicariance, and then cited as support for a centre of origin/dispersal model. This is not accepted here.

The pattern shown in palms, with different New Caledonian clades having sister-groups in different areas, also occurs in other groups. New Caledonian Diospyros (Ebenaceae) provides a good example (Duangjai et al., 2009).

One clade (Diospyros balansae, etc.) has its sister in eastern Australia (Cairns to Sydney), indicating a Cretaceous split with the opening of the Tasman Sea. This clade is basal to a global group (the entire genus except for Diospyros maingayi and Diospyros puncticulosa). A second clade (Diospyros calciphila, etc.) has its sister in the Hawaiian islands, indicating evolution around the central Pacific igneous plateaus. A third clade comprises Diospyros fasciculosa of New Caledonia and its sister Diospyros ehretioides of Southeast Asia (cf. the affinities of the fan palm Pritchardiopsis), also Australia, Vanuatu and Fiji. The fourth clade (Diospyros olen) has its sister in the Solomon Islands, Vanuatu, Fiji, Tonga and Samoa. This is explained by terranes accreting in New Caledonia from the north-east (Heads, 2008a).

The largely allopatric distribution of the four clades can be explained by original vicariance of a widespread ancestor followed by juxtaposition in New Caledonia of the four clades with terrane accretion. The only evidence for local range

**Figure 7** Distribution of the Trachycarpeae and Phoeniceae (Arecaceae). Line ‘a’ indicates the affinity of Pritchardiopsis with western Malesian genera. Line ‘b’ indicates the affinity of Pritchardia with Copernicia of Cuba, Hispaniola and South America. †Areas with fossil records only. Distributions from Uhl & Dransfield (1987).
expansion is in *D. ehretioides* and, in all four clades, within New Caledonia itself. The overall process is one of juxtaposition rather than radiation.

**EVOLUTIONARY ECOLOGY OF THE TRACHYCARPEAE**

In traditional analyses geographical centres of origin are assumed and their location is calculated with reference to the location of centres of diversity, `basal’ clades and grades, minimizing the number of founder dispersal events, and so on. In the same way, an ecological centre of origin or ancestral niche of a group is often estimated and the group is proposed to have spread from there into other niches. In contrast, vicariance analysis assumes that the ancestor of a group was already widespread and so may have already occupied a wide ecological range before the modern groups existed. In the palm tribe Trachycarpeae, the New Caledonian *Pritchardia* occurs on soils derived from ultramafic rock. Other members include the Central American *Brahea* and the Asian *Maddockia*, *Guihaia*, *Rhapis* and *Trachycarpus*, all on limestone and karst (the ecological data cited here for palms are from Uhl & Dransfield, 1987). The close physiological, ecological and tectonic relationship between limestone and ultramafic floras is examined in more detail elsewhere (Heads, 2008a). Both rock types characterize belts of subduction and accretion, where taxa of uplifted coral reefs are pre-adapted for life on obducted ultramafic terranes. The ecological ranges of the other genera of Trachycarpeae are as follows.

1. *Pritchardia*: rain forest (Hawaii), uplifted coral reef near sea (other Pacific Islands). In Fiji, plants occur only on limestone islets and limestone lagoon cliffs, where they grow right to the edge of the sea and are subject to salt spray (Heads, 2006).
2. *Johannesteijsmannia*: undisturbed, primary rain forest; kerangas heath forest (*Johannesteijsmannia altifrons*).
4. *Licuala*: mostly rain forest; *Licuala calciophila* is a calcicole, *Licuala spinosa* occupies the landward fringe of mangrove, *Licuala paludosa* is in peat swamp forest.
5. *Livistona*: rain forest, freshwater and peat swamp forest, montane forest, woodland, savanna, permanent water bodies in desert.
7. *Serenoa* (south-eastern USA): pinelands, prairies, coastal sand-dunes, often forming dense swards; the architecture is unusual: `stem subterraneean and prostrate or surface creeping’. Similar plagiotropic axes occur in many mangroves, for example the mangrove palm *Nypa*, with `prostrate or subterranean’ stems.
8. *Rhapidophyllum*: low, moist to wet areas with rich humus, calcareous clay or sandy soils in woods or swamps. In grottos, limestone sinks, shaded pinelands, but usually associated with limestone.
9. *Copernicia*: savanna, woodland; *Copernicia prunifera* forms vast stands in South America in areas subject to annual flooding.
10. *Colpothrinax*: open, sandy country, open forest on ridges.
12. *Chamaerops* (western Mediterranean): sandy or rocky ground usually near the sea.

The sister tribe of Trachycarpeae is Phoeniceae, with only one genus, *Phoenix* (including the date palm). Species occur around oases and watercourses in semi-arid areas with a few in tropical monsoon areas. *Phoenix paludosa* is in perhumid parts of Asia where it is confined to the landward fringe of the mangrove.

To summarize, Trachycarpeae/Phoeniceae occupy a series of habitats that is typical of tropical groups: back-mangrove, limestone/ultramafic sites, monsoon forest, savanna, swamp forest, rain forest, montane forest. This may have resulted from a weedy group of back-mangrove and associated habitats spreading through inland areas with the advance of Cretaceous seas, later becoming stranded there with the retreat of the seas and onset of Cenozoic orogeny (cf. Heads, 2006). It is often suggested that the biogeography of a group is determined by its ecology, but in the model proposed here a group’s current ecology is determined by its location. Populations derived from a widespread Trachycarpeae/Phoeniceae ancestor have ended up being stranded in areas that became desert in Arabia, flood plains in South America, atolls in the Pacific, and rain forests in Southeast Asia.

**CONCLUSIONS**

New Caledonian terranes derived from the west (Gondwana, i.e. Australia) include the `basement’ terranes. Those derived from the east (Pacific) include the Loyalty Ridge, formerly an active island arc. This history is reflected in the composite nature of the New Caledonian biota, which shows connections with areas to the west (Figs 1, 5 & 6c) and to the east (Figs 2 & 6d). Affinities with taxa to the north-west (Figs 6a & 7) may reflect evolution associated with the former Tethys basins. The old Pacific plate/Indian plate margin ran through New Zealand, New Caledonia and New Guinea, and so this arc represents both a tectonic and a biogeographical edge of intercontinental significance.

In the dispersal paradigm, the standard questions asked for any group in an area are: `Where is its centre of origin?’ and `Which route and which means of dispersal did the group use to disperse to the area?’ For example, Keast (1996) proposed the `fundamental question’: `When, and how, did the archaic southern elements reach New Caledonia?’. It is suggested here that neither the `archaic’ nor any other indigenous elements ever `reached’ New Caledonia using `means of dispersal’. They evolved there, or rather on arc and intraplate islands associated with the different component terranes. The groups differentiated out of already widespread ancestors before the terranes were assembled as modern New Caledonia in the Jurassic and the Eocene. The different global patterns involving New Caledonian taxa reflect areas around which differentiation took place, not centres of origin.

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REFERENCES


Heads, M. (2008b) Biological disjunction along the West Caledonian Fault, New Caledonia: a synthesis of molecular


Oginuma, K., Munzinger, J. & Tobe, H. (2006) Exceedingly high chromosome number in Strasburgeriaceae, a


BIOSKETCH

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