Biogeographical affinities of the New Caledonian biota: a puzzle with 24 pieces

Michael Heads*

Buffalo Museum of Science, 1020 Humboldt Parkway, Buffalo, NY 14211, USA

ABSTRACT

Aim The distributions of many New Caledonian taxa were reviewed in order to ascertain the main biogeographical connections with other areas.

Location Global.

Methods Panbiogeographical analysis.

Results Twenty-four areas of endemism (tracks) involving New Caledonia and different areas of Gondwana, Tethys and the central Pacific were retrieved. Most are supported by taxa of lower and higher plants, and lower and higher animals.

Main conclusions Although parts of New Caledonia were attached to Gondwana for some time in the mid-Cretaceous, most of the New Caledonian terranes formed as oceanic island arcs and sections of sea floor bearing seamounts. The flora and fauna have evolved and survived for tens of millions of years as metapopulations on ephemeral islands. Later, the biotas were juxtaposed and fused during terrane accretion. This process, together with the rifting of Gondwana, explains the biogeographical affinities of New Caledonia with parts of Gondwana, Tethys and the Pacific.

Keywords

Australia, New Caledonia, New Guinea, New Zealand, panbiogeography, Solomon Islands, tectonics, Vanuatu, vicariance.

*Correspondence: Michael Heads, Buffalo Museum of Science, 1020 Humboldt Parkway, Buffalo, NY 14211, USA.
E-mail: michael.heads@yahoo.com

INTRODUCTION

The aim of this paper is to document the biogeographical connections that New Caledonian taxa show with other regions. Distribution patterns within New Caledonia and the tectonic development of the country have been discussed in more detail elsewhere (Heads, 2008a,b, 2009a,b, 2010a). The biological and geological history of New Caledonia has involved the fusion of different types of structures (island arcs, sections of ocean floor, seamounts) that were either Gondwanan or central Pacific in origin. New Caledonia, New Guinea and New Zealand all straddle past or present plate boundaries and all three are geological and biological 'hybrids'. Affinities with the lands to the west (Gondwana) are understood more easily than those to the east (central Pacific). The Cretaceous emplacement of large igneous plateaus in the central Pacific and their subsequent dispersal eastward (to America) and westward (to the western Pacific) has been important for terrestrial biogeography, as many islands (now seamounts) existed on the plateaus. Island chains in the central

Pacific (east of Fiji) were formerly interpreted as the result of mantle-plume hot spots, but many geologists now attribute them to stress-induced propagating fissures. This process would enhance the opportunities for the long-term survival and evolution of central Pacific taxa more or less *in situ*, as metapopulations on ephemeral islands.

METHODS OF ANALYSIS IN HISTORICAL BIOGEOGRAPHY

Spatial analysis of phylogeny

In most modern studies, the spatial analysis of phylogeny has been based on the idea of a centre of origin, and so authors employ programs, such as DIVA, that will usually find one (for example, at the location of a basal grade). Nevertheless, there is no logical necessity for interpreting a phylogeny as dispersal from a centre of origin. Grandcolas *et al.* (2008, p. 3311) argued that 'within certain New Caledonian groups, multiple species are nested within larger clades with taxa from Australia,

New Zealand or New Guinea, calling for explanations in terms of recent dispersal [to New Caledonia]'. But although the location of a basal grade is often assumed to be the centre of origin, the phylogeny (Australia (Australia (Australia + New Caledonia))), for example, would also result from differentiation within a widespread ancestor already in Australia and New Caledonia, with basal splits occurring within Australia (and possibly followed by secondary, local overlap there). This principle is discussed elsewhere (Heads, 2009c).

Chronological analysis of phylogeny

Many authors use a methodology that will provide young dates for clades. One popular method is to use the age of islands with endemic taxa to calibrate a clock. Islands form at subduction zones and other tectonic structures that continuously produce islands, and so using individual islands to date clades endemic to them is almost guaranteed to give clade ages that are much too young. Equating the age of the clade with its oldest fossil also underestimates ages (Heads, 2005a,b).

Grandcolas et al. (2008) suggested that 'Dating [of taxa] can be obtained from a molecular hypothesis with careful calibration of substitution rates [e.g. using fossils] or a geological hypothesis based on some physical measurements (e.g. K–Ar dating for some islands).' With the first method, instead of 'careful calibration', most authors 'transmogrify' fossil-calibrated molecular clock dates (minimum ages) into absolute ages and then use these to rule out earlier events (vicariance) instead of later ones (Heads, 2005a,b, 2010b). For example, Richardson et al. (2004) calibrated phylogenies based on fossil material, and early in their paper 'emphasized that all timings are therefore minimum ages'. Nevertheless, following transmogrification, they were able to conclude that 'most lineages within Annonaceae are too young to have had their distribution patterns influenced by break-up of previously connected Gondwanan landmasses … long-distance dispersal appears to have played a more significant role … than had previously been assumed'. A subsequent study of New Caledonian Annonaceae by Saunders & Munzinger (2007, p. 502) accepted the transmogrification. The authors wrote that 'The exceptionally young age of only 3.6–4.8 (±1.5) Mya recently postulated for Goniothalamus by Richardson et al. (2004) clearly indicates that the genus cannot represent an ancient lineage derived before the separation of New Caledonia from Australia.' A fossil-calibrated date is a minimum age and cannot rule out an earlier origin of the taxon, only a later one.

Many authors have accepted the idea that fossil ages are minimum ages, but only in theory and not in practice. They may accept the minimum (oldest fossil) ages as approximately accurate, and add a margin of, say, a few million years. But this misunderstands the nature of 'minimum age' – the extent of the margin is completely unknown. It is not at all unusual for fossils to turn up that are tens of millions of years older than the previously oldest known fossil. Authors often accept the oldest fossil dates as a working basis, an interim measure, and agree that when older fossils are discovered new calculations of

the chronology can be made. But this overlooks the point that 'transmogrification' is flawed. Authors argue that they use it because there is no other alternative. In fact, there are several methods for establishing chronology that do not use fossils at all (Heads, 2005a). The method favoured here relies on the correlation of biogeographical patterns with tectonic events.

With respect to K–Ar dating, even apart from problems with resetting and argon leakage that result in ages that are too young, this method gives the age of the rock, not the age of the island. Younger eruptions cover older ones and older rocks may also be removed by erosion or subsidence as the island grows. But in any case, the age of individual islands is irrelevant to the age of the taxa endemic there and many taxa have been shown to be older than the island they are endemic to (see 'Metapopulations and dispersal', below).

'Dispersal': one word, two distinct concepts

With the exception of some colonial taxa, all individual organisms have reached their present position by dispersing there. The organism's new position may lie within the former range of the taxon or it may lie outside it and represent a range expansion. This normal movement ('ecological dispersal') is seen every day. Some biogeographers have proposed that a similar process of physical movement also explains biogeographical patterns of allopatry, endemism and so on, but this is more problematic. In particular, this second process ('biogeographical dispersal') involves differentiation, which does not occur in the first process, and so hypotheses of founder dispersal (dispersal over barriers) and founder speciation (genetic revolutions) have had to be added.

Dispersalist theorists accept both types of dispersal as occurring in nature, whereas vicariance theorists accept only the first. But in any case it is important to distinguish between the two processes and many authors have failed to do this. For example, the inability to distinguish between contiguous range expansions (normal movement) and across-barrier dispersals is one of several serious drawbacks with DIVA (Kodandaramaiah, 2010). This conflation of the two processes is a key aspect of dispersal biogeography and is the basis of the confusing criticism that panbiogeography denies 'dispersal'. This paper accepts normal ecological movement (including range expansion and overlap of taxa) and allopatric differentiation. It does not accept the process of 'founder dispersal/founder speciation'.

Metapopulations and dispersal

Oceanic island and reef taxa exist as metapopulations, constantly dispersing from older islands to younger ones as these become available and older ones subside. Oceanic islands do not develop at random locations but usually form in the vicinity of other islands, around persistent tectonic features such as subduction zones and propagating fissures. The dispersalist model of Pacific biogeography argues that because individual volcanic islands were not joined, vicariance is impossible (e.g. van Balgooy et al., 1996). Thus it rejects

ordinary, local dispersal among populations but supports extraordinary, long-distance dispersal (founder speciation). In contrast, the model used here accepts local dispersal among populations and vicariance between metapopulations, but denies founder speciation. The metapopulation in a region may be much older than any of the individual, ephemeral islands that it survives on.

This model indicates that evolution does not proceed by founder speciation but by repeated cycles involving phases of vicariance of metapopulations causing general allopatry followed by phases of overlap (the overlap is often only marginal). There is no founder dispersal or centre of origin and the biogeographical phases are determined not by chance but by events in Earth history.

Modern centre of origin/dispersal theory

Modern versions of centre of origin/dispersal theory use clocks calibrated with fossils and island age to give young dates and use dispersal–vicariance analysis to find a centre of origin. This approach has proposed that nearly all biogeographical patterns are pseudopatterns as they are all held by groups that evolved at different times and so are the result of repeated chance dispersal (cf. Wen & Ickert-Bond, 2009); community-wide allopatry caused by vicariance is not accepted. The only exceptions permitted are those required for purposes of calibration, as in the case of divergence at the Isthmus of Panama.

In a recent example of the neodispersalist approach, Jønsson et al. (2010) studied the Asian–Pacific passerine family Pachycephalidae that includes three species on New Caledonia. The authors adopted a centre of origin model and so used an appropriate program (DIVA). They found that the family 'clearly' originated in the Australo-Papuan region, but this is simply a consequence of using a centre of origin program. Instead of New Guinea being the centre of origin for Pachycephala, with long-distance colonizing flights to Samoa and New Caledonia, New Guinea can be interpreted as a centre of differentiation in a widespread ancestor. Jønsson et al. (2010) calibrated a molecular clock using endemics on very young Indonesian islands near active plate margins. They concluded it is 'fairly clear' that much of the diversity in Pachycephala 'was generated recently, probably in the Pleistocene' (p. 252), but this result simply reflects the calibration method. The authors admitted the calibration is 'complicated by the possibility of recently submerged islands in such a dynamic region', and admitted that the problem is 'impossible to remedy'. Island age is probably not suitable for calibration and other methods should be used.

Data selection in biogeographical analysis

Sanmartín & Ronquist's (2004) analysis of Southern Hemisphere biogeographical patterns included New Caledonian groups and has been widely cited. The authors wrote that 'recent methodological developments have made it possible to study complex biogeographical patterns in much more detail than previously' (p. 217). The method used by Sanmartín & Ronquist (2004) required well-sampled, fully resolved phylogenies and they made a thorough search of the literature for these. Nevertheless, comparatively few were found and so there is a statistical problem. For example, in their analysis of New Zealand and New Caledonia the authors concluded: 'our results … do not support the notion of a common relict late Cretaceous Gondwanan biota in the two land masses' (p. 240). This was because none of the sampled plant or animal taxa showed New Zealand and New Caledonia as sister areas. The authors explained any affinities between the two areas as due to dispersal between the two areas rather than vicariance of a New Caledonia/New Zealand group from, say, an Australian one. But this conclusion has little support as their sample of taxa was so small. The authors themselves acknowledged 'The shortcomings of studies based on only a few groups and the necessity of large data sets in separating general biogeographical patterns from distributional noise…' (p. 217).

Methods used in this paper

The advantages of well-sampled, fully resolved phylogenies are obvious, but there are even fewer of these available for smaller regions, such as New Caledonia and the surrounding islands, than there are for larger regions such as the Southern Hemisphere. As in Sanmartín & Ronquist's (2004) study, the panbiogeographical method used in this paper is based on a survey of published accounts of taxa, but all available accounts were examined whether or not they provided fully resolved phylogenies or indeed any statistical analysis of the taxonomy. (Of course, detailed studies were included wherever available.) The hypothesis here is that by including traditional accounts, the potentially lower quality of some of the data would be more than compensated by the large number of data that would become available. Hundreds of thousands of collections have been made from the Pacific islands and identified more or less accurately, but although only a minute fraction of these have been included in a detailed phylogenetic study it is already evident that a New Zealand–New Caledonia distribution, for example, is a standard pattern seen in taxa of different groups (see section 11, New Caledonia–New Zealand, below).

Many taxonomic accounts attribute a different species to each of the different Pacific archipelagos, including New Caledonia. These contribute no information on the affinities of the New Caledonian taxon and so are not cited in this paper. Studies that propose a sister-group relationship between a New Caledonian endemic and a world-wide clade also provide no geographical information and are not cited (they are discussed elsewhere; Heads, 2009a). In contrast, any studies which do link a New Caledonian population or taxon with a particular area are cited, along with the geographical affinity. In this study it is accepted that the biogeographical patterns are real and that spatial correlation of these with tectonic events provides a better base for calibrating the time-course of evolution than either oldest fossils or island ages (cf. Heads, 2010b).

BIOGEOGRAPHICAL AFFINITIES OF THE NEW CALEDONIAN BIOTA

Affinities with Australia and New Guinea are relatively well known and have often been explained by dispersal. Affinities restricted to the east, including central Pacific endemism, are discussed less often. Many of these tracks are poorly known, for example van Steenis (1981, p. 248) described the distribution of *Phyllanthus bourgeoisii* (Phyllanthaceae) in New Caledonia and New Guinea (section 12, New Caledonia–(Rennell Island)–New Guinea, below) as 'most peculiar' and 'an unusual distribution; it should then also occur in east Australia'. Achille (2006) described the New Caledonia–Vanuatu connection (section 15, New Caledonia–Vanuatu, below) as rare and Boyer *et al.* (2007) suggested that a connection between New Caledonia and northern South America (section 24, New Caledonia (± south-west Pacific)–South America, below) had not been proposed before. If a biogeographical distribution pattern is unusual this is often taken as evidence for chance dispersal and so it is important to establish which patterns are in fact shown by many groups.

A review of the literature revealed 24 distribution patterns that involve New Caledonia and other regions. Brief discussions of these are given below and documentation of the taxa defining each one (lower plants, seed plants, invertebrates and vertebrates) is given in Appendix S1 in the Supporting Information. Unless otherwise stated, records of plants are from Aubréville *et al.* (1967–present) and *Australia's virtual herbarium* (Council of Heads of Australasian Herbaria, 2009), while records of birds are from Dickinson (2003).

1. New Caledonia–south-west Indian Ocean

Many New Caledonian and other south-west Pacific taxa belong to groups that are based around the Indian Ocean. This often involves a direct, disjunct relationship between New Caledonia and the south-west Indian Ocean (especially Madagascar and South Africa). An example is *Cunonia* (Cunoniaceae), restricted to New Caledonia and South Africa (Fig. 1; Pillon *et al.*, 2008). Discussing an example in *Geniostoma* (Loganiaceae), Conn (1980) felt that 'no satisfactory explanation has been given' for the floristic similarities of Madagascar/Mascarenes and New Caledonia. Crisp *et al.* (1999) also acknowledged the disjunctions, describing them as 'rather bizarre'.

Another example is *Acridocarpus* (Malpighiaceae), which comprises about 30 species of Africa and Madagascar, and one disjunct species endemic to New Caledonia (sister to two Madagascan species). Davis *et al.* (2002) used an Oligocene fossil species of Malpighiaceae to calibrate a molecular clock for the genus and they dated the Madagascar–New Caledonia affinity at 15–8 Ma. After transmogrifying this minimum age into a maximum age, they concluded that the affinity evolved 'well after any known land route was available between these two areas'. Relying on this transmogrified date led them to infer a long-distance dispersal event from Madagascar to New Caledonia.

2. Tethyan affinities: New Caledonia–Mediterranean

Manconi & Serusi (2008) mapped the lithistid sponge *Neophrissospongia* (Fig. 1) and proposed that it 'confirms the existence of a biogeographic track', representing 'the remnants of an ancient Tethyan marine fauna' (p. 79). This and one other lithistid sponge (see Appendix S1) were the only examples of a New Caledonia–Tethyan affinity found in the present study. Nevertheless, other cases can be predicted as Australian and New Zealand taxa often show affinities with groups in localities such as Afghanistan and the Mediterranean [examples include clades in Cucurbitaceae (Schaefer *et al.*, 2008) and Caryophyllaceae (Smissen *et al.*, 2003)].
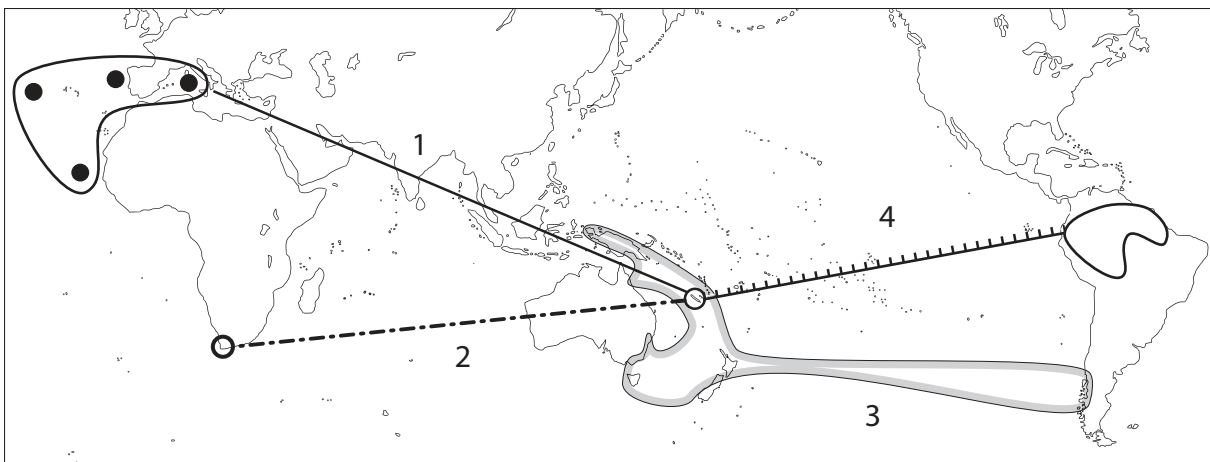

Figure 1 Some intercontinental connections of New Caledonian taxa: 1, the sponge *Neophrissospongia* (from Manconi & Serusi, 2008); 2, *Cunonia* (Pillon *et al.*, 2008); 3, one of the two main clades of Atherospermataceae: *Atherosperma*, *Dryadodaphne*, *Laurelia* and *Nemuaron* (Renner *et al.*, 2000); 4, *Montrouziera* of New Caledonia and its relatives in America (phylogeny from Gustafsson *et al.*, 2002; Sweeney, 2008; distributions from Global Biodiversity Information Facility, 2010).

3. Southern South Pacific: Australia–New Zealand–New Caledonia–southern South America

In one example of this pattern, the main clade of Atherospermataceae (Fig. 1), Renner *et al.* (2000) wrote that 'Calibration with a [fossil] pollen-based minimal family age of 90 MY … implied arrivals of *Laurelia novae-zelandiae* in New Zealand at ∼ 33 MYA and arrival of *Nemuaron* in New Caledonia at ∼ 25 MYA.' These dates are in fact estimates of minimum ages, as they are based on fossil calibrations. 'Arrival' is assumed in a dispersal model, but the South Pacific-based Atherospermataceae/Gomortegaceae are sister to an Atlantic group, the Siparunaceae of tropical America and West Africa, indicating allopatric evolution at family level between the South Pacific and Atlantic clades, as well as at generic level.

The tribe Adeliini of tenebrionid beetles is a Pacific group distributed in Australia (25 genera), New Zealand (9), New Caledonia (8) and Chile (4) (Matthews, 1998). The probable sister group is the Indian Ocean tribe Laenini of Sri Lanka, India, Madagascar and southern Africa, and together the two groups form what Matthews described as 'a remarkably complete Gondwanan pattern'. After discussing relevant geology, Matthews concluded: 'All these [distribution] facts taken together leave no doubt that the present distribution of the two tribes is the result of vicariance and not recent dispersal.'

4. Coral Sea (New Caledonia, north-eastern Queensland, Papuan Peninsula, Solomon Islands)

The Coral Sea and Tasman Sea together form one of the world's most important biogeographical nodes (Heads, 2004, 2009a). In the tree family Cunoniaceae, widespread in tropical and Southern Hemisphere regions, the basal group is *Spiraeanthemum* s. lat. (Fig. 2; Pillon, 2008). The two main clades in the genus occur, respectively, around the Coral Sea and along the outer Melanesian arc (track 19 below), with overlap in New Caledonia. *Fontainea* (Euphorbiaceae; Fig. 3) is another example, with its relatives largely vicariant to the west, south and east. In a similar pattern, the clade comprising *Lenbrassia*,
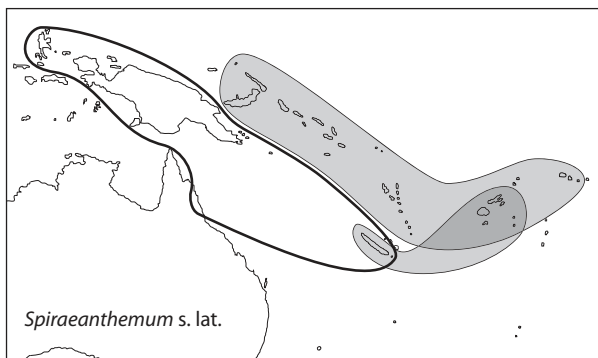
Figure 2 *Spiraeanthemum* s. lat. (Cunoniaceae; from Pillon *et al.*, 2009). *Spiraeanthemum densiflorum* group (Coral Sea–New Guinea); *S. brongniartianaum* group (Fiji–New Caledonia) and its sister *Spiraeanthemum* s. str. (outer Melanesian arc).
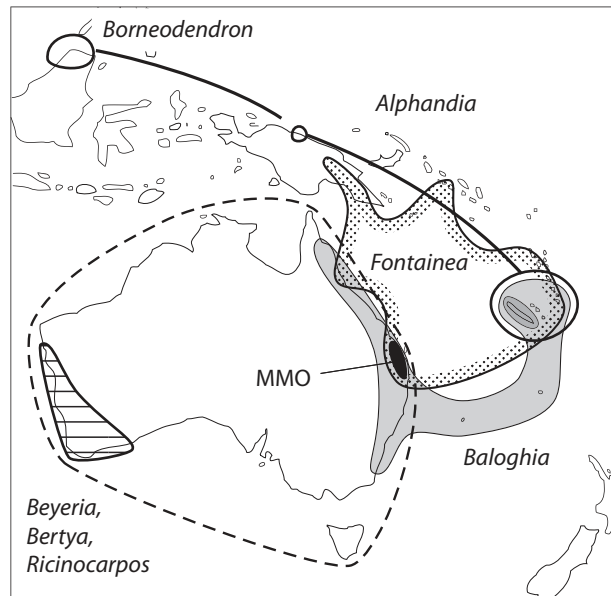
Figure 3 *Bertya*, *Beyeria* and *Ricinocarpos* (Australia) form a clade sister to *Baloghia*, *Fontainea* (sisters) and *Borneodendron* (Euphorbiaceae; Avé, 1984a,b; Wurdack *et al.*, 2005; K.J. Wurdack pers. comm., 15 May 2008). *Alphandia* (New Caledonia–New Guinea) and the New Caledonian endemics *Myricanthe* and *Cocconerion* were not sampled but probably belong here also. The sister of this whole group is *Reutealis*: Philippines, plus *Aleurites*: India to Polynesia including Hawaii (often cultivated, original distribution unclear). All these genera comprise the tribe Ricinocarpeae. The centres of diversity for *Beyeria* (south-western Australia), *Fontainea* (McPherson-Macleay Overlap) and *Baloghia* (New Caledonia) are indicated.

Negria and *Depanthus* (Gesneriaceae; Fig. 4) is allopatric, with its relatives to the west and east.

5. Tasman Basin

Many taxa are centred around the Tasman Basin and are absent from apparently suitable montane areas further north in the Solomon Islands and New Guinea. The only parasitic gymnosperm, *Parasitaxus* (Podocarpaceae), is endemic to New Caledonia and is related to *Lagarostrobos* (including *Manoao*; Kelch, 2002) of New Zealand and Tasmania (Sinclair *et al.*, 2002). The monocot family Campynemataceae, one of the three clades of the large order Liliales, comprises *Campynema* of Tasmania and *Campynemanthe* of New Caledonia (Kubitzki, 1998; Fay *et al.*, 2006).

6. New Caledonia–Australia

Many New Caledonian taxa show clear affinities with Australian groups, although no examples of taxa found in all regions of Australia and New Caledonia have been found. Most Australian/New Caledonian groups are absent in, for example, south-western Australia, Tasmania or the Loyalty Islands. In many taxa, eastern Australia is more closely related to New
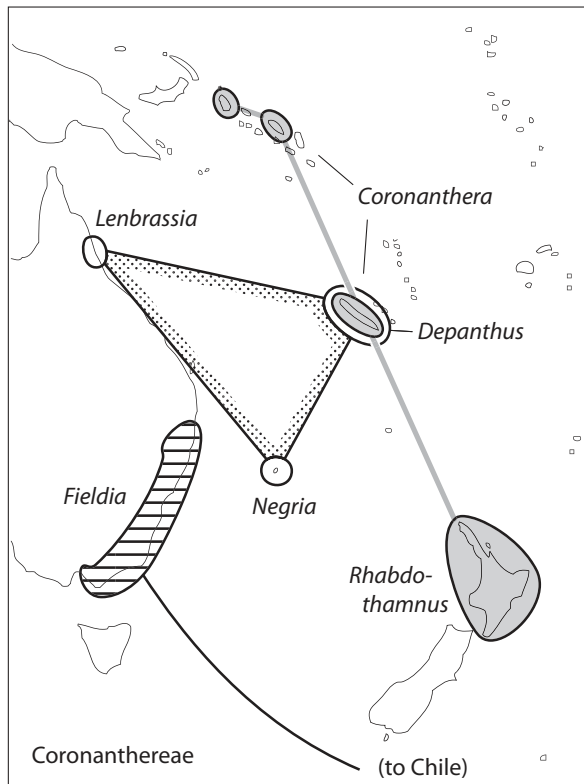
Figure 4 Coronanthereae (Gesneriaceae). The tribe also includes *Mitraria*, *Asteranthera* and *Sarmienta* of central Chile. *Titanotrichum* of Okinawa, Taiwan, and adjacent China is also involved although its exact position is unclear. Coronanthereae are sister to the large New World group Gesnerioideae. (Phylogeny from Wang *et al.*, 2004; and Smith *et al.*, 2006; distribution from van Balgooy, 1984.)

Caledonia than to western Australia. For example, the regional members of the *Allothereua/Parascutigera* clade of centipedes have a phylogeny (south-western Australia (north-western Australia (eastern Australia + New Caledonia))) (Edgecombe & Giribet, 2009).

Australia–New Caledonia affinities are often explained by dispersal from Australia. In the sandalwood genus *Santalum* (Santalaceae), widespread in the Pacific, Harbaugh & Baldwin (2007, p. 1031) wrote that 'A well-supported basal grade of Australian taxa indicates an origin of the genus on that continent. Multiple long distance dispersal events must be postulated to account for the current natural distribution of *Santalum* across the Pacific.' The idea that a basal grade occurs at the centre of origin and that the affinities represent dispersal events is not accepted here (see Methods). Instead, it is emphasized that the three clades in the main group of *Santalum* are allopatric in, respectively, northern Australia, New Caledonia and Vanuatu; southern Australia, New Guinea and Hawaii; and the Bonin Islands, Hawaii and south-eastern Polynesia.

In another example, Nyári *et al.* (2009) found that the passerine *Rhipidura* subgen. *Rhipidura* has a phylogeny (New Guinea (New Caledonia, Vanuatu, Fiji (south-eastern Solomon Islands (south-western Solomon Islands (New Caledonia,

Solomon Islands, Vanuatu (Australia, New Zealand)))))). There is a basal grade in the islands and so the authors interpreted the phylogeny as representing a recolonization of Australia from a centre of origin in the islands (cf. Jønsson *et al.*, 2010, on *Pachycephala* and Filardi & Moyle, 2005, on monarch flycatchers). Instead, the phylogeny may represent early differentiation in the island region within an ancestor that was already widespread in both the island region and Australia/New Zealand, with the final differentiation occurring between the two regions.

There are profound differences between the plants and animals of Australia and those of New Caledonia. Guillaumin (1928) emphasized the remarkable absence in New Caledonia of the diverse Australian groups *Eucalyptus*, Lobeliaceae, Stylidiaceae, Xanthorrhoeaceae, Restionaceae and Centrolepidaceae, and the paucity of *Acacia* and Myoporaceae. *Eucalyptus* has hundreds of species in Australia but is entirely absent in New Caledonia, although Myrtaceae is the richest plant family there (236 species). The monotypic *Arillastrum*, endemic to New Caledonia, is sister to the mainly Australian *Eucalyptus*, *Angophora* and *Corymbia* (Ladiges *et al.*, 2003) or *Angophora/Corymbia* (Wilson *et al.*, 2005). Ladiges *et al.* (2003) argued that this split is the result of vicariance following rifting of the Norfolk Ridge away from eastern Australia/Lord Howe Rise in the Late Cretaceous (cf. Ladiges & Cantrill, 2007).

Some of the differences between Australia and New Caledonia may be the result of extinction. It is difficult to know to what extent extinction has framed overall biogeographical patterns. At one extreme, if 'everything was everywhere' originally, extinction alone could have produced all patterns. But in many cases, such as precise, multi-taxon patterns, allopatry does seem to be the result of allopatric differentiation. A study of living and fossil records of *Nothofagus* suggested that extinction has occurred throughout the range of the genus. This has tended to eliminate subgenera where they were less diverse to start with, while centres of main diversity in the subgenera have remained more or less in place since their allopatric evolution (Heads, 2006). Several diverse Australian groups, such as *Eucalyptus* and Casuarinaceae, are absent from the extant biota of New Zealand but are known there from a few fossil species; two each for *Eucalyptus* (Pole, 1993) and Casuarinaceae (Campbell & Holden, 1984). There are no known Tertiary plant fossils from New Caledonia and so similar patterns are possible there. On the other hand, although there are many studies of New Zealand plant fossils very few species of *Eucalyptus* and the others have been found; there are hundreds of species in Australia and so the fossils do not substantially change the overall pattern of differential diversity. In addition, while the Australian fossil record is also well studied, there are no records of New Caledonian taxa such as the plant family Amborellaceae or the bird family Rhynochetidae.

Australasian skates are highly diverse and endemic. Last & Yearsley (2002) cited 'striking' differences between the faunas of New Zealand/New Caledonia (dominated by members of the subfamily Arhynchobatinae) and the fauna of Australia

(dominated instead by members of the subfamily Rajinae). The two show little overlap in species composition and 'the main ancient mechanism of derivation is almost certainly vicariance' (Last & Yearsley, 2002).

The bird family Aegothelidae (owlet-nightjars) comprises one clade in New Zealand (Holocene fossil) and New Caledonia, and one in Tasmania, Australia and New Guinea (Dumbacher *et al.*, 2003). Rather than emphasizing the simple east/west vicariance around the Tasman and Coral Seas, Dumbacher *et al.* based their interpretation on the theory that the family has dispersed to New Zealand and New Caledonia from a restricted centre of origin in Australia or New Guinea. In support they noted that the earliest known fossil is from Australia, the family is unknown outside Australasia and most of the species occur in New Guinea, but in fact none of these constitute good evidence for a centre of origin. On the other hand, the phylogeny provides excellent evidence for evolution by vicariance and there is an obvious geological mechanism, the opening of the Tasman Basin.

7. New Caledonia–McPherson-Macleay Overlap/north-eastern Queensland

Chance, long-distance dispersal does not explain many aspects of the Australia–New Caledonia connection, such as repeated affinities of New Caledonian taxa with the McPherson-Macleay Overlap (MMO), a biogeographical region straddling the eastern New South Wales/Queensland border (Ladiges, 1998). For example, *Dysoxylum bijugum* (Meliaceae) of New Caledonia, Vanuatu and Norfolk Island is closely related to *Dysoxylum fraseranum* locally endemic at the MMO (Mabberley, 1998). The MMO comprises an exotic terrane, the Gympie terrane, equivalent to the Téremba terrane of New Caledonia, and the Brook Street terrane of New Zealand (Spandler *et al.*, 2005). Other New Caledonian taxa are related to forms of north-eastern Queensland rather than the MMO (for example, *Lethedon*: Thymelaeaceae, of New Caledonia and the Cairns region; a large clade of New Caledonian *Planchonella* species sister to *Planchonella euphlebia* of Cairns; Swenson *et al.*, 2007), but sometimes all three are involved as disjunct, related localities. For example, in Rutaceae, five genera keyed together by Hartley (2001) range in New Caledonia (*Dutailliopsis*, *Dutailleya*, *Zieridium*, *Comptonella*) and in eastern Australia (*Pitaviaster*), disjunct at Fraser Island by the MMO and in north-eastern Queensland.

8. New Caledonia–Lord Howe Island/Norfolk Island

Lord Howe Island is a high point on one ribbon of continental crust stretching north-west of New Zealand (Lord Howe Rise), while Norfolk and New Caledonia are high points on another (Norfolk Ridge). The Lord Howe Rise and the Norfolk Ridge separated from Australia and from each other in the Late Cretaceous (Schellart *et al.*, 2006). Lord Howe and Norfolk Islands are both volcanic islands, but their small size and young age belie their biogeographical significance (cf. *Baloghia*,

Fig. 3). Keast (1966) outlined the 'puzzle' of the Lord Howe flora and fauna, which have several 'bewildering' distributions. He wrote that 'normally [Lord Howe Island] would simply be regarded as a volcanic island, but it has several forms of life that could hardly have been transported over the sea; hence certain biologists postulate that at some time in the past it [or precursors] must have had connections with New Zealand to the south and New Caledonia to the north…'. In fact, land connections are unnecessary if taxa survive as metapopulations dispersing (by normal means, not founder dispersal) among the ephemeral islands of a region.

Lord Howe and Norfolk Islands together form an important centre of endemism, and many groups show connections between this centre and New Caledonia. For example, in the freshwater shrimp genus *Paratya* the Norfolk and Lord Howe species form a pair, and this is sister to three New Caledonian species (Page *et al.*, 2005). Page *et al.* (2005) wrote 'Initially, the continent of Australia would appear to be a likely source for the island populations, but our data does not support this. Rather, the New Caledonian and other island [Norfolk and Lord Howe] populations are sister clades and not derived from Australian *Paratya*.' This supports the idea of a common ancestor rather than direct derivation by dispersal. Nevertheless, the authors concluded 'This means that the islands may have been colonized contemporaneously with Australia.' This would not explain why the Australian and island groups together form a clade. Nor would it explain why the sister of this group is in New Zealand, or why the sister group of this whole Tasman Basin clade has its sister in yet another region, the north-west Pacific. As usual, there is a simple pattern of pervasive vicariance in which the entire west Pacific is divided into numerous allopatric areas of endemism, some of which are very local.

9. New Caledonia–Lord Howe Island

This connection may relate to the separation of the Lord Howe Rise from the Norfolk Ridge/New Caledonia by the rifting open of the New Caledonia Basin.

10. New Caledonia–Norfolk Island

The Norfolk Ridge runs from New Zealand to Norfolk Island and New Caledonia. Herzer *et al.* (1997) found evidence for Oligocene uplift along the length of the Norfolk Ridge which could have provided land between New Zealand and New Caledonia. Meffre *et al.* (2007) confirmed this with evidence (including a fossil leaf from seafloor rocks) for the existence of a large island 100 km across just east of Norfolk Island from 38–21 Ma. This suggests that Holloway's (1996) model of a 'stochastic pattern of dispersal' from present-day land areas to the present-day Norfolk Island needs to be revised.

11. New Caledonia–New Zealand

The basal angiosperm *Amborella* is a New Caledonian endemic, while the basal passerines Acanthisittidae are a New Zealand

group and so the strong biogeographical affinity between the two countries is of special interest. Chambers *et al.* (2001) concluded that their molecular studies of *Cyanoramphus* parakeets, cicadas and geckos 'point to a relationship between the biota of New Zealand and New Caledonia that is closer than previously acknowledged .... The finding that the closest living relative of many of the [New Zealand] taxa that we have examined reside in New Caledonia was unexpected....' In fact, many authors from Hutton (1872) onwards have commented on this connection and it is seen in diverse taxa.

In the plant family Balanophoraceae, *Hachettea* of New Caledonia is sister to *Dactylanthus* of New Zealand (and this pair is sister to *Mystropetalon* of South Africa, cf. track 1) (Nickrent, 1998). In the basal clade of Lepidoptera (Micropterigidae), *Sabatinca* s. str. occurs in New Caledonia and New Zealand (Gibbs, 1990). In New Zealand it is disjunct along the Alpine fault (south-western South Island–north-western South Island–north-eastern North Island) and Gibbs (citing Heads, 1990) noted that similar patterns often occur in groups that are disjunct from New Zealand to New Caledonia, Australia etc. (Another example is the moss *Dicranoloma billardieri*, disjunct in south-western and north-western South Island, also in New Caledonia, Australia, Malesia, Africa and South America; Klazenga, 1999.) New Caledonian *Sabatinca* pollinates an equally archaic plant, *Zygogynum* (Winteraceae). Both have Cretaceous fossils and Thien *et al.* (1985) accepted that their association is an ancient one.

A clade in cicadas comprises *Maoricicada*, *Rhodopsalta* and *Kikihia* of New Zealand (including Norfolk and the Kermadec Islands) and *Pauropsalta* and *Myersalna* of New Caledonia (Arensburger *et al.*, 2004). The authors attributed the range to trans-oceanic dispersal, and they described this as a 'remarkable feat', since these insects are not known for their dispersal abilities. This conclusion was based solely on the estimated age for the clade (<11.6 Ma). This in turn was based on an unspecified 'geological calibration' supplied as a personal communication from one of the authors, C. Simon. Other studies of the authors (also personal communications) 'demonstrate' that *Kikihia* has shown 'incredible dispersal abilities' by colonizing Norfolk Island and the Kermadec Islands, 1000 km north-west and north-east of New Zealand. 'Remarkable' and 'incredible' means of dispersal are often inferred in centre of origin/dispersal theory; in this case they are all based on (unspecified) clock calibrations.

Simon has co-authored two other studies on members of the group in which two different calibrations were used, and these are possibly the source of the Arensburger *et al.* (2004) calibration. In one of the papers, Buckley *et al.* (2001) assumed that *Maoricicada* species were no older than 5 Ma, because this is the age of the New Zealand alpine habitat, the Southern Alps. This argument is flawed; while *Maoricicada* species are mainly alpine, four species are found below 100 m elevation and it is quite possible that substantial diversity already existed in New Zealand before the latest mountains were uplifted. In another study, Buckley & Simon (2007) used the age of the Kermadec Islands (3 Ma) and Norfolk Island (3 Ma) to date

the endemic *Kikihia* species on each of the islands, but this assumes that the species are no older than the current rocks, which is dubious. The Kermadec Islands are a typical active island arc, generated by the subduction of the Pacific plate under the Australian plate. It is the age and history of the subduction zone which is important for the cicadas and other 'subduction zone weeds', not the age of particular islands they currently inhabit. Buckley & Simon's (2007) other calibration point, Norfolk Island, is not located at an active subduction zone but evidence of Tertiary uplift and former islands along the Norfolk Ridge was cited above (Herzer *et al.*, 1997). (Buckley & Simon cited this work earlier in Arensburger *et al.*, 2004.)

Using the age of islands, strata or habitat to which taxa are currently endemic (for example, Norfolk Island, the Kermadec Islands or the Southern Alps) to calibrate a molecular clock will usually give a date that is much too young, as will the use of fossils. By surviving as dynamic metapopulations in ephemeral microrefugia, living taxa such as the cicada clade of New Zealand–New Caledonia (including Norfolk and the Kermadec Islands) can survive more or less *in situ* in tectonically disturbed environment for tens of millions of years and be much older than individual landscape features such as islands or even mountain ranges. There is no need to invoke the 'remarkable' or 'incredible' dispersal abilities that Arensburger *et al.* (2004) proposed.

For geckos, Bauer & Jackman (2006) suggested that differentiation among the New Zealand–New Caledonia diplodactylids could indicate response to Cretaceous–Palaeogene geological events. In contrast, more recent ages have been proposed for differentiation in the skinks of the region, despite their similar disjunctions (Bauer & Jackman, 2006; Smith *et al.*, 2007). Smith *et al.* (2007) described a skink clade (*Oligosoma*, *Cyclodina* etc.) endemic to New Zealand, Lord Howe Island, New Caledonia and southern Vanuatu. This is a large group, with 44 species in 14 genera, but is absent from Australia. The authors observed that the group's distribution (apart from Vanuatu) defines a block of continental crust, termed Tasmantis or Zealandia, that includes the Lord Howe Rise, the Norfolk Ridge, and the New Zealand plateau. This was rifted from Australia in the Cretaceous–Palaeogene. Accepting a young age for the Tasmantis skink clade (on the basis of unreliable calibrations) leads to the inevitable problem that 'specific candidate cladogenetic events remain elusive' (Bauer & Jackman, 2006, p. 12). Instead, the range of the Tasmantis clade can be related to the same Mesozoic–Palaeogene rifting and convergence that produced the gecko distributions and also the extreme levels of endemism seen in New Caledonian lizards overall – there are 106 endemic species and only three non-endemics.

Cyanoramphus parakeets are recorded in New Zealand, Lord Howe Island and Norfolk Island, New Caledonia and the Society Islands (recently extinct). Boon *et al.* (2001) found that the New Caledonian species was sister to the entire New Zealand/Norfolk Island clade. Because the New Caledonian clade is much smaller, Boon *et al.* regarded it as 'basal' and so

they inferred a New Caledonian centre of origin followed by dispersal to New Zealand. They argued that if *Cyanoramphus* was 'Gondwanic', the nearest living relatives of the New Zealand species would instead 'probably [be] one of the Australian parrot taxa', such as *Platycercus*. This does not follow, as a Gondwanan origin is compatible with a phylogeny (Australia (New Zealand + New Caledonia)). The New Zealand–New Caledonia relationship, the relationship of the Pacific *Cyanoramphus* with the Australian *Platycercus*, and the absence of the latter from New Zealand and New Caledonia (a fact which Boon *et al.* did not mention) could all be explained by a simple vicariant origin of *Cyanoramphus* (a Pacific group) and the related *Platycercus* (a Gondwanan group).

As already noted, prior land existed along the Norfolk Ridge. Herzer *et al.* (1997) suggested that this constituted a 'land-bridge' or series of 'stepping stones' for dispersal between New Caledonia and New Zealand. Instead, the central Norfolk Ridge/Norfolk Basin region was probably an important biogeographical centre in its own right, not simply a pathway between two already formed countries.

In Sanmartín & Ronquist's (2004) study of Southern Hemisphere biogeography, none of the sampled plant or animal taxa showed New Zealand and New Caledonia as sister areas, and the authors concluded 'our results … do not support the notion of a common relict late Cretaceous Gondwanan biota in the two land masses'. They explained any affinities between the two areas as due to either long-distance dispersal or dispersal via stepping stones along the Norfolk Ridge. As discussed above, this conclusion has little support as their sample of taxa was so small.

12. New Caledonia–(Rennell Island)–New Guinea

The New Caledonia–New Guinea connection is not as well known as that between New Caledonia and New Zealand and also has a less obvious geological basis, but occurs frequently (e.g. in lichens, Fig. 5) and clades endemic here can be basal to worldwide groups. In the fig family (Moraceae), *Sparattosyce* of New Caledonia and *Antiaropsis* of New Guinea comprise the basal clade in the pantropical tribe Castilleae (Zerega *et al.*, 2005).

The traditional idea is that the 'Malesian element' in the New Caledonian biota 'arrived over water' (e.g. Keast, 1996), but Polhemus (1996) proposed an alternative explanation in which volcanic island arcs, together with their biota, have been incorporated into continental areas by accretion. As an example, Polhemus (1996) discussed the *Rhagovelia novacaledonica* group (Hemiptera) of New Caledonia, New Guinea and the Philippines (Mindanao). Another hemipteran genus, *Phrynovelia*, is restricted to New Caledonia and north-eastern New Guinea (Andersen & Polhemus, 2003). Island arc accretion has probably been fundamental for the biogeography of New Zealand, New Caledonia and New Guinea. Polhemus (1996) and Hartley (2000) suggested that Eocene islands may have been present between New Caledonia and New Guinea prior to the opening of the Coral Sea along the Rennell Island Ridge (south-western Solomon Islands) and the Pocklington Rise
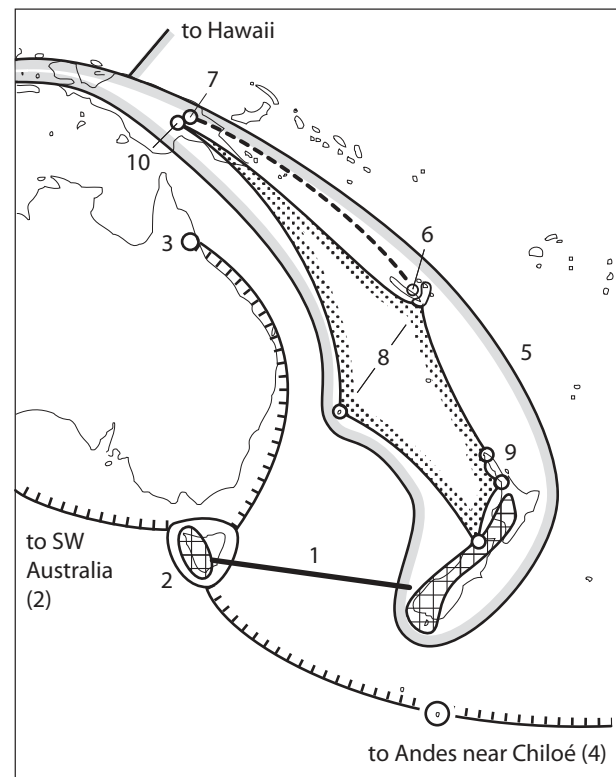

Figure 5 Some groups in Megalosporaceae (from Sipman, 1983 and Galloway, 2007): 1, *Austroblastenia*; 2, *Megalospora lopadioides*; 3, *M. queenslandica*; 4, *M. kalbii* (2, 3 and 4 share a distinctive spore type); 5, *M. atrorubicans*; 6, *M. hillii*; 7, *M. weberi* (6 and 7 share a distinctive combination of characters); 8, *M. sulphureorufa*; 9, *M. bartlettii*; 10, *M. granulans* (8, 9 and 10 share a distinctive combination of characters).

(eastern Papua New Guinea, between Alotau and Sudest/Rossel Islands). In this region the sea-floor topography is complex and there is much endemism. As with the central Norfolk Ridge/Norfolk Basin, this part of the Coral Sea has been an important zone of evolution, not just a 'land bridge' from one point to another. The connection among New Caledonia, Rennell Island (south-western Solomon Islands) and the Louisiade Islands may have involved the large, submarine Louisiade Plateau that lies between Rennell and the Louisiade group (separated from the latter by the Pocklington Trough). (Louisiade–New Caledonia endemism in Chrysobalanaceae and Loranthaceae is cited in Appendix S1.) Quarles van Ufford & Cloos (2005) interpreted the New Guinea–Rennell Island–New Caledonia–New Zealand 'inner Melanesian arc' as an Eocene–Oligocene subduction zone along which there was nearly coeval collisional orogenesis in the Oligocene.

Disjunctions around New Guinea conform to a series of parallel, nested arcs attributed to accretion of island arcs and the associated large-scale lateral movement of terranes on strike-slip faults (Heads, 2001, 2003). A similar series of parallel arcs connects New Caledonia with New Guinea (Fig. 6). In the fruit bat genus *Pteropus* the species groups in the south-west Pacific (Fig. 7) have a complex distribution that
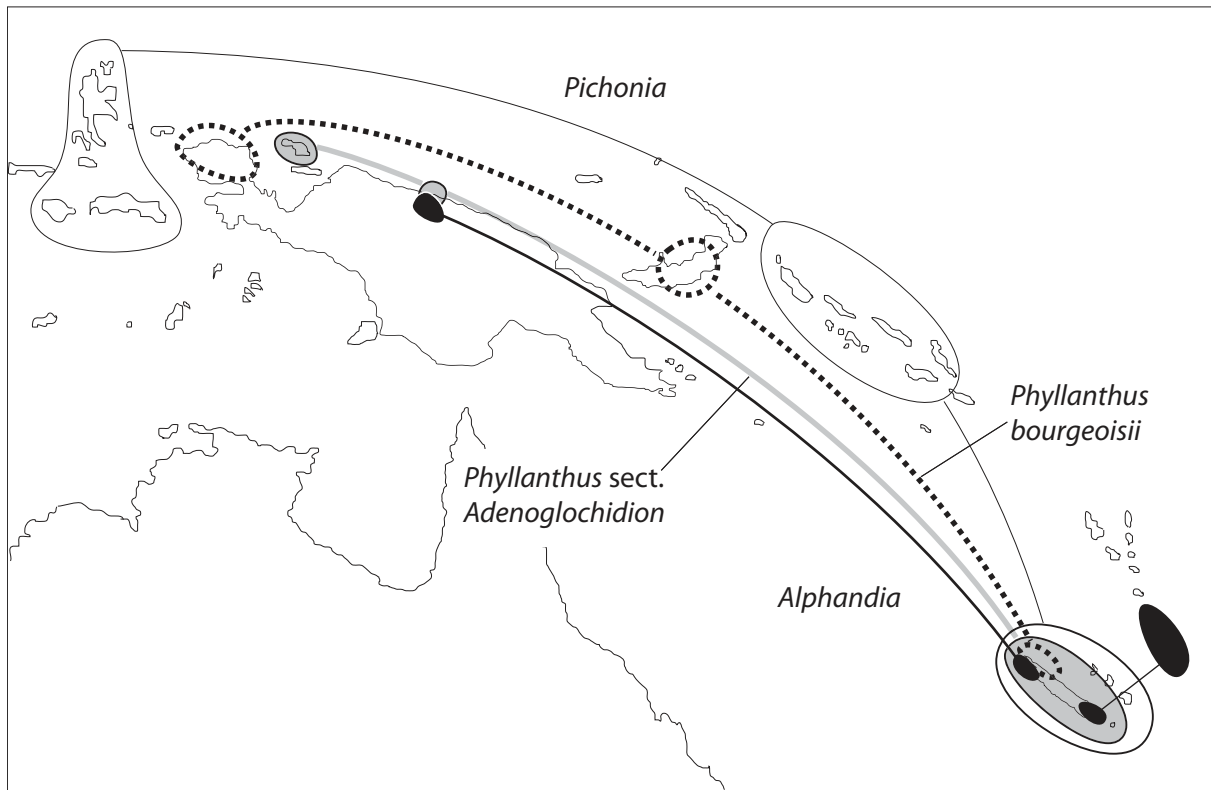
Figure 6 Distribution of *Alphandia* (Euphorbiaceae, see Fig. 3), *Phyllanthus* sect. *Adenoglochidion* (Phyllanthaceae) (Holm-Nielsen, 1979), *Phyllanthus bourgeoisii* (Webster & Airy Shaw, 1971) and *Pichonia* (Sapotaceae; including *Rhamnoluma* – Swenson *et al.*, 2007; Govaerts *et al.*, 2001).

can be resolved into a series of nested arcs. The three species on New Caledonia each belong to a different species group distributed on a different arc (tracks 1, 4 and 5 in Fig. 7).

In passerine birds, a study of the *Zosterops griseotinctus* species complex and allies (Moyle *et al.*, 2009) linked *Zosterops inornatus* of the Loyalty Islands, New Caledonia, with *Zosterops rennellianus* of Rennell Island. Moyle *et al.* (2009) used the island age of New Georgia, one of the Solomon Islands to calibrate the tree, and 'checked' this with calibrations based on the ages of Indian Ocean islands and Socorro Island, Mexico (Arbogast *et al.*, 2006). All these islands occur near long-lived geological features that have been producing ephemeral islands since long before the current islands existed and so the calibrations are likely to give dates that are much too young. Thus the conclusion of Moyle *et al.* (2009) that *Zosterops* had 'extremely high speciation rates early in the Pleistocene' is doubtful. Moyle *et al.* discussed the 'paradox' that the species show a high degree of differentiation and stark geographical boundaries, despite its 'excellent' dispersal ability. The latter is inferred rather than demonstrated. The idea that *Zosterops* first colonized New Zealand from Australia in the early 1800s is often cited in text-books as fact but was not accepted by Buller (1870) or Mees (1969).

Members of the *Z. griseotinctus* complex have been regarded as 'supertramps', as they occur on small, young islands (Loyalty Islands, Rennell Island, islets off northern and eastern New Guinea, possibly Norfolk Island). But the question remains: why do they only occur on *these* small islets when there are so many others in the region? The regional distribution of the group may not reflect the ecology of the group so much as an important biogeographical sector brought into existence by tectonic history such as arc accretion, and the small islets are currently the only land available in the sector. For groups to persist as metapopulations in such regions, they must be able to survive on ephemeral islets and colonize these as they appear, but this small-island ecology did not necessarily cause the distribution pattern to begin with. Other examples of New Caledonia–Vanuatu–Rennell distribution are cited under section 13, New Zealand–New Caledonia–New Guinea/ Bismarck Archipelago in Appendix S1 and some of these may involve direct New Caledonia–Rennell links, as in *Zosterops*.

13. New Zealand–New Caledonia–New Guinea/ Bismarck Archipelago

For insects, Gressitt (1958) found that 'There appear to be relationships between New Guinea and New Zealand, through New Caledonia, which do not involve Australia.' This 'inner Melanesian arc' is important in many groups, for example in the lichen *Megalospora* (Fig. 5). The liane genus *Mearnsia* (Myrtaceae) has a predominantly inner arc distribution: New Zealand, New Caledonia, Solomon Islands, New
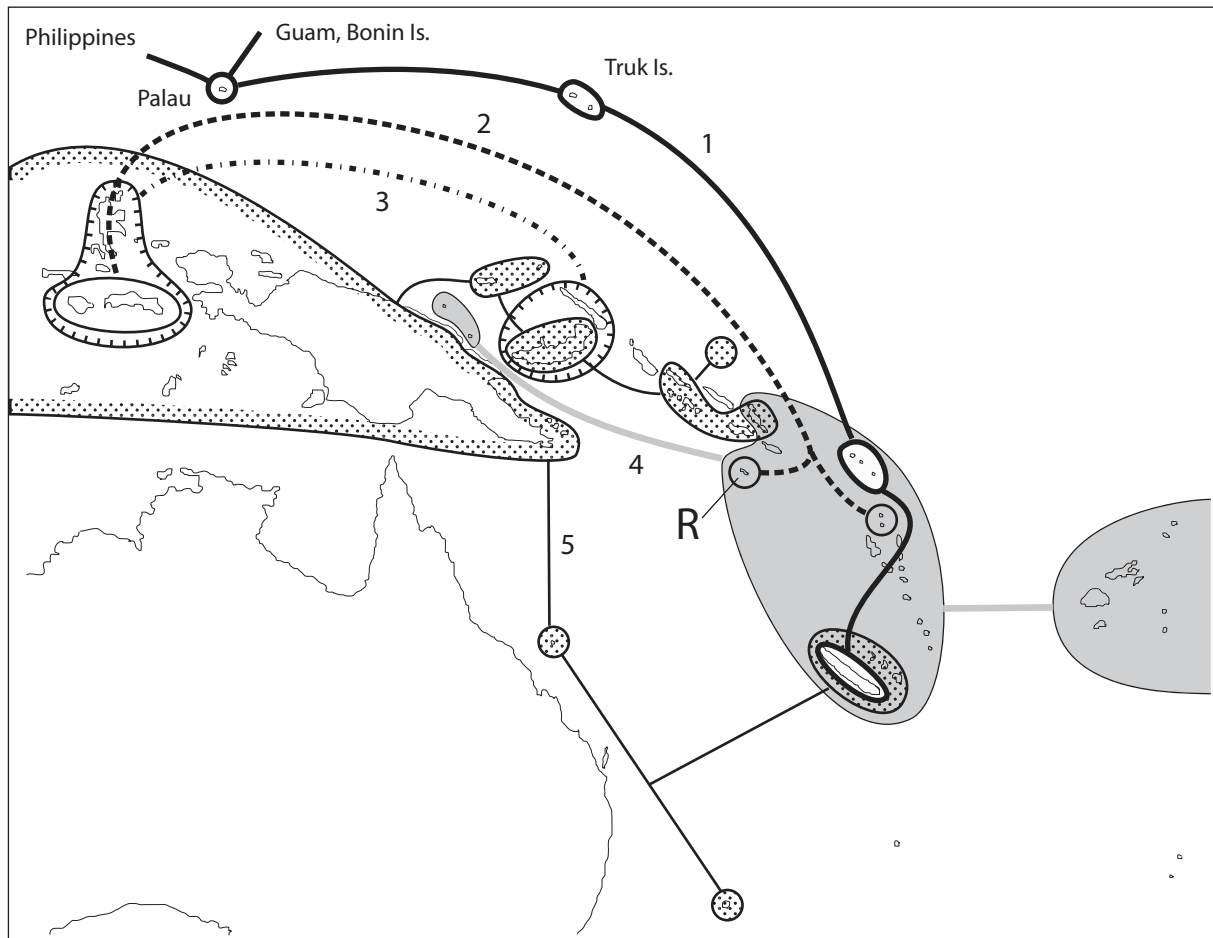
Figure 7 Some clades in *Pteropus* fruit bats: 1, *P. pselaphon* group; 2, *P. chrysoproctus* group; 3, *P. personatus* group; 4, *P. tonganus*; 5, *P. subniger* group (Simmons, 2005). R, Rennell Island.

Britain, New Guinea and the Philippines (Wilson, 1996) with relatives to the east (in the central Pacific; *Metrosideros* s. str.) and to the west (in Australia; Backhousieae etc.) (see Appendix S1).

Outer Melanesian arc groups absent in New Caledonia

The outer Melanesian arc comprises the Bismarck Archipelago, the Solomon Islands, Vanuatu, Fiji and Tonga. These may once have formed a continuous island arc, the Vitiaz arc, that was later rifted apart. The nearest part of the outer arc to New Caledonia is Vanuatu. Although the southern Vanuatu islands are only 200 km from the Loyalty Islands of New Caledonia, there are considerable biogeographical differences between the two countries. Many conspicuous rain forest genera range widely on the outer arc from New Guinea to Vanuatu and often Fiji but are notably absent from New Caledonia. Many of these are also absent in Queensland despite suitable habitat there, indicating an ancient absence in the region, Queensland–New Caledonia, complementing its status as a centre of endemism. In Melastomataceae, for example, members of the tribe Astronieae are conspicuous, large-leaved trees and

Maxwell & Veldkamp (1990) observed that 'It is very remarkable' that there are none in Queensland, when there are so many in New Guinea, the Solomon Islands, Vanuatu and Fiji. Their absence from New Caledonia is also remarkable.

14. New Caledonia/outer arc vicariants

The absence of many outer arc taxa from New Caledonia is not absolute, as many have a closely related vicariant there. *Faradaya* (Labiatae) ranges widely in north-eastern Queensland, New Guinea, the Bismarck Archipelago, the Solomon Islands, Vanuatu and Fiji/Samoa/Tonga (de Kok & Mabberley, 1999a). While it is absent as such from New Caledonia, it is replaced there by the closely related *Oxera*, with 20 species in New Caledonia and two in Vanuatu (de Kok & Mabberley, 1999b).

In the blackfly genus *Simulium*, Craig *et al.* (2001) mapped the subgenus *Nevermannia* from Asia, Australia and New Guinea east to Norfolk Island and New Caledonia. Its sister groups are the subgenus *Hebridosimulium* in Vanuatu and Fiji and the subgenus *Inseliellum* in Micronesia (Mariana and Caroline Islands) and Polynesia. Craig *et al.* did not mention the well-defined vicariance among the subgenera (note, for example, the break between New Caledonia and Vanuatu) and

instead explained the overall distribution as the result of 'routes of colonisation' into the Pacific from a Southeast Asian centre of origin.

15. New Caledonia–Vanuatu

Despite the major biogeographical break between New Caledonia and the outer arc, numerous groups are endemic to New Caledonia plus Vanuatu, especially the southern islands Aneityum, Erromango and Tanna. *Oxera*, cited in section New Caledonia/outer arc vicariants, is one example. Another is the genus *Tinadendron* (Rubiaceae), comprising one species on Grande Terre and another on the Loyalty Islands and southern Vanuatu (Achille, 2006). The close connection between the Loyalty Islands and Vanuatu and its tectonic basis are discussed elsewhere (Heads, 2008a).

16. New Caledonia–Vanuatu–Fiji (/Samoa/Tonga)

Authors who have employed a vicariance explanation for this region include Woodland (1983) and Valdés (2001a,b,c), both working on marine biota. The rifting apart of the Melanesian (Vitiaz) arc was cited as an important biogeographical mechanism by Springer (1999, 2002) for reef fishes and Zug (1991) for Fiji–Vanuatu reptiles.

17. New Caledonia–Fiji/Samoa/Tonga

Morat *et al.* (1984) cited strong affinities between the rain forest plant genera of New Caledonia and, respectively, New Guinea (60% shared), Australia (57%), Malesia (56%) and Fiji (44%). As well as the overall similarity between New Caledonia and Fiji there is also a direct connection, avoiding southern Vanuatu (e.g. *Spiraeanthemum* 'brongniartianaum Group', Fig. 2).

Kroenke (1996) suggested that 'Eua (Tonga) and a portion of the modern Tonga forearc were attached to the eastern end of the New Caledonia arc in the Palaeocene and were detached by the upper Eocene. (In Kroenke's model the rest of the Vitiaz arc lay far to the east at this time.) This could account for ties between New Caledonia and Tonga, and New Caledonia–Fiji (Lau)/Tonga connections. (The Lau Ridge in eastern Fiji was part of the Tonga Ridge until it was separated by backarc basin formation.) Springer (1989) cited similar ideas to explain the distribution of the reef fish *Ecsenius fourmanoiri* in New Caledonia and eastern Fiji/Tonga. Sdrolias *et al.* (2003) gave another model of the regional tectonics in which the entire outer Melanesian arc formed more closely to New Caledonia.

18. New Caledonia–Samoa

New Caledonia and Samoa are linked by a clade of *Crossostylis* (Rhizophoraceae) (Setoguchi *et al.*, 1998), and several bryophytes, ferns and invertebrates are also only known from these two localities (see Appendix S1). Samoa is an archipelago of high islands located just east of the current plate margin and near the Melanesian Border igneous plateau. This formed in the Cretaceous along with the vast Ontong Java plateau (Heads, 2009b).

19. New Caledonia–outer Melanesian arc (accreted terranes of New Guinea, Bismarck Archipelago, Solomon Islands, Vanuatu, Fiji/Tonga/Samoa)

So far the Melanesian region as a whole has received little attention as a centre of endemism, and most authors have assumed that the very diverse flora and fauna are all the result of chance dispersal from Australia and the Malay Archipelago. Nevertheless, the regional endemics are notably absent from Australia and so are not simply Gondwanan, and they are also absent west of New Guinea/Moluccas and so are not simply Indomalaysian (or Tethyan).

Biogeographers have traditionally followed geologists and treated New Caledonia as part of the inner Melanesian belt (the old plate margin, New Zealand–New Caledonia–New Guinea) and not the outer or Vitiaz arc (the current plate margin). But New Caledonian rocks and taxa show relationships with both inner and outer arcs. This is seen to different degrees in the different terranes of New Caledonia, with the Loyalty Islands having many Pacific elements that are absent on the New Caledonian mainland (Grande Terre) (Heads, 2008a).

A glance at the geography shows that the archipelagos of the Solomon Islands, Vanuatu, New Caledonia and Fiji are not simple arcs. In early plate tectonics interpretations the outer arc was represented as a single structure, the Vitiaz arc, that has been disrupted, but it is more likely to have been derived from a series of arc systems that had disparate origins and were juxtaposed later in their history (Kroenke, 1996; Polhemus, 1996). Although most exposed rocks in the Vitiaz arc are no older than Eocene, part of the arc system may have been initiated as early as the late Cretaceous, perhaps as part of the Loyalty Ridge (Heads, 2008a). The place of origin of the arc(s) is also controversial; it may have formed within the Pacific plate far from New Caledonia/Norfolk Ridge (explaining the absence of groups from New Caledonia) or alternatively along the eastern edge of the New Caledonian/Norfolk Ridge (explaining the presence of outer arc groups there). As a third possibility, different component arcs may have formed in different places before integration with other arcs.

If the Vitiaz arc is a complex of accreted and rifted arc fragments, this would explain why some otherwise widespread outer arc groups are absent from the Solomon Islands, from Vanuatu, or along the important Solomon Islands–Fiji track, a former plate margin. It might also explain the highly structured internal biogeography of the Solomon Islands and Vanuatu. For example, there are biogeographical connections of northern Vanuatu with Fiji and the Solomon Islands, which are quite distinct from those of southern Vanuatu with Fiji and New Caledonia.

Of the three main clades in *Spiraeanthemum* (Cunoniaceae; Fig. 2), the two around the Coral Sea and the outer Melanesian arc are neatly vicariant, while the third, in New Caledonia and

Fiji, overlaps both. New Caledonian and Fiji are both tectonic composites formed by the fusion of several island arcs and the secondary overlap probably followed initial allopatry of all three clades. Pillon (2008, p. 32) wrote that the divergence between the outer arc group in *Spiraeanthemum* and the Fiji–New Caledonia group would date to about 21 Ma, but this is a minimum date as the Warren & Hawkins (2006) dates it is based on were calibrated with fossils. Warren & Hawkins wrote: 'Fossils always provide only a minimum estimate of when a taxon existed. However, under relaxed clocks, rates frequently appear to change too readily across a tree in the absence of an upper constraint on divergence times …. Therefore, we compromised by fixing the age of the basal-most calibration point(s) to their minimal age(s).'

In Araliaceae, New Caledonia has more species per unit area than anywhere else in the world (Bernardi, 1979). A clade of 50 species including *Plerandra* and allies (sometimes termed 'Melanesian *Schefflera*' although it does not include *Schefflera*) ranges from New Guinea to Fiji and has a centre of diversity in New Caledonia. Plunkett & Lowry (2007; cf. Plunkett *et al.*, 2005) took the phylogeny to represent dispersal events from a centre of origin in New Caledonia. But even apart from problems basing date calibrations on fossil age and island age, chance dispersal does not explain the significant overall allopatry between the Melanesian *Plerandra* s. lat. and its Micronesian–Polynesian sister group *Meryta* to the east (on islands north of New Zealand and east of Fiji in the central Pacific). There is secondary overlap around the break, on New Caledonia, Vanuatu and Fiji. The third group in the complex, *Pseudopanax* of mainland New Zealand, is allopatric with both *Plerandra* s. lat. and *Meryta*.

In another clade of Araliaceae, *Polyscias* sect. *Tieghemopanax*, Eibl *et al.* (2001) described affinities between certain New Caledonian species and their respective relatives on Lord Howe, Vanuatu, Fiji and the Solomon Islands, and interpreted these as dispersal events because of the young age of the islands. Nevertheless, as they admitted, 'Perhaps what is most surprising is the apparent rarity of successful dispersal events from New Caledonia to other islands….' This observation is critical; if normal ecological dispersal were the mechanism establishing the geographical range of modern taxa, these fleshy fruited taxa would be found throughout the Pacific.

In Sylvioidea (passerine birds), *Megalurulus* (including *Cichlornis*, *Trichocichla* and *Ortygocichla*) and *Cettia* both range widely through Melanesia (except mainland New Guinea) but the localities are markedly disjunct (Fig. 8; Dickinson, 2003; Lecroy & Barker, 2006) and may reflect the complex history of the Vitiaz arc. For *Cettia*, at least, Orenstein & Pratt (1983) concluded that the distribution gaps 'cannot be entirely explained by accidents of dispersal or unsuitability of habitat on the unoccupied islands'. The apparent connection between New Caledonia and northern Vanuatu (Santo)/southern Solomon Islands in *Megalurulus* and the apparent absence in southern Vanuatu (the usual connection with New Caledonia) may reflect the history of the d'Entrecasteaux Ridge. This is an extension of the Norfolk Ridge that continues
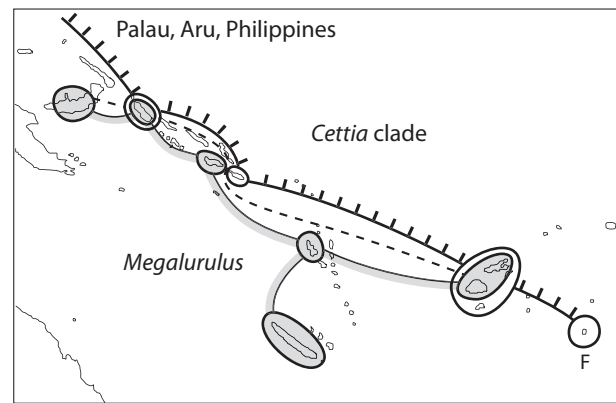

Figure 8 Two clades in Sylvioidea (Passerines): *Megalurulus* (Megaluridae) and the south-west Pacific clade of *Cettia* (Cettiidae) (Lecroy & Barker, 2006). Broken line indicates possible affinity between 'Ortygocichla' of New Britain and 'Trichocichla' of Fiji (Mayr, 1933), currently both placed in *Megalurulus*. F, fossil.

north of New Caledonia and curves eastward to Santo, where it is currently being destroyed by subduction at the New Hebrides trench. Alternatively, the connection could be New Caledonia–Fiji–Santo–southern Solomon Islands.

20. New Caledonia–Micronesia

Taxa with this distribution often occur on atolls, the only land present in much of this region. The distributions are often interpreted as recent, but the whole sector extending from Micronesia to eastern Polynesia represents a vast area of subsidence, with the seafloor cooling and sinking as it moves away from the ridge that produces it (the East Pacific Rise). Thus the area may represent an old centre of endemism.

In *Cupaniopsis* (Sapindaceae), the largest New Caledonian clade (14 species) is sister to a group in Fiji, Samoa and Micronesia (Truk Island) (Adema, 1991). van Balgooy *et al.* (1996) described the genus as ranging 'strangely enough even to Truk', but this is quite a common pattern and is seen, for example, in fruit bats (Fig. 7) and mosses (*Fissidens scabrisetus*: Fiji, Samoa, Tonga, Truk; Miller *et al.*, 1978). Adema (1991) wrote that Australia was the main centre of origin for *Cupaniopsis*, supplying New Caledonia 'several times'. New Caledonia was a secondary centre and Truk, Fiji and Samoa 'were reached by dispersal'. Overall, 'Distribution patterns of the *Cupaniopsis* species are produced by dispersal'; but if this were true, the genus would be expected east of Samoa and west of Sulawesi.

Other groups with the New Caledonia–Melanesia–Micronesia connection also include central Pacific representation and are cited under section 22, New Caledonia/Melanesia–central South Pacific, below.

21. New Caledonia–Philippines/western Malesia

In many families, genera and species of freshwater fishes, Séret (1997) observed a similar disjunction between vicariants in the

South Pacific (New Caledonia, Fiji and Tahiti) and the western Malay Archipelago (western Indonesia, Philippines, also Taiwan and the Ryukyu Islands), that are nevertheless absent from New Guinea, Borneo and Sulawesi. This pattern does not involve Australia and is probably related to the New Caledonia–Micronesia connections (section 20, New Caledonia–Micronesia). Séret (1997) explained it as a result of tectonic processes and the track: New Caledonia–Philippines lies at the margins of the Pacific and Philippine plates.

22. New Caledonia/Melanesia–central South Pacific

Many taxa are restricted to New Caledonia and further east in the central Pacific. Some taxa with similar distributions also extend north to northern Melanesia and Micronesia, but are absent from Australia and often mainland New Guinea (for example, *Pteropus tonganus*; track 4 in Fig. 7). Again, this is not predicted under the usual model of dispersal from Asia/Australia and is probably not due simply to extinction in Australia, as the Pacific taxa often have close relatives there.

Meryta (Araliaceae) was cited in section New Caledonia–outer Melanesian arc (accreted terranes of New Guinea, Bismarck Archipelago, Solomon Islands, Vanuatu, Fiji/Tonga/Samoa) as a central Pacific vicariant of its Melanesian and New Zealand sister groups. It has a centre of diversity in New Caledonia (11 species) (Lowry, 1988). The two main clades in the genus are strictly allopatric; one is in Fiji and islets off north-eastern New Zealand, the other is in Micronesia (Yap), New Caledonia, Vanuatu, Fiji and east to eastern Polynesia (Marquesas). Tronchet *et al.* (2005) accepted 'ancient vicariance' as the basic process. On the other hand, within the second clade, Tronchet *et al.* concluded that a group of species found on young volcanic islands (in Micronesia, Vanuatu, and eastern Polynesia) 'almost certainly' reached these by long-distance dispersal. While these current islands themselves are young, they are all generated at subduction zones, spreading ridges and propagating fissures that have been producing islands throughout the history of the Pacific. Local dispersal within a metapopulation is all that is necessary. Tronchet *et al.* (2005) argued that the volcanic islands clade of *Meryta* is nested in an otherwise New Caledonian clade and so it has been derived by long-distance dispersal from that island, but this reasoning is not accepted here (see Methods).

23. New Caledonia–Polynesia–Hawaii

In *Cyrtandra* (Gesneriaceae, *c.* 600 species), Cronk *et al.* (2005) suggested that 'Because all oceanic Pacific island species form a well-supported clade, these species apparently result from a single initial colonization into the Pacific, possibly by a species from the eastern rim of SE Asia….' The sister of the Pacific clade is endemic to the strip: Ryukyu Islands–Philippines-Sulawesi Java (Fig. 9; Clark *et al.*, 2009), but a small sister clade (a 'basal' clade) does not indicate a centre of origin. There is no evidence that the Pacific was ever 'colonized' by the Pacific clade of *Cyrtandra*, which is a simple
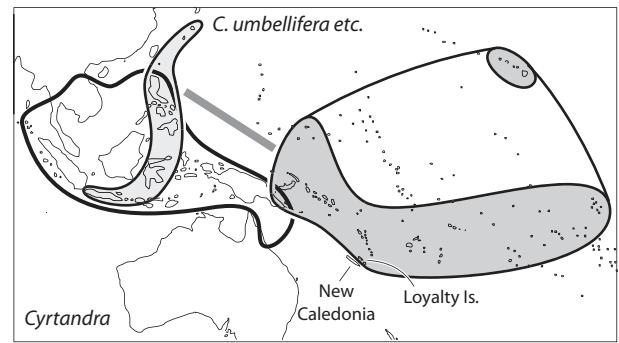

Figure 9 Distribution of *Cyrtandra* (Gesneriaceae), showing the Pacific clade (grey), its sister (*C. umbellifera* etc.) (light grey), and other clades (bold line).

vicariant. In New Caledonia, *Cyrtandra* occurs only on the low, flat Loyalty Islands and is absent from Grande Terre, despite the steep, montane gullies there that provide much more typical habitat for the genus. This difference between Grande Terre and the Loyalty Islands is standard and can be attributed to the independent history of the Loyalty Ridge with respect to Grande Terre rather than to chance dispersal.

A group of monarch flycatchers form a clade that is endemic over a wide area of the central Pacific (Fig. 10; Filardi & Moyle, 2005). For one of the genera, *Clytorhynchus* (New Caledonia to Samoa), Dutson (2006) suggested a centre of origin in the south-eastern Solomon Islands (Santa Cruz Islands) followed by radiation to the south and east. Instead, the genus can be interpreted as having evolved by allopatry with the other central Pacific members of the clade in Hawaii and south-eastern Polynesia, with secondary overlap around Vanuatu and Fiji.

In the plant genus *Scaevola* (Goodeniaceae; 130 species) the largest clade comprises two subclades (Fig. 11): *Scaevola plumieri* and allies centred around the Atlantic Ocean and in Australia, and *Scaevola taccada* and allies mainly in the Pacific (including a clade on New Caledonia, Fiji, Samoa, Tahiti and the Marquesas) (Howarth *et al.*, 2003). The *plumieri* and
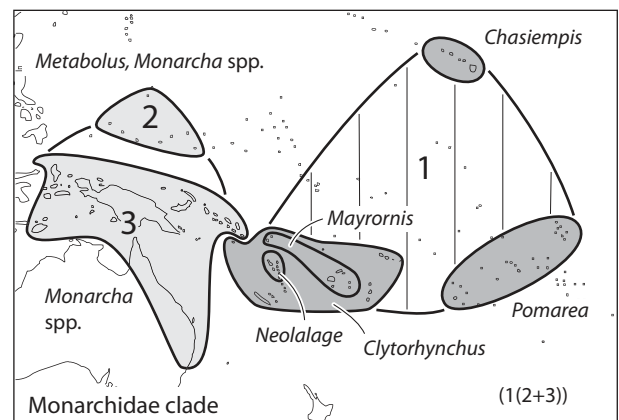

Figure 10 Distribution of *Monarcha* and allies (Monarchidae; Filardi & Moyle, 2005). Phylogeny indicated by numbers.
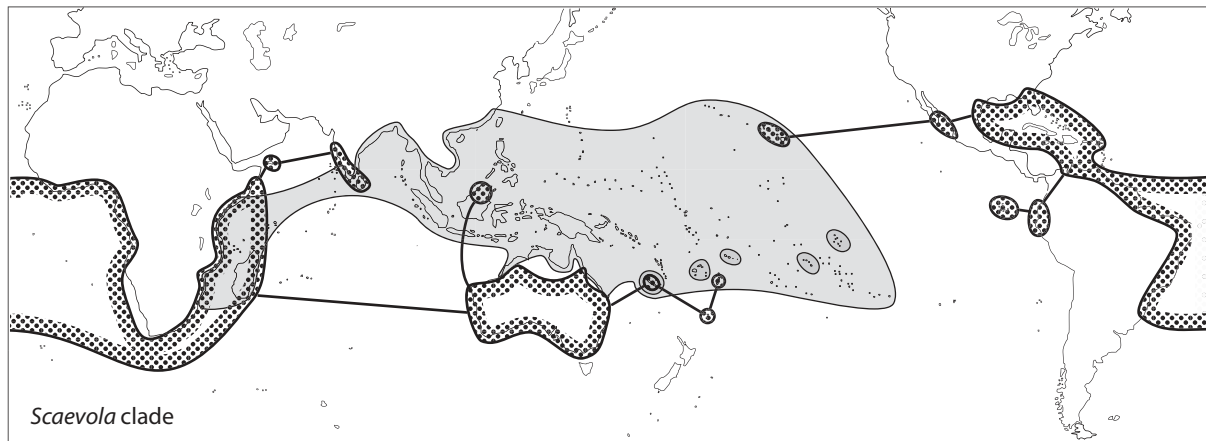
Figure 11 Distribution of the largest clade in *Scaevola* (Goodeniaceae), comprising two subclades (1) the widespread *S. taccada* (= *S. sericea*) and allies (grey; endemics from New Caledonia to the Marquesas Islands are indicated), and (2) the widespread *S. plumieri* and allies (stippled) (Howarth *et al.*, 2003; Caribbean records from Flora of the West Indies at http://botany.si.edu/antilles/WestIndies/results.cfm).

taccada groups are largely vicariant and can be derived more simply by the allopatric break-up of a pantropical ancestor than by chance dispersal from an Australian centre of origin, as suggested by Howarth *et al.* Overlap of the two clades occurs mainly in the south-west Indian Ocean, New Caledonia and the Hawaiian islands, but only New Caledonia has endemic species in both clades. The overlap is interpreted here as the result of secondary range expansion, terrane juxtaposition or both, following the original break. Howarth *et al.* regarded the 'efficient' means of dispersal in the genus as a key factor in explaining the distribution, but in fact these are so efficient that they cannot account for the extensive local endemism, the regional endemism in the central South Pacific or the overall allopatry between the two main clades.

24. New Caledonia (± south-west Pacific)–South America

Many groups are in Australia, New Caledonia and America. Several of these have greater diversity in New Caledonia than in Australia (see Appendix S1). Related patterns do not involve Australia but connect New Caledonia/Melanesia directly with South America. The New Caledonia/New Zealand–Chile track has been well known for over a century, but New Caledonian connections are often with tropical America in a pattern that is much less familiar and seldom cited.

A clade in Opiliones comprises Troglosironidae of New Caledonia plus Neogoveidae of tropical America/West Africa (Boyer *et al.*, 2007) and, as Boyer & Giribet (2007) wrote, the connection is 'intriguing'.

Montrouziera (Clusiaceae) is endemic to New Caledonia (where *M. gabriellae* has the largest flowers in the flora) and forms a clade with *Platonia*, *Lorostemon* and *Moronobea* of tropical South America (Ecuador to the Guianas and eastern Brazil) (Fig. 1; Gustafsson *et al.*, 2002). Sweeney (2008) found representatives of this clade to be basal to a pantropical clade comprising *Garcinia* and relatives.

A similar pattern occurs in Polygalaceae. Tribe Moutabeeae comprises *Balgoya* of New Caledonia, *Eriandra* of New Guinea and the Solomon Islands and *Barnhartia*, *Diclidanthera* and *Moutabea* of northern South America (Fig. 12; van Balgooy & van der Meijden, 1993). The tribe is basal in the world-wide Polygalaceae (minus *Xanthophyllum*) (Eriksen, 1993; Forest *et al.*, 2007). Groups such as Moutabeeae and the *Montrouziera* group indicate that the trans-tropical Pacific region is an important centre in its own right; the groups are of global significance and are not simply secondary derivatives of Asian or Australian groups.

In orchids, the New Caledonian genera *Clematepistephium* and *Eriaxis* are sister taxa, and the pair is sister to *Epistephium*, widespread in tropical South America between Paraguay and Colombia (Cameron, 2003). These genera belong to the tribe Vanilleae, a group that 'exhibits one of the most intriguing continental disjunctions in the Orchidaceae' (Cameron, 2003). *Vanilla* is pantropical while other genera occur around the Pacific in Southeast Asia, Malesia, Australia, Oceania and South America. Cameron (2000) attributed the general distribution of the group to evolution prior to the break-up of Gondwana and a series of vicariance events. This type of distribution based in and around the central Pacific may be related to persistent central Pacific volcanic centres and Cretaceous large igneous plateaus. The emplacement of these
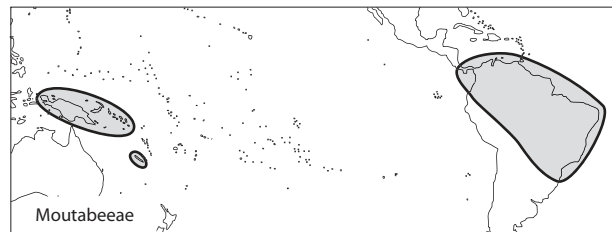

Figure 12 Tribe Moutabeeae (van Balgooy & van der Meijden, 1993).

plateaus – the largest igneous event in Earth's history – was followed by their dismemberment and dispersal eastward to New Zealand (Hikurangi plateau), the Solomon Islands (Ontong Java plateau) and elsewhere, and westward to Colombia and the Caribbean (Heads, 2009a).

Augusta (including *Lindenia*) (Rubiaceae) has a trans-tropical Pacific distribution: New Caledonia, Fiji and tropical America (Mexico to Panama, also Brazil; Motley *et al.*, 2005). Also in Rubiaceae, the Catesbaeeae–Chiococceae complex occurs in the Philippines, Micronesia, Melanesia, including New Caledonia, and throughout tropical America (Motley *et al.*, 2005). These authors wrote that 'There is no other lineage of flowering plants that appears to have a similar distribution pattern', but similar, trans-tropical Pacific distributions are cited here. Within the Catesbaeeae–Chiococceae complex, a New Caledonian clade composed of *Bikkia* species plus *Morierina* is sister to a group comprising *Schmidottia*, *Ceratopyxis* and *Siemensia*, all endemic to Cuba, and *Phialanthus* of the West Indies. Geologically the Caribbean crust was formed in the Pacific and this history is reflected here in the biogeography.

Motley *et al.* (2005) suggested that 'a New World origin for the Catesbaeeae–Chiococceae complex is indicated by the [New World] distribution of the taxa in the basal polytomy', but as indicated this line of argument is not convincing (Heads, 2009c). Since the Greater Antilles are the most species-rich area, Motley *et al.* proposed this as the ultimate centre of origin and suggested long-distance dispersal from here to the West Pacific (from Cuba to New Caledonia is about 12,000 km). Instead, the Catesbaeeae–Chiococceae complex could have arisen *in situ* by vicariance with a sister group in, say, Asia, or in America with secondary overlap. The identity of the sister group is still unclear, and solving this problem should be more useful for elucidating the history of the Catesbaeeae–Chiococceae complex than speculating on centres of origin and long-distance dispersal events.

A pantropical clade of trees and lianes in Violaceae is made up of *Hybanthus* s. str. and its allies (Fig. 13; Feng, 2005;

Tokuoka, 2008). The group is divided into two clades; one is a Gondwanan group distributed around the Indian Ocean, the other is a trans-tropical Pacific group. The breaks between the two groups are located in the Atlantic Ocean and around New Caledonia/McPherson-Macleay Overlap. Secondary overlap occurs only at the last two localities, perhaps due to the juxtaposition of Gondwanan and Pacific biotas there following terrane accretion.

BIOGEOGRAPHICAL PATTERNS, GEOLOGICAL EVENTS AND THE AGE OF TAXA

As discussed above ('Chronological analysis of phylogeny'), the age of taxa has usually been established on the basis of the fossil record or clocks calibrated with this. But this approach and the use of island age to date island endemics will give estimates of clade age that are too young by some unknown factor. Cretaceous–Cenozoic fossils are abundant and so many clades have been interpreted as this old and no older. These clades have been assumed to be too young to have been affected by events in the mid or lower Mesozoic. This was a period of major tectonic activity in the south-west Pacific with accretion of basement terranes and associated orogeny in New Zealand and New Caledonia. Vicariance studies of New Zealand (e.g. Heads, 1990) attributed many extant biogeographical patterns to these events and have sometimes been criticized for suggesting that groups could be so much older than is indicated by the fossil record. But recent revisions of ideas on phylogeny have also changed ideas on the age of groups. Angiosperms provide an illustrative example of this and the predictive power of biogeographical analysis.

The macrofossil record of angiosperms begins with flower assemblages from the late Early Cretaceous period, with unpublished records extending back to the Upper Jurassic (E.-M. Friis, personal communication cited in Frohlich & Chase, 2007). The oldest fossil angiosperm pollen is dated as 136 Ma (middle Early Cretaceous), about 10 Myr older
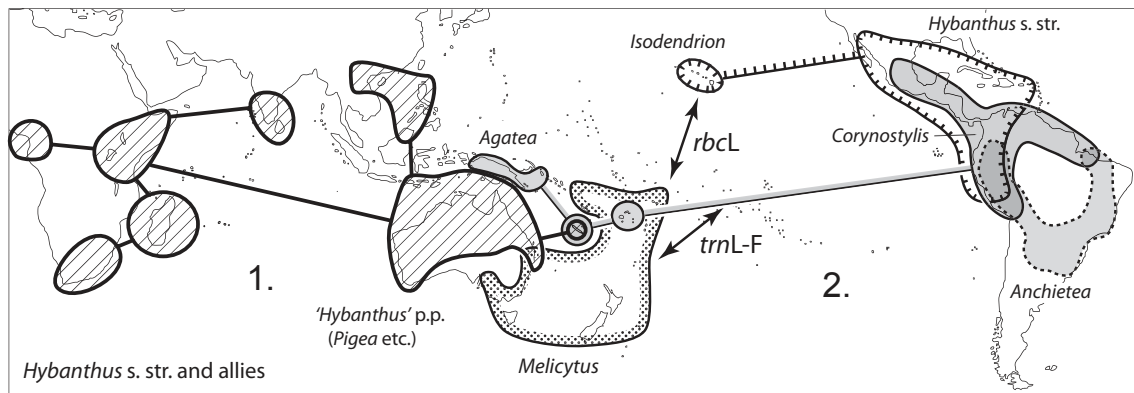

Figure 13 Distribution of *Hybanthus* s. str. and allies (Violaceae: Feng, 2005; Tokuoka, 2008). Of the two subclades, the first (1) comprises 'Indian Ocean *Hybanthus*' (oblique lines), the second (2) comprises *Melicytus* (stippled line), sister to either *Isodendrion* + 'American *Hybanthus*' (*rbc*L) or to *Agatea* (New Guinea, New Caledonia, Fiji) + *Corynostylis* and *Anchietea* (tropical America) (*trn*L-F).

than the earliest published flower fossils (Frohlich & Chase, 2007).

Molecular studies have found that angiosperms are not nested in extant gymnospems, but are basal either to all extant gymnosperms, to all extant gymnosperms except gnetophytes, or to cycads (Mathews, 2009). Of the extant gymnosperm groups, conifers are known from fossils back to the late Carboniferous, gnetophytes to the Permian and cycads also back to the Permian (*c.* 265–290 Ma; Brenner *et al.*, 2003). Even if angiosperms are sister to cycads alone, cycads, and thus angiosperms, existed at *c.* 265–290 Ma. Thus there is a period of *c.* 129–154 Myr until the first undisputed fossil angiosperms at *c.* 136 Ma during which time angiosperms probably existed, although fossils are either unknown or not recognized. If groups known only from fossils are considered, angiosperms may be sister to corystosperms (Upper Permian to Eocene) and so, again, are likely to be Permian in origin.

Molecular clock dating uses the principle of cross-calibration. This is based on the idea that the fossil record of a group with known fossils (such as gymnosperms) can be used to calibrate the age of a related clade without known fossils (such as angiosperms), whether the record of the latter is poor or misinterpreted. This means that dating a group based on the fossil record of the group itself can be avoided. Nevertheless, in studies of angiosperms this principle has been lost sight of; recent papers date angiosperms and calibrate phylogenetic trees for the group using fossil calibrations from the angiosperm fossil record alone (e.g. Bell *et al.*, 2005; Magallón & Castillo, 2009). Thus angiosperms are still regarded as Cretaceous – the same age they were given before the new phylogeny was established – and the significance of this important breakthrough has been overlooked by many researchers.

It is unknown whether the angiosperms in the gap between the molecular date and the oldest fossil date belong to the stem group (sister clades to the known group) or crown group (belonging to the extant clade). It is sometimes assumed that they belong to the stem group, but the only justification for this is the fossil record of angiosperms themselves which, as indicated, must be either flawed or misinterpreted.

For some authors the new phylogenies and their implications for angiosperm age have stimulated critical re-examination of pre-Cretaceous fossils. Doyle (2005) wrote that Triassic pollen in the *Crinopolles* group has 'remarkably angiosperm-like' features. Hochuli & Feist-Burckhardt (2004) described Triassic pollen belonging to angiosperms or an extinct group, possibly a sister group of angiosperms. Vasanthy *et al.* (2004) described Triassic 'angiospermid' pollen from the United States. In a review, Zavada (2007) concluded that Triassic pollen types 'exhibit a full inventory of angiosperm pollen synapomorphies' (p. 124) and that association with certain insect groups suggests modern ecological relationships. He concluded in favour of 'a Triassic origin of the angiosperm clade' (p. 127).

CONCLUSIONS

Although New Caledonia is composed of continental crust and part of the island was attached to Gondwana for some time in the mid-Cretaceous, most of the New Caledonian terranes originally formed as oceanic island arcs or sections of seafloor that included seamounts. The flora and fauna have evolved on these and survived for tens of millions of years, usually on very young islands. The separate arcs and other terranes, with their biotas, were eventually juxtaposed and fused during accretion. The rifting of basement terranes from Gondwana (eastern Australia), together with accretion of geological structures arriving from the Pacific side explains the double biogeographical affinities seen in New Caledonia and also in New Zealand and New Guinea. Affinities among New Zealand, New Caledonia and the central east coast of Australia (the McPherson-Macleay Overlap) can be explained with reference to the correlated Brook Street (New Zealand), Téremba (New Caledonia) and Gympie (Australia) terranes. Biogeographical connections of New Caledonia with Australia and New Zealand have often been explained with reference to tectonics, but areas of endemism involving New Caledonia with New Guinea and the central Pacific have usually been accounted for by chance dispersal. Instead, New Caledonian affinities with New Guinea via Rennell Island can be related to former subduction zones and orogeny along this sector. New Caledonian affinities with the outer Melanesian arcs may be the result of collision between New Caledonia and island arc/s such as the Vitiaz arc and the Loyalty ridge, following their arrival from the north-east. Trans-tropical Pacific endemism has seldom been discussed but the emplacement of the large igneous plateaus in the central Pacific (the largest igneous event in Earth's history) and their dispersal is probably implicated with trans-tropical Pacific distributions such as New Caledonia/ New Guinea–Colombia/Caribbean plate. In the model proposed here, the diversity and biogeography of the New Caledonian biota is due not to chance dispersal events and recent, adaptive radiation but to Mesozoic–Tertiary vicariance together with phases of juxtaposition caused by the accretion of arcs and other geological structures.

REFERENCES

Achille, F. (2006) *Tinadendron*, nouveau genre de Rubiaceae, Guattardeae de Mélanésie orientale. *Adansonia*, sér. 3, **28,** 167–180.

Adema, F.A.C.B. (1991) *Cupaniopsis* Rdlk. (Sapindaceae): a monograph. *Leiden Botanical Series*, **15,** 1–190.

Andersen, N.M. & Polhemus, D.A. (2003) A new genus of terrestrial Mesoveliidae from the Seychelles (Hemiptera: Gerromorpha). *Journal of the New York Entomological Society*, **111,** 12–21.

Arbogast, B.S., Drovetski, S.V., Curry, R.L., Boag, P.T., Suetin, G., Grant, P.R., Grant, B.R. & Anderson, D.J. (2006) The origin and diversification of Galapagos mockingbirds. *Evolution*, **60,** 370–382.

Arensburger, P., Buckley, T.R., Simon, C., Moulds, M. & Holsinger, K. (2004) Biogeography and phylogeny of the New Zealand cicada genera (Hemiptera: Cicadidae) based on nuclear and mitochondrial DNA data. *Journal of Biogeography*, **31**, 557–569.

Aubréville, A., Leroy, J.-F., Morat, Ph. & MacKee, H.S. (eds) (1967–present) *Flore de la Nouvelle-Calédonie et dépendances*. Muséum National d'Histoire Naturelle, Paris.

Avé, W. (1984a) *Baloghia. Pacific Plant Areas*, **4**, 180–181.

Avé, W. (1984b) *Fontainea. Pacific Plant Areas*, **4**, 184–185.

van Balgooy, M.M.J. (1984) Coronanthereae and Mitrarieae. *Pacific Plant Areas*, **4**, 186–187.

van Balgooy, M.M.J. & van der Meijden, R. (1993) Moutabeeae. *Pacific Plant Areas*, **5**, 166–167.

van Balgooy, M.M.J., Hovenkamp, P.H. & van Welzen, P.C. (1996) Phytogeography of the Pacific – floristic and historical distribution patterns in plants. *The origin and evolution of Pacific Island biotas, New Guinea to Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 191–213. SPB Academic, Amsterdam.

Bauer, A.M. & Jackman, T. (2006) Phylogeny and microendemism of the New Caledonian lizard fauna. *Herpetologica Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica* (ed. by M. Vences, J. Köhler, T. Ziegler and W. Böhme), pp. 9–13. Societas Herpetologica Bonnensis, Bonn.

Bell, C.D., Soltis, D.E. & Soltis, P.S. (2005) The age of the angiosperms: a molecular timescale without a clock. *Evolution*, **59**, 1245–1258.

Bernardi, L. (1979) The New Caledonian genera of Araliaceae and their relationships with those of Oceania and Indonesia. *Tropical botany* (ed. by K. Larsen and L.B. Holm-Nielsen), pp. 315–325. Academic Press, London.

Boon, W.M., Kearvell, J.C., Daugherty, C.H. & Chambers, G.K. (2001) Molecular systematics and conservation of kakariki (*Cyanoramphus* spp.). *Science for Conservation*, **176**, 1–46.

Boyer, S.L. & Giribet, G. (2007) A new model Gondwanan taxon: systematics and biogeography of the harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand. *Cladistics*, **23**, 337–361.

Boyer, S.L., Clouse, R.M., Benavides, L.R., Sharma, P., Schwendinger, P.J., Karunatathna, I. & Giribet, G. (2007) Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *Journal of Biogeography*, **34**, 2070–2085.

Brenner, E.D., Stevenson, D.W. & Twigg, R.W. (2003) Cycads: evolutionary innovations and the role of plant derived neurotoxins. *Trends in Plant Science*, **8**, 446–452.

Buckley, T.R. & Simon, C. (2007) Evolutionary radiation of the cicada genus *Maoricicada* Dugdale (Hemiptera: Cicadoidea) and the origins of the New Zealand alpine biota. *Biological Journal of the Linnean Society*, **91**, 419–435.

Buckley, T.R., Simon, C. & Chambers, G.K. (2001) Phylogeography of the New Zealand cicada *Maoricicada campbelli* based on mitochondrial DNA sequences: ancient clades associated with Cenozoic environmental change. *Evolution*, **55**, 1395–1407.

Buller, W.L. (1870) On *Zosterops lateralis* in New Zealand with an account of its migrations. *Transactions of the New Zealand Institute*, **3**, 15–23.

Cameron, K.M. (2000) Gondwanan biogeography of Vanilloideae (Orchidaceae). *Southern Connections Congress, programme and abstracts*, pp. 25–26. Wickliffe Press, Lincoln, New Zealand.

Cameron, K.M. (2003) Tribe Vanilleae: distribution, *Clematepistephium*, *Epistephium*, *Eriaxis. Genera Orchidacearum. Vol. 3. Orchidoideae (Part 2). Vanilloideae* (ed. by A.M. Pridgeon, P.J. Cribb, M.W. Chase and F.N. Rasmussen), pp. 299–302, 306–311. Oxford University Press, New York.

Campbell, J.D. & Holden, A.M. (1984) Miocene casuarinacean fossils from Southland and Central Otago, New Zealand. *New Zealand Journal of Botany*, **22**, 159–167.

Chambers, G.K., Boon, W.M., Buckley, T.R. & Hitchmough, R.A. (2001) Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. *Australian Journal of Botany*, **49**, 377–387.

Clark, J.R., Wagner, W.L. & Roalson, E.H. (2009) Patterns of diversification and ancestral range reconstruction in the southeast Asian–Pacific angiosperm lineage *Cyrtandra* (Gesneriaceae). *Molecular Phylogenetics and Evolution*, **53**, 982–994.

Conn, B.J. (1980) A taxonomic revision of *Geniostoma* subgenus *Geniostoma* (Loganiaceae). *Blumea*, **26**, 245–364.

Council of Heads of Australasian Herbaria (2009) *Australia's virtual herbarium*. Available at: http://www.ersa.edu.au/avh/ (accessed August 2009).

Craig, D.A., Currie, D.C. & Joy, D.A. (2001) Geographical history of the central-western Pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae: *Simulium*) based on a reconstructed phylogeny of the species, hot-spot archipelagos and hydrological considerations. *Journal of Biogeography*, **28**, 1101–1127.

Crisp, M.D., West, J.G. & Linder, H.P. (1999) Biogeography of the terrestrial flora. *Flora of Australia*, Vol. 1, 2nd edn (ed. by A.E. Orchard), pp. 321–367. Australian Biological Resources Study/CSIRO, Canberra.

Cronk, Q.C.B., Kiehn, M., Wagner, W.L. & Smith, J.F. (2005) Evolution of *Cyrtandra* (Gesneriaceae) of the Pacific Ocean: the origin of a supertramp clade. *American Journal of Botany*, **92**, 1017–1024.

Davis, C.C., Bell, C.D., Fritsch, P.W. & Mathews, S. (2002) Phylogeny of *Acridocarpus-Brachylophon* (Malpighiaceae): implications for Tertiary tropical floras and Afroasian biogeography. *Evolution*, **56**, 2395–2405.

Dickinson, E.C. (ed.) (2003) *The Howard & Moore complete checklist of the birds of the world*, 3rd edn. Princeton University Press, Princeton, NJ.

Doyle, J.A. (2005) Early evolution of angiosperm pollen as inferred from molecular and morphological phylogenetic analyses. *Grana*, **44**, 227–251.

Dumbacher, J.P., Pratt, T.K. & Fleischer, R.C. (2003) Phylogeny of the owlet-nightjars (Aves: Aegothelidae) based on mitochondrial DNA sequence. *Molecular Phylogenetics and Evolution*, **29**, 540–549.

Dutson, G. (2006) The Pacific shrikebills (*Clytorhynchus*) and the case for species status for the form *sanctaecrucis*. *Bulletin of the British Ornithologists' Club*, **126**, 299–308.

Edgecombe, G.D. & Giribet, G. (2009) Phylogenetics of scutigeromorph centipedes (Myriapoda: Chilopoda) with implications for species delimitation and historical biogeography of the Australian and New Caledonian forms. *Cladistics*, **25**, 406–427.

Eibl, J.M., Plunkett, G.M. & Lowry, P.P., II (2001) Evolution of *Polyscias* sect. *Tieghemopanax* (Araliaceae) based on nuclear and chloroplast DNA sequence data. *Adansonia*, series 3, **23**, 23–48.

Eriksen, B. (1993) Phylogeny of the Polygalaceae and its taxonomic implications. *Plant Systematics and Evolution*, **186**, 33–55.

Fay, M.F., Chase, M.W., Rønsted, N., Devey, D.S., Pillon, Y., Pires, J.C., Petersen, G., Seberg, O. & Davis, J.I. (2006) Phylogenetics of Liliales: summarized evidence from combined analyses of five plastid and one mitochondrial loci. *Aliso*, **22**, 559–565.

Feng, M. (2005) *Floral morphogenesis and molecular systematics of the family Violaceae*. PhD Thesis, Ohio University, Athens, OH.

Filardi, C.E. & Moyle, R.G. (2005) Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature*, **438**, 216–219.

Forest, F., Chase, M.W., Persson, C., Crane, P.R. & Hawkins, J.A. (2007) The role of biotic and abiotic factors in evolution of ant dispersal in the milkwort family (Polygalaceae). *Evolution*, **61**, 1675–1694.

Frohlich, M.W. & Chase, M.W. (2007) After a dozen years of progress the origin of angiosperms is still a great mystery. *Nature*, **450**, 1184–1189.

Galloway, D.J. (2007) *Flora of New Zealand: lichens*, 2nd edn. Manaaki Whenua, Lincoln, New Zealand.

Gibbs, G.W. (1990) Local or global? Biogeography of some primitive Lepidoptera in New Zealand. *New Zealand Journal of Zoology*, **16**, 689–698.

Global Biodiversity Information Facility (2010) Available at: www.gbif.org (accessed January 2010).

Govaerts, R., Frodin, D.G. & Pennington, T.D. (2001) *World checklist and bibliography of Sapotaceae*. Royal Botanic Gardens, Kew, UK.

Grandcolas, P., Murienne, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E. & Deharveng, L. (2008) New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 3309–3317.

Gressitt, J.L. (1958) *New Guinea and insect distribution. Proceedings of the Tenth International Congress of Entomology*, Vol. 1, Montreal, pp. 767–773.

Guillaumin, A. (1928) Les régions floristiques du Pacifique d'après leur endémisme et la répartition de quelques plantes phanérogames. *Proceedings of the 3rd Pan-Pacific Science Congress* [Tokyo], pp. 920–938.

Gustafsson, M.H.G., Bittrich, V. & Stevens, P.F. (2002) Phylogeny of Clusiaceae based on *rbc*L sequences. *International Journal of Plant Science*, **163**, 1045–1054.

Harbaugh, D.T. & Baldwin, B.G. (2007) Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): repeated dispersals throughout the Pacific. *American Journal of Botany*, **94**, 1028–1040.

Hartley, T.G. (2000) On the taxonomy and biogeography of *Euodia* and *Melicope* (Rutaceae). *Allertonia*, **8**, 1–319.

Hartley, T.G. (2001) Morphology and biogeography in Australasian-Malesian Rutaceae. *Malayan Nature Journal*, **55**, 197–219.

Heads, M. (1990) Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand Journal of Zoology*, **16**, 549–586.

Heads, M. (2001) Birds of paradise, biogeography and ecology in New Guinea: a review. *Journal of Biogeography*, **28**, 893–927.

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

Heads, M. (2004) What is a node? *Journal of Biogeography*, **31**, 1883–1891.

Heads, M. (2005a) A review of R.T. Pennington, Q.C.B. Cronk, and J.A. Richardson (eds) (2004) 'Plant phylogeny and the origin of major biomes'. *The Systematist*, **24**, 19–22.

Heads, M. (2005b) Dating evolutionary events: a critique of the molecular clock approach. *Cladistics*, **21**, 62–78.

Heads, M. (2006) Panbiogeography of *Nothofagus* (Nothofagaceae): analysis of the main species massings. *Journal of Biogeography*, **33**, 1066–1075.

Heads, M. (2008a) Panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic arcs, and old taxa endemic to young islands. *Journal of Biogeography*, **35**, 2153–2175.

Heads, M. (2008b) Biological disjunction along the West Caledonian Fault, New Caledonia: a synthesis of molecular phylogenetics and panbiogeography. *Botanical Journal of the Linnean Society*, **158**, 470–488.

Heads, M. (2009a) Globally basal centres of endemism: the Tasman-Coral Sea region (south-west Pacific), Latin America and Madagascar/South Africa. *Biological Journal of the Linnean Society*, **96**, 222–245.

Heads, M. (2009b) Vicariance. *Encyclopedia of islands* (ed. by R.G. Gillespie and D.A. Clague), pp. 947–950. University of California Press, Berkeley.

Heads, M. (2009c) Inferring biogeographic history from molecular phylogenies. *Biological Journal of the Linnean Society*, **98**, 757–774.

Heads, M. (2010a) The endemic plant families and the palms of New Caledonia: a biogeographical analysis. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2010.02292.x.

Heads, M. (2010b) Evolution and biogeography of primates: a new model based on plate tectonics, molecular phylogenetics and vicariance. *Zoologica Scripta*, **39**, 107–127.

Herzer, R.H., Chaproniere, G.C.H., Edwards, A.R., Hollis, C.J., Pelletier, B., Raine, J.I., Scott, G.H., Stagpoole, V., Strong, C.P., Symonds, P., Wilson, G.J. & Zhu, H. (1997) Seismic stratigraphy and structural history of the Reinga Basin and its margins, southern Norfolk Ridge system. *New Zealand Journal of Geology and Geophysics*, **40**, 425–451.

Hochuli, P.A. & Feist-Burckhardt, S. (2004) A boreal early cradle of angiosperms? Angiosperm-like pollen from the Middle Triassic of the Barents Sea (Norway). *Journal of Micropalaeontology*, **23**, 97–104.

Holloway, J.D. (1996) The Lepidoptera of Norfolk Island, actual and potential, their origins and dynamics. *The origin and evolution of Pacific Island biotas, New Guinea to Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 123–151. SPB Academic, Amsterdam.

Holm-Nielsen, L.B. (1979) Comments on the distribution and evolution of the genus *Phyllanthus* (Euphorbiaceae). *Tropical botany* (ed. by K. Larsen and L.B. Holm-Nielsen), pp. 277–290. Academic Press, London.

Howarth, D.G., Gustafsson, M.H.G., Baum, D.A. & Motley, T.J. (2003) Phylogenetics of the genus *Scaevola* (Goodeniaceae): implications for dispersal patterns across the Pacific Basin and colonization of the Hawaiian Islands. *American Journal of Botany*, **90**, 915–923.

Hutton, F.J. (1872) On the geographic relations of the New Zealand fauna. *Transactions of the New Zealand Institute*, **5**, 227–256.

Jønsson, K.A., Bowie, R.C.K., Moyle, R.G., Christidis, L., Norma, J.A., Benz, B.W. & Fjeldså, J. (2010) Historical biogeography of an Indo-Pacific passerine bird family (Pachycephalidae): different colonization patterns in the Indonesian and Melanesian archipelagos. *Journal of Biogeography*, **37**, 245–257.

Keast, A. (1966) *Australia and the Pacific Islands: a natural history*. Random House, New York.

Keast, A. (1996) Pacific biogeography: patterns and processes. *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 477–512. SPB Academic, Amsterdam.

Kelch, D.G. (2002) Phylogenetic assessment of the monotypic genera *Sundacarpus* and *Manoao* (Coniferales: Podocarpaceae) utilising evidence from 18S rDNA sequences. *Australian Systematic Botany*, **15**, 29–35.

Klazenga, N. (1999) A revision of the Malesian species of *Dicranoloma* (Dicranaceae, Musci). *Journal of the Hattori Botanical Laboratory*, **87**, 1–130.

Kodandaramaiah, U. (2010) Use of dispersal–vicariance analysis in biogeography – a critique. *Journal of Biogeography*, **37**, 3–11.

de Kok, R.P.J. & Mabberley, D.J. (1999a) The genus *Faradaya* (Labiatae). *Blumea*, **44**, 321–342.

de Kok, R.P.J. & Mabberley, D.J. (1999b) A synopsis of *Oxera* Labill. (Labiatae). *Kew Bulletin*, **54**, 265–300.

Kroenke, L.W. (1996) Plate tectonic development of the Western and Southwestern Pacific: Mesozoic to the present. *The origin and evolution of Pacific island biotas* (ed. by A. Keast and S.E. Miller), pp. 19–34. SPB Academic, Amsterdam.

Kubitzki, K. (1998) Campynemataceae. *The families and genera of vascular plants*. Vol. 3. *Flowering plants. Monocotyledons: Lilianae* (ed. by K. Kubitzki) pp. 173–175. Springer, Berlin.

Ladiges, P. (1998) Biogeography after Burbidge. *Australian Systematic Botany*, **11**, 231–242.

Ladiges, P.Y. & Cantrill, D. (2007) New Caledonia–Australian connections: biogeographic patterns and geology. *Australian Systematic Botany*, **20**, 383–389.

Ladiges, P.Y., Udovicic, F. & Nelson, G. (2003) Australian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. *Journal of Biogeography*, **30**, 989–998.

Last, P.R. & Yearsley, G.K. (2002) Zoogeography and relationships of Australasian skates (Chondrichthyes: Rajidae). *Journal of Biogeography*, **29**, 1627–1641.

Lecroy, M. & Barker, F.K. (2006) A new species of bush-warbler from Bougainville Island and a monophyletic origin for southwest Pacific *Cettia*. *American Museum Novitates*, **3511**, 1–20.

Lowry, P.P., II (1988) Notes on the Fijian endemic *Meryta tenuifolia* (Araliaceae). *Annals of the Missouri Botanic Garden*, **75**, 389–391.

Mabberley, D.J. (1998) On *Neorapinia* (*Vitex* sensu lato, Labiate-Viticoideae). *Telopea*, **7**, 313–317.

Magallón, S. & Castillo, A. (2009) Angiosperm diversity through time. *American Journal of Botany*, **96**, 349–365.

Manconi, R. & Serusi, A. (2008) Rare sponges from marine caves: discovery of *Neophrissospongia nana* nov. sp. (Demospongiae, Corallistidae) from Sardinia with an annotated checklist of Mediterranean lithistids. *ZooKeys*, **4**, 71–87.

Mathews, S. (2009) Phylogenetic relationships among seed plants: persistent questions and the limits of molecular data. *American Journal of Botany*, **96**, 228–236.

Matthews, E.G. (1998) Classification, phylogeny and biogeography of the genera of Adeliini (Coleoptera: Tenebrionidae). *Invertebrate Taxonomy*, **12**, 685–824.

Maxwell, J.F. & Veldkamp, J.F. (1990) Notes on the Astronieae (Melastomataceae) – II. Astronidium, Beccarianthus. *Blumea*, **35**, 115–165.

Mayr, E. (1933) Birds collected during the Whitney South Sea Expedition. XXII. Three new genera from Polynesia and Melanesia. *American Museum Novitates*, **590**, 1–6.

Mees, G.F. (1969) A systematic review of the Indo-Australian Zosteropidae (part III). *Zoologische Verhandelingen*, **102**, 1–390.

Meffre, S., Crawford, A.J. & Quilty, P.G. (2007) *Arc continent collision forming a large island between New Caledonia and*

New Zealand in the Oligocene. ASEG Extended Abstracts 2006, doi:10.1071/ASEG2006ab111.

Miller, H.A., Whittier, H.O. & Whittier, B.A. (1978) *Prodromus florae Muscorum Polynesiae: with a key to genera.* Cramer, Vaduz.

Morat, P., Veillon, J.-M. & MacKee, H.S. (1984) Floristic relationships of New Caledonian rain forest phanerogams. *Biogeography of the tropical Pacific* (ed. by P. Raven, F. Radovsky and S. Sohmer), pp. 71–128. Association of Systematics Collections and Bernice P. Bishop Museum, Honolulu.

Motley, T.J., Wurdack, K.J. & Delprete, P.G. (2005) Molecular systematics of the Catesbaeeae–Chiococceae complex (Rubiaceae): flower and fruit evolution and biogeographic implications. *American Journal of Botany*, **92**, 316–329.

Moyle, R.G., Filardi, C.E., Smith, C.E. & Diamond, J. (2009) Explosive Pleistocene diversification and hemispheric expansion of a 'great speciator'. *Proceedings of the National Academy of Sciences USA*, **106**, 1863–1868.

Nickrent, D. (1998) *Intrafamilial phylogeny of Balanophoraceae.* Available at: http://www.parasiticplants.siu.edu/Balanophoraceae/ (accessed August 2009).

Nyári, A.S., Benz, B.W., Jønsson, K.A., Fjeldså, J. & Moyle, R.G. (2009) Phylogenetic relationships of fantails (Aves: Rhipiduridae). *Zoologica Scripta*, **38**, 553–561.

Orenstein, R.I. & Pratt, H.D. (1983) The relationships and evolution of the southwest Pacific warbler genera *Vitia* and *Psamathia* (Sylviinae). *Wilson Bulletin*, **95**, 184–198.

Page, T.J., Baker, A.M., Cook, B.D. & Hughes, J.M. (2005) Historical transoceanic dispersal of a freshwater shrimp: the colonization of the South Pacific by the genus *Paratya* (Atyidae). *Journal of Biogeography*, **32**, 581–593.

Pillon, Y. (2008) *Biodiversité, origine et evolution des Cunoniaceae: implications pour la conservation de la flore de Nouvelle-Calédonie.* Unpublished PhD Thesis, Université de la Nouvelle-Calédonie, Nouméa.

Pillon, Y., Hopkins, H.C.F. & Bradford, J.C. (2008) Two new species of *Cunonia* (Cunoniaceae) from New Caledonia. *Kew Bulletin*, **63**, 419–431.

Pillon, Y., Hopkins, H.C.F., Munzinger, J. & Chase, M.W. (2009) A molecular and morphological survey of generic limits of *Acsmithia* and *Spiraeanthemum* (Cunoniaceae). *Systematic Botany*, **34**, 141–148.

Plunkett, G.M. & Lowry, P.P., II (2007) *Evolution and biogeography in Melanesian Schefflera (Araliaceae): a preliminary assessment based on ITS and ETS sequence data.* Abstract only. Botany and Plant Biology 2007 Joint Congress, Chicago. Available at: http://www.2007.botanyconference.org/engine/search/index.php?func=detail&aid=1425.

Plunkett, G.M., Lowry, P.P., II, Frodin, D.G. & Wen, J. (2005) Phylogeny and biogeography of *Schefflera*: pervasive polyphyly in the largest genus of Araliaceae. *Annals of the Missouri Botanic Garden*, **92**, 202–224.

Pole, M. (1993) Early Miocene flora of the Manuherikia Group, New Zealand. 7. Myrtaceae, including *Eucalyptus. Journal of the Royal Society of New Zealand*, **23**, 313–328.

Polhemus, D.A. (1996) Island arcs, and their influence on Indo-Pacific biogeography. *The origin and evolution of Pacific Island biotas, New Guinea to eastern Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 51–66. SPB Academic Publishing, Amsterdam.

Quarles van Ufford, A. & Cloos, M. (2005) Cenozoic tectonics of New Guinea. *Bulletin of the American Association of Petroleum Geology*, **98**, 119–140.

Renner, S.S., Murray, D. & Foreman, D. (2000) Timing transantarctic disjunctions in the Atherospermataceae (Laurales): evidence from coding and noncoding chloroplast sequences. *Systematic Biology*, **49**, 579–591.

Richardson, J.E., Chatrou, L.W., Mols, J.B., Erkens, R.H.J. & Pirie, M.D. (2004) Historical biogeography of two cosmopolitan families of flowering plants Annonaceae and Rhamnaceae. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 1495–1508.

Sanmartín, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology*, **53**, 216–243.

Saunders, R.M.K. & Munzinger, J. (2007) A new species of *Goniothalamus* (Annonaceae) from New Caledonia, representing a significant range extension for the genus. *Botanical Journal of the Linnean Society*, **155**, 497–503.

Schaefer, H., Telford, I.R.H. & Renner, S.S. (2008) *Austrobryonia* (Cucurbitaceae), a new Australian genus, is the closest living relative to the Eurasian and Mediterranean *Bryonia* and *Ecballium. Systematic Botany*, **33**, 125–132.

Schellart, W.P., Lister, G.S. & Toy, V.G. (2006) A Late Cretaceous and Cenozoic reconstruction of the Southwest Pacific region: tectonics controlled by subduction and slab rollback processes. *Earth Science Reviews*, **76**, 191–233.

Sdrolias, M., Müller, R.D. & Gaina, C. (2003) Tectonic evolution of the southwest Pacific using constraints from backarc basins. *Geological Society of America Special Paper*, **372**, 343–359.

Séret, B. (1997) Les poissons d'eau douce de Nouvelle-Calédonie: implications biogéographiques de récentes découvertes. *Zoologia Neocaledonica*, Vol. 4 (ed. by J. Najt and L. Matile), pp. 369–378. Mémoires du Muséum National d'Histoire Naturelle, Paris, No. 171.

Setoguchi, H., Ohba, H. & Tobe, H. (1998) Evolution in *Crossostylis* (Rhizophoraceae) on the South Pacific Islands. *Evolution and speciation of island plants* (ed. by T.F. Stuessy and M. Ono), pp. 203–229. Cambridge University Press, Cambridge.

Simmons, N.B. (2005) *Pteropus. Mammal species of the world: a taxonomic and geographic reference*, 3rd edn (ed. by D.E. Wilson and D.A.M. Reeder), pp. 334–346. Johns Hopkins University Press, Baltimore, MD.

Sinclair, W.T., Mill, R.R., Gardner, M.F., Woltz, P., Jaffré, T., Preston, J., Hollingsworth, M.L., Ponge, A. & Möller, M. (2002) Evolutionary relationships of the New Caledonian heterotrophic conifer *Parasitaxus usta* (Podocarpaceae), inferred from chloroplast *trn*L-F intron/spacer and nuclear

rDNA ITS2 sequences. *Plant Systematics and Evolution*, **233,** 79–104.

Sipman, H.J.M. (1983) *A monograph of the lichen family Megalosporaceae.* Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht, Vol. 482. Cramer, Vaduz.

Smissen, R.D., Garnock-Jones, P.J. & Chambers, G.K. (2003) Phylogenetic analysis of ITS sequences suggests a Pliocene origin for the bipolar distribution of *Scleranthus* (Caryophyllaceae). *Australian Systematic Botany*, **16,** 301–313.

Smith, J.F., Funke, M.M. & Woo, V.L. (2006) A duplication of g*cyc* predates divergence within tribe Coronanthereae (Gesneriaceae): phylogenetic analysis and evolution. *Plant Systematics and Evolution*, **261,** 245–256.

Smith, S.A., Sadlier, R.A., Bauer, A.M., Austin, C.C. & Jackman, T. (2007) Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: evidence for a single origin of the endemic skinks of Tasmantis. *Molecular Phylogenetics and Evolution*, **43,** 1151–1166.

Spandler, C., Worden, K., Arculus, R. & Eggins, S. (2005) Igneous rocks of the Brook Street Terrane, New Zealand: implications for Permian tectonics of eastern Gondwana and magma genesis in modern intra-oceanic volcanic arcs. *New Zealand Journal of Geology and Geophysics*, **48,** 167–183.

Springer, V.G. (1989) *Ecsenius*: the world's most interesting genus of marine fishes, part II. *Tropical Fish Hobbyist*, **37,** 50–61.

Springer, V.G. (1999) *Ecsenius polystictus*, new species of blenniid fish from Mentawai Islands, Indonesia, with notes on other species of *Ecsenius*. *Revue Français Aquariologie*, **16,** 39–48.

Springer, V.G. (2002) *Ecsenius niue*, new species of blenniid fish, and new distribution records for other species in the *Opsifrontalis* species group. *Zootaxa*, **72,** 1–6.

van Steenis, C.G.G.J. (1981) *Rheophytes of the world.* Sijthoff and Noordhoff, Alpen aan den Rijn, The Netherlands.

Sweeney, P.W. (2008) Phylogeny and floral diversity in the genus *Garcinia* (Clusiaceae) and relatives. *International Journal of Plant Science*, **169,** 1288–1303.

Swenson, U., Munzinger, J. & Bartish, I.V. (2007) Molecular phylogeny of *Planchonella* (Sapotaceae) and eight new species from New Caledonia. *Taxon*, **56,** 329–354.

Thien, L.B., Bernhardt, P., Gibbs, G.W., Bergström, G., Groth, I. & McPherson, G. (1985) The pollination of *Zygogynum* (Winteraceae) by a moth, *Sabatinca* (Micropterigidae): an ancient association? *Science*, **227,** 540–543.

Tokuoka, T. (2008) Molecular phylogenetic analysis of Violaceae (Malpighiales) based on plastid and nuclear DNA sequences. *Journal of Plant Research*, **121,** 253–260.

Tronchet, F., Plunkett, G.M., Jérémie, J. & Lowry, P.P., II (2005) Monophyly and major clades of *Meryta* (Araliaceae). *Systematic Botany*, **30,** 657–670.

Valdés, Á. (2001a) Depth-related adaptations, speciation processes and evolution of color in the genus *Phyllidiopsis* (Mollusca: Nudibranchia). *Marine Biology*, **139,** 485–496.

Valdés, Á. (2001b) Deep-water phyllidiid nudibranchs (Gastropoda: Phyllidiidae) from the tropical south-west Pacific Ocean. *Tropical deep-sea benthos*, Vol. 22 (ed. by P. Bouchet and B.A. Marshall), pp. 331–368. Mémoires du Muséum National d'Histoire Naturelle, Paris, No. 185.

Valdés, Á. (2001c) Deep-sea cryptobranch dorid nudibranchs (Mollusca, Opisthobranchia) from the tropical west Pacific, with descriptions of two new genera and eighteen new species. *Malacologia*, **43,** 237–311.

Vasanthy, G., Cornet, B. & Pocock, S.A.J. (2004) Evolution of proangiosperms during Late Triassic: pre-Cretaceous pollen trends towards mono- and dicotyledonous taxa diversification. *Geophytology*, **33,** 99–113.

Wang, C.-N., Möller, M. & Cronk, Q.C.B. (2004) Phylogenetic position of *Titanotrichum oldhamii* (Gesneriaceae) inferred from four different gene regions. *Systematic Botany*, **29,** 407–418.

Warren, B.H. & Hawkins, J.A. (2006) The distribution of species diversity across a flora's component lineages: dating the Cape's 'relics'. *Proceedings of the Royal Society B: Biological Sciences*, **273,** 2149–2158.

Webster, G.L. & Airy Shaw, H.K. (1971) A provisional synopsis of the New Guinea taxa of *Phyllanthus* (Euphorbiaceae). *Kew Bulletin*, **26,** 85–109.

Wen, J. & Ickert-Bond, S.M. (2009) Evolution of the Madrean-Tethyan disjunctions and the North American and South American amphitropical disjunctions in plants. *Journal of Systematics and Evolution*, **47,** 331–348.

Wilson, P.G. (1996) Myrtaceae in the Pacific, with special reference to *Metrosideros*. *The origin and evolution of Pacific Island biotas, New Guinea to eastern Polynesia: patterns and processes* (ed. by A. Keast and S.E. Miller), pp. 233–245. SPB Academic Publishing, Amsterdam.

Wilson, P.G., O'Brien, M.M., Heslewood, M.M. & Quinn, C.J. (2005) Relationships within Myrtaceae *sensu lato* based on a *mat*K sequence. *Plant Systematics and Evolution*, **251,** 3–19.

Woodland, D.J. (1983) Zoogeography of the Siganidae (Pisces): an interpretation of distribution and richness patterns. *Bulletin of Marine Science*, **33,** 713–717.

Wurdack, K.J., Hoffmann, P. & Chase, M.W. (2005) Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae *sensu stricto*) using plastid *rbc*L and *trn*L-F DNA sequences. *American Journal of Botany*, **92,** 1397–1420.

Zavada, M.S. (2007) The identification of fossil angiosperm pollen and its bearing on the time and place of the origin of angiosperms. *Plant Systematics and Evolution*, **263,** 117–134.

Zerega, N.J.C., Clement, W.L., Datwyler, S.L. & Weiblen, G.D. (2005) Biogeography and divergence times in the mulberry family (Moraceae). *Molecular Phylogenetics and Evolution*, **37,** 402–416.

Zug, G.R. (1991) *Lizards of Fiji: natural history and systematics*. Bishop Museum Press, Honolulu.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary notes on New Caledonian biogeography.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

Michael Heads has taught ecology and systematics at universities in Papua New Guinea, Zimbabwe, Ghana and Fiji. His main research interests are in tree architecture, biogeography and the evolution of rain forest plants and animals.

Editor: Malte Ebach