

# Globally basal centres of endemism: the Tasman-Coral Sea region (south-west Pacific), Latin America and Madagascar/South Africa

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The New Zealand wrens (Acanthisittidae) are basal in passerine birds and in New Caledonia, the closest country to New Zealand, *Amborella* is basal in angiosperms. A review of molecular studies indicates that 29 other locally or regionally endemic clades around the Tasman and Coral Sea basins have cosmopolitan or globally widespread sister groups. Other areas that have local endemics basal to diverse global groups include Borneo, Madagascar/South Africa/Tanzania, southern China–Taiwan–Japan, and different parts of Latin America, especially the Guayana Plateau and western Mexico. Basal clades are widely interpreted as ancestral and their location is generally taken to represent a centre of origin for the group as a whole. In the present study, basal groups are treated simply as small (less speciose) sister groups. The Tasman and western Mexico/Caribbean regions have important biogeographic and tectonic ties with each other and with the central Pacific. Large igneous provinces (Ontong Java, Hikurangi-Manihiki, and Gorgona Plateaus) formed in the central Pacific in the Cretaceous. Fossil wood is found on the Ontong Java Plateau, and formerly emergent seamounts up to 24 km across occur on Hikurangi Plateau. Many terranes in New Zealand, New Caledonia, New Guinea and western America represent former island arcs (or their products) that formed in the central Pacific and later accreted to the Pacific margins. Long-term survival of taxa as metapopulations on the ephemeral volcanic islands and atolls of plate margins and fissures may explain the biogeographical connections among the Tasman region, the central Pacific, and the accreted terranes of western America. Branching sequences in cladograms and phylogenetic trees have been interpreted as dispersal events, but instead probably indicate the sequence of differentiation in an already widespread ancestor. Major disjunctions of tens of thousands of kilometres often occur between taxa at consecutive nodes on a tree and dispersal by physical movement is unlikely. The break between the globally basal centres and the rest of the world marks the initial site of differentiation of a widespread ancestor, with subsequent or more or less simultaneous differentiation occurring in other areas. Differentiation of the modern angiosperms, passerines and other groups first took place around the Tasman region, or at least the terranes now accumulated there, and then around other centres, especially Madagascar–South Africa and Mexico–north-west South America. Angiosperms are now recognized as basal to extant gymnosperms and major tectonic dynamism around the globally basal centres during the Mesozoic, involving terrane accretion, orogeny, and rifting could have been involved with the last important modernization of angiosperms, birds and other groups. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 96, 222–245.

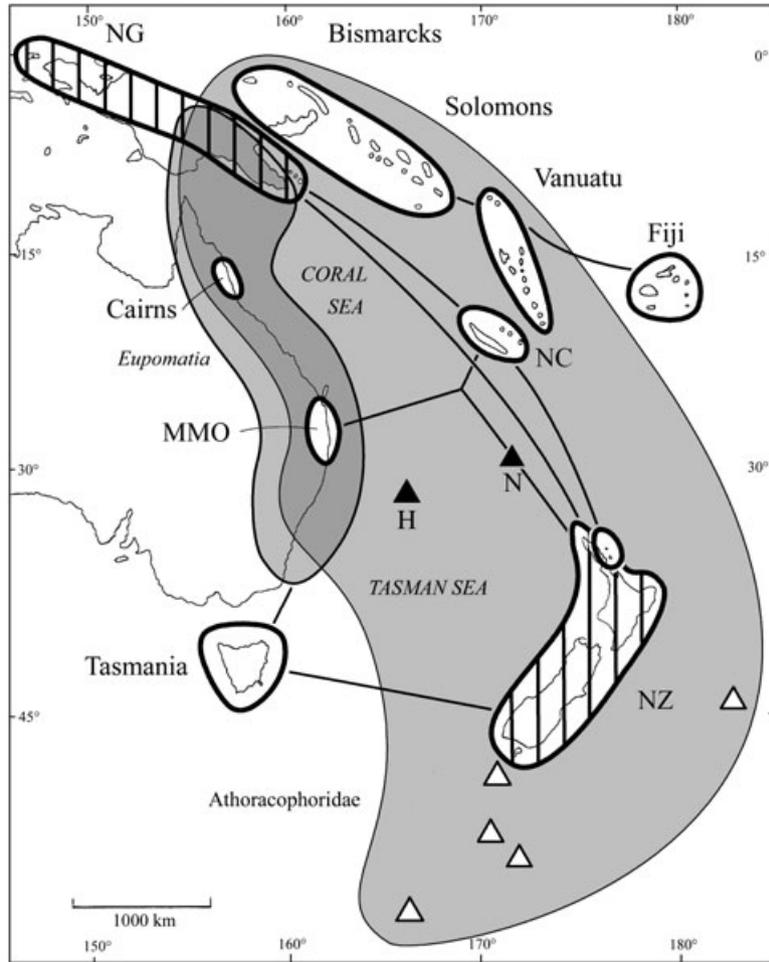
**ADDITIONAL KEYWORDS:** *Amborella* – Acanthisittidae – biogeography – distribution – ecology – molecular phylogeny – panbiogeography – vicariance.

## INTRODUCTION

The basal passerines (Acanthisittidae) are endemic to New Zealand and the basal angiosperm (*Amborella*) is endemic to New Zealand's nearest neighbour, New

Caledonia. These discoveries, both made in the period 1999–2002, concern two major groups and presumably have significance for ideas on evolution. But what exactly do they mean? The intriguing geographical pattern, with the two groups located closely together in the south-west Pacific islands, is the theme of the present study. Is the juxtaposition really

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**Figure 1.** The Tasman-Coral Sea region, with the centres of endemism of the basal groups. MMO, McPherson–Macleay Overlap; NG, New Guinea; NC, New Caledonia; NZ, New Zealand. White triangles, islands occupied by Athoracophoridae. Black triangles (Athoracophoridae not present): H, Lord Howe I., N, Norfolk I.

just a coincidence? It may have no significance; the two groups might only be the results of chance dispersal or chance survival. Alternatively, their location might be part of a general pattern and could be a clue to understanding global evolution in birds, trees, and other groups.

**MATERIAL AND METHODS**

To establish whether there are other taxa like *Amborella* and the wrens, recent literature was scanned for more or less local endemics in the south-west Pacific region with widespread (especially cosmopolitan or pantropical) sister groups.

A basal group is just a small sister group (Krell & Cranston, 2004; Crisp & Cook, 2005; Santos, 2007) and the phrases ‘sister to the rest of’ and ‘basal in’ are used here more or less interchangeably. The difference between the two is mainly nomenclatural: a

basal group is considered to be part of the sister group and has the same name, a sister has a different name.

Maps of Australian plants were accessed at: <http://www.anbg.gov.au/avh/> and at: <http://florabase.calm.wa.gov.au/>. Maps of tropical American plants based on Missouri Botanical Garden records are at: <http://mobot.mobot.org/W3T/Search/vast.html>. Distributions of plant genera in Chile are given in Moreira-Muñoz (2007).

**SYSTEMATIC BIOGEOGRAPHY**

Globally basal endemic taxa in the Tasman-Coral Sea region are listed below and their local centres of endemism are shown in Fig. 1.

**FLORA**

1. In red algae, *Apophlaea* is endemic to New Zealand (subantarctic islands, Chathams and

- main islands) and is sister to a group of *Hildenbrandia* which is widespread through northern and southern temperate zones at least (Sherwood & Sheath, 1999, 2003).
2. In liverworts, *Goebeliella*, monotypic in New Zealand (the subantarctic Auckland Islands, the main islands and the Chathams) and New Caledonia is sister to a large group: Radulaceae, Frullaniaceae, Jubulaceae plus Lejeuneaceae (Hodgson, 1949; He-Nygrén *et al.*, 2006; D. Glenny, pers. comm.).
  3. In angiosperms, *Amborella trichopoda* is a shrub or small tree of New Caledonia and is basal in angiosperms (Mathews & Donoghue, 1999; Müller, Borsch & Hilu, 2006; Stevens, 2007). Occasionally, it is placed as sister to Nymphaeales, and these two are basal in angiosperms. Nymphaeales are more or less worldwide (not in New Zealand or New Caledonia).
  4. *Eupomatia* is a liane or scandent shrub. One species, *Eupomatia laurina*, occurs in eastern Australia (east of the Great Dividing Range) and Papua New Guinea, the other, *Eupomatia bennettii*, is restricted to south-east Queensland and north-east New South Wales, a region known to biogeographers as the McPherson Range–Macleay River Overlap (MMO). It is sister to Annonaceae, a pantropical family of lowland rain-forest lianes and trees (Sauquet *et al.*, 2003).
  5. In monocots, *Blandfordia* of south-east Australia (MMO to Tasmania) is sister to Lanariaceae of South Africa, Asteliaceae of Mascarenes, Pacific islands and Chile, and Hypoxidaceae, of the seasonal tropics especially southern Africa (Graham *et al.*, 2006).
  6. *Doryanthes* has two species of massive, agave-like plants at the MMO, one of which is also in north-east Queensland. The genus is sister to the cosmopolitan clade comprising Iridaceae, Xeronemataceae, and others (Janssen & Bremer, 2004).
  7. *Xeronema* comprises *Xeronema moorei* of New Caledonia and *Xeronema callistemon* of the Poor Knights and Hen and Chicken Islands, northern New Zealand. It is basal in a large, cosmopolitan clade of Asparagales (Fay *et al.*, 2000; Janssen & Bremer, 2004).
  8. *Isophysis*, a monotype from southern and western Tasmania, is basal in the more or less cosmopolitan Iridaceae (Davies, Goldblatt & Barraclough, 2005).
  9. The orchid *Pachyplectron* comprises three species endemic to New Caledonia and is sister to the rest of the subtribe Goodyerinae, a virtually cosmopolitan group (Cribb, Pridgeon & Chase, 2003).
  10. There are three clades in Liliales. One is Campynemataceae, with one species in Tasmania (*Campynema*) and two in New Caledonia (*Campynema* and *Campynemanthe*) (Fay *et al.*, 2006).
  11. *Petermannia*, monotypic, is a climber with a woody rhizome found at the MMO and is sister to a cosmopolitan clade of Liliales (Colchicaceae, Alstroemeriaceae, Luzuriagaceae) (Fay *et al.*, 2006).
  12. Berberidopsidaceae comprise *Streptothamnus*, monotypic at the MMO, and *Berberidopsis*, with one species at the MMO and one in Central Chile (by Concepción) (Savolainen *et al.*, 2000). This family is sister to *Aextoxicon*, also in Central Chile (I. Chiloé to approximately Coquimbo). The two families (forming Berberidopsidales) may be basal to a very large, cosmopolitan clade of core eudicots (Soltis *et al.*, 2003).
  13. In eudicots, *Canacomyrca* is endemic to New Caledonia and is sister to the rest of the subcosmopolitan family Myricaceae (Herbert *et al.*, 2006). *Canacomyrca* is extant only in New Caledonia, but pollen from Eocene to Miocene strata in New Zealand has been identified with it (Lee, Lee & Mortimer, 2001). The rest of the family is widespread globally but notably absent from Australia, eastern New Guinea, New Caledonia, New Zealand and southern South America.
  14. The tree *Balanops*, sole genus of Balanopaceae, ranges in New Caledonia (seven spp.), Vanuatu and Fiji (one spp.), and north-east Queensland (one spp.). It is sister to a large pantropical complex comprising Chrysobalanaceae, Dichapetalaceae, Euphroniaceae, and Trigoniaceae (Stevens, 2007).
  15. *Athrotaxis* (Tasmania) is sister to all other Cupressaceae s.l. except *Cunninghamia* and *Taiwania* (Gadek *et al.*, 2000).
  16. *Sparattosyce* (New Caledonia) and *Antiaropsis* (New Guinea) form the basal clade in the pantropical tribe Castilleae (Moraceae) (Zerega *et al.*, 2005).
  17. *Tetracarpaea*, monotypic, is a shrub of subalpine woodland in Tasmania, and is sister to the cosmopolitan clade Haloragaceae plus Penthoraceae (Stevens, 2007).
  18. *Pennantia* has one species in the South Island and the North Island of New Zealand, one on Three Kings Islands, one on Norfolk Island, and one in eastern Australia (eastern New South Wales, disjunct in north-east Queensland) (Gardner & de Lange, 2002). The genus is sister to a cosmopolitan clade including Umbelliferae/Araliaceae, Pittosporaceae, Griseliniaceae, and Torricelliaceae (Kårehed, 2003).

19. *Teucrium* (Lamiaceae) of central New Zealand (North and South Islands) is sister to another monotype, *Oncinocalyx* of the MMO (Cantino, Wagstaff & Olmstead, 1999). This pair is sister to the almost cosmopolitan *Teucrium*, usually credited with 300 species and especially diverse in the Mediterranean but absent in New Zealand.

## FAUNA

- In molluscs, Athoracophoridae are a family of terrestrial slugs that are sister to the cosmopolitan Succineidae (Wade, Mordan & Naggs, 2006). Athoracophorids are widespread around the Tasman-Coral Sea region (not Tasmania): New Zealand (including the subantarctic Macquarie, Auckland, Campbell, Snares and Chatham Islands; Burton, 1963, 1980), New Caledonia (these two countries have most of the species), Vanuatu, Solomons, New Britain, Manus Island (west of New Britain), Papua New Guinea mainland ('Schroder' – probably Schrader – Mts), and eastern Australia (north-east Queensland to Woolongong, south of Sydney). Their sister group, Succineidae, are widespread worldwide and are the landsnails most closely associated with water, being found in swampy areas and by rivers and lakes (not actually in the water). In New Zealand, the single representative, *Austrosuccinea*, occurs in flats behind coastal dunes. Athoracophorids are not found in this habitat but occur in forest and at higher altitude. An alpine population survives at 1500 m near Gertrude Saddle, New Zealand, on alga-covered rockfaces under large overhanging rims of ice (M. Heads, pers. observ.). The athoracophorids are, at least in New Zealand, an altitudinal and phylogenetic vicariant of the widespread coastal succineids.
- In centipedes, some genes show *Craterostigma* as basal in centipedes, others have it near the base (Giribet & Edgecombe, 2006). *Craterostigma* has one or two species in Tasmania and New Zealand (North, South and Stewart Islands; G. Edgecombe, pers. comm.).
- In Lepidoptera, three clades branch off sequentially at the base below the main group: the worldwide Micropterigidae; *Agathiphaga*, with one species in north-east Queensland and one in the Solomons, Vanuatu, and Fiji feeding mainly on Araucariaceae; and *Heterobathmia* of southern South America (Valdivia, etc.) on *Nothofagus* (Wiegmann, Regier & Mitter, 2002).
- In the worldwide Micropterigidae, the basal clade comprises 11 species in Tasmania and east coast Australia (north to Daintree), two species in New Caledonia, and one in northern North Island, New Zealand (Gibbs, 1989, 2006; G.W. Gibbs pers. comm.). The next basal clade is *Sabatinea* s.s. of New Zealand and New Caledonia.
- In other Lepidoptera, the family Mnesarchaeidae is endemic to New Zealand (North and South Islands) and is sister to the globally widespread Hepialoidea (ghost moths; not in the Caribbean, western Africa or Madagascar) (Gibbs, 1989, 2006; G.W. Gibbs pers. comm.; J. R. Grehan pers. comm.).
- In reptiles, *Sphenodon*, the tuatara of New Zealand, and its widespread, fossil relatives (Sphenodontia) comprise the sister group of all other extant lizards and snakes (Squamata). Sphenodontians were widespread globally in the Mesozoic (Gibbs, 2006: 156) but Cenozoic fossils are restricted to New Zealand and South America.
- In parrots, the New Zealand genera *Strigops* (kakapo; South Island, Stewart Island) and *Nestor* (kaka and kea; North, South and Stewart Island, formerly Norfolk and Chatham Island) form a clade that is sister to all other parrots (de Kloet & de Kloet, 2005). The kakapo is a flightless, nocturnal bird that favours forest margins, kaka species are widespread in lowland and montane forest, the kea is common in alpine regions.
- After the ratites and Galliformes/Anseriformes are split off, passerines may be sister to all other birds (Slack *et al.*, 2006). The basal passerines are the New Zealand wrens Acanthisittidae (Barker, Barrowclough & Grouth, 2002; Ericson *et al.*, 2002; Slack *et al.*, 2007). Four species were extant in historical times. The rifleman is widespread in lowland forests of North, South and Stewart Islands. The rock wren is restricted to the alpine zone of the South Island. Bush wrens were seen on Mt Luxmore, Fiordland in 1978 (M. Heads, pers. observ.) but none have been sighted subsequently and the species is regarded as extinct. A fourth species, the Stephen's Island wren, was extinct by the end of the 19th Century. Fossil representatives are also known but only in New Zealand (Millener, 1988; Millener & Worthy, 1991); their bizarre morphology (more beak than bird) is well-illustrated in Tennyson & Martinson (2006).
- A clade of 'wattlebirds' found in New Zealand (Callaeatidae plus *Notiomystis*, formerly in Meliphagidae) and New Guinea (Cnemophilinae, formerly in birds of paradise, plus Melanocharitidae) are basal to the worldwide 'crown Corvidae' (Barker *et al.*, 2004; Ewen, Flux & Ericson, 2006). There are no extra-limital fossils. In New Zealand, the group was found widely in

North, South, and Stewart Islands. In New Guinea, the group is widespread on the mainland, on the Vogelkop islands (Waigeo, Japen, Misool and Aru) and, with *Oedistoma*, on the D'Entrecasteaux Archipelago. However, as with birds of paradise and bowerbirds, it is notably absent from the nearby Bismarck Archipelago. Irestedt & Ohlson (2008) found Callaeatidae plus Cnemophilidae, and then Melanocharitidae to be basal branches in the cosmopolitan 'core Corvoidea' for the nuclear genes RAG-1 and RAG-2, but for other genes these New Zealand–New Guinea families form a basal grade in another large, worldwide group of passerines, the Passerida.

10. *Melonycteris* of the Bismarck Archipelago and Solomon Islands is basal or near basal in fruit bats, a conspicuous group throughout the Old World tropics (Pulvers & Colgan, 2007).

#### OTHER AREAS WITH GLOBALLY BASAL LOCAL ENDEMICS

A less detailed global survey of literature on angiosperms and some other groups revealed the following additional areas which have local endemics with cosmopolitan sisters (Figs 2, 3).

#### Old World

*South-west Western Australia: Emblingia*, monotypic, is sister to a global clade of Brassicales (Hall, Iltis &

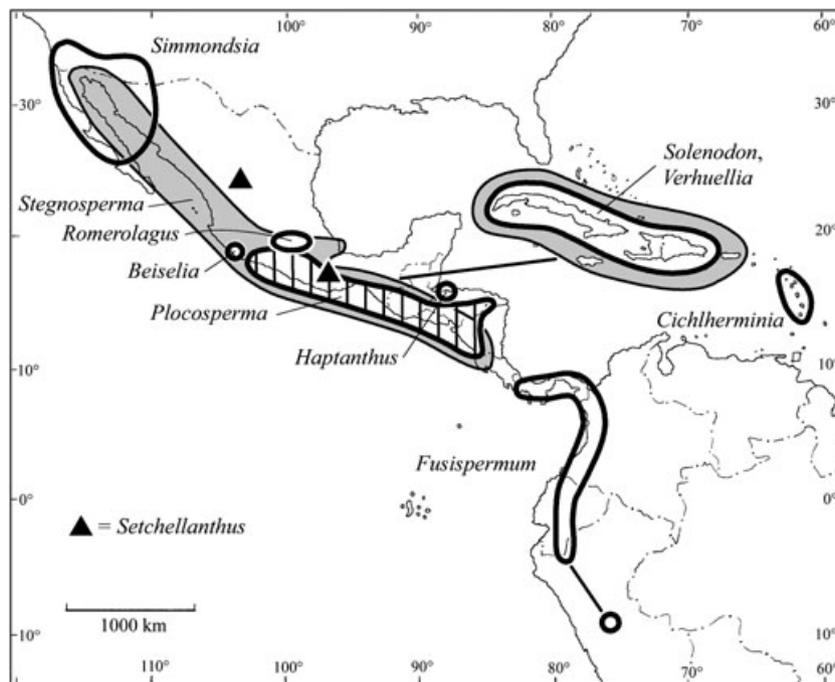
Sytsma, 2004) or, alternatively, basal in the global Gentianaceae (Savolainen *et al.*, 2000). *Nuytsia*, monotypic, is basal in the mistletoes Loranthaceae which are subcosmopolitan (rare in northern temperate countries).

*Sumatra/Borneo: Scyphostegia* (Borneo, north of the 'Lupar line') is sister to Salicaceae, a cosmopolitan group including most of the old Flacourtiaceae (Stevens, 2007). *Combretocarpus* (Sumatra and Borneo) is sister to the rest of the pantropical Anisophylleaceae (Zhang, Simmons & Renner, 2007).

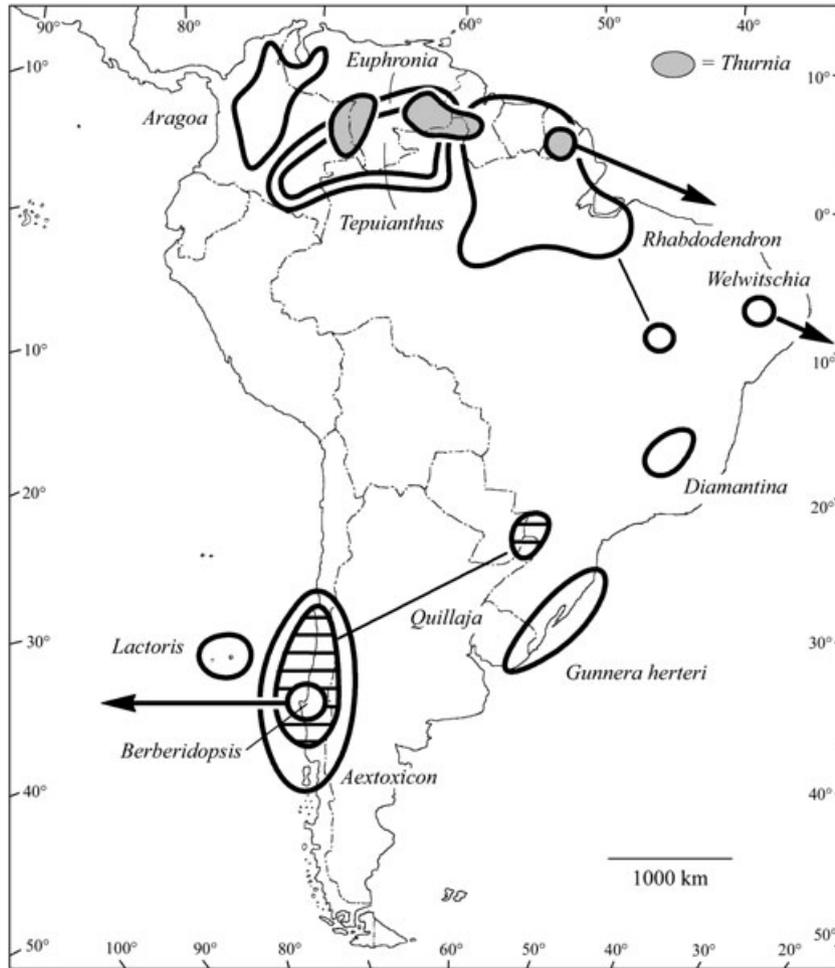
*Southern China–Taiwan–Japan: Euptelea*, with two species in southern China, is basal in the cosmopolitan Ranunculales (Stevens, 2007). The conifer *Sciadopitys*, monotypic in southern Japan, is sister to the widespread Cupressaceae and Taxaceae. In bats, the Taiwan endemic *Myotis latirostris* is basal in the genus, which is more or less worldwide (Stadelmann *et al.*, 2007). (Only 66 of 100 species have been sampled so far, but *M. latirostris* has distinctive morphology).

*South Africa: Agapanthus* (Cape Town to Swaziland) is sister to the subcosmopolitan Alliaceae and Amaryllidaceae (Givnish *et al.*, 2006).

*Madagascar: Humbertia*, monotypic, is a tree of Madagascar that is basal in the cosmopolitan



**Figure 2.** Globally basal groups on accreted terranes of the Americas.



**Figure 3.** Globally basal groups in cratonic South America. Arrows: *Welwitschia* is fossil in Brazil and living in south-western Africa, Thurniaceae are in South America (*Thurnia*) and South Africa (*Pronium*), *Berberidopsis* and its sister at the McPherson Range–Macleay River Overlap form a globally basal clade.

Convolvulaceae (Stefanović & Olmstead, 2005). *Didymeles*, north-east Madagascar, is sister of the subcosmopolitan Buxaceae (not in Australia or New Zealand). Asteropeiaceae/Physenaceae (two genera, nine spp.) is sister to a cosmopolitan clade of Caryophyllales. In the same order, *Barbeuia* (monotypic) is also sister to cosmopolitan clade (Aizoaceae, Nyctaginaceae, etc.). Sarcolaenaceae (eight genera, 60 spp.) are sister to Dipterocarpaceae, pantropical (but rare in South America). In the vertebrates, the coelacanth of Mozambique Channel and Sulawesi is (with some or all of the fossil crossopterygians) sister to the lungfishes plus tetrapods.

*South-eastern Tanzania–Cameroon:* The pantropical Triuridaceae have no chloroplasts and molecular systematics studies have given equivocal results. Morphological studies indicate that the tribe Kupeaeae is

basal. It comprises three very rare species of Cameroon and south-eastern Tanzania (Cheek, 2003; Rudall & Bateman, 2006).

*South Africa and Guayana shield:* This area of endemism is intercontinental but covers a small total area. It is occupied by Thurniaceae (four species), with *Thurnia* on the Guayana shield and *Pronium* in South Africa. The group is sister to the cosmopolitan Cyperaceae plus Juncaceae.

*Western Mediterranean:* The monocot *Aphyllanthes* of southern France, southern Spain, and northern Algeria is sister either to Laxmanniaceae (incl. *Lomandra*, *Cordyline* etc.) of Australia, India, Madagascar and South America (Givnish *et al.*, 2006) or to the subcosmopolitan Agavaceae (not in New Zealand or southern Australia) (Graham *et al.*, 2006).

*Americas: Allochthonous terranes (Mexico–western Colombia/western Ecuador) (Fig. 2)*

*Mexico: Beiselia* is a tree with a succulent trunk discovered in south-west Mexico in 1982. It occurs in dry forest near Aquila on the Michoacán coast (D. Espinosa, pers. comm.) and is basal in Burseraceae, widespread throughout warmer countries. *Setchellanthus* is a monotypic, microphyllous shrub of Mexico (mainly Durango and Oaxaca; Iltis, 1999) that is sister to a global clade of Brassicales. The monotypic *Plocosperma*, distributed from Guerrero to Nicaragua, is putative sister to the rest of Lamiales. *Simmondsia*, monotypic in north-western Mexico, Arizona, and California, is sister to a cosmopolitan clade of Caryophyllales (Caryophyllaceae, Aizoaceae, Portulacaceae etc.). (Distal to this branch is Asteropeiaceae/Physenaceae from Madagascar, also basal to a large clade, giving a trans-Atlantic, California–Madagascar sequence of differentiation). *Pterostemon*, with three species on Guerrero terrane (Guanajuato to Guerrero and Oaxaca; Jiménez Ramírez & Martínez Gordillo, 1997) is sister to the widespread Iteaceae: eastern USA, eastern Africa, and eastern Asia/western Malesia.

*Stegnosperma* (three species) is distributed along the Pacific coast of Mexico, Guatemala, and Costa Rica, and also in the Greater Antilles. It is sister to a cosmopolitan clade of Caryophyllales (Aizoaceae, Portulacaceae, etc.; Stevens, 2007).

*Romerolagus*, the ‘volcano rabbit’, is restricted to Popocatepetl and three other volcanoes near Mexico City (Lagomorph Specialist Group, 1996). It is basal to a large group of rabbits and hares (*Lepus*, *Sylvilagus*, etc.) found throughout the world except Australasia/Pacific (Stoner, Bininda-Emonds & Caro, 2003).

These taxa (Fig. 2; *Pterostemon* not shown) are mainly restricted in Mexico to the Guerrero terrane (in a broad sense; Umhoefer, 2003), which makes up most of the western half of the country. The taxa extend to the east only on the trans-Mexican volcanic belt (Torres Miranda & Luna Vega, 2006; Corona, Toledo & Morrone, 2007).

*Honduras: Haptanthus* is a tree collected once in northern Honduras in 1980, which is currently unplaced in angiosperms (Stevens, 2007). It has very distinctive flowers (there is no perianth, the males comprise single stamens, and the ovary is three-partite with parietal placentas). The species could conceivably be sister to a cosmopolitan group but it has proved hard to relocate.

*Greater Antilles: Verhuellia* has two species in Cuba and Hispaniola and is sister to all other Piperaceae (including *Peperomia*), a pantropical group (Wanke *et al.*, 2007). In mammals, *Solenodon* also has two

species of Cuba and Hispaniola and is sister to shrews, moles, and hedgehogs (Roca *et al.*, 2004), widespread globally but absent from Australasia and South America south of Peru.

*Lesser Antilles:* In *Turdus* thrushes, ‘*Cichlherminia*’ has one species in St Lucia, Dominica, Guadeloupe, and Montserrat. It is basal to a widespread clade of *Turdus* ranging in southern and central America, Africa, Eurasia and the Pacific islands (Voelker *et al.*, 2007).

*North-western South America–Southern Costa Rica: Fuispermum* of southern Costa Rica to western Colombia, Ecuador and central Peru (four spp.) is basal in the family Violaceae (Feng, 2005).

*Americas: Cratonic South America (Fig. 3)*

*Northern Colombia/western Venezuela: Aragoa* comprises 19 species of shrubs found in the high Andes of Colombia and western Venezuela, and is sister to the cosmopolitan *Plantago* (Plantaginaceae) (Fernández-Alonso, 1995; Rønsted *et al.*, 2002; Bello *et al.*, 2004).

*Guayana shield: Euphronia* (two species) occurs in a small area of the shield centred on southern Venezuela and is sister to the pantropical Chrysobalanaceae. *Tepuianthus* (seven species) of the southern Venezuela highlands is basal in the cosmopolitan Thymelaeaceae. *Rhabdodendron*, eastern Amazon/Guianas (three species) is basal in Caryophyllales. Thurniaceae (South Africa–Guayana Shield) are cited above.

*North-eastern Brazil–south-western Africa: Welwitschia*, a bizarre gymnosperm endemic to the Namib desert of south-western Africa is also known from good fossil material in north-eastern Brazil (Ceará/Pernambuco; Dilcher *et al.*, 2005). *Welwitschia* is sister to the pantropical *Gnetum* (Bowe, Coat & Depamphilis, 2000; Chaw *et al.*, 2000).

*Minas Gerais, Brazil:* The genus *Diamantina* may be basal in the pantropical Podostemaceae subfam. Podostemoidae (Rutishauser *et al.*, 2005). It is endemic to the Rio Prêto basin, Minas Gerais.

*Southernmost Brazil (Rio Grande do Sul/Santa Catarina)–north-eastern Argentina–Central Chile: Quillaja*, sister to the cosmopolitan Leguminosae, is a tree with three species in north-eastern Argentina (Misiones) and adjacent parts of Brazil, and disjunct in Central Chile (Coquimbo to Temuco). (Populations further north are usually regarded as human introductions). *Gunnera* is basal to the other eudicots and the basal species in *Gunnera* is *G. herteri*. This very

small plant occurs in the coastal sand dunes of Uruguay and southern Brazil (Rio Grande do Sul, Santa Catarina), forming dense mats on seepages (Rutishauser, Wanntorp & Pfeifer, 2004).

*Juan Fernandez Is. (Chile): Lactoris* is sister of the pantropical *Aristolochioideae* (Aristolochiaceae).

#### DESCRIPTION OF AREAS

##### *New Zealand, New Caledonia, and New Guinea*

These are all geologically polyphyletic, each comprising several terranes with distinct affinities. For example, the correlated Brook Street, Téremba and Gympie terranes (Permian-Triassic) have accreted to New Zealand, New Caledonia, and the McPherson-Macleay Overlap (Spandler *et al.*, 2005). In one sense, the taxa have 'dispersed' to these areas with the accreting terranes or their associated volcanic islands. But geological dispersal (at approximately 10 cm year<sup>-1</sup>) is much slower than biological long-distance dispersal and is an orderly process involving the entire community.

Some geologists have considered the possibility that New Zealand might have been totally covered by a very shallow sea (150–200 m in many parts) at some time in the Oligocene, as characteristic sedimentary strata are widespread (Campbell & Hutching, 2007; Landis *et al.*, 2008). However, they concluded that current geological data are not sufficient to permit definite confirmation or denial that some land existed, and they conceded that biological arguments can be made for the continuous presence of islands. Biogeographic and paleontological patterns that are incompatible with total flooding of New Zealand and the rest of the New Zealand plateau have been stressed by many recent studies (Craw, Grehan & Heads, 1999; Lee, Lee *et al.*, 2001; Gibbs, 2006; Heads, 2006b; Worthy *et al.*, 2006; Knapp *et al.*, 2007; Edgecombe & Giribet, 2008; McDowall, 2008). The survival of pre-Oligocene biogeography can perhaps be reconciled with widespread Oligocene sediments if minor, local tectonic variation led to a changing archipelago of many, small, low-lying islands and shifting coastlines. Landis *et al.* (2008) found no evidence for large, persistent islands, but small, ephemeral islands would preserve taxa as metapopulations and also allow local differentiation. Regional heterogeneity has characterized most of New Zealand's history and minor local uplift and subsidence, together with former emergent areas of the New Zealand plateau off the mainland are likely.

The Chatham Islands, east of mainland New Zealand, are well-known for both marked endemism and conspicuous absence. Chatham endemics are sometimes related to taxa in the subantarctics but

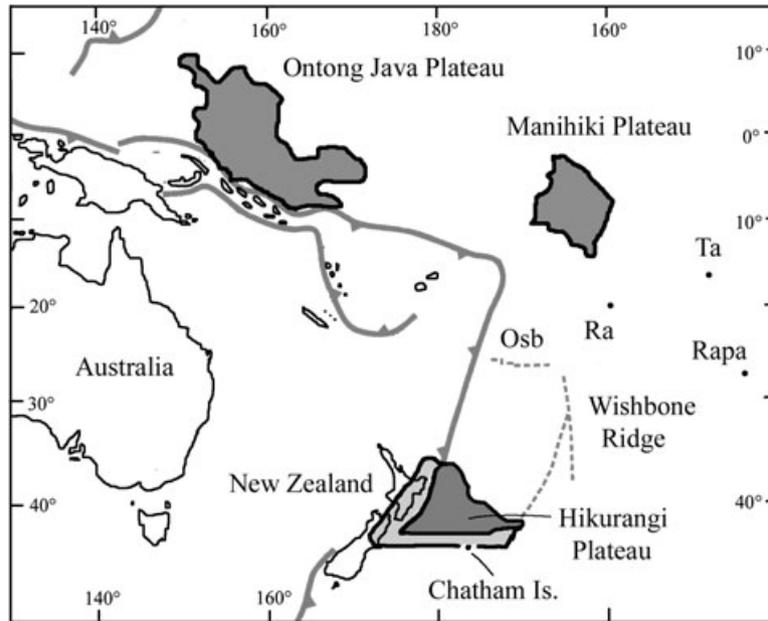
are often most closely related to groups of the north-eastern New Zealand islands and central Pacific, rather than mainland New Zealand. For example, the only Chatham Islands species of *Hebe* (Veronicaceae) are most closely related to the Rapa I. species, not to species of mainland New Zealand (Bayly & Kellow, 2006) (Fig. 4). The Chathams lie above a former subduction zone. The Hikurangi Plateau has encroached on this from the north-east (central Pacific) and, at approximately 86 Ma, choked the subduction zone, leading to movement on the Emerald fracture zone south-west of New Zealand and later on the Alpine fault (Schellart, Lister & Toy, 2006). The Hikurangi Plateau is currently located off the east coast of New Zealand and the portion exposed covers an area the size of New Zealand. Other parts are subducted beneath the North Island and the Chatham Rise. What are now Chathams/East Coast/Northland taxa with central Pacific affinities may have been 'scraped off' the descending plate at the subduction zone and piled up as the biogeographic equivalent of an accretionary wedge. Marshall (2001) used this process to explain the great diversity in New Caledonian marine molluscs.

##### *Bismarck Archipelago and Solomon Islands*

These islands are rarely visited and their biogeography is poorly understood. The biota is highly diverse but traditionally regarded as made up of minor variants recently derived from Australia and New Guinea. The flora and fauna are seldom seen as having any real significance for global evolution and Pulvers & Colgan (2007) wrote that the restriction of the basal fruit bat *Melonycteris* to these 'geographically remote' islands is 'puzzling'. Pulvers & Colgan concluded that if the bat has occupied these archipelagos during its evolution, suitable habitat 'must have been permanently available in the Melanesian Arc for many millions of years, either as continuously emergent land or as successively emergent, geographically proximal islands'. This latter process is typical of subduction zones and would help explain how the rain-forests of the Solomon Islands contain more endemic bird species than any other area of similar size in the world (Filardi & Smith, 2005).

##### *The Ontong Java Plateau*

This is a very large, almost entirely submarine plateau which abuts the eastern side of the Solomons (Fig. 4). Several geological reconstructions (Hall, 2002) have the Bismarcks–Solomons basement originating in the central Pacific, thousands of kilometers off Gondwana and their biota is probably more closely related to the original biota of the Ontong Java Plateau than to that of Gondwana.



**Figure 4.** Present position of the three large igneous plateaus (the subducted portion of the Hikurangi plateau in light grey). Osb, Osbourn Trough. Three biogeographically significant localities are also shown: Rapa I., Rarotonga (Ra), and Tahiti (Ta). (Simplified from IFM-GEOMAR, 2007). The grey line represents the current boundary of Indo-Australian plate (west) and the Pacific plate (east).

The Early Cretaceous Ontong Java Plateau is the world's largest 'large igneous province' and covers an area of some 2 million km<sup>2</sup>, the size of Alaska or western Europe. Its formation was the largest known magmatic event on Earth (Fitton *et al.*, 2004). The few geological investigations of the plateau have been described as 'pinpricking the elephant' and at present 'no simple model appears to account satisfactorily for all of the observed first-order features' (Tejada *et al.*, 2004). One of the most interesting recent discoveries on the plateau was a thick succession of volcanoclastic rocks, the result of eruptions in a subaerial setting (Thordarson, 2004). Fossilized or carbonized wood fragments have been found near the bottom of four of the eruptive members (Fitton *et al.*, 2004).

On-going collision of the Ontong Java Plateau with the Solomon arc has resulted in uplift of the plateau's southern margin and created on-land exposures of the plateau on the islands of Malaita, Ulawa, northern Santa Isabel and Makira (= San Cristobal). The fauna of the last island is regarded as a biogeographic mystery in dispersal accounts (Mayr & Diamond, 2001); Pulvers & Colgan (2007) cited the 'unexpected' placement of the Makira species basal in the Solomons clade of *Melonycteris* fruit bats. The island of Makira is also a special case within the Solomon block because, whereas Ontong Java Plateau material dating back 90 Mya is present, there is little or no pelagic sedimentation, as would be expected. This

suggests deep erosion of a subaerial edifice (Craig, Englund & Takaoka, 2006).

#### *Tasman–tropical America connections*

The highly endemic flora and fauna of the Tasman–Coral Sea region show affinities with areas to the west and also to the east, especially with Chile, the central Pacific islands, and north-west South America. Trans-tropical Pacific connections are generally discussed with reference to south-east Asia–tropical America. For example, the most diverse areas for angiosperm families are in southern Yunnan/Cambodia and southern Mexico (Gaston *et al.*, 1995).

However, many other trans-tropical Pacific tracks involve Melanesia. For example, a clade in Opiliones comprises Troglósironidae of New Caledonia plus Neogoveidae of tropical America/western Africa (Boyer *et al.*, 2007). Boyer & Giribet (2007) wrote that the relationship of New Caledonia and 'tropical Gondwana has never been proposed based on geological or biological data' and, as they say, the connection is 'intriguing'. A New Caledonia–tropical South America track is standard (Hheads, 2006b). In plants, the tribe Moutabeeae is in New Guinea, New Caledonia, and tropical America. It is basal in the worldwide Polygalaceae (minus *Xanthophyllum*) (Forest *et al.*, 2007). *Oncotheca*, monotypic in New Caledonia, and the Metteniusaceae: Costa Rica to Ecuador, mainly in Colombia, form the first and second basal branches in

a cosmopolitan clade of Lamiales, Solanales, etc. This topology (from a strict consensus tree) indicates a trans-tropical Pacific sequence of initial differentiation but statistical support is weak and the two small trans-Pacific groups may instead be sisters, forming a basal clade (González & Rudall, 2007; González *et al.*, 2007). In birds, the family Rhynochetidae is endemic to New Caledonia and related to *Aptornis* of New Zealand (fossil) and Eurypygidae of Guatemala to Brazil (Ladiges & Cantrill, 2007). In a similar pattern, iguanid lizards are in Fiji, Tonga (fossil), the Galapagos, and the Americas, where they are mainly in the west.

#### *Madagascar/South Africa/eastern Tanzania*

There is a standard biogeographic connection between Madagascar and the Usambara–Uluguru node in eastern Tanzania. For example, three Madagascar genera of Myristicaceae (*Brochoneura*, *Mauloutchia* and *Doyleanthus*) form a clade with *Cephalosphaera* of the Usambara, Uluguru, Udzungwa, and southern Nguru Mts in Tanzania and the Shimba Hills in south-east Kenya (Lovett & Clarke, 1998; Sauquet *et al.*, 2003). The South Africa–Madagascar biogeographic connection is well-known, so there may be an arc: South Africa–Madagascar–Tanzania of general biogeographic/phylogenetic significance.

This list of taxa and areas only gives a preliminary outline, but apart from the Tasman-Coral Sea area, the importance of western Mexico and Madagascar/South Africa is already evident. By contrast, the large blocks of rain-forest in the Congo basin and central-west Amazon basin hardly feature. One Amazon group of birds, the trumpeters (Psophiidae), are sister to a worldwide complex, the limpkin and crane families (Aramidae, Gruidae) (Fain, Krajewski & Houde, 2007). However, trumpeters are widespread over a vast area of the Amazon and Orinoco basins. The western Amazon basin and the foot hills of the central Andes are often accepted as having the most biodiverse plots in the world for tree species. However, a recent assessment of plant biodiversity in the Amazon Basin instead predicted maximum levels in the area of northern Brazil (in Roraima and Pará) from the border with southern Venezuela to near the border with Surinam (i.e. the core of the Guayana Shield; Hopkins, 2007). This region is also highly significant for its globally basal endemics (Fig. 3).

North of Mexico, there appear to be fewer locally endemic groups with widespread sisters. The northernmost example noted in this study was the boojum tree family, Fouquieriaceae, of south-western USA and north-western Mexico. It is sister to Polemoniaceae, fairly widespread in the Andes (to Tierra del Fuego) and the northern hemisphere.

## DISCUSSION

The more or less adjacent localities of the basal angiosperm and the basal passerine are part of a more general pattern, as the Tasman region is a centre for many other globally basal groups. Why are the Tasman and the other globally basal centres located where they are? They may represent centres of survival, centres of origin from which their widespread sisters have dispersed, or centres of differentiation in widespread groups.

#### BASAL CENTRES AS CENTRES OF SURVIVAL

Assessing this option requires the integration of fossil distributions and extant distributions. The globally basal groups might be relics of previously widespread taxa which have gone extinct everywhere else. For example, the New Zealand tuatara has fossil relatives (the other Sphenodontia) which were globally widespread in the Mesozoic. The plant *Canacomyrica* is extant only in New Caledonia, but has Cenozoic fossils in New Zealand. There is little if any fossil evidence that the other Tasman globally basal endemics were formerly more widespread. Probably some were and some were not.

Chance, local ecology, and the location of prior diversity have all been suggested as factors causing the survival of relic taxa in particular regions, such as around the Tasman or in western Mexico, and not others.

1. Any distribution can be explained by chance survival in the locality and extinction everywhere else. However, although it is impossible to disprove, chance survival does not explain the apparent concentration of basal groups in certain areas.
2. The survival in these regions may be due to certain ambient conditions. This seems unlikely as the Tasman region, western Mexico, etc., each share similar ecological conditions with many others in different parts of the world.
3. Relics of declining taxa may survive in areas where the taxa had prior centres of diversity. This is more likely. On average, taxa do not go extinct first at the geographical core of their diversity but at less diverse, peripheral areas. For example, *Nothofagus* is a wind-pollinated tree which is dominant in many South Pacific rain-forests and has an exceptional fossil record. The four extant subgenera are all known from Cretaceous fossils. The main species concentrations of the four subgenera occur in the same four localities (New Zealand; New Guinea and New Caledonia; Chile north of I. Chiloé; and Chile south of Valdivia) whether extant species only or all species (extant plus fossil) are counted (Heads, 2006b). Subgenus

*Brassospora* has its centre of total species diversity in New Guinea and New Caledonia, with a small number of extinct species in New Zealand, Australia, Antarctica, and South America. The pattern indicates that the subgenera have gone extinct in areas where they were less diverse to start with, whereas the main centres of diversity have persisted largely *in situ*.

In accordance with this reasoning, sphenodontians may have survived in New Zealand to modern times (two or three species) and in South America until Miocene time (recently reported fossils) because there were prior centres of diversity in these localities (despite the poverty of the New Zealand fossil record of sphenodontians).

This brings us back to the original question concerning the location of the globally basal centres of endemism. This is discussed further under 'Pacific geology', below.

#### BASAL CENTRES AS CENTRES OF ORIGIN

In centre of origin theory, the basal taxon in a group is usually interpreted as the ancestor of the group (rather than just a small sister group). The location of the basal taxon is taken to represent the centre of origin of the whole group, the members of which attain their respective distributions by physical movement away from the centre. In a group of taxa ( $a(b(c, d))$ ) found in areas A, B, C, D, the taxa have attained their distributions by a series of dispersal events from A to B to C and D. This concept of the evolutionary process is almost universally assumed by ecologists (Levin, 2000) and paleontologists (Eldredge *et al.*, 2005). However, it has been criticized by biogeographers because the simple allopatry among  $a-d$  could be due to *in situ*, sequential differentiation of a widespread ancestor, rather than dispersal. For example, populations of  $a$  could have been separated from the others by a newly rising mountain range leading to the two groups differentiating. Here the pattern is not caused by  $a$  dispersing into the territory of  $b-d$  and then differentiating there, and there is no centre of origin.

Good examples of centre of origin analysis are seen in the extensive literature discussing dispersal both into and out of the Caribbean. In mockingbirds, a Yucatán endemic is basal to a largely Caribbean clade. Lovette & Rubenstein (2007) argued that this 'is suggestive of a pathway of colonization into the Antilles from central America via Cuba . . .'. Conversely, in butterflies, the Greater Antilles genus *Antillea* is basal to a widespread clade (Phyciodina) of northern, southern, and central America. So, from a centre of origin in the Antilles, 'The ancestral

Phyciodina colonized the [Antilles–Venezuela] land-span and spread south to the Guyanan Shield and then quickly to the Brazilian Shield' (Wahlberg & Freitas, 2007). (The subsequent scenario involved a convoluted history of transcontinental dispersals and back-dispersals, although the authors wrote that these butterflies are 'well-known to be relatively sedentary').

In fact, no migration into or out of the Caribbean is required for the mockingbirds or the butterflies. In both groups, the location of the basal break between Yucatán and the Greater Antilles can be explained by simple vicariance in an already widespread ancestor.

The idea that basal groups are ancestral is not accepted here and neither is the idea that the location of basal groups represents a centre of origin. They are simply small (less speciose) sister groups and their distribution limits represent early centres of differentiation in already widespread groups, not centres of origin.

#### *Ecological dispersal versus biogeographic dispersal*

Every individual plant and animal moves by virtue of its normal means of survival, at least during one stage of its life-cycle. In addition, the ranges of taxa expand and contract. However, ecological movement should not be confused with biogeographic dispersal, which involves genetic differentiation. Dispersalists argue that 'When lineages arrive in new habitats they will usually diverge and sometimes speciate' (Renner, 2006). However, any patch of newly cleared ground will soon be colonized by 'weedy' flora and fauna and later by less weedy taxa, none of which will differentiate there. The biogeographic process of long distance, chance or founder dispersal is a theoretical process quite distinct from the movement observed as a normal component of an organism's life. Authors supporting the centre of origin view have often concentrated on proving that ecological dispersal, or ordinary movement, does occur, but this is already well-known. The main problem with biogeographic or founder dispersal is explaining how movement between populations could be occurring at one time, but then at some point stop (leading to differentiation). What is the reason for the change? In theory, it could be due to changing behavioural patterns in animals, but this cannot explain repeated patterns in unrelated animals and plants. Geological or climatic change is one obvious possibility and this is the basis of vicariance or simple allopatric speciation. In the centre of origin/dispersal theory, speciation instead occurs by chance dispersal: the change from movement to no movement simply involves a 'barrier' that is permeable to chance crossing by a founder but subsequently becomes impermeable.

*Dispersal in the ancestors*

If most groups are the result of vicariance in a widespread ancestor during a phase of population immobilism, how did the ancestor achieve its range? Possibilities include phases of population mobilism and range expansion by normal ecological dispersal (not founder dispersal) into new landscapes. These would have emerged following the devastation of the Permo-Carboniferous ice ages (much more severe than the present ice ages, and centred in the southern hemisphere) and along dramatically extended coastlines during extensive Mesozoic flooding of the continents. Cycles of mobilism of widespread groups into new habitat followed by immobilism and local differentiation, and eventually further phases of mobilism, may take tens of millions of years to complete, as in the geological cycles of mountain uplift, erosion, deposition, and further uplift.

BASAL CENTRES AS CENTRES OF INITIAL  
DIFFERENTIATION IN WIDESPREAD ANCESTORS

In the freshwater fish family Cichlidae, Chakrabarty (2004) proposed a vicariance interpretation of the biogeographic evolution and compared the process with a mirror being struck two or three times with a hammer. There is no movement of the individual shards, which are all neatly vicariant. The sequence of the hammer blows (phases of differentiation) is seen in the cladogram or phylogenetic tree.

Tree topology probably indicates the sequence of differentiation in an already widespread ancestor, not dispersal by physical movement. Major disjunctions of tens of thousands of kilometres often occur between taxa at consecutive nodes on a phylogram and long-distance, colonizing dispersal is very unlikely.

If differentiation in a widespread ancestor follows a sequence proceeding from one area (basal clade in area A) to another area (next basal clade in area B), and so on, this will give a cladogram that may convey the impression of a centre of origin at A and 'dispersal' from A to B. However, movement is not necessarily involved. Following this line of reasoning, Brown, Nelson & Ladiges (2006) illustrated the process leading to the distribution of Malesian *Rhododendron* as a sequence of differentiation in a widespread ancestor, and Doan (2003) suggested a south-to-north sequence of speciation (not dispersal) in Andean lizards.

Around the Tasman Sea, the cosmopolitan Apiales provide a transparent example of sequential differentiation of a global ancestor around different basins. Pennantiaceae, a Tasman Sea clade, branches off first. The second branch is an Indian Ocean group, Torricelliaceae, comprising the western Malesian

*Aralidium* and its relatives in Madagascar. The third branch, Griselinaceae, occupies a South Pacific track: New Zealand–Chile/south-eastern Brazil. Finally, there are three widespread groups, Pittosporaceae (wide in the Old World), Araliaceae (cosmopolitan), and Umbelliferae (cosmopolitan). The sequence of differentiation is: Tasman basin, Indian Ocean basin, Pacific basin, world.

An important Tasman–south-west Indian Ocean pattern is illustrated by Gnaphalieae, a tribe of Compositae with greatest diversity in South America, Southern Africa, and Australia. The basal members are South African. In the Australian members (84 genera), there is massive species diversity in south-west western Australia but the basal clades are dominated by perennial shrubs and alpine cushion-plants from south-east Australia (Bayer, Greber & Bagnall, 2002). The most basal is the monotypic *Parantennaria*, restricted to the mountains on the border of Victoria and New South Wales (Bogong High Plains–Snowy Mts–Mt Bimber). (It is a dioecious cushion-plant and would traditionally have been regarded as very derived). Bayer *et al.* accepted that the pattern: South Africa, south-east Australia, south-west western Australia, was attained through long-distance, chance colonization. Instead, it is suggested here that the topology represents a sequence of differentiation in a widespread ancestor, first around South Africa, then south-east Australia (Tasman node), and then south-west western Australia, where a final phase of extensive, low-rank evolution has taken place.

The Tasman Sea region is diverse because there has been a pool of diversity, or at least genetic propensity for diversity, on and around the component terranes since before the last major modernization of the major groups in the Mesozoic. The region does not represent a 'centre of origin' for the cosmopolitan groups in which Tasman clades are basal, but it may well be the area, or one of the areas, where differentiation began. The original centre of genetic diversity on the Tasman region terranes has been exposed to exceptionally high levels of tectonic activity in the Mesozoic, including subduction, obduction, rifting, orogeny, metamorphism and massive igneous emplacements. Similar processes have occurred in the South Africa/Madagascar region and western Mexico.

PACIFIC GEOLOGY

*Tasman Sea–central Pacific–America affinities and accreted terranes*

Apart from the biological and geological connections of the Tasman region with Madagascar/South Africa on one hand and southern South America on the other (both parts of Gondwana), many Tasman

groups have affinities in and around the central Pacific. Other Tasman groups show connections with western tropical America. Neither the central Pacific nor Mexico–Central America was ever part of Gondwana. Likewise, the island arc-derived terranes that make up large parts of modern eastern Australia, New Zealand (Eastern Province rocks), New Caledonia and New Guinea formed in the Pacific Ocean (or its precursor oceans on the Phoenix plate), not in Gondwana.

The south-west Pacific island arcs are probably a good analogue of the arc complexes that have accreted to western North America and form large parts of the continent. The idea that the Tasman Sea accreted-arc taxa are simply Gondwanan has an exact parallel in traditional interpretations of western Mexican groups as Laurasian. Several basal groups cited above are endemic to the Guerrero terrane, a large island arc complex that accreted to Mexico from the Pacific in the Jurassic–Cretaceous and forms the western half of the country (Umhoefer, 2003). Weeks, Dal & Simpson (2005) wrote that ‘Laurasian vicariance can account for the distribution patterns among the basal lineages in *Burseraceae*’ (i.e. *Beiselia* of Michoacán) but, like the Gondwanan explanation of the Tasman Sea groups, this emphasizes something that is not relevant and overlooks the fundamental importance of Pacific accreted arcs for American biogeography. Escalante *et al.* (2007) concluded that biogeographic differentiation between western Mexico (Guerrero terrane) and eastern Mexico is more fundamental than the north and south difference in the country. This is expected in accreted terrane theory but is not predicted in dispersal theory which is based on north–south and south–north dispersal (the ‘Great American Biotic Interchange’). The basal endemics in Mexico–central America are concentrated in the Michoacán–Guanajuato–Oaxaca sector of the Guerrero terrane, around the Motagua fault in Honduras/Nicaragua, and in the Antilles. Many of these survive on limestone and young volcanics, the typical rock types of their ancestral island arc habitat. In parts of the Guerrero terrane occupied by *Setchellanthus* (basal in a large clade of *Capparales*), levels of local endemism ‘approximate the rates found in insular floras’ (Iltis, 1999).

As with the south-west Pacific terranes and western Mexico (Guerrero) terrane, the sectors of accreted Pacific terranes in Colombia (east to the Romeral fault zone; Chicangana, 2005) are highly significant for biogeography. Also of interest are the Jurassic–Lower Cretaceous island arc rocks that form the Coast Range in Central Chile (at the basal endemic centre; Fig. 3). These are possibly allochthonous (Moores, Wakabayashi & Unruh, 2002).

#### *The Pacific plate*

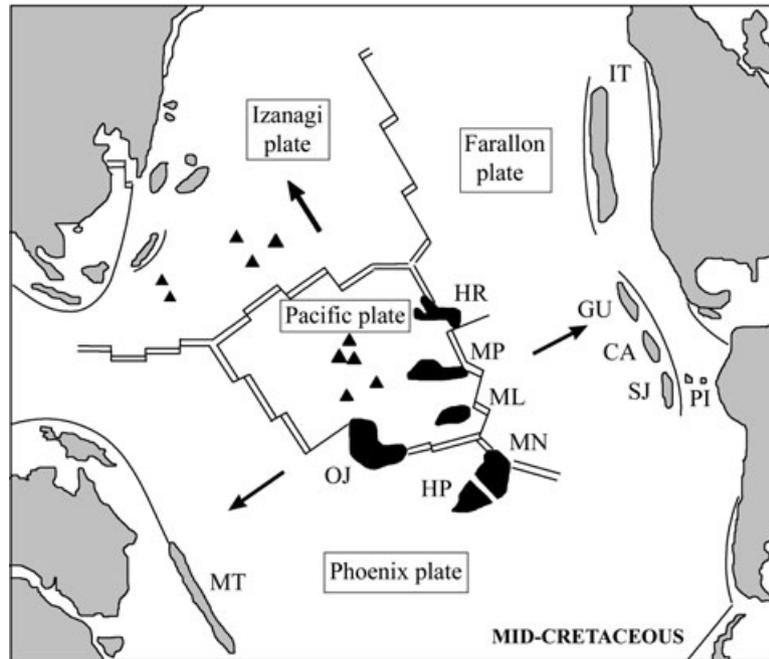
The Pacific plate began to form in the mid-Jurassic at the Tongareva ridge–ridge–ridge triple junction (Larson *et al.*, 2002). From here, the Pacific plate expanded at the expense of the Phoenix, Farallon and Izanagi plates that surrounded it (Fig. 5). Some of the old biota preserved on the islands of the Phoenix plate will have been transferred to the Tasman islands as the Phoenix plate was subducted below New Zealand, generating arcs and other terranes. For example, the Mt Camel terrane of the Far North Peninsula and Three Kings Islands (Nicholson & Black, 2004), maintains notable endemism and may represent a relic of the Phoenix–Pacific ridge, the arrival of which blocked subduction (Bradshaw, 2004). Similar processes took place in the East Pacific/western Americas as the Farallon plate was almost entirely subducted.

#### *Large igneous plateaus in the central Pacific*

In the Early Cretaceous, when the new Pacific plate was still relatively small, the Ontong Java, Manihiki, and Hikurangi plateaus were emplaced. The three may have originally formed a single, very large plateau (Taylor, 2006; Ingle *et al.*, 2007). The Hikurangi and Manihiki plateaus may have been separated by spreading at the Osborn trough (Worthington *et al.*, 2006). The Earth’s largest oceanic igneous province (the Ontong Java Plateau) and the largest silicic igneous province (the Whitsunday igneous province of north-east Queensland, Lord Howe Rise, New Zealand, and Antarctica) were emplaced at the same time (Early Cretaceous, approximately 120 Ma; Bryan & Ernst, 2007) and these great tectonic events must have had a profound impact on the contemporary biota.

In another type of tectonism, Vaughan & Livermore (2005) discussed episodicity of terrane accretion on the Gondwana–Pacific margin. They cited two major Mesozoic pulses, a Late Triassic–Early Jurassic deformation associated with Pangaea breakup, and a mid-Cretaceous deformation associated with the eruption of the oceanic plateaus, core-complex formation, and the rifting of New Zealand from Gondwana. Possible effects of the last event are well-known to biogeographers but the earlier one was probably just as important.

The Greater Ontong Java event covered approximately 1% of the earth’s surface with volcanic rocks within a few million years. This is the largest volcanic event in earth’s history and had a dramatic impact on the life of the earth’s oceans. However, it is not associated with a mass extinction (Hoernle *et al.*, 2004). Many populations and taxa will have been extirpated, but the new volcanic strata, both submarine and terrestrial, will have soon been occupied by plants and animals. Many types of vegetation thrive



**Figure 5.** The mid-Cretaceous positions of the central Pacific plateaus and the three spreading ridges that produced the Pacific plate (simplified from Smith, 2007). The Pacific plate now occupies almost the entire Pacific basin. Spreading ridges as double lines joined by single lines (transforms). Subduction zones as single lines around the Pacific margin. HR, Hess Rise; MP, Mid-Pacific Mountains; ML, Magellan Plateau; MN, Manihiki Plateau; HP, Hikurangi Plateau (the last two separated by the Osborn Trough); OJ, Ontong Java Plateau; IT, Insular terrane; GU, Guerrero terrane; CA, Central America arc; SJ, San Juan Plateau; PI, Piñón plateau; MT, Median Tectonic arc.

around active volcanism, for example rain-forest in the islands off northern New Guinea and alpine vegetation in New Zealand. New lava flows and ash deposits are quickly colonized by the weedy taxa in a region. Three-dimensional projections of the Hikurangi Plateau show a spectacular rifted north-eastern margin and, in the interior of the plateau, massive seamounts up to 24 km across (Hoernle *et al.*, 2004). The seamounts are flat-topped guyots, indicating they were formerly island volcanoes that were eroded to sea-level by wave-action and later subsided to 2000 m below sea-level. Fossils of montane moss-forest taxa (e.g. land snails) are known from several Pacific atolls, again indicating islands that were formerly mountainous (Heads, 2006a).

In the north of New Zealand, emplacement of the Northland–East Cape allochthon from the north-east probably occurred in response to the collision of the Hikurangi Plateau with eastern New Zealand (Whattam *et al.*, 2005). The Wishbone Ridge runs north-east from the Hikurangi Plateau and is an Early Cretaceous intra-oceanic arc (Fig. 4.; Mortimer *et al.*, 2006). Similar to the Hikurangi Plateau it has collided with the Chatham Rise. Another arc, the Loyalties–Three Kings Ridge, was active in the Cretaceous and at some stage accreted to New Caledonia

and New Zealand (east of the Three Kings Island). Its history is important for biogeographically as the biota of the Loyalties is so different from that of the main New Caledonian island (Heads, *in press a*).

Some geologists have made the interesting suggestion that the Ontong Java Plateau formed in the central Pacific near the Gorgona Plateau, now accreted in western Ecuador, western Colombia, and the Caribbean. The Ontong Java Plateau former moved westwards and eventually accreted with the Solomons, whereas the Gorgona Plateau moved north-east and collided with north-west South America/Caribbean (Chicangana, 2005; Kerr & Tarney, 2005). Chicangana discussed the possibility of a single, great igneous province in the Cretaceous central Pacific which subsequently split. These authors used geochemical, geophysical and microfossil evidence, but their ideas would also account for the Melanesia–tropical America connections of many extant groups.

#### *New models of intraplate magmatism and the biogeography of Polynesia*

In traditional dispersalist interpretations of oceanic island biotas, a volcanic island just ‘pops up’ and its location (apart from its distance from the mainland) is not considered relevant. Islands are assumed to be

populated from the nearest mainland and endemism is explained by isolation from the mainland. However, if volcanism is not spatially random but recurs in certain areas, volcanic islands might instead 'inherit' flora and fauna from prior volcanic islands in the same region. This probably happens at subduction zones. But even admitting that old metapopulations might survive on young strata along arcs at plate margins, as in Melanesia, surely populations on intraplate volcanics, as in Polynesia and Micronesia, are the result of long distance dispersal?

The plate tectonic model was proposed in the mid-1960s and accounted for the distribution of most of the volcanism on Earth's surface, that at plate boundaries. However, it did not explain areas of unusually profuse volcanism within plates (e.g. at Hawaii and other Pacific islands). Hotspots and a mechanism for producing them (i.e. mantle plumes) were proposed as a second, independent mode of convection to account for this type of volcanism and widely accepted. Recently, however, explanations for 'anomalous' volcanism based instead on effects of plate tectonics have come to rival the plume model (Foulger & Natland, 2003). In these alternative models, stresses produce patterns of great fissures and systems of fissures through the lithosphere along which seamount provinces and linear chains form (Anderson, 2005, Anderson & Natland, 2005; Foulger *et al.*, 2005; Foulger, 2007; Foulger & Jurdy, 2007).

Hot spot theory is one explanation for intraplate volcanism, and some biogeographic patterns may be caused by 'integration' of hot spot traces. However, the hot spot theory only accounts well for one subset of biogeographic tracks, those running parallel to plate movement. The new ideas on volcanism are an interesting alternative. They explain intraplate volcanism not by plumes and hotspots but by stress- and crack-controlled propagation of fractures and fissures. These are set up by normal plate tectonics processes rather than movement over fixed hotspots. In this model, changes in patterns of stress orientation (rather than shifts in plate motion over fixed hotspots) result in changes in directions of volcanic chains (Natland & Winterer, 2005). In the hotspot model, the youngest island lies nearest the hotspot, the oldest island is furthest away. However, this is also explained easily by fissure propagation, and many islands arranged in linear chains do not conform to age sequences. The new model accounts for other geological 'anomalies' such as the large igneous plateaus, and also accords much better with biogeographic patterns in the Pacific because these resemble a network rather than a simple pattern of parallel lines.

The islands of Polynesia and Micronesia are some of the most isolated in the world. Despite their small size they maintain many, well-marked regional

endemics. For example, *Fitchia* (Compositae/Asteraceae) is a small tree endemic to montane forest in south-eastern Polynesia and is very distinctive. It has stilt roots, the largest fruits in the family (5 cm long not including the awns), and is viviparous (M. Heads, pers. observ.; Rarotonga, Cook Islands). It has presumably survived as a metapopulation on the volcanic islands and atolls which have come and gone around the Manihiki plateau (Cook Islands/Tokelau) and other localities in south-eastern Polynesia. Its ancestors may date back to the origin of the Pacific plate and the Cretaceous plateaus. *Fitchia* is probably derived from weedy mangrove ancestors which would have colonized any subaerial parts of the plateaus and their seamounts in the Cretaceous from other arcs and islands the region. Some of their descendants have survived largely *in situ*. Others may have been transported to north-east New Zealand/Chatham Rise and accreted with this part of the New Zealand plateau soon after its split from Gondwana.

AGE OF TAXA: CALIBRATIONS BASED ON AGE OF STRATA AND ISLANDS ON WHICH TAXA ARE ENDEMIC  
Donoghue & Benton (2007) claimed that 'all molecular clock analyses rely on palaeontological data for calibration', but this is incorrect. Many studies have acknowledged the problems with fossil dates, especially the absence of a fossil record in most groups. Some have adopted another method and used the age of islands on which taxa are endemic to calibrate clocks. However, this will give dates that are much too young, as in fossil-based calibrations. Murienne *et al.* (2005) used the age of the Loyalty Island, the young atolls off New Caledonia which currently cap the Loyalty Ridge, to calibrate a clock for endemic insects there, but the Loyalty Ridge itself was active back to the Cretaceous. Monaghan *et al.* (2006) used a suggested age of Kadavu I. in Fiji as 1.5–2.5 Ma but, prior to the current period of 'ocean island basalt' eruptions, which cover earlier strata, Fiji was part of a major arc (producing andesites) which lasted from Eocene to Miocene time (Colley & Hindle, 1984, Cronin, Ferland & Terry, 2003). In New Zealand, Bayly *et al.* (2000) wrote that 'The distribution of *Hebe stenophylla* in the North Island cannot predate the formation of the landscapes that it occupies'. Again, this view is based on a literal reading of available stratigraphy and overlooks tectonics. Most of the south-west Pacific islands are young but have formed at subduction zones and fissures which have existed for tens of millions of years longer than the individual islands.

The Lesser Antilles, like many Pacific islands, have formed at a subduction zone. Endemics on the Lesser Antilles (including '*Cichlherminia*', basal to a

global clade of thrushes) are generally assumed to be no older than current rocks, which are young volcanics and limestone. However, there is good geological evidence for earlier arcs lying buried beneath the southern Lesser Antilles (Speed *et al.*, 1993).

Endemic taxa survive as populations of populations (metapopulations) on the individually ephemeral islands which come and go around zones of subduction, rifting, etc. It is the age and tectonic history of the different cracks and margins, not the particular products (i.e. the islands), that are of primary relevance for biogeography. Calibrating a tree using the age of volcanic islands will almost automatically give dramatic underestimates for taxon ages. Basing calibration on the fossil record will also generally give underestimates, so the reciprocal 'corroboration' often found in studies using these two essentially stratigraphic methods is meaningless.

Many of the examples cited in the present study are from angiosperms. From the 1970s until recently, the angiosperms as a whole were thought to have originated in the Cretaceous, the age of the earliest accepted fossils. However, molecular studies have now shown that angiosperms are basal to the extant gymnosperms (conifers, cycads, and Gnetales), a group with many Paleozoic fossils (Chaw *et al.*, 2000; Bowe *et al.*, 2000). Angiosperms were formerly assumed to have been derived from within the gymnosperms and so angiosperms are probably much older than was thought.

#### ARE THE GLOBALLY BASAL GROUPS THE RESULT OF LONG ISOLATION?

Many studies have attributed endemism around the Tasman Sea to long isolation on the islands, which they interpret simply as 'fragments of Gondwana'. However, it is not isolation in itself that has led to the evolution of basal groups and other endemics there. The location of any group is primarily related to the distribution of its ancestor and, in particular, the distribution in the ancestor of genetic propensity or predisposition for diversification (Lovette, Bermingham & Ricklefs, 2002; Davies *et al.*, 2004). In any case, the east Australian nodes intimately associated with the Tasman Sea centres all occur on mainland, as do the South African and Tanzanian parts of the node centred on Madagascar. Biogeographers have known about the great diversity of South Africa and Madagascar (i.e. mainland and island) for centuries. Traditionally, the two have been explained as separate phenomena. However, the last main differentiation of taxa in South Africa, the Mozambique Channel, and Madagascar may instead all be the result of Jurassic–Early Cretaceous folding and rifting (Craw *et al.*, 1999) as in the Tasman.

#### ARE THE TASMAN-CORAL SEA GROUPS GONDWANAN?

Despite the central Pacific endemism, the idea that Tasman Sea groups are simply Gondwanan persists. Barker *et al.* (2002) found Acanthisittidae to be sister to all other passerines. They also noted that the earliest passerine fossils are from the early Eocene of Australia, and they supported a Gondwana origin for the passerines. They also suggested an Australo-Papuan centre of origin for oscines (the largest group of passerines), with the radiations of the large crown clades Corvida and Passerida the result of dispersal northwards. Ericson *et al.* (2002) also found that the New Zealand wrens were sister of all the other passerines, 'supporting a Gondwanan origin and early radiation of passerines'. Edwards & Boles (2002) argued that 'Both papers find that the New Zealand wrens fall at the base of the passerine radiation, implying an origin of this clade in Gondwana'.

However, jumping from the recognition of basal clades in New Zealand and Australasia to the idea of a Gondwana origin and dispersal northwards may not be as logical as it seems. With respect to the role of Gondwana, Australia was part of the supercontinent, but many terranes in New Guinea, New Caledonia and New Zealand formed in the ocean and were only accreted to Gondwana in the earliest Cretaceous, rifting away again in the mid-Cretaceous.

With respect to origin and dispersal, the 'basal' New Zealand wrens are not the ancestor of the passerines, just a small sister group, and their location in New Zealand does not represent the centre of origin of the passerines, only of Acanthisittidae. It is likely that pre-passerines were already globally widespread when the differentiation between Acanthisittidae and the others occurred, somewhere near the terranes now assembled around the Tasman-Coral basins. This process does not require improbable, one-off colonizing flights over tens of thousands of kilometres, only local movement leading to sympatry of the wrens and other passerines in New Zealand, and *Amborella* and other angiosperms in New Caledonia, etc.

In another example, the wattlebirds of New Zealand and New Guinea may be basal in a large, cosmopolitan clade, 'Crown Corvida'. Despite the notable absence of the wattlebirds from Australia (there is plenty of suitable habitat there) Cracraft *et al.* (2004) wrote that 'The basal position of these groups relative to the remaining Corvida provides persuasive evidence that the group as a whole had its origin in Australia (and perhaps adjacent Antarctica) . . .'. In fact, the topology is good evidence that the basal group at least has *not* been involved with Australia. Differentiation in proto-Crown Corvida may well have begun around the New Zealand–New Guinea region, but this does not mean that the Crown

Corvida had its origin here. Other dispersal interpretations of the New Zealand–New Guinea wattlebirds assume these (Shepherd & Lambert, 2007) or their last common ancestor (Ewen *et al.*, 2006) migrated to New Zealand, but no evidence or discussion was given to support the idea.

In geology, as in biogeography, New Zealand, New Caledonia and New Guinea are not simply ‘parts of Gondwana’. Some of their terranes are fragments of the margin or edge of Gondwana, but others were never part of Gondwana (the Northland–East Coast allochthon in New Zealand, the Loyalties–Three Kings Ridge, the Ontong Java–Manihiki–Hikurangi plateau, many terranes in New Guinea). Dispersalist accounts often emphasize that some New Zealand terranes are made up of deep sea sediments and so are not relevant to terrestrial biogeography. However, the history of a terrane after its formation is often more relevant for biogeography than its origin. In addition, the oceanic terranes typically include at least small amounts of material derived from, or associated with, island arcs or seamounts. This material and the biogeographic patterns are the only trace of a former geography.

Until the 1970s, New Zealand was seen as the vertical development of a single landscape feature, the New Zealand geosyncline. However, the New Zealand continent is now recognized as a zone of lateral accretion with arc after arc having arrived in the region from the east (Pacific) and being added to the pile. Unfortunately, the history of the Pacific region itself during this time is very poorly understood as there are no rocks there older than the Jurassic. The formation and growth of the Pacific plate has completely destroyed the prior geography, the only fragments left are traces of arcs and seamounts in terranes and slivers now accreted around the margins of the basin. The significance of arcs in the Pacific region even before the formation of the modern Pacific basin is undeniable though. Even the oldest basement rocks of mainland New Zealand (the lower Paleozoic Western Province terranes) include arc-derived material. After their formation somewhere in the ‘pre-Pacific’ Ocean (Panthalassa), these arc terranes were fused to Gondwana (eastern Australia/Antarctica) and a series of arcs, plateaus, blocks of ocean floor, etc. were added through the Paleozoic and Mesozoic. The whole sequence eventually rifted away from Gondwana but continued to collide with further accreting terranes in the Cenozoic (Northland–East Coast allochthon, etc.).

It is often assumed that the Pacific arc terranes were all sterile at the time of their accretion with Gondwana; the terranes formed and emerged immediately off the Gondwana coast and were colonized solely by the Gondwana biota. Describing

this process, Winkworth *et al.* (2002) wrote that ‘the origins of the earliest colonists seem straightforward’ and the biota of New Zealand, when it eventually rifted from Gondwana, was ‘identical’ to that of Gondwana (Campbell & Hutching, 2007). However, there is no need to assume that the arcs were only populated from the Gondwana mainland (or that the biota of Gondwana was homogeneous). The plants and animals of the Pacific and pre-Pacific arcs and intra-plate volcanics would have been just as significant. The idea that Gondwana was full of life and the Pacific and pre-Pacific were empty is very unlikely. There were always many islands in the Pacific region, even before the formation of the current Pacific basin, and even a small tropical island, let alone an entire arc, can maintain a diverse biota. The history of the old central Pacific biota together with the Gondwana biota is key to understanding the biogeography of the Tasman region.

## CONCLUSIONS

### PACIFIC TECTONICS

The Tasman region is more likely to be a centre of juxtaposition than a centre of origin or radiation. The Pacific biotas are now piled up in and around the south-west Pacific but the arcs and plateaus that they arrived on were originally widespread over the pre-Pacific and Pacific (cf. Kerr & Tarney, 2005). Subsequent to continued terrane accretion and tectonic erosion, many terranes in New Zealand and New Guinea have been reduced to thin slivers. Others have disappeared altogether with subduction, although some of their taxa may have survived by being ‘scraped off’ or obducted.

Biologists often regard New Zealand as ‘part of Gondwana’, but it is more complex than that and geologists are often more careful, describing it as ‘part of the edge of Gondwana’. In the present study, it is stressed that parts of New Zealand and New Caledonia formed part of the edge of Gondwana for part of the Cretaceous. It is also emphasized that the Pacific side of the edge is just as important for the biogeography as the Gondwana side. New Zealand, New Caledonia and New Guinea, along with eastern Australia and the Bismarcks/Solomons, are thus part of a globally significant geological ‘edge’, and the fauna and flora represent a globally significant biological ‘edge’ or ‘split’, clearly marked by the basal endemics. It is likely that the two phenomena are causally related. The Mesozoic geological revolution (the Rangitata orogeny, etc.) was also the last major phase of modernization in the earth’s plants and animals and resulted in the old biota being metamorphosed into the new, Cenozoic biota.

Important new geological discoveries in the Tasman include fossil wood on the vast Ontong Java Plateau, evidence for a large, long-lived Paleogene island between New Zealand and New Caledonia (Meffre, Crawford & Quilty, 2007), and many large, drowned seamounts on the Hikurangi and Manihiki Plateaus. These are all compatible with the initial differentiation of passerines and angiosperms having taken place around the terranes currently located in the south-west Pacific region.

The island arcs in the south-west Pacific are usually interpreted as landbridges or 'stepping-stones', merely providing routes of dispersal into the Pacific or from one part of it to another. However, the basal endemism on these islands shows that this is unlikely. Old endemic taxa have survived *in situ*, subsequent to their origin, on young islands. This hardly seems possible, but although the islands and arcs are individually ephemeral, new ones are constantly being produced and regional endemics survive and evolve as metapopulations. In this way, the different centre of endemism in the Pacific can be much older than the islands and reefs currently in the area (M. Heads, in press b).

Traditional, fossil-based biogeographic narratives have always used the twin concepts of centre of origin and chance dispersal. These explained all patterns easily but attention was deflected away from underlying tectonics and onto the details and vagaries of stratigraphy. However, it is suggested here that island biogeographers should turn from studying the ages and extrapolated ages of individual islands to re-examining the general history and evolution of subduction zones, spreading centres, fissures, arcs, back-arc basins, and accreted terranes.

#### MOLECULAR PANBIOGEOGRAPHY

The fundamental importance of geography is a recurring theme in current molecular studies. Many studies are finding clades that are radically incongruent with earlier morphological classifications but are instead strikingly geographic, often much more so than the earlier arrangements (e.g. Larsen *et al.*, 2007; Stadelmann *et al.*, 2007; Stefanović, Kuzmina & Costea, 2007). In most large groups, for example mammals (Wildman *et al.*, 2007), the importance of geographical allopatry among the main clades is recognized. This discovery has already impressed some (Avice, 2007) but its full implications have yet to sink in. It provides some of the strongest evidence yet that geographical distribution has a determined, genetic relationship with phylogeny and is not the result of chance movement or founder dispersal. Recognition of this relationship should encourage authors to map their clades and lead to a renewed interest in comparative biogeography.

With on-going work, the distribution patterns in most groups are becoming more and more clearly geographic, but this satisfying progress in describing the patterns of distribution and phylogeny has not been matched by increased understanding of the process which has given rise to them. Traditional scenarios base chronology on oldest fossil calibrations and clock-like models of evolution (neither is accepted here). They usually conclude in favour of chance processes or admit that the means of dispersal are not evident. In a typical example, Mayr & Diamond (2001) frankly admitted that bird distribution in the southern Solomons (San Cristobal and Rennell) is a mystery and a paradox. However, they interpreted the birds of the Solomons and Bismarcks as the result of recent dispersal from the mainland and did not consider pre-Pleistocene geology. In fact, the Solomons are a major centre of bird endemism. The pantropical tree genus *Ficus* (figs) is another group with exceptionally high diversity in the Solomons rain-forests. Corner (1967) wrote that the classification of *Ficus* in the area 'is too closely-knit with geography to admit the prevalence of random dispersal'. He also observed that 'as the islands are very far away, we are led to think of their problems as marginal and irrelevant to the mainspring of life'. Corner (1969) argued instead that they held 'important keys to the evolution of flowering forest' and he also related the problem to the trans-tropical Pacific connection. In the Americas, the number of plant species in each country relative to the country's area is much higher in Costa Rica and Panama than in any South American country (Prance, 1994). This significant pattern is probably associated with prior diversity around the accreting Costa Rica–Panama–Chocó terranes (Chicangana, 2005) and biogeographic/tectonic affinities with the central and south-west Pacific.

Geologists do not agree about many aspects of the Cretaceous-Cenozoic history of the south-west Pacific, let alone earlier periods when the basal groups originated. Many tectonic models for the region have been proposed (Schellart *et al.*, 2006). They stress different sets of data and reach different conclusions. For example, some models have the Australia/Pacific plate boundary (i.e. a subduction zone with its attendant island arcs) developing near the coast of Australia, others have it much further offshore from an early time (Kroenke, 1996; Hall, 2002). Johnston's (2004) orocline model is quite different from all the others and proposes direct connections between New Caledonia and New Guinea, the two comprising an important centre of endemism.

Biogeography offers an independent data set. Craw *et al.* (1999) suggested that life is the uppermost geological layer which differs from other strata

through its 'stickiness' or 'weediness', and hence its resistance to erosion, but which evolves with the terranes it survives on as metapopulations. In this way, the geography of a group can represent inherited information, passed on with minor modifications for tens of millions of years. If this is true, distributions and relationships like those reviewed here can contribute to a coherent synthesis of tectonics and biogeography in the south-west Pacific.

The 'invasion from the north' theory of Asian–Australasian–Pacific biogeography denied the flora and fauna of the south-west Pacific and the region itself any fundamental significance in the global evolution of the main groups. By contrast, a synthesis of biogeography and molecular biology which focuses on clade distribution and tectonics rather than fossil-based clock dates, branch lengths, and species numbers, indicates that the Tasman-Coral Sea region is one of the primary evolutionary centres of modern life. A preliminary survey indicates that the south-west Indian Ocean region and parts of Latin America, especially western Mexico, are the others.

## REFERENCES

- Anderson DL. 2005.** Scoring hotspots: the plume and plate paradigms. In: Foulger GR, Natland JH, Presnall DC, Anderson DL, eds. *Plates, plumes, and paradigms*. Geological Society of America Special Paper, Vol. 388. Boulder, CO: Geological Society of America, 31–54.
- Anderson DL, Natland JH. 2005.** A brief history of the plume hypothesis and its competitors: concept and controversy. In: Foulger GR, Natland JH, Presnall DC, Anderson DL, eds. *Plates, plumes, and paradigms*. Geological Society of America Special Paper, Vol. 388. Boulder, CO: Geological Society of America, 119–145.
- Avise JC. 2007.** Twenty-five key evolutionary Insights from the phylogeographic revolution in population genetics. In: Weiss S, Ferrand N, eds. *Phylogeography of southern European refugia*. New York, NY: Kluwer, 7–21.
- Barker FK, Barrowclough GF, Grouth JG. 2002.** A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of analysis of nuclear DNA sequence data. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 295–308.
- Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J. 2004.** Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 11040–11045.
- Bayer RJ, Greber DG, Bagnall NH. 2002.** Phylogeny of Australian Gnaphalieae (Asteraceae) based on chloroplast and nuclear sequences, the *trnL* intron, *trnL/trnF* intergenic spacer, *matK*, and ETS. *Systematic Botany* **27**: 801–814.
- Bayly M, Kellow A. 2006.** *An illustrated guide to New Zealand hebes*. Wellington: Te Papa Press.
- Bayly MJ, Garnock-Jones PJ, Mitchell KA, Markham KR, Brownsey PJ. 2000.** A taxonomic revision of the *Hebe parviflora* complex (Scrophulariaceae), based on morphology and flavonoid chemistry. *New Zealand Journal of Botany* **38**: 165–190.
- Bello MA, Rudall PJ, González F, Fernández-Alonso JL. 2004.** Floral morphology and development in *Aragoa* (Plantaginaceae) and related members of the Order Lamiales. *International Journal of Plant Science* **165**: 723–738.
- Bowe LM, Coat G, Depamphilis CW. 2000.** Phylogeny of seed plants based on all three genomic compartments: extant gymnosperms are monophyletic and Gnetales' closest relatives are conifers. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 4092–4097.
- Boyer SL, Clouse RM, Benavides LR, Sharma P, Schwendinger PJ, Karunathna 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.
- Boyer SL, 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.
- Bradshaw JD. 2004.** Northland Allochthon: an alternative hypothesis of origin. *New Zealand Journal of Geology and Geophysics* **47**: 375–382.
- Brown GK, Nelson G, Ladiges PY. 2006.** Historical biogeography of *Rhododendron* section *Vireya* and the Malesian Archipelago. *Journal of Biogeography* **33**: 1929–1944.
- Bryan S, Ernst R. 2007.** Revised definition of large igneous province (LIP). *Earth-Science Reviews* **86**: 175–202.
- Burton DW. 1963.** A revision of the New Zealand and subantarctic Athoracophoridae. *Transactions of the Royal Society of New Zealand* **3**: 47–75.
- Burton DW. 1980.** Anatomical studies on Australian, New Zealand, and subantarctic Athoracophoridae (Gastropoda: Pulmonata). *New Zealand Journal of Zoology* **7**: 173–198.
- Campbell H, Hutching G. 2007.** *In search of ancient New Zealand*. Auckland: Penguin, and Lower Hutt: Institute of Geological and Nuclear Sciences.
- Cantino PD, Wagstaff SJ, Olmstead RG. 1999.** *Caryopteris* (Lamiaceae) and the conflict between phylogenetic and pragmatic considerations in botanical nomenclature. *Systematic Botany* **23**: 369–386.
- Chakrabarty P. 2004.** Cichlid biogeography: comment and review. *Fish and Fisheries* **5**: 97–119.
- Chaw S-M, Parkinson CL, Cheng Y, Vincent TM, Palmer JD. 2000.** Seed plant phylogeny inferred from all three plant genomes: monophyly of extant gymnosperms and origin of Gnetales from conifers. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 4086–4091.
- Cheek M. 2003.** Kupeaeae, a new tribe of Triuridaceae from Africa. *Kew Bulletin* **58**: 939–949.
- Chicangana G. 2005.** The Romeral fault system: a shear and deformed extinct subduction zone between oceanic and continental lithospheres in northwestern South America. *Earth Science Research Journal* **9**: 51–66.

- Colley H, Hindle WH. 1984.** Volcano-tectonic evolution of Fiji and adjoining marginal basins. *Geological Society of London Special Publication* **16**: 151–162.
- Corner EJH. 1967.** *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Philosophical Transactions of the Royal Society of London Series B* **253**: 23–159.
- Corner EJH. 1969.** Introduction to 'A discussion on the results of the Royal Society Expedition to the British Solomon Islands Protectorate, 1965'. *Philosophical Transactions of the Royal Society of London Series B* **255**: 187–189.
- Corona AM, Toledo VH, Morrone JJ. 2007.** Does the Trans-Mexican Volcanic Belt represent a natural biogeographic unit? An analysis of the distribution patterns of Coleoptera. *Journal of Biogeography* **34**: 1008–1015.
- Cracraft J, Barker FK, Braun M, Harshman J, Dyke G, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, García-Moreno J, Sorenson MD, Yuri T, Mindell DP. 2004.** Phylogenetic relationships among modern birds (Neornithes): toward an avian tree of life. In: Cracraft J, Donoghue MJ, eds. *Assembling the tree of life*. New York, NY: Oxford University Press, 468–489.
- Craig DA, Englund RA, Takaoka H. 2006.** Simuliidae (Diptera) of the Solomon Islands: new records and species, ecology, and biogeography. *Zootaxa* **1328**: 1–26.
- Craw RC, Grehan JR, Heads MJ. 1999.** *Panbiogeography: tracking the history of life*. New York, NY: Oxford University Press.
- Cribb P, Pridgeon AM, Chase MW. 2003.** *Pachyplectron*. In: Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN, eds. *Genera Orchidacearum, Vol. 3. Orchidoideae (Part 2). Vanilloideae*. New York, NY: Oxford University Press, 131–133.
- Crisp MD, Cook LG. 2005.** Do early branching lineages signify ancestral traits? *Trends in Ecology and Evolution* **20**: 122–128.
- Cronin SJ, Ferland MA, Terry JP. 2003.** Nabukelevu volcano (Mt. Washington), Kadavu – a source of hitherto unknown volcanic hazard in Fiji. *Journal of Volcanology and Geothermal Research* **131**: 371–396.
- Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE. 2004.** Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 1904–1909.
- Davies TJ, Goldblatt P, Barraclough TG. 2005.** Environment, area and diversification in the species rich flowering plant family Iridaceae. *American Naturalist* **186**: 418–425.
- Dilcher DL, Bernardes-De-Oliveira ME, Pons D, Lott TA. 2005.** Welwitschiaceae from the Lower Cretaceous of northeastern Brazil. *American Journal of Botany* **92**: 1294–1310.
- Doan TM. 2003.** A south-to-north biogeographic hypothesis for Andean speciation: evidence from the lizard genus *Proctoporus* (Reptilia, Gymnophthalmidae). *Journal of Biogeography* **30**: 361–374.
- Donoghue PCJ, Benton MJ. 2007.** Rocks and clocks: calibrating the tree of life using fossils and molecules. *Trends in Ecology and Evolution* **22**: 424–431.
- Edgecombe GD, Giribet G. 2008.** A New Zealand species of the trans-Tasman centipede order Craterostigmomorpha (Arthropoda: Chilopoda) corroborated by molecular evidence. *Invertebrate Systematics* **22**: 1–15.
- Edwards SV, Boles WE. 2002.** Out of Gondwana: the origin of passerine birds. *Trends in Ecology and Evolution* **17**: 347–349.
- Eldredge N, Thompson JN, Brakefield PM, Gavrillets S, Jablonski D, Jackson JBC, Lenski RE, Lieberman BS, McPeck MA, Miller W, III. 2005.** The dynamics of evolutionary stasis. *Paleobiology* **31**: 133–145.
- Ericson PGP, Christidis L, Cooper A, Irestedt M, Jackson J, Johansson US, Norman JA. 2002.** A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 235–241.
- Escalante T, Rodríguez G, Cao N, Ebach MC, Morrone JJ. 2007.** Cladistic biogeographic analysis suggests an early Caribbean diversification in Mexico. *Naturwissenschaften* **94**: 561–565.
- Ewen JG, Flux I, Ericson PGP. 2006.** Systematic affinities of two enigmatic New Zealand passerines of high conservation priority, the hihi or stitchbird *Notiomystis cincta* and the kokako *Callaeas cinerea*. *Molecular Phylogenetics and Evolution* **40**: 281–284.
- Fain MG, Krajewski C, Houde P. 2007.** Phylogeny of 'core Gruiformes' (Aves: Grues) and resolution of the Limpkin-Sungrebe problem. *Molecular Phylogenetics and Evolution* **43**: 515–529.
- Fay MF, Chase MW, Rønsted N, Devey DS, Pillon Y, Pires JC, Petersen G, Seberg O, Davis JL. 2006.** Phylogenetics of Liliales: summarized evidence from combined analyses of five plastid and one mitochondrial loci. *Aliso* **22**: 559–565.
- Fay MF, Rudall PJ, Sullivan S, Stobart KL, de Bruijn AY, Reeves G, Qamaruz-Zaman F, Hong W-P, Joseph J, Hahn WJ, Conran JG, Chase MW. 2000.** Phylogenetic studies of Asparagales based on four plastid DNA regions. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Collingwood: CSIRO, 360–371.
- Feng M. 2005.** Floral morphogenesis and molecular systematics of the family Violaceae. PhD Thesis, Ohio University.
- Fernández-Alonso JL. 1995.** Scrophulariaceae-Aragoaeae. *Flora de Colombia* **16**: 1–224. Instituto de Ciencias Naturales, Universidad Nacional, Bogotá.
- Filardi CE, Smith CE. 2005.** Molecular phylogenetics of monarch flycatchers (genus *Monarcha*) with emphasis on Solomon Island endemics. *Molecular Phylogenetics and Evolution* **37**: 776–788.
- Fitton JG, Mahoney JJ, Wallace PJ, Saunders AD. 2004.** Origin and evolution of the Ontong Java Plateau: introduction. In: Fitton JG, Mahoney JJ, Wallace PJ, Saunders AD, eds. *Origin and evolution of the Ontong Java Plateau*, Vol. 229. London: Geological Society of London Special Publication, 1–8.
- Forest F, Chase MW, Persson C, Crane PR, Hawkins JA. 2007.** The role of biotic and abiotic factors in evolution of

- ant dispersal in the milkwort family (Polygalaceae). *Evolution* **61**: 1675–1694.
- Foulger GR. 2007.** The ‘plate’ model for the genesis of melting anomalies. *Geological Society of America Special Paper* **430**: 1–28.
- Foulger GR, Jurdy DM, eds. 2007.** Plates, plumes, and planetary processes. *Geological Society of America Special Paper* **430**: 1–998.
- Foulger GR, Natland JH. 2003.** Is ‘hotspot’ volcanism a consequence of plate tectonics? *Science* **300**: 921–922.
- Foulger GR, Natland JH, Presnall DC, Anderson DL, eds. 2005.** Plates, plumes, and paradigms. *Geological Society of America Special Paper* **388**: 1–881.
- Gadek PA, Alpers DL, Heslewood MM, Quinn CJ. 2000.** Relationships within Cupressaceae sensu lato: a combined morphological and molecular approach. *American Journal of Botany* **87**: 1044–1057.
- Gardner RO, de Lange PJ. 2002.** Revision of *Pennantia* (Icacinaeae), a small isolated genus of Southern Hemisphere trees. *Journal of the Royal Society of New Zealand* **32**: 669–695.
- Gaston KJ, Williams PH, Eggleton P, Humphries CJ. 1995.** Large scale patterns of biodiversity: spatial variation in family richness. *Proceedings of the Royal Society of London Series B, Biological Sciences* **260**: 149–154.
- Gibbs GW. 2006.** *Ghosts of Gondwana: the history of life in New Zealand*. Nelson: Craig Potton.
- Gibbs GW. 1989.** Local or global? Biogeography of some primitive Lepidoptera in New Zealand. *New Zealand Journal of Zoology* **16**: 689–698.
- Giribet G, Edgecombe GD. 2006.** Conflict between datasets and phylogeny of centipedes: an analysis based on seven genes and morphology. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 235–241.
- Givnish TJ, Pires JC, Graham SW, McPherson MA, Prince LM, Petterson T, Rai HS, Roalson EH, Evans TM, Hahn WJ, Millam KC, Meerow AW, Molvray M, Kores PJ, O’Brien HE, Hall JC, Kress WJ, Sytsma KJ. 2006.** Phylogenetic relationships of monocots based on the highly informative plastid gene *ndhF*: evidence for widespread concerted convergence. *Aliso* **22**: 28–51.
- González F, Betancur J, Maurin O, Freudenstein JV, Chase MW. 2007.** Metteniusaceae, an early-diverging family in the lamiid clade. *Taxon* **56**: 795.
- González F, Rudall PJ. 2007.** Floral morphology of the neotropical family Metteniusaceae, an isolated member of the lamiids. *Plant biology and botany 2007. Program and abstract book*. Chicago, IL.
- Graham SW, Zgurski JM, McPherson MA, Cherniawsky DM, Saarela JM, Horne EFC, Smith SY, Wong WA, O’Brien HE, Biron VL, Pires JC, Olmstead RG, Chase MW, Rai HS. 2006.** Robust inference of monocot deep phylogeny using an expanded multigene plastid data set. *Aliso* **22**: 3–21.
- Hall JC, Iltis HH, Sytsma KJ. 2004.** Molecular phylogenetics of core Brassicales, placement of orphan genera *Emblingia*, *Forchammeria*, *Tirania*, and character evolution. *Systematic Botany* **29**: 654–669.
- Hall R. 2002.** Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Science* **20**: 353–431.
- He-Nygrén X, Juslén A, Ahonen I, Glennly D, Piippo S. 2006.** Illuminating the evolutionary history of liverworts (Marchantiophyta) – towards a natural classification. *Cladistics* **22**: 1–31.
- Heads M. 2006a.** Seed plants of Fiji: an ecological analysis. *Biological Journal of the Linnean Society* **89**: 407–431.
- Heads M. 2006b.** Panbiogeography of *Nothofagus* (Nothofagaceae): analysis of the main species massings. *Journal of Biogeography* **33**: 1066–1075.
- Heads M. In press a.** Panbiogeography of New Caledonia, SW Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs, and old taxa endemic to young islands. *Journal of Biogeography*.
- Heads M. In press b.** Vicariance. In: Gillespie R, ed. *Encyclopedia of islands*. Berkeley, CA: University of California Press.
- Herbert J, Chase MW, Möller M, Abbott RJ. 2006.** Nuclear and plastid DNA sequences confirm the placement of the enigmatic *Canacomyrica monticola* in Myricaceae. *Taxon* **55**: 349–357.
- Hodgson EA. 1949.** New Zealand Hepaticae (liverworts). VI. A review of the New Zealand species of the genus *Frullania*. *Transactions of the Royal Society of New Zealand* **77**: 361–389.
- Hoernle K, Werner R, Hauff F, van den Bogaard P. 2004.** The Hikurangi Oceanic Plateau: a fragment of the largest volcanic event on earth. *IFM-GEOMAR report 2002–2004*: 51–54.
- Hopkins MJG. 2007.** Modelling known and unknown plant diversity of the Amazon Basin. *Journal of Biogeography* **34**: 1400–1411.
- IFM-GEOMAR. 2007.** *The Research Project SO193 Manihiki*. Available at: <http://www.ifm-geomar.de>. Accessed November 2007.
- Iltis HH. 1999.** *Setchellanthus* (Capparales), a new family for a relictual, glucosinolate-producing endemic of the Mexican deserts. *Taxon* **48**: 257–275.
- Ingle S, Mahoney JJ, Sato H, Coffin MF, Kimura J-I, Hirano N, Nakanishi M. 2007.** Depleted mantle wedge and sediment fingerprint in unusual basalts from the Manihiki Plateau, central Pacific Ocean. *Geology* **35**: 595–598.
- Irestedt M, Ohlson JI. 2008.** The division of the major songbird radiation into Passerida and ‘core Corvoidea’ (Aves: Passeriformes) – the species tree vs. gene trees. *Zoologica Scripta* **37**: 305–313.
- Janssen T, Bremer K. 2004.** The age of major monocot groups inferred from 800+ *rbcl* sequences. *Botanical Journal of the Linnean Society* **146**: 385–398.
- Jiménez Ramirez J, Martínez Gordillo M. 1997.** Una especie nueva del genero *Pterostemon* (Grossulariaceae) del Estado de Guerrero, México. *Acta Botanica Mexicana* **41**: 21–25.
- Johnston ST. 2004.** The New Caledonia-d’Entrecasteaux orocline and its role in clockwise rotation of the Vanuatu-

- New Hebrides arc and formation of the North Fiji Basin. In: Sussman AJ, Weil AB, eds. *Orogenic curvature: integrating paleomagnetic and structural analyses* Vol. 384, Geological Society of America Special Paper. Boulder, CO: Geological Society of America, 225–236.
- Kerr AC, Tarney J. 2005.** Tectonic evolution of the Caribbean and northwestern South America: the case for accretion of two Late Cretaceous oceanic plateaus. *Geology* **33**: 269–272.
- de Kloet RS, de Kloet SR. 2005.** The evolution of the spindlin gene in birds: sequence analysis of an intron of the spindlin W and Z gene reveals four major divisions of the Psittaciformes. *Molecular Phylogenetics and Evolution* **36**: 706–721.
- Knapp M, Mudaliar R, Havell D, Wagstaff SJ, Lockhart PJ. 2007.** The drowning of New Zealand and the problem of *Agathis*. *Systematic Biology* **56**: 862–870.
- Krell F-T, Cranston PS. 2004.** Which side of the tree is more basal? *Systematic Entomology* **29**: 279–281.
- Kroenke LW. 1996.** Plate tectonic development of the western and southwestern Pacific: Mesozoic to the present. In: Keast A, Miller SE, eds. *The origin and evolution of Pacific island biotas*. Amsterdam: SPB Academic, 19–34.
- Kårehed J. 2003.** The family Pennantiaceae and its relationship to Apiales. *Botanical Journal of the Linnean Society* **141**: 1–24.
- Ladiges PY, Cantrill D. 2007.** New Caledonia–Australian connections: biogeographic patterns and geology. *Australian Systematic Botany* **20**: 383–389.
- Lagomorph Specialist Group. 1996.** *Romerolagus diazi*. In: 2007 IUCN Red List of Threatened Species. Available at: <http://www.iucnredlist.org>. Accessed at 10 October 2007.
- Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA. 2008.** The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geological Magazine* **145**: 173–197.
- Larsen C, Speed M, Harvey N, Noyes HA. 2007.** A molecular phylogeny of the nightjars (Aves: Caprimulgidae) suggests extensive conservation of primitive morphological traits across multiple lineages. *Molecular Phylogenetics and Evolution* **42**: 789–796.
- Larson RL, Pockalny RA, Viso RF, Erba E, Abrams LJ, Luyendyk BP, Stock JM, Clayton RW. 2002.** Mid-Cretaceous tectonic evolution of the Tongareva triple junction in the southwestern Pacific Basin. *Geology* **30**: 67–70.
- Lee DE, Lee WG, Mortimer N. 2001.** Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany* **49**: 341–356.
- Levin DA. 2000.** *The origin, expansion, and demise of plant species*. New York, NY: Oxford University Press.
- Lovett J, Clarke GP. 1998.** *Cephalosphaera usambarensis*. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. Available at: <http://www.iucnredlist.org>. Accessed on 16 August 2007.
- Lovette IJ, Bermingham E, Ricklefs RE. 2002.** Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 37–42.
- Lovette IJ, Rubenstein DR. 2007.** A comprehensive molecular phylogeny of the starlings (Aves: Sturnidae) and mockingbirds (Aves: Mimidae); congruent mtDNA and nuclear trees for a cosmopolitan radiation. *Molecular Phylogenetics and Evolution* **44**: 1031–1056.
- Marshall BA. 2001.** Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. *Mémoires du Muséum national d'Histoire naturelle* [Paris] **150**: 41–109.
- Mathews S, Donoghue MJ. 1999.** The root of angiosperm phylogeny inferred from duplicate phytochrome genes. *Science* **286**: 947–950.
- Mayr E, Diamond J. 2001.** *The birds of northern Melanesia: speciation, ecology and biogeography*. New York, NY: Oxford University Press.
- McDowall RM. 2008.** Process and pattern in the biogeography of New Zealand – a global microcosm? *Journal of Biogeography* **35**: 197–212.
- Meffre S, Crawford AJ, Quilty PG. 2007.** Arc continent collision forming a large island between New Caledonia and New Zealand in the Oligocene. Extended Abstracts, Australian Earth Sciences Convention 2006. Melbourne. 3 pp.
- Millener PD. 1988.** Contributions to New Zealand's Late Quaternary avifauna. I. *Pachyplechus*, a new genus of wren (Aves: Acanthisittidae), with two new species. *Journal of the Royal Society of New Zealand* **18**: 383–406.
- Millener PD, Worthy TH. 1991.** Contributions to New Zealand's Late Quaternary avifauna. II. *Dendroscansor decurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). *Journal of the Royal Society of New Zealand* **21**: 179–200.
- Monaghan MT, Balke M, Pons J, Vogler AP. 2006.** Beyond barcodes: complex DNA taxonomy of a South Pacific radiation. *Proceedings of the Royal Society of London Series B, Biological Sciences* **273**: 887–893.
- Moore EM, Wakabayashi J, Unruh JR. 2002.** Crustal-scale cross-section of the U.S. Cordillera, California and beyond, its tectonic significance, and speculations on the Andean orogeny. *International Geology Review* **44**: 479–500.
- Moreira-Muñoz A. 2007.** Plant geography of Chile: an essay on postmodern biogeography. PhD Thesis, Friedrich-Alexander University, Erlangen-Nürnberg.
- Mortimer N, Hoernle K, Hauff F, Palin JM, Dunlap WJ, Werner R, Faure K. 2006.** New constraints on the age and evolution of the Wishbone Ridge, southwest Pacific Cretaceous microplates, and Zealandia-West Antarctica breakup. *Geology* **34**: 185–188.
- Murienne J, Grandcolas P, Piulachs MD, Bellés X, d'Haese C, Legendre F, Pellens R, Guilbert E. 2005.** Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* **21**: 2–7.
- Müller KF, Borsch T, Hilu KW. 2006.** Phylogenetic utility of rapidly evolving DNA at high taxonomical levels: contrasting *matK*, *trnT-F*, and *rbcL* in basal angiosperms. *Molecular Phylogenetics and Evolution* **41**: 99–117.

- Natland JH, Winterer EL. 2005.** Fissure control on volcanic action in the Pacific. *Geological Society of America Special Paper* **388**: 687–710.
- Nicholson KN, Black PM. 2004.** Cretaceous–Early Tertiary basaltic volcanism in the Far North of New Zealand: geochemical associations and their tectonic significance. *New Zealand Journal of Geology and Geophysics* **47**: 437–446.
- Prance G. 1994.** A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. *Philosophical Transactions of the Royal Society of London Series B* **345**: 89–99.
- Pulvers JN, Colgan DJ. 2007.** Molecular phylogeography of the fruit bat genus *Melonycteris* in northern Melanesia. *Journal of Biogeography* **34**: 713–723.
- Renner SS. 2006.** Relaxed molecular clocks for dating historical plant dispersal events. *Trends in Plant Science* **10**: 550–558.
- Roca AL, Bar-Gal GK, Eizirik E, Helgen KM, Maria R, Springer MS, O'Brien SJ, Murphy WJ. 2004.** Mesozoic origin for West Indian insectivores. *Nature* **429**: 649–651.
- Rudall PJ, Bateman RM. 2006.** Morphological phylogenetic analysis of Pandanales: testing contrasting hypotheses of floral evolution. *Systematic Botany* **31**: 223–238.
- Rutishauser R, Pfeifer E, Novelo RA, Philbrick CT. 2005.** *Diamantina lombardii* – an odd Brazilian member of the Podostemaceae. *Flora* **200**: 245–255.
- Rutishauser R, Wanntorp L, Pfeifer E. 2004.** *Gunnera herteri* – developmental morphology of a dwarf from Uruguay and S Brazil (Gunneraceae). *Plant Systematics and Evolution* **248**: 219–241.
- Rønsted N, Chase MW, Albach DC, Bello MA. 2002.** Phylogenetic relationships within *Plantago* (Plantaginaceae); evidence from nuclear ribosomal ITS and plastid trnL-F sequence data. *Botanical Journal of the Linnean Society* **139**: 323–338.
- Santos CMD. 2007.** On basal clades and ancestral areas. *Journal of Biogeography* **34**: 1470–1471.
- Sauquet H, Doyle JA, Scharaschkin T, Borsch T, Hilu KW, Le Thomas A. 2003.** Phylogenetic analysis of Magnoliales and Myristicaceae based on multiple data sets: implications for character evolution. *Botanical Journal of the Linnean Society* **142**: 125–186.
- Savolainen V, Fay MF, Albach DC, Backlund A, van der Bank M, Cameron KM, Johnson SA, Lledó MD, Pintaud J-C, Powell M, Shehan MC, Soltis DE, Soltis PS, Weston P, Whitten WM, Wurdack KJ, Chase MW. 2000.** Phylogeny of the eudicots: a nearly complete familial analysis based on *rbcL* gene sequences. *Kew Bulletin* **55**: 257–309.
- Schellart WP, Lister GS, Toy VG. 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.
- Shepherd LD, Lambert DM. 2007.** The relationships and origins of the New Zealand wattlebirds (Passeriformes, Callaeatidae) from DNA sequence analysis. *Molecular Phylogenetics and Evolution* **43**: 480–492.
- Sherwood AR, Sheath RG. 1999.** Biogeography and systematics of *Hildenbrandia* (Rhodophyta, Hildenbrandiales) in North America: inferences from morphometrics and *rbcL* and 18S rRNA gene sequence analyses. *European Journal of Phycology* **34**: 523–532.
- Sherwood AR, Sheath RG. 2003.** Systematics of the Hildenbrandiales (Rhodophyta): gene sequence and morphometric analyses of global collections. *Journal of Phycology* **39**: 409–422.
- Slack KE, Delsuc F, Mclenachan PA, Arnason U, Penny D. 2007.** Resolving the root of the avian mitogenomic tree by breaking up long branches. *Molecular Phylogenetics and Evolution* **42**: 1–13.
- Slack KE, Jones CM, Ando T, Harrison GL, Fordyce RE, Arnason U, Penny D. 2006.** Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Molecular Biology and Evolution* **23**: 1144–1155.
- Smith AD. 2007.** A plate model for Jurassic to Recent intra-plate volcanism in the Pacific Ocean basin. *Geological Society of America Special Paper* **430**: 471–495.
- Soltis DE, Senter AE, Zanis MJ, Kim S, Thompson JD, Soltis PS, Ronse de Craene LP, Endress PK, Farris JS. 2003.** Gunnerales are sister to other core eudicots: implications for the evolution of pentamery. *American Journal of Botany* **90**: 461–470.
- 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.
- Speed RC, Smith-Horowitz PL, Perch-Nielsen KvS, Saunders JB, Sanfilippo AB. 1993.** Southern Lesser Antilles arc platform: pre-Late Miocene stratigraphy, structure, and tectonic evolution. *Geological Society of America Special Paper* **277**: 1–98.
- Stadelmann B, Lin L-K, Kunz TH, Ruedi M. 2007.** Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution* **43**: 32–48.
- Stefanović S, Kuzmina M, Costea M. 2007.** Delimitation of major lineages within *Cuscuta* subgenus *Grammica* (Convolvulaceae) using plastid and nuclear DNA sequences. *American Journal of Botany* **94**: 568–589.
- Stefanović S, Olmstead RG. 2005.** Down the slippery slope: plastid genome evolution in Convolvulaceae. *Journal of Molecular Evolution* **61**: 292–305.
- Stevens PF. 2007.** *Angiosperm phylogeny website*, Version 8. Available at: <http://www.mobot.org/MOBOT/Research/APweb/> Accessed July 2007.
- Stoner CJ, Bininda-Emonds ORP, Caro T. 2003.** The adaptive significance of coloration in lagomorphs. *Biological Journal of the Linnean Society* **79**: 309–328.
- Taylor B. 2006.** The single largest oceanic plateau: Ontong Java-Manihiki-Hikurangi. *Earth and Planetary Science Letters* **241**: 372–380.
- Tejada MLG, Mahoney JJ, Castillo PR, Ingle SP, Sheth HC, Weis D. 2004.** Pin-pricking the elephant: evidence on

- the origin of the Ontong Java Plateau from Pb-Sr-Hf-Nd isotopic characteristics of ODP Leg 192 basalts. *Geological Society of London, Special Publication* **229**: 33–150.
- Tennyson A, Martinson P. 2006.** *Extinct birds of New Zealand*. Wellington: Te Papa Press.
- Thordarson T. 2004.** Accretionary-lapilli-bearing pyroclastic rocks at ODP Leg 192 Site 1184: a record of subaerial phreatomagmatic eruptions on the Ontong Java Plateau. *Geological Society of London, Special Publication* **229**: 275–306.
- Torres Miranda A, Luna Vega I. 2006.** Análisis de trazos para establecer áreas de conservación en la Faja Volcánica Transmexicana. *Interciencia* **31**: 849–855.
- Umhoefer PJ. 2003.** A speculative model for the North American cordillera in the Early Cretaceous: tectonic escape related to arc collision of the Guerrero terrane and a change in North America plate motion. *Geological Society of America Special Paper* **374**: 117–134.
- Vaughan APM, Livermore RA. 2005.** Episodicity of Mesozoic terrane accretion along the Pacific margin of Gondwana: implications for superplume-plate interactions. *Geological Society of London Special Publication* **246**: 143–178.
- Voelker G, Rohwer S, Bowie R, Outlaw DC. 2007.** Molecular systematics of a speciose, cosmopolitan songbird genus: defining the limits of, and relationships among, the *Turdus* thrushes. *Molecular Phylogenetics and Evolution* **42**: 422–434.
- Wade CM, Mordan PB, Naggs F. 2006.** Evolutionary relationships among the pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society* **87**: 593–610.
- Wahlberg N, Freitas AVL. 2007.** Colonization and radiation in South America by butterflies in the subtribe Phycioidina (Lepidoptera: Nymphalidae). *Molecular Phylogenetics and Evolution* **44**: 1257–1272.
- Wanke S, Venderschaeve L, Mathieu G, Neinhuis C, Goetghebeur P, Samain MS. 2007.** From forgotten taxon to missing link? The position of the genus *Verhuellia* (Piperaceae) revealed by molecules. *Annals of Botany* **99**: 1231–1238.
- Weeks A, Dal DC, Simpson BB. 2005.** The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. *Molecular Phylogenetics and Evolution* **35**: 85–101.
- Whattam SA, Malpas J, Ali JR, Lo C-H, Smith IEM. 2005.** Formation and emplacement of the Northland ophiolite, northern New Zealand: SW Pacific tectonic implications. *Journal of the Geological Society* **162**: 225–241.
- Wiegmann BM, Regier JC, Mitter C. 2002.** Combined molecular and morphological evidence on the phylogeny of the earliest lepidopteran lineages. *Zoologica Scripta* **31**: 67–81.
- Wildman DE, Uddin M, Opazo JC, Liu G, Lefort V, Guindon S, Gascuel O, Grossman LI, Romero R, Goodman M. 2007.** Genomics, biogeography, and the diversification of placental mammals. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 14395–14400.
- Winkworth R, Wagstaff SJ, Glenny D, Lockhart PJ. 2002.** Plant dispersal N.E.W. S. from New Zealand. *Trends in Ecology and Evolution* **17**: 514–520.
- Worthington TJ, Hekinian R, Stoffers P, Kuhn T, Hauff F. 2006.** Osbourn Trough: structure, geochemistry, and implications of a mid-Cretaceous paleospreading ridge in the South Pacific. *Earth and Planetary Science Letters* **245**: 685–701.
- Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD. 2006.** Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 19419–19423.
- Zerega NJC, Clement WL, Datwyler SL, Weiblen GD. 2005.** Biogeography and divergence times in the mulberry family (Moraceae). *Molecular Phylogenetics and Evolution* **37**: 402–416.
- Zhang L-B, Simmons MP, Renner SS. 2007.** A phylogeny of Anisophylleaceae based on six nuclear and plastid loci: ancient disjunctions and recent dispersal between South America, Africa, and Asia. *Molecular Phylogenetics and Evolution* **44**: 1057–1067.