Biological disjunction along the West Caledonian fault, New Caledonia: a synthesis of molecular phylogenetics and panbiogeography

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This paper documents a newly discovered pattern of biological disjunction between NW and SE New Caledonia. The disjunction occurs in 87 (mapped) taxa, including plants, moths and lizards, and correlates spatially with the West Caledonian fault. This fault is controversial; some geologists interpret it as a major structure, others deny that it exists. It may have undergone 150–200 km of lateral movement and it is suggested that this has caused the biological disjunction by pulling populations apart. The disjunction matches similar dextral disjunctions of taxa along transform faults in New Zealand, New Guinea, California and Indonesia. Major biogeographic patterns – whether centres of diversity, boundaries of allopatric taxa or disjunctions – all include taxa with many different degrees of differentiation. Studies using a clock model of evolution will therefore interpret a biogeographic pattern as the result of many disparate events. However, this line of reasoning reaches the untenable conclusion that biogeographic patterns, including normal allopatry, are always caused by chance dispersal, never by vicariance. A more productive approach, avoiding the pitfalls of a fossil-based molecular clock, involves a close examination of molecular clades, comparative biogeography and tectonics. The New Caledonia example documented here shows that this can lead to novel, testable predictions. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **158**, 470–488.

ADDITIONAL KEYWORDS: biogeography – distribution – ecology – lizard – molecular clock – molecular systematics – Pacific – tectonics – vicariance.

INTRODUCTION

The concept of sister groups in phylogeny has a parallel in the idea of sister areas in biogeography. What exactly is the geographic and evolutionary relationship between two sister areas? In the case of South America and Africa, or New Zealand and Australia, areas have been pulled apart by rifting around spreading centres. Movement on transform faults is connected with rifting and subduction and it is suggested in this paper that lateral strike-slip movement on transforms, like rifting, may have separated biological populations and clades.

New Caledonia is a French territory in the SW Pacific comprising one large island, Grande Terre, and three smaller islands, the Loyalties, with a total area approximately that of Wales or Massachusetts. The flora and fauna are of special interest through their diversity, endemism and geographic affinities. For seed–plants, no other region of comparable area has such a rich, archaic and peculiar flora (Thorne, 1965; Good, 1974). There are about 3700 indigenous species, including 2324 endemic species, 105 endemic genera and five endemic families (Jaffré, Rigault & Dagostini, 2001). New Caledonia must also be one of the smallest areas in the world with an endemic bird family (Rhynochetidae), the kagu.

Notwithstanding oddities such as the kagu, the vertebrates of New Caledonia were assumed to be rather depauperate. However, work by A. M. Bauer,

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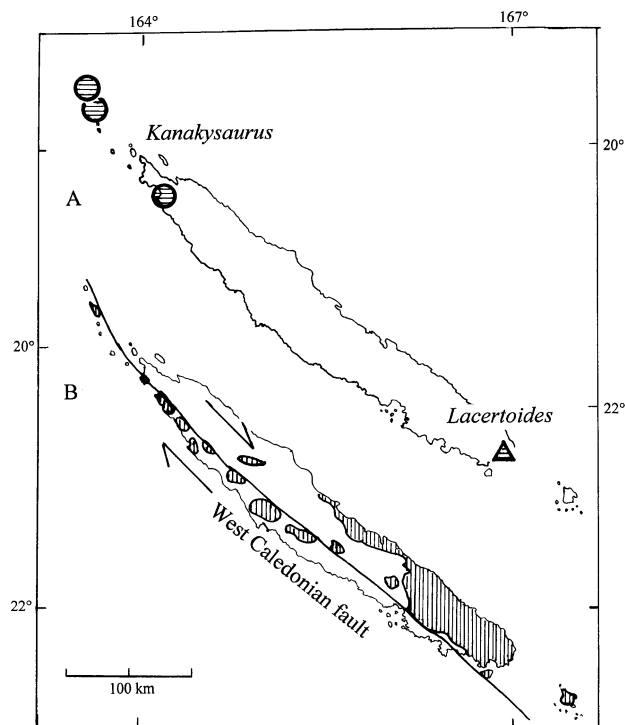
Figure 1. A, distribution of the scincid lizards *Kanakysaurus* (circles) and *Lacertoides* (triangle) (Sadlier *et al.*, 2004). B, Grande Terre, New Caledonia, showing the West Caledonian fault and massifs of ultramafic rock (vertical lines).

R. A. Sadlier and colleagues has revealed major diversity in the lizards (Bauer & Sadlier, 2000) and recent molecular studies indicate some fascinating relationships. For example, Sadlier *et al.* (2004) wrote that 'in overall appearance and biology' the recently discovered scincid *Kanakysaurus* endemic to NE Grande Terre and the offshore Iles Bélep is 'most similar to the forest-dwelling species of the endemic New Caledonian genus *Marmorosphax*'. However, in the phylogeny (Sadlier *et al.*, 2004), based on mitochondrial DNA (*ND2*) and nuclear DNA (*RAG-1*), *Kanakysaurus* appears as sister to *Lacertoides*, endemic to the southern tip of Grande Terre (Fig. 1A) (bootstrap support 96%). Sadlier *et al.* did not comment on this link, but it represents a striking disjunction of 320 km. (Generic groupings in another analysis were slightly different but had bootstrap support less than 50% and are not discussed here; Smith *et al.* 2007.)

One way of testing phylogenetic hypotheses such as the *Kanakysaurus*–*Lacertoides* pairing is to sequence more DNA. Another test is to establish whether the geographic distribution is unusual or unique, or whether it follows a pattern repeated in many groups. For the lizards, the molecular work has indicated or at least suggested an interesting distribution, but there

are few if any other molecular studies for comparison. However, for plants, New Caledonia is perhaps the most intensively collected forested country in the tropics and hundreds of detailed (dot) maps of species distributions have been published in an ongoing flora series (Aubréville *et al.*, 1967–present). This work may lack phylogenetic precision, especially in some difficult groups, but the sheer bulk of the sample size (hundreds of thousands of specimens) means that many patterns are clearly evident. In any case, it is unusual to come across a molecular clade with a distribution that is not already documented in traditional monographs (cf. Avise, 2007). Biogeography can best be served by using the strengths of both approaches – the penetration of molecular phylogenetic analysis and the intensive geographic sampling of traditional, morphological taxonomy.

MATERIAL AND METHODS

No two distributions are exactly the same. However, distributions often share distinctive attributes and so can be grouped together like clades. Biogeographic patterns are often based around tectonic features (Craw, Grehan & Heads, 1999). Centres of biological endemism, diversity and disjunction have been correlated with belts of subduction, terrane accretion, back-arc basin formation, igneous activity and metamorphism. It was observed that the lizard disjunction in New Caledonia (Fig. 1A) follows a major geological structure, the *sillon* or furrow, interpreted by some authors as a major rift or West Caledonian fault (Fig. 1B). A review was made of other groups to determine whether this is a common disjunction or not. New Caledonian plants are especially well mapped (Aubréville *et al.*, 1967–present) and provide most of the examples cited below.

RESULTS

Some taxa have a boundary at the West Caledonian fault; for example, the mutual boundary of *Stephania* and *Tinospora* (Menispermaceae) follows it closely and a species pair in *Dubouzetia* (Elaeocarpaceae) is separated by it (Fig. 2). In addition, many taxa show a notable disjunction (> 100 km) along the fault. This pattern could be explained by the dextral displacement along the fault proposed by several geologists cited below. (In dextral movement, the land on the other side of the fault to that of the observer moves to the observer's right.)

Apart from *Kanakysaurus*–*Lacertoides*, 86 plant and animal taxa displaying the disjunction were found and are mapped here (Figs 3–11). All individual species from the flora that show the pattern clearly are mapped. Several examples of possible sister
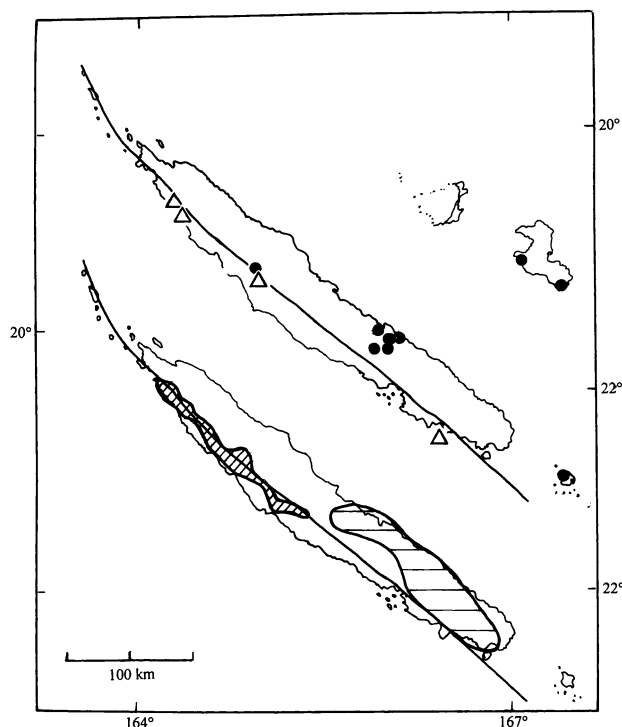
Figure 2. A, two of the four genera of Menispermaceae in New Caledonia: *Stephania* (dots) and *Tinospora* (triangles). B, *Dubouzetia campanulata* (horizontal hatching) and *D. caudiculata* (oblique hatching) (Elaeocarpaceae) (from Aubréville *et al.*, 1967–present).

species that show the disjunction are included, but no attempt was made to retrieve all of these. Most of the taxa shown here are species, but the absence of clades with other ranks is simply because these are seldom mapped (or even well established).

DISCUSSION

Soils and climate

Disjunctions can often be attributed to disjunctions in ecological conditions. Many of the taxa involved in the West Caledonian fault disjunction occur on soils developed over ultramafic substrate. However, ultramafic massifs are found along the length of Grande Terre, including central areas where the disjuncts are absent (Fig. 1B). Because of this distribution it is unlikely that edaphic factors can explain the disjunction. With respect to climate, the far western strip of the island is drier than the rest. Again, there is no obvious relationship to the fault disjunction, in which taxa are missing from central localities.

The West Caledonian fault

Routhier (1953) first drew attention to the New Caledonia *sillon* as an elongated, fault-aligned trough that runs along western Grande Terre, 10–20 km inland of the coast. Guillon & Routhier (1971) emphasized its structural importance. The *sillon* separates the southern ultramafic massif from the belt of smaller massifs along the northwest coast (Fig. 1B) and is 'apparently a radical line in the country's structural pattern' (Lillie & Brothers, 1970). These authors suggested that it is a major fault zone which may be regarded 'as a rift or a median line.' They compared it with structure in New Guinea, where northern ranges are separated from central ranges by a great depression occupied by a fault line which shows evidence of transcurrent displacement. They also made comparisons with the Median Tectonic Line in Japan.

Brothers & Blake (1973) made the interesting suggestion that the *sillon* is a transcurrent fault zone with a dextral offset of at least 150 km. They interpreted the NW peridotite belt as the offset south-west margin of the southern massif. Lateral movement on the fault (named the West Caledonian fault; Brothers, 1974) was suggested to be Early Miocene or younger. Brothers & Blake (1973) cited features that the fault has in common with the Alpine fault of New Zealand and the San Andreas fault of California: a relatively young geologic age, an apparently abrupt change in regional tectonic regimes from thrusting to transcurrent faulting and a great inferred displacement. Like Lillie & Brothers (1970), they noted that both Eocene ophiolite obduction and post-Oligocene dextral transcurrent faulting also occurred in New Guinea.

van Bemmelen (1974) suggested the *sillon* is 'a deep fault, an old line of weakness' belonging to the numerous dextral offsets formed in the Tethys belt in the Late Palaeozoic. Rod (1974) argued that, whatever the details of its history are, 'tectonic models which neglect to show this geosuture as the most prominent structural feature of New Caledonia are certainly unrealistic'. Guérangé, Lozes & Autran (1977) mapped it as a 'Main longitudinal fault = median line'. Brothers (1987) described the *sillon* as 'A major late-stage NW–SE Fault, possibly with a large right-lateral strike-slip component'. Brothers & Lillie (1988: fig. 15) mapped it as a 'fracture zone'.

Carey (1996) described the *sillon* as a great geosuture and suggested that, while it marks an important shear in the diapirism and a very significant transcurrent fault, it is only one component of a megashear system. Rawling & Lister (1997, 1999) also accepted 'major strike slip movements on the sillon fault'. Rawling (1998) wrote that the fault formed in the Miocene and has offset the ultramafics by up to 200 km (about half the length of Grande Terre). Rawling suggested that movements on the fault probably occurred in response to relocation of regional subduction to the New Hebrides Trench and major change in plate motions.
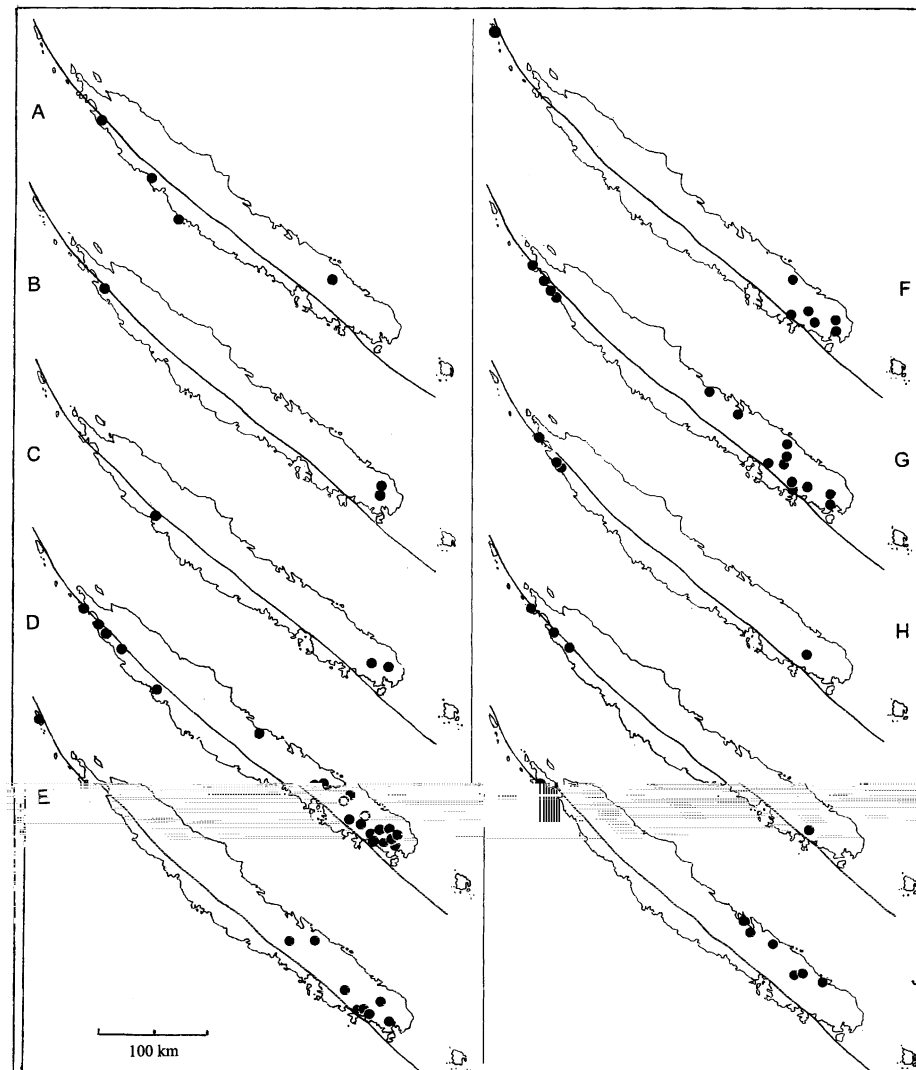
Figure 3. Various Sapotaceae. A, *Leptostylis filipes*. B, *Sebertia acuminata*. C, *S. gatopensis* (these two comprise the genus); D, *Trouettia* [*T. lissophylla* (dots) and *T. heteromera* (circles)]. E, *Bureavella endlicheri*. F, *B. wakere*. G, *Pichonia* (incl. *Rhamnoluma*; Swenson, Bartish and Munzinger, 2007) (all three Grande Terre species). H, *Iteiluma pinifolium*. I, *Planchonella daenikeri*. J, *Planchonella crassinervia*.

In a radical contradiction of these ideas, Cluzel, Aitchison & Picard (2001) argued 'there is no evidence that the so-called West Caledonian Fault exists' and Chardon & Chevillote (2006) did not map it as a single structure (they showed a number of unrelated faults along different sectors of the *sillon*). However, the idea of 150–200 km of dextral displacement is compatible with the biogeographic analysis given here.

Recently, Baldwin, Rawling & Fitzgerald (2007) described the feature as a 'major structural break'. They concluded that 'Movement along this fault is a subject of continued controversy, but it may provide a critical constraint on the tectonic evolution of this part of the SW Pacific.' They noted that different authors have interpreted the *sillon* as a downbuckle, a median fault line, a dextral transcurrent fault zone, a thrust, the trace of a subduction surface and, of particular relevance for biogeography, a long-lived fracture zone with some 150 km of dextral offset and a major vertical component of offset. The high-pressure (HP) metamorphic terrane of NE Grande Terre lies east of the West Caledonian fault. Unfortunately, a possible genetic relationship between the fault and metamorphism/exhumation of the HP terrane is obscured by poor exposure. NW and NE Grande Terre are major centres of endemism and biogeographic data may eventually shed some light on
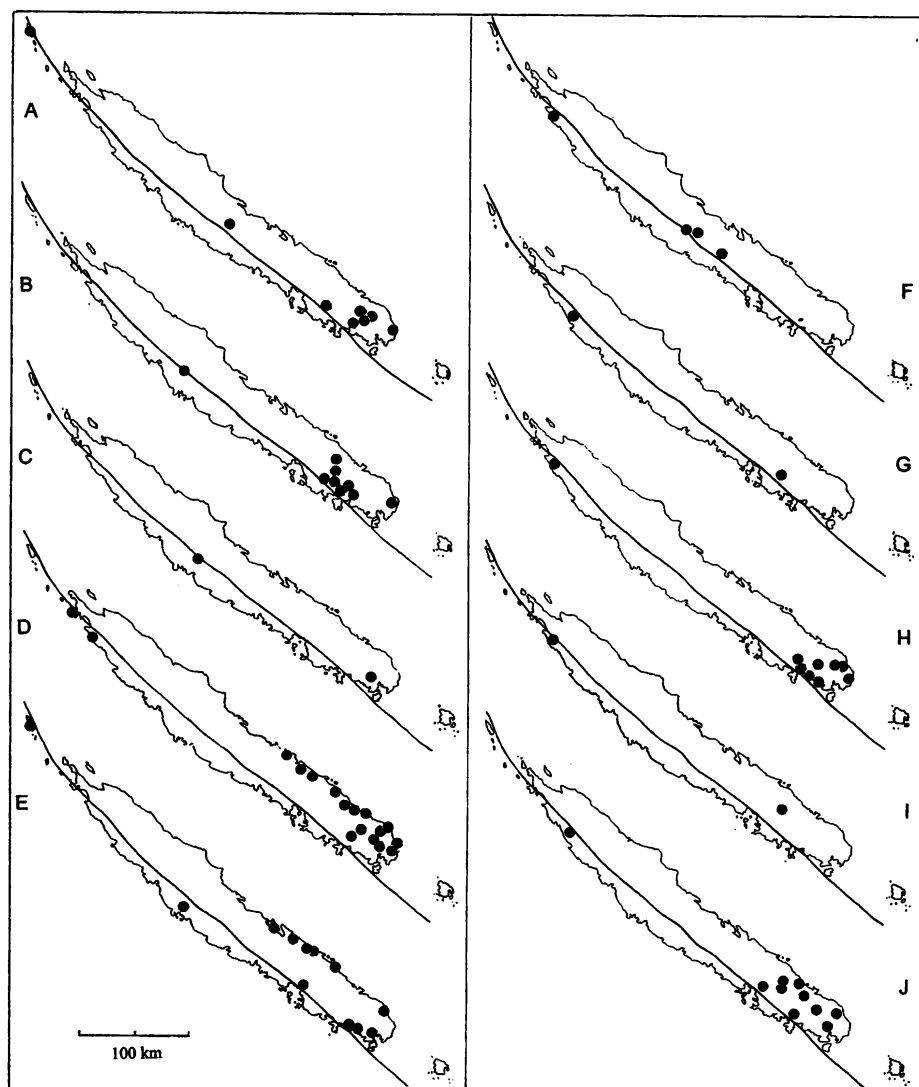
Figure 4. A, *Planchonella microphylla* (Sapot.). B, *Beauprea pancheri* (Prot.). C, *Kermadecia pronyensis* (Prot.); D, *Araucaria bernieri* (Araucar.). E, *A. luxurians*. F, *Cryptocarya pluricostata* (Laur.). G, *Litsea pentaflora* (Laur.). H, *L. ripidion*. I, *L. humboldtiana*, J, *Styphelia coryphila* (Epacrid.).

this aspect of the problem also. Baldwin *et al.* (2007) inferred that the HP terrane and the ultramafic rocks were spatially separated prior to exhumation of the HP terrane but were subsequently juxtaposed in post-Oligocene time as the result of movement on the West Caledonian fault.

THE AGE OF TAXA

If the West Caledonian fault does exist, its age is controversial. The fault may have developed during the Cretaceous orogeny and have been reactivated later in the Cenozoic, during or after emplacement of the ophiolite nappe (Paris, 1981). The ages of taxa endemic to different parts of New Caledonia are also

controversial. Murienne *et al.* (2005) concluded that endemic New Caledonian cockroach species were less than 2 million years old, but the clock calibrations used in the study were based on the assumption that taxa endemic to the Loyalty Islands were no older than the islands. The Loyalties are low, flat, islands composed of very recent limestone. However, they are merely the emergent parts of the Loyalty Ridge, a volcanic island arc which has been active back to at least the Cretaceous (Sdrolias, Müller & Gaina, 2003). The Loyalty Ridge extends to NE North Island, New Zealand, as the Three Kings Ridge (Schellart, 2007). Grande Terre is the emergent part of a second rise, the Norfolk Ridge, that reaches NW North Island. The Loyalties and Grande Terre biotas are highly endemic and very
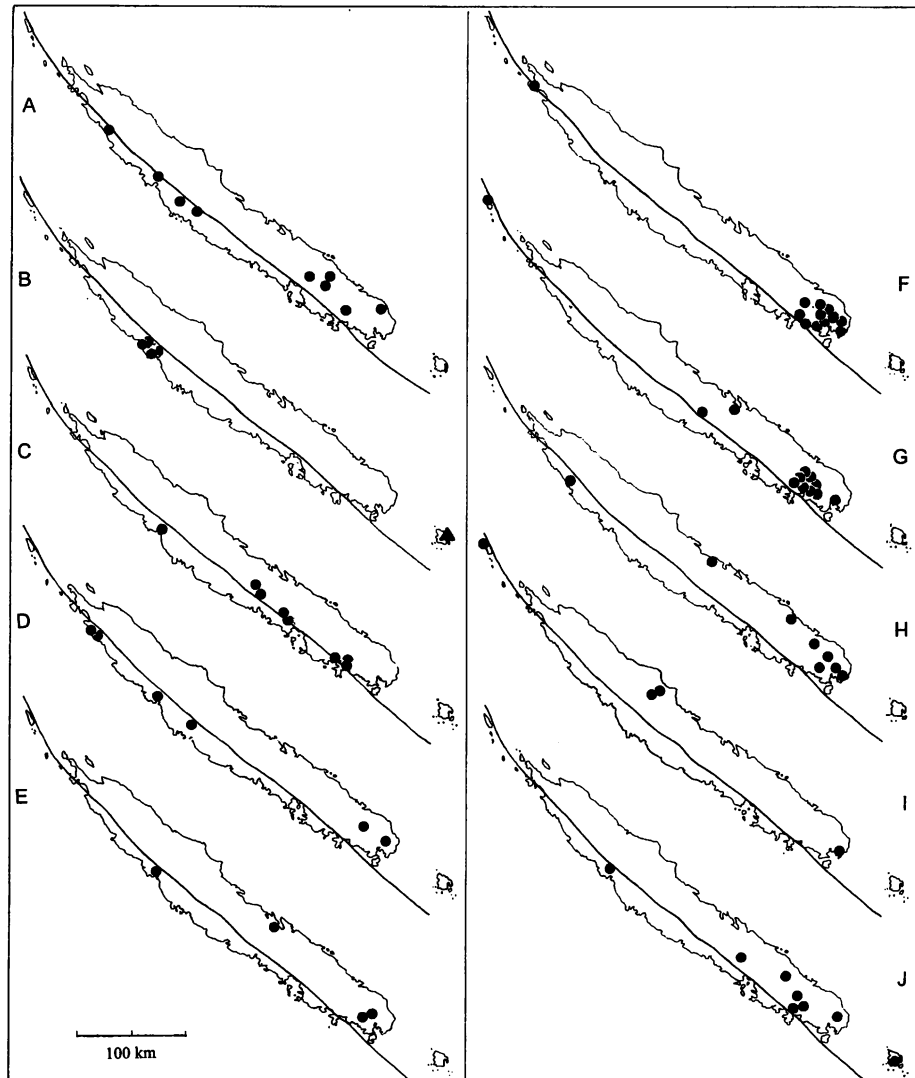
Figure 5. A, *Styphelia macrocarpa* var. *macrocarpa* (Epacrid.). B, *Solanum vaccinioides* (dots) and *S. insulae–S. pinorum* (triangle) (keyed together) (Solan.). C, *Pseuderanthemum repandum* (Acanth.). D, *Dendrobium sarchochilus* var. *megalorhizum* (Orchid.). E, *D. polycladium* var. *polycladium*. F, *D. verruciferum*, G, *D. virotii*. H, *D. ngoyense*. I, *Ephemeranthera comata* (Orchid.). J, *Liparis chalandei* (Orchid.).

different from each other and this can be attributed to the tectonic histories of the two ridges being independent until their collision in the Eocene/Oligocene (Cluzel *et al.*, 2006; Heads, in press) (these arcs are not shown separately in Fig. 15).

Bauer *et al.* (2006) calculated the ages of eight species of *Dierogekko* lizards endemic to New Caledonia that were very different from the cockroach ages proposed by Murienne *et al.* (2005). Bauer *et al.* concluded that all differentiation in the New Caledonian diplodactylid geckos goes back to 30 Ma, the earliest differentiation in *Dierogekko* to 19 Ma and the most recent speciation to 10–6 Ma.

Calibrating evolutionary events using either oldest fossil or the age of strata that taxa are currently

endemic to, will lead to dates that are generally much too young (Heads, 2005). Assuming total extinction of New Caledonian life by Palaeogene marine transgressions will also lead to dates that are too young. There is an old controversy about whether islands such as New Caledonia, New Zealand, New Guinea and Jamaica were or were not totally covered by sea during the Palaeocene–Oligocene. However, Bauer *et al.* (2006) dated differentiation between New Zealand and New Caledonian gecko lineages as Late Cretaceous to Palaeogene and ruled out the possibility that New Caledonia was completely submerged by the sea during the Palaeocene. Aspects of the New Caledonian flora also indicate that plant life cannot have been eliminated at this time (Lowry, 1998). With respect to
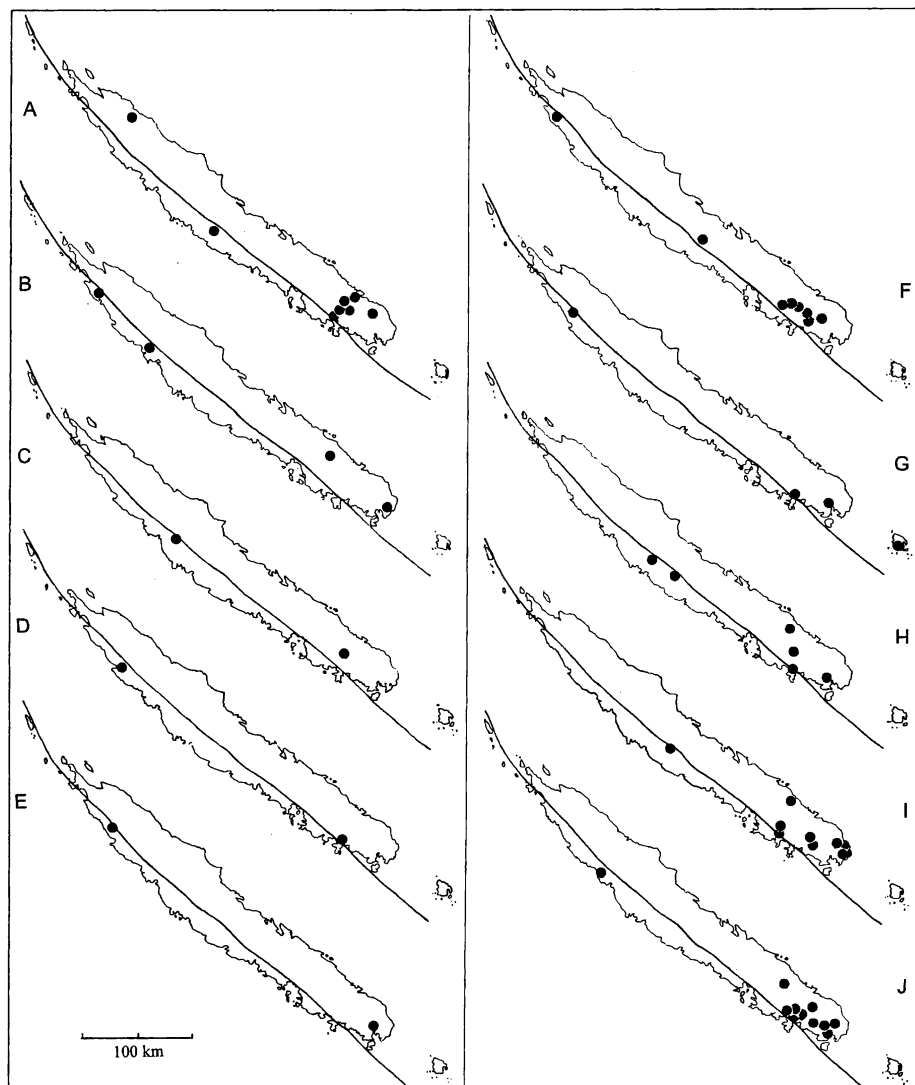
Figure 6. *Octarrhena oberonioides* (Orchid.; with an additional S massif – NE Grande Terre disjunction). B, *Sarcochilus rarus* (Orchid.). C, *S. hillii*. D, *Acianthus amplexicaulis*. E, *A. aegeridantennatus*. F, *A. macroglossus*. G, *A. halleanus* (*Acianthus* maps from Kores, 1995). H, *Calochilus neocaledonicus* (Orchid.) I, *Megastylis rara* (Orchid.). J, *Pachyplectron neocaledonicum* (Orchid.).

New Zealand, a 'mouse-like' mammal discovered there in Miocene strata and identified as an endemic relic basal to the monotreme–marsupial–placental lineage (Worthy *et al.*, 2006) provides good evidence that the country was not totally submerged at any one time.

BIOGEOGRAPHIC DISJUNCTIONS ON TRANSFORM FAULTS

Major biological disjunctions similar to the West Caledonian fault example occur along transform fault zones in New Zealand (Fig. 12; Heads, 1998b) and New Guinea (Fig. 13; Heads, 1999, 2001, 2002, 2003). All three disjunctions are dextral (Fig. 14); in New

Guinea sinistral disjunctions are also frequent. The location of the Pacific/Australia plate boundary through the Cretaceous/Cenozoic is a topic of debate, but New Zealand, New Caledonia and New Guinea have all been associated with subduction and also with Palaeogene obduction (ramping up onto land) of ophiolite sequences (Parrot & Dugas, 1980). The three islands (the Inner Melanesian Arc of Avias, 1973; cf. Coleman, 1997) may mark the axis of a Palaeogene orogeny (Rawling & Lister, 1997, 1999).

A recent model proposed two 'lithospheric beams' or ribbon continents in the SW Pacific bending and buckling as the Ontong Java Plateau crashes into them (Fig. 15; Johnston, 2004). The first beam
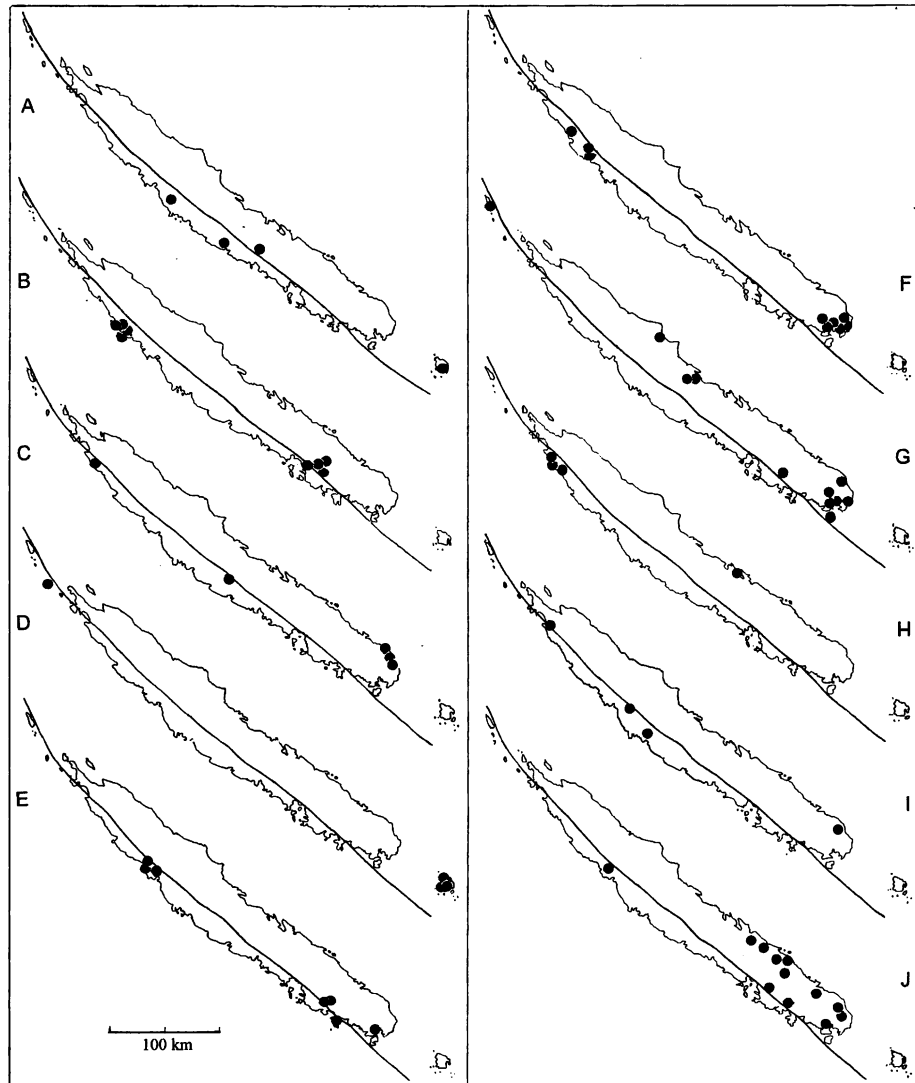
Figure 7. A, *Cheirostylis montana* (Orchid.). B, *Melodinus reticulatus* (Apocyn.). C, *Alstonia veillardii* var. *glaberrima* (Apocyn.). D, *Alyxia spathulata* (Apocyn.). E, *A. affinis* (these last two species were sunk by Middleton, 2002 in an 'enormously variable' *A. tisserantii*). F, *Elaeocarpus leratii* (Elaeocarp.). G, *Hedycarya baudouinii* (Monim.). H, *Serianthes margaretae* (Mimos.). I, *Hunga mackeeana* (Chrysobalan.). J, *Hunga minutiflora*.

comprises Northland (New Zealand)–Norfolk I.–New Caledonia–d'Entrecasteaux Ridge and, before collision of the Ontong Java Plateau with the Solomons, also included the Papuan Peninsula. The second beam included the Tonga–Kermadec Ridge and Fiji; before collision this was continuous with the Solomons and the Bismarcks. This model explains the curvature of the d'Entrecasteaux Ridge through its having been pinned by the Vanuatu Arc as this moved south. The model also explains several puzzling biogeographic ranges. The first beam as a whole is also an important biogeographic sector. Within it, there is a distinct biotic connection: New Caledonia–Papuan Peninsula, seen in several groups. The seafloor

topography here is complex and many features, for example the South Rennell Trough, remain poorly understood. The history of the second beam proposed in Johnston's model would also account for the separate biogeographic connections of Fiji with the Solomons/N Vanuatu and with S Vanuatu.

In New Zealand, biological disjunction along the Alpine fault was previously explained by glacial extirpation of central populations, but this does not explain the fact that many of the taxa involved thrive around glaciers or that there are generally closely related vicariants in the gap. The disjunction may have been caused, not by extirpation, but by strike-slip movement on the fault pulling apart populations
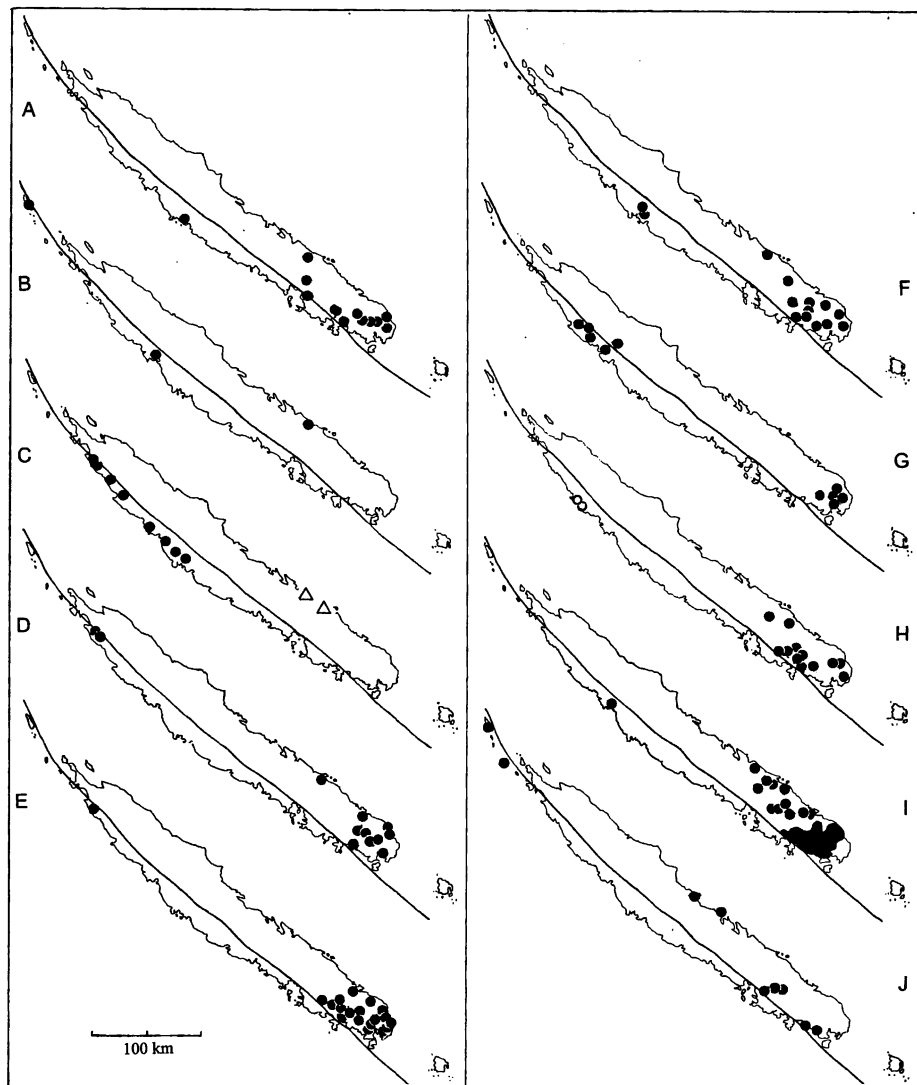
Figure 8. A, *Neoguillauminia* (Euphorb.). B, *Alphandia* in New Caledonia (Euphorb.). C, *Baloghia neocaledonica* and *B. drimiflora* (Euphorb.) (keyed together). D, *Bocquillonia spicata* (Euphorb.). E, *Dysoxylum minutiflorum* (Mel.). F, *Oncotheca humboldtiana* (Oncothec.). G, *Elaphanthera baumannii* (Santal.). H, *Hibbertia ebracteata* and *H. rubescens* (Dillen.) (keyed together). I, *Hibbertia trachyphylla*. J, *Phyllanthus tenuipedicellatus* (Phyllanth.).

(Heads, 1998b; Heads & Craw, 2004). The idea was criticized by Wallis & Trewick (2001), although they accepted that it may be true for some taxa. It should be noted that only a small subset of all clades can potentially show disjunction. Undifferentiated clades that are were widespread before fault movement will be widely distributed after it and so will not show any change. Clades that only occurred on one side of the fault before movement will also show no change in their distribution after fault movement. Only taxa with certain kinds of prior distributions – more or less localized, but found on both sides of the fault – can potentially show fault movement. Gibbs (2006: 181) has found the pattern in various insects and is sym-

pathetic to the Alpine fault hypothesis and Fenwick & Marshall (2006) mapped what they called a 'classic' Alpine fault disjunction in two freshwater bivalve species. A molecular dating study of freshwater gastropods concluded that fault disjunction could have been caused by fault movement (Haase, Marshall & Hogg, 2007).

In New Guinea, the disjunction has been attributed to chance extinction although, again, this is contradicted by the repetition of the pattern and by the presence of closely related vicariants in the gap (Heads, 2001).

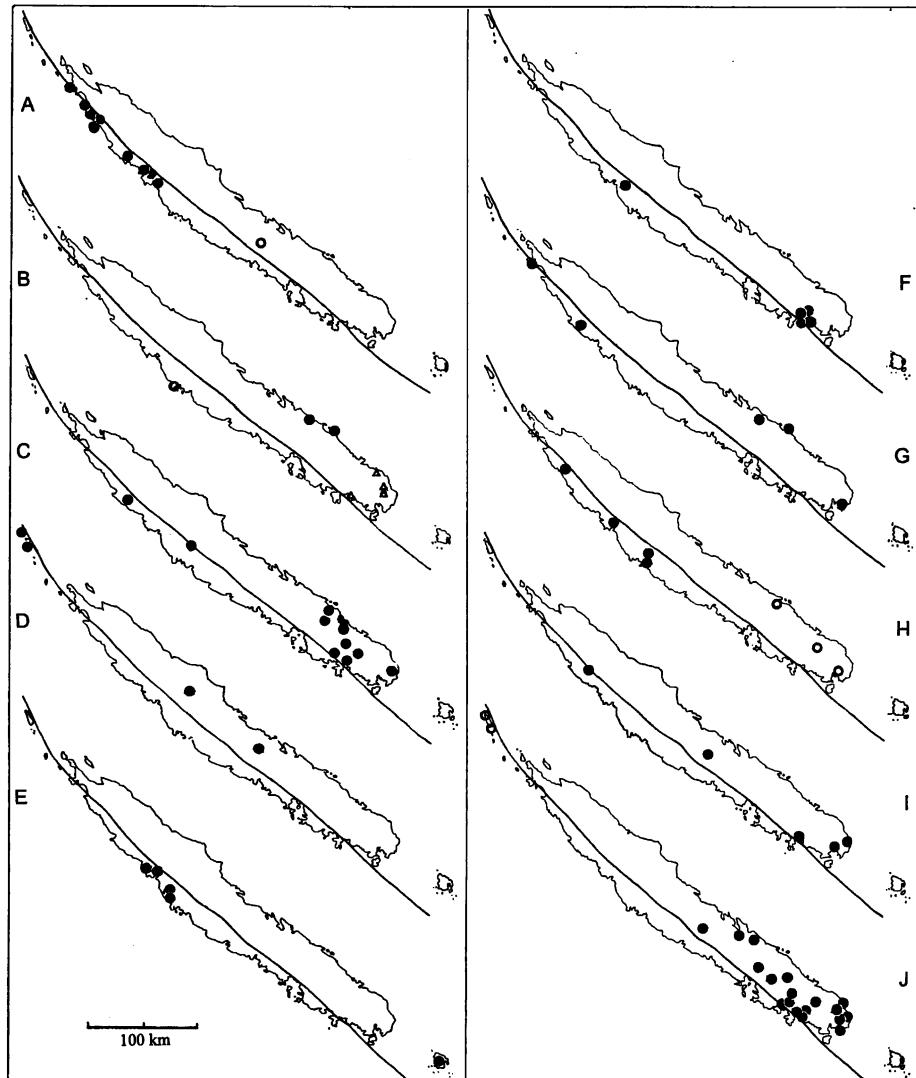Other cases of disjunction along transforms occur along the Great Sumatra fault in Indonesia (Heads,

Figure 9. A, *Phyllanthus poumensis* (dots), *P. koniamboensis* (dots) and *P. unioensis* (circle) (the three keyed together). B, *Phyllanthus aeneus* var. *nepouiensis* (circle), var. *longistylus* (dots) and var. *cordifolius* (triangles) (keyed together). C, *Metrosideros engleriana* (Myrt.). D, *Diospyros tireliae* (Eben.). E, *Jasminum kriegeri* (Olea.). F, *Syzygium acre* (Myrt.). G, *Syzygium pterocalyx.* H, *Syzygium koniamboense* (dots) and *S. xanthostemifolium* (circles) (keyed together). I, *Syzygium capillaceum.* J, *Pittosporum artense* (circles) and *P. leratii* (dots) (Pittospor.) (keyed together).

2003: 399), in southern Patagonia along the margin of the Scotia and South American plates (Heads, 1999), in the Caribbean along the southern margin of the Caribbean plate (Heads, 1990a) and in California along the San Andreas fault (Baldwin & Kyhos, 1990; Craw *et al.*, 1999: figs 2–8).

Some interesting taxa that show Alpine fault disjunction in New Zealand also have disjunct localities across the Tasman Sea, in SE Australia (Heads, 1998b). Similarly, the orchid *Acianthus amplexicaulis* occurs in New Caledonia, where it is disjunct along the West Caledonian fault (Fig. 6D) and is also in NE Australia. Here it occurs at the McPherson–Macleay

Overlap (the accreted Gympie terrane; eastern end of the Queensland/New South Wales border) and in NE Queensland, another common disjunction. The New Caledonia–E Australia disjunction is accounted for by Cretaceous–Palaeogene rifting (Ladiges & Cantrill, 2007).

INTERPRETING THE BIOGEOGRAPHY OF CLADES

In the dispersalist philosophy which has guided most biogeographic studies over the last century, clade distributions have often lacked status as hard data. They might be a 'stimulus to suggest hypotheses' but
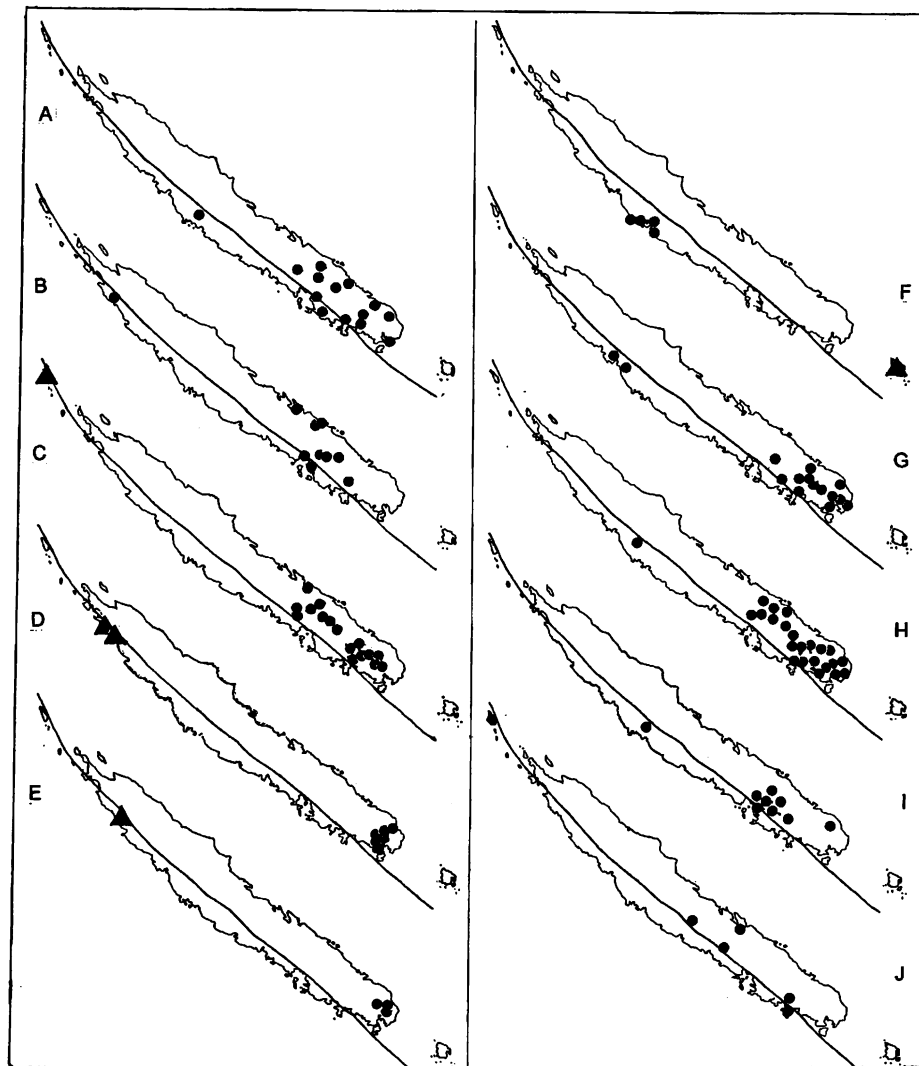
Figure 10. *Lasiochlamys reticulata* (Flacourt.). B, *Xylosma nervosum* (Flacourt.). C, *Phyllanthus artensis* (triangle) and *P. vulcani* (dots). D, *Phyllanthus guillauminii* (triangles) and *P. pronyensis* (dots). E, *Tristaniopsis minutiflora* (triangle) and *T. yateensis* (dots) (Myrt.). F, *Cassine pininsularis* subsp. *pininsularis* (triangle) and subsp. *poyaensis* (dots) (Celastr.). G, *Euroschinus elegans* (Anacard.). H, *E. rubromarginatus.* I, *Semecarpus riparia* (Anacard.). J, *Jasminum promunturianum* and *J. elatum* (Olea.).

could not in themselves answer questions or even test hypotheses (Wallis & Trewick, 2001). However, like the early advocates of geographic subspecies, many molecular workers have realized the fundamental significance of biogeographic structure and allopatry (Avise, 2007). Some have suggested that species be defined as well-supported lineages in a haplotype phylogeny that are 'concordant with geography' (Wiens & Penkrot, 2002; Sites & Marshall, 2003). This concordance is a major discovery (or rediscovery) of molecular systematics, although many analyses of 'geographic concordance' are still based simply on measures of spatial spread or coherence, rather than on geographic distribution (e.g. Templeton, 1998,

2001). Spatially significant biogeographic patterns, such as the *Kanakysaurus–Lacertoides* disjunction along the West Caledonian fault, are neither coherent nor concordant with geography and are easily overlooked. Sadlier *et al.* (2004) may have hesitated to highlight the disjunction because at first sight it seems unlikely to be real. A similar case occurred in studies on birds of paradise. In the standard theory, these birds had a centre of origin in the main axial range of New Guinea and dispersed from there to outlying mountainous peninsulas in the north-west (Vogelkop Peninsula) and north-east (Huon Peninsula). These peninsulas are not far from the main range but separated from each other by 1500 km. The
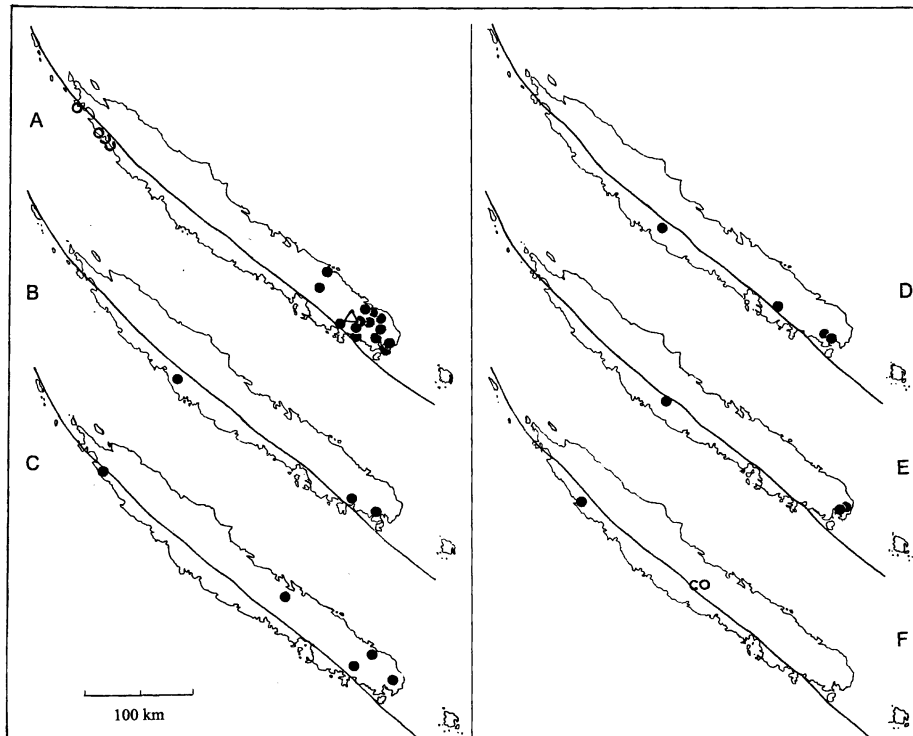
Figure 11. A, *Gmelina evoluta* (in the north) keyed with *G. ligneum–G. vitreum* and *G. neocaledonica*. (in the south) (Labiatae). B, *Sarcomelicope simplicifolia* (Ruta.) (the same subspecies is also in Vanuatu; map from Hartley, 1982). Moths (all Geometridae, from Holloway, 1979): C, *Parosteodes grisea*. D, *Chloroclystis scintillata*. E, *Caledophia pauli*. F, the lizard *Bavayia pulchella* (dots) and its putative sister species, *B. exsuccida* (circles) (Diplodactylidae; Bauer & Sadlier, 2000).
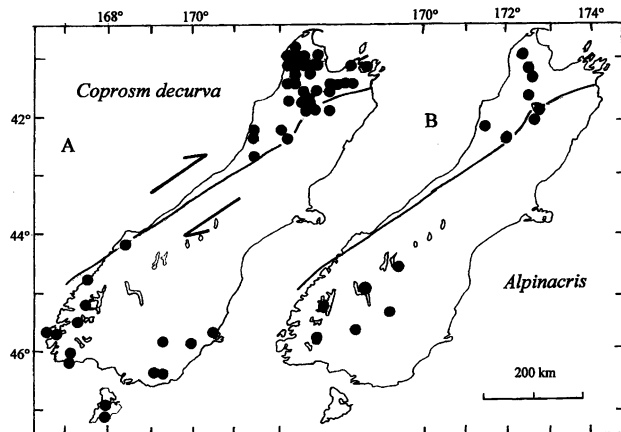

Figure 12. Two examples of disjunction in New Zealand along the Alpine fault. A, the lowland–montane shrub, *Coprosma decurva* (Rubiaceae; Heads, 1998a). B, the alpine grasshopper *Alpinacris* (Acrididae, Bigelow, 1967), with new records from S. J. Morris, Christchurch, pers. comm., 10.vi.2007).

endemic taxa of each peninsula should thus be related to birds of the nearby central range. However, Frith & Beehler's (1998) cladogram of *Paradisaea* instead showed taxa of the two peninsulas to be

sisters. The authors glossed over this interesting anomaly but the same, distinctive pattern was found to occur in two other bird of paradise genera and many other taxa (Heads, 2001, 2002). This major disjunction is best accounted for by lateral displacement of the peninsula terranes around the craton margin on transform faults.

As well as overlooking the distribution of clades, workers sometimes even map groups to fit dispersalist preconceptions rather than to show monophyletic clades. To cite just one example: a study of Caribbean anole lizards included a distribution map in which Saba Island is linked with nearby St Kitts and St Martin, although the cladogram indicates that the only Saba I. species, endemic there, is in fact related to forms of distant west Guadeloupe (Stenson, Thorpe & Malhotra, 2004: fig. 1).

INTERPRETING THE BIOGEOGRAPHY OF
DIFFERENT GENES

Different sections of DNA, like morphological characters, show interesting differences in their geographic structure. For example, the disjunct affinity between *Kanakysaurus* and *Lacertoides* is supported by some homologous sequences and not others. Unfortunately,
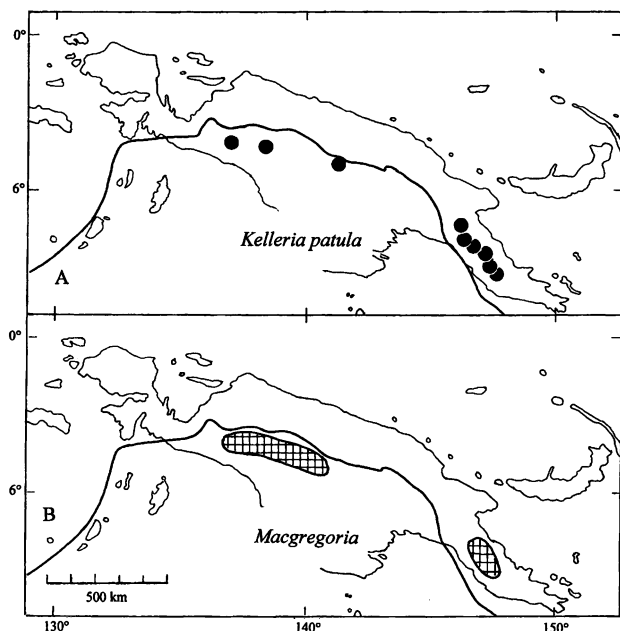
Figure 13. Two examples of disjunction in New Guinea along the craton margin (line). A, the alpine shrub *Kelleria patula* (Thymelaeaceae; Heads, 1990b). B, the subalpine bird *Macgregoria* (Meliphagidae; Heads, 2002).
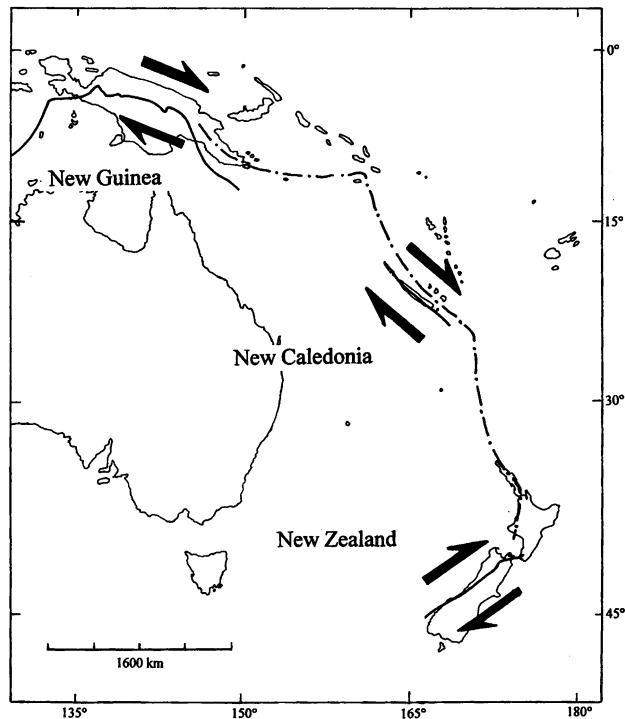

Figure 14. New Zealand, New Caledonia and New Guinea, showing the faults and dextral disjunctions in each. The axis of a late Mesozoic–Palaeogene orogeny is indicated by the broken dotted line.

these different character geographies will always be obscured in combined trees. For example, in the main clade of *Fagonia* (Zygophyllaceae), a genus of desert shrubs, a *trnL* tree indicates an American/South African clade sister to a north African/Eurasian clade, whereas an ITS tree (and the combined *trnL*/ITS tree) have an American clade sister to an Old World clade (Beier *et al.*, 2004). The America–southern African affinity indicated in the *trnL* tree is of considerable interest but was not mentioned in the text.

In other cases, incongruent results that do not fit with biogeographic preconceptions are left out of the analysis. In *Phyllanthus* (Euphorbiaceae), *matK* sequences link New Caledonian members of subgen. *Gomphidium* with another New Caledonian clade of *Phyllanthus* (Kathriarachchi *et al.*, 2006), giving 'geographic coherence'. However, an ITS tree instead placed the New Caledonian *Gomphidium* with the Madagascan *Phyllanthus betsileanus* (92% bootstrap support) and this distribution pattern has many precedents. Kathriarachchi *et al.* (2006) do not appear to have realized this and instead concluded, without any further discussion, that the New Caledonia–New Caledonia tie in *matK* is 'biogeographically more plausible' than the New Caledonian–Madagascar disjunction in ITS. Following this reasoning, they simply removed the ITS data of the Madagascan species from their combined (ITS and *matK*) matrix and even suggested that the ITS information is 'most likely spurious because it does not fit the general patterns of geographical relationships observed'. In the same way, they removed the *matK* information for the African species *Phyllanthus kaessneri* from the combined analysis because it showed a link with Neotropical species. The ITS data instead linked *P. kaessneri* and other African species and were included as this link was deemed 'more consistent with its current geographical distribution'. However, many African taxa are more closely related to American taxa than to other African groups. Determining, on the basis of biogeography, which molecular data should be ignored and which highlighted requires a good understanding of regional biogeographic patterns and molecular workers sometimes overlook this. In another example, Kathriarachchi *et al.* (2006) described the disjunct distribution of *Phyllanthus pinnatus* in South Africa/Kenya and Sri Lanka/India as 'remarkable', although this pattern is also very common.

THE CLOCK MODEL OF EVOLUTION AND MOLECULAR CLOCK THEORY

The fundamental advances that molecular biogeography has made in clarifying major distribution patterns have often been overlooked in the flood
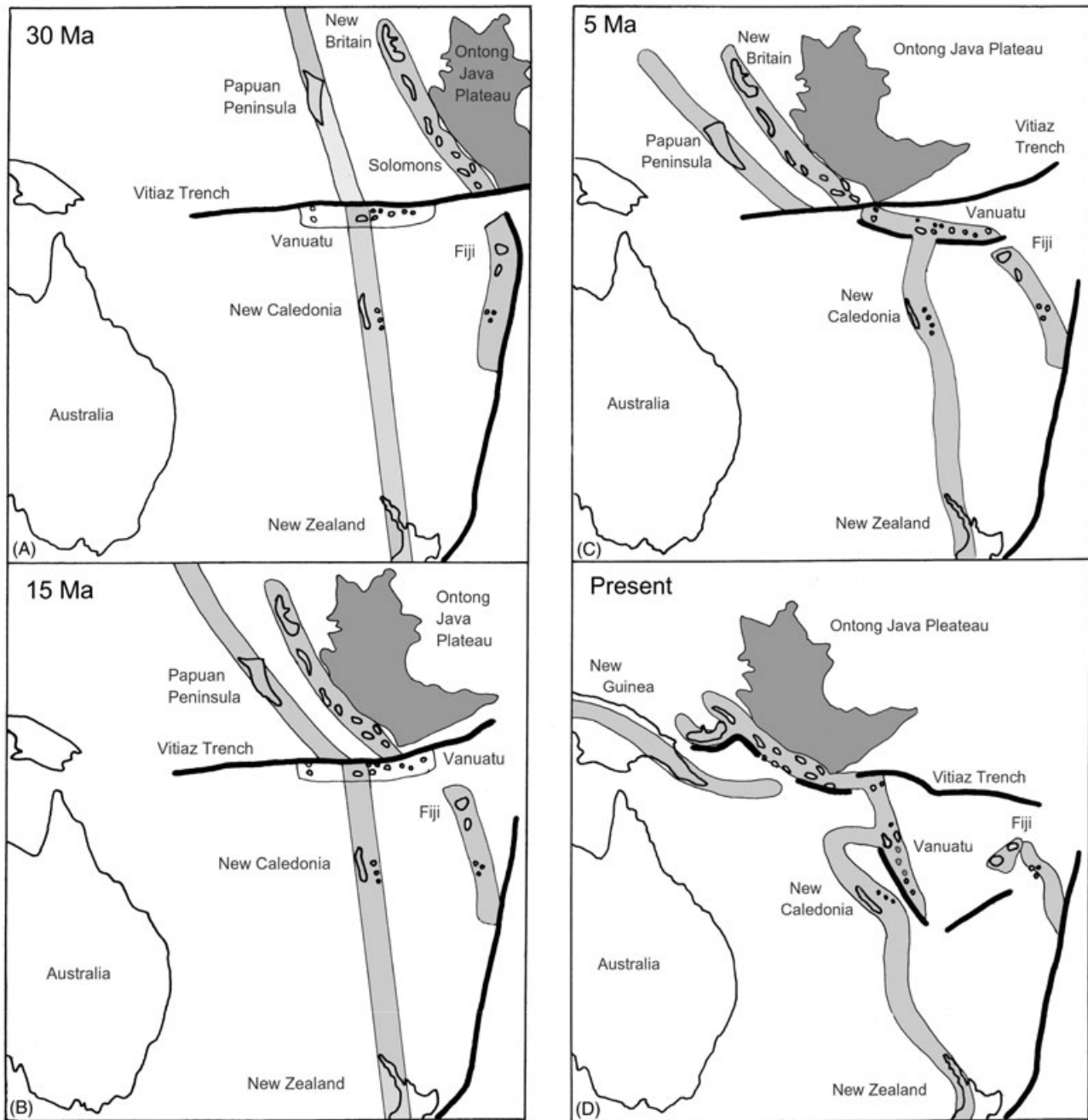
Figure 15. A–D, palaeogeographic reconstruction – tectonic model showing evolution of the Melanesian region from 30 Ma to present (Johnston, 2004). Light grey regions indicate 'lithospheric beams'. Heavy lines are trenches.

of dubious 'clock' studies. The main aim of these is to test for chance dispersal vs. vicariance, but the techniques used are flawed (Heads, 2005). The particular model of evolution assumed is crucial (just how 'relaxed' can the clock be?) and fossil record sampling error can be huge. It is important to note that the new dating method is based primarily on the age of oldest fossils, not on molecular phylogenetics per se. If a new oldest fossil is found pushing back the date of a clade from, say, 10 to 100 Ma, the so-called 'molecular' clock dates will all automatically change too, as fossils are crucial. Conversely, two groups with coeval oldest fossils but showing different degrees of molecular differentiation would be interpreted as having the same age but different rates of evolution; again, fossils trump molecules.

Another point is often overlooked. Molecular work has shown clearly that many morphological features traditionally used to identify clades are of much less systematic significance (or are much more poorly understood) than was thought. Many well-established molecular clades have only obscure or microscopic morphological defining features, if any. However, assignment of fossils to nodes in clades is still based largely on the traditional morphological homologies and so molecular workers at least would admit it is likely that many fossil identifications (and clocks based on them) are misleading. In particular, many Palaeogene clades are probably closer phylogenetically to modern groups than palaeontologists acknowledge. Dramatic morphological stasis since the Cretaceous is often reported in groups with better fossil records (cf. Rydin *et al.*, 2006) and is probably much more widespread than has been thought.

Apart from all the problems with the clock, the extent and precision of allopatry that molecular analysis reveals is itself excellent evidence for allopatry by simple vicariance rather than by chance processes.

'DEGREE OF DIFFERENTIATION' AND ITS SIGNIFICANCE

The same disjunction held by the two New Caledonian lizard genera is common in many plants. However, the plant examples (Figs 3–11) generally involve individual species or species pairs. Most biologists now accept that the taxonomic ranks have no absolute significance. While a hierarchical system of nomenclature is desirable for practical purposes, a 'genus' in one group may well be the equivalent of a 'species' or a 'family' in another in terms of degree of divergence. This does not pose a problem for analytical methods of biogeography that are not based on rank or degree of differentiation. In fact, simple morphological observation suggests that the different West Caledonia fault disjuncts show widely differing degrees of differentiation between the disjunct populations. A clock model would conclude that the repeated disjunction has no single evolutionary cause and the distributions' resemblance to each other is a chance coincidence. But this conclusion is drawn only because the model assumes degree of differentiation is somehow proportional to time.

The disjunction along the New Zealand Alpine fault, like that along the West Caledonian fault, involves disjunct populations and taxa showing many differing degrees of divergence. Molecular clock analyses of several taxa disjunct along the Alpine fault have concluded that the disjunction could be Miocene (in freshwater gastropods; Haase *et al.*, 2007) or as recent as 200 000 years ago (in beetles; Leschen *et al.*,

2008) (cf. Trewick & Wallis, 2001). Clock studies will probably find similar spreads of ages in all major biogeographic patterns, but this is probably an artefact of the model.

THE LOGICAL CONCLUSION OF DISPERSALIST BIOGEOGRAPHY: VICARIANCE DOES NOT OCCUR (EXCEPT IN PANAMA)

As noted, all biogeographic patterns, whether centres of diversity, boundaries or disjunctions, involve taxa that show many different degrees of differentiation. Morphological systematists have known this for over a century and, not surprisingly, it also holds for molecular differentiation. For any important biogeographic pattern, when enough clock studies are available for comparison they inevitably indicate that the taxa involved developed over a wide range of different times. This is true in the Alpine fault disjunctions cited above, in SW/SE Australia (Crisp & Cook, 2007; cf. Morgan, Roberts & Keogh, 2007) and in a sample of fishes with distributions spanning the east Pacific 'barrier' (Lessios & Robertson, 2006). Lessios & Robertson (2006) interpreted the different degrees of molecular differentiation to mean that all the individual trans-Pacific disjunctions were produced at different times and so formed 'a pattern consistent with dispersal [a series of dispersal events] but not with vicariance [a single event]'. This conclusion relies on degree of differentiation being proportional to either the time involved in differentiation or the age of the differentiation, but it probably never is. Short branch lengths are widely assumed to represent recent, rapid evolution rather than ancient, rapid evolution, slow evolution or parallel evolution, but this literal reading of genetic differentiation is just as misleading as the literal reading of appearance times in the fossil record.

Dispersalist analyses assume the clock model of evolution and attribute differing degrees of differentiation in the endemic members of a biota to 'waves of migration' at different times. For example, Mayr & Phelps (1967) argued that the different taxonomic ranks (degrees of differentiation) of the bird taxa endemic to the southern Venezuelan mountains (genera, species, subspecies) indicate that their dispersal to the mountains took place at different times. This assumption, made in all clock analyses, marks the logical conclusion of dispersalist biogeography, because using it, and given that almost all taxa in any pattern show different levels of differentiation, every biogeographic pattern would be interpreted as meaningless coincidence caused by as many separate, unrelated events of chance dispersal as there are taxa involved in the pattern. There would no longer be any

point in producing or studying distribution maps. Earth history would be assumed to be irrelevant for evolution or biogeography and new geological or any other barriers would never be interpreted as causing general allopatric differentiation through a community. All spatial structure in a clade distribution not correlated with ecology would be as a result of chance alone. Every clade would have had its own, independent centre of origin and not be due simply to differentiation of a prior, widespread group. Paradoxically there is a single exception: Lessios & Robertson (2006) found different degrees of divergence between east and west Pacific fishes and hence inferred dispersal events. However, like many authors they calculated their mutation rates on the assumption that all differentiation between E Pacific and Caribbean taxa is as a result of vicariance following the rise of the Panamanian Isthmus at just 3.3 Ma. (This conclusion is itself flawed, as many pairs of E Pacific/Caribbean taxa show different ages when dated using independent calibrations; (Heads, 2005). Thus, the clock method, after basing its analysis on the assumption of allopatric speciation by a geographic barrier (Panama), shows, and will probably always show, that allopatric speciation by barrier formation does not occur.

Fossil-based molecular clock dates vs. radiometric dates

The clock-based dates are taken very seriously by some biologists and have even been used to challenge standard dates in geology. For example, in two large clades of frogs Bocxlaer *et al.* (2006) found typical Gondwanic patterns, such as Africa–India, and regarded evolution in the two groups as involving a general history of vicariance associated with Gondwana breakup rather than founder, over-sea dispersal. This seems unproblematic. However, clock calculations for the frogs indicated Late Cretaceous dates for the main break-up of the group, rather than the Jurassic/Early Cretaceous dates for Gondwana break-up accepted by geologists. Having correctly eliminated chance dispersal, Bocxlaer *et al.* had to decide between the clock dates or geological dates for Gondwana break-up and they suggested that the geological dates were wrong. Nevertheless, these are based on radiometric dating and the decay of one isotope to another is a much simpler process than organic evolution. Analysis of different U-Pb isotope ratios gives dates with very small errors. The so-called 'molecular clock' dates will not be taken seriously by tectonicists when they realize how closely they are based on oldest fossils. This will effectively hinder collaboration just when biology has developed a revolutionary molecular biogeography that should lead to a new phase of synthesis with geology. Criticism of the molecular clock appears regularly (Heads, 2005; Roger & Hug, 2006; Schwartz & Maresca, 2007). Pulquério & Nichols (2007) subtitled their article on the clock 'how wrong could we be?' and concluded that clock dates could contain serious errors. Linder (2005), reviewing explanations for the famously diverse Cape flora of South Africa, also concluded that methods of molecular dating are flawed and there is little understanding of possible error in age estimates. He also found that methods of inferring the ecologies and distributions of ancestral taxa are still 'crude'. These two criticisms involve fundamental aspects of evolutionary study – the analysis of time and space with respect to a given phylogeny – and are serious objections which deserve wider discussion.

CONCLUSIONS

In contrast with the fossil-based molecular clock studies, the beautifully delineated distributions of most molecular clades constitute a large and rapidly growing source of invaluable biogeographic data. Unfortunately, this is still badly neglected as most workers and editors have been seduced by the elaborate calculations of the clock approach. A more realistic synthesis of biogeography, genetics and tectonics can begin instead with close comparison of the geographic distributions of clades with the main aspects of tectonics.

Different groups probably respond differently during phases of evolutionary modernization. The degrees of differentiation between and within taxa are as a result of differing levels of what is termed 'evolutionary potential' (Whitaker, 2006) or genetic 'propensity for diversification' in an ancestor (Lovette, Bermingham & Ricklefs, 2002; Arbogast *et al.*, 2006). The differing extent of evolution seen in different taxa during phases of modernization is because of variation in this prior aspect of genomic architecture, not because of time since divergence. However, by correlating aspects of distribution with tectonics, likely dates of phylogenesis can eventually be arrived at. Wegener (1924) used biogeographic data in framing the idea of continental drift and molecular biogeographic data, if interpreted rationally, should be even more effective in solving general problems in tectonics, including the complex history of the SW Pacific.

Croizat (1984) characterized evolution as 'molecular biology plus panbiogeography'. Biogeographers certainly appreciate the relatively unbiased classifications of the molecular revolution. Many traditional morphological concepts, such as ideas on organ homologies, are inherited from the 18th century and are often misleading. Also, it is easy to deliberately

skew morphological trees by selecting favourite characters and leaving others out. On the one hand, a vast number of molecular clades provide important new evidence for significant biogeographic patterns. On the other hand, molecular biology can benefit from comparative biogeography. The informative distributions of new clades are often overlooked by authors not familiar with the biogeographic patterns and tectonics in a region. However, there is an increasing interest in the biogeographic structure of groups and many recent molecular studies map the clades. Correlation of the clade distributions with others in the region and with tectonics can lead to novel, testable hypotheses, such as the idea of the West Caledonian fault pulling apart populations. The case of the New Caledonian lizards shows that the successful core of the molecular work, the phylogenetic analysis, will contribute more to a long-term, fruitful synthesis of biology and geology if integrated with panbiogeography rather than with the simplistic procedures of the molecular clock.

ACKNOWLEDGEMENTS

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