



Inferring biogeographic history from molecular phylogenies

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The present study illustrates a method for analysing the biogeography of a group that is based on the group's phylogeny but does not invoke founder dispersal or centre of origin. The case studies presented include groups from many different parts of the world, but most are from the south-west Pacific. The idea that basal groups are ancestral is not valid as a generalization. Neither the basal group, nor the oldest fossil represents the centre of origin, the time of origin or the ancestral ecology. Basal groups comprise less diverse sister groups and their distributions occur around centres of differentiation in already widespread ancestors, and not centres of origin for the whole group. Thus, the sequence of nodes in a phylogeny may indicate the spatial sequence of differentiation in a widespread ancestor rather than a series of founder dispersal events. Allocation of clades to a priori geographic areas, such as the continents, in the initial stages of biogeographic analysis has often involved incorrect assumptions of sympatry. This has led to the idea that the 'areas of sympatry' were centres of origin. Areas other than those defined by the taxa themselves need not be used in analysis. The fossil-calibrated molecular clock, with dates transmogrified from minimum to maximum dates, has been used to test for vicariance. Recent work in population genetics, however, indicates that allopatry is caused by vicariance rather than founder dispersal, and so vicariance can instead be used to test the clock. Deriving evolutionary chronology by calibrating spatial vicariance in molecular clades with associated tectonic events is more reasonable than relying on the fossil record to give maximum (absolute) dates. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 98, 757–774.

ADDITIONAL KEYWORDS: dispersal – distribution – endemism – Gondwana – rifting – speciation – tectonics – vicariance.

INTRODUCTION

Almost every week, new molecular phylogenies are published that describe intriguing new clades with fascinating distributions. Among the highlights of the last decade's research are several small, more or less locally endemic clades that have diverse, cosmopolitan sister groups. These small clades include *Amborella* of New Caledonia, basal in angiosperms, and the nearby New Zealand wrens (*Acanthisittidae*), basal in passerine birds. Parrots are the sister group of passerines (Hackett *et al.*, 2008) and the basal parrots are also a New Zealand clade (*Nestor* and *Strigops*). Patterns such as this (Fig. 1) could hardly be clearer, although their meaning, in particular the biogeographic

interpretation of these phylogenies, remains controversial (Heads, 2009). The chronological aspect of evolution is discussed elsewhere (Heads, 2005); the present study focuses on the spatial component of phylogeny and investigates methods used to analyse biogeographic patterns.

MODES OF SPECIATION: DISPERSAL AND VICARIANCE

The interpretation of biogeographic and phylogenetic patterns requires some basic concept of the 'mode of speciation' and cladogenesis in general. This is well-known as a problematic area where there is intense debate about even the simplest cases. Two allopatric clades can be explained as the result of either vicariance of a widespread ancestor (dichopatric speciation)

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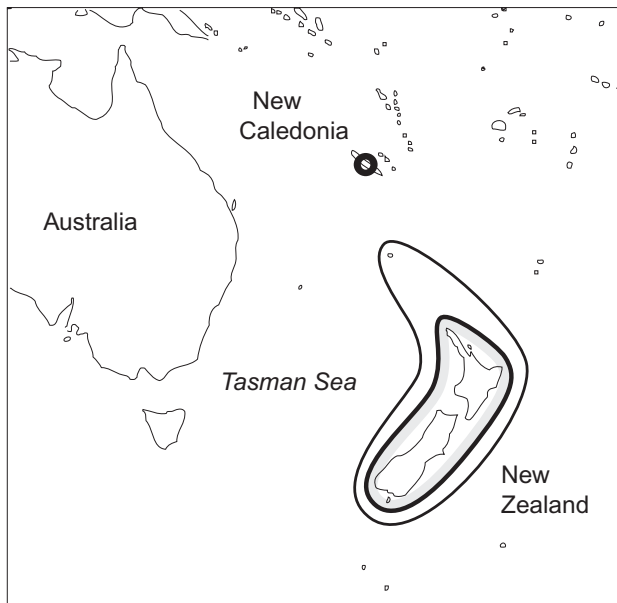


Figure 1. The basal angiosperm *Amborella* (circle), the basal passerine clade Acanthisittidae (New Zealand; grey), and the basal parrot clade *Nestor* and *Strigops* (thin line; New Zealand and Norfolk Island). (Hheads, 2009).

or founder dispersal (= peripatric speciation, = chance dispersal). Overlap of two clades has been explained either by range expansion via normal ecological dispersal (a process which does not involve differentiation), or by sympatric evolution.

Of these four processes, allopatry by vicariance and normal, ecological dispersal observed every day are both accepted as important processes. Sympatric evolution was controversial, but is now accepted in some cases (Schluter, 2001; Bolnick & Fitzpatrick, 2007; Friesen *et al.*, 2007). It may be quite rare and many supposed cases of sympatry between sister groups prove, on closer examination, to involve minor, geographic overlap of clades that are mainly allopatric. Some examples are discussed below. Other apparent cases of sympatry may involve allopatry at a small scale, termed microallopatry (McKinnon *et al.*, 2004). Unlike the three processes that are accepted here (i.e. vicariance, ecological dispersal, and sympatric evolution), the fourth process, founder speciation, is controversial and may not exist.

CRITIQUE OF FOUNDER DISPERSAL IN POPULATION GENETICS STUDIES

In founder dispersal, unlike normal ecological dispersal, once the founder individual has been isolated from its parent population by dispersing over a barrier (an apparent contradiction), it then diverges

into a new species. This is achieved by a second unlikely process, the 'genetic revolution' produced by the founder effect. Modern dispersal theory is based on this genetic revolution, which was introduced as a mode of geographic speciation in island birds (Mayr, 1954) and became very popular, at least in explanations of island taxa. There are hundreds of *Drosophila* fruit-fly species on Hawaii and an evolutionary explanation for this anomaly based on Mayr's theory has been the paradigm for founder speciation/chance dispersal (Templeton, 1980, 1998; Carson & Templeton, 1984).

Although many biogeographers have accepted the argument of these geneticists, geneticists themselves have remained less convinced; Tokeshi (1999) argued that founder dispersal does not appear to be an effective means of speciation and Nei (2002) cited 'one of the most important findings in evolutionary biology in recent years: that speciation by the founder principle may not be very common after all'. Orr (2005) wrote that despite the early popularity of the idea, 'it is difficult to point to unambiguous evidence for founder effect speciation, and the idea has grown controversial'. Experiments conducted by Moya, Galiana & Ayala (1995) failed to corroborate predictions of founder effect speciation and subsequent studies have also found no evidence for this (Rundle *et al.*, 1998; Mooers, Rundle & Whitlock, 1999; McKinnon & Rundle, 2002; Rundle, 2003).

Even in birds, founder effects 'may be unnecessary' (Grant, 2001, cf. Walsh, Jones & Friesen, 2005). For example, the passerine genus *Zosterops* is often cited as the classic case of a taxon that has evolved by founder speciation (Mayr & Diamond, 2001). However, a study of south-western Pacific clades concluded that the focus on founder effects in this group 'has been overemphasized' (Clegg *et al.*, 2002). It may be even less significant than the authors thought. Their suggestion that a 'detailed record' exists for the New Zealand species back to the early 19th Century is incorrect; its ecology and distribution at this time are shrouded in obscurity (Buller [1888] 1967; Mees, 1969).

Florin (2001) described how 'The vicariance model of allopatric speciation has been repeatedly confirmed empirically, while peripatric [founder effect] speciation has suffered severe criticism for being both implausible and empirically unsupported'. In her own studies on flies, she found 'no support for speciation through founder effects'. In recent years, the debate has heated up and advocates of dispersal theory have even found it necessary to publish an article stressing 'The reality and importance of founder speciation in evolution' (Templeton, 2008). This was a reply to the conclusion of Coyne & Orr (2004: 401) that 'there is little evidence for founder effect speciation'.

Templeton's (1998) nested clade analysis incorporated founder effect dispersal (as 'range expansion') and promised to distinguish between this process and fragmentation of populations (i.e. between dispersal and vicariance). This raised considerable interest in the method but, in addition to its use of founder effect speciation, it has been criticized on other grounds by different research groups (Knowles & Maddison, 2002; Beaumont & Panchal, 2008; Petit, 2008).

CRITIQUE OF FOUNDER DISPERSAL IN BIOGEOGRAPHIC STUDIES

Biogeographers have known for a long time that similar distribution patterns are held by different taxa, each with different means of dispersal and ecology. For this reason, and the fact that the shared patterns are often idiosyncratic and precise, many biogeographers have criticized the concept of chance dispersal. The vicariance biogeography produced by 19th Century authors such as T. H. Huxley and J. D. Hooker was later criticized by the dispersalists of the 20th Century as 'land-bridge building'; however, in retrospect, the earlier analyses were more than a century ahead of their time and it was this research tradition, and not that of dispersalism, which Wegener (1915) used in his prescient synthesis.

FOUNDER DISPERSAL AND NEW IDEAS ON RIFT TECTONICS

Apart from the problems with founder effect speciation that genetics and biogeography have raised, new developments in geology indicate that founder dispersal may not be required. Mayr developed founder theory to account for marked differences between bird taxa on mainland and nearby offshore islands, even where ecological differences between the two environments are not apparent (Mayr, 1942, 1992). Mayr's immediate inspiration for the idea came from the bird faunas of northern New Guinea and its offshore islands. However, this region is one of the most mobile parts of the Earth's crust and is now interpreted as a plate margin or series of margins. It is traversed by major transform faults and strike-slip movement on these has transported terranes, fault slivers, and biota over hundreds of kilometers. This has produced a series of dramatic disjunctions and juxtapositions (Heads, 2001, 2002), such as the 'strange' and 'intriguing' distributions reported by Musser, Helgen & Lunde (2008). Another important study of New Guinea birds (Diamond, 1972) involved a transect across the main tectonic boundary in the whole island, the craton margin. However, following Mayr's methodology, Diamond did not refer to struc-

tural geology at all and attributed the many faunistic and phylogenetic differences found along the transect to other factors. Some of the geology was only clarified more recently, after these two biologists were writing. Yet, a later, book-length collaboration explaining evolution and biogeography in the region (Mayr & Diamond, 2001) continued to rely on founder dispersal over current or recent geography, with no mention of pre-Pleistocene geology or plate tectonics.

Founder theory and a later reincarnation, the 'equilibrium' theory of island biogeography, both assume that volcanic islands appear at random with respect to other islands. In fact, volcanism and volcanic islands tend to recur around the same tectonic features (subduction zones, propagating fissures, hotspots, etc.). It is easy to date individual lava flows, but much harder to date the age of an island, parts of which may emerge as others subside or are buried beneath fresh lava flows. Dating the age of individual islands by extrapolating assumed rates of erosion and subsidence is fraught with problems and is not a firm enough basis to establish timing in biogeographic analysis. Taxa survive and evolve more or less *in situ* as metapopulations around subduction zones, propagating fissures and other centres of volcanism, and the age of the structure producing the volcanism is more relevant than the age of individual islands. New ideas on volcanism in the Pacific, for example, emphasize the importance of the large, igneous plateaus emplaced in the Cretaceous. These are mainly submarine but intercalated sedimentary strata include fossil wood, and the plateaus have many large, flat-topped seamounts that were once high islands (Heads, 2009). The simple hotspot model is not sufficient to explain many aspects of intraplate volcanism and, in addition to the traditional mantle-plume hotspots, new tectonic models cite propagating fissures caused by plate tectonics-induced stress fields (Foulger & Jurdy, 2007).

VICARIANCE, FOUNDER DISPERSAL, AND MOLECULAR CLOCK DATING

Some studies have attempted to decide between vicariance and founder dispersal in particular cases by dating the clades concerned. However, molecular clocks have been calibrated using either the fossil record or the age of strata (or islands) that taxa are endemic to, and both these methods will give drastic underestimates (tens of millions of years). Uncritical correlations with geography can also be misleading. The isthmus of Panama rose at ~3.5 Mya, but assuming that all taxa currently separated by the isthmus occurred at this time will, again, give underestimates of clade age (Heads, 2005). None of these calibration

methods are anywhere near reliable enough to base analysis on. However, the geographic distribution of the molecular clades and the geometry of the vicariance seen in them provides a growing body of more or less uncontroversial evidence and a solid foundation for comparative biogeography.

The vicariance versus dispersal debate is an old one; in his 1789 classic work, *The natural history of Selborne*, Gilbert White referred to it with reference to trans-Atlantic affinities and he regarded it as a difficult question (White, 1977: 65). Over two centuries later, the question is still unresolved. In the present study, normal, ecological dispersal is accepted, along with range expansion and contraction. These processes do not involve cladogenesis, which could be caused by vicariance or sympatric evolution. In most of the examples provided here, sympatric evolution is not necessary to explain overlap, although it cannot be ruled out. However, for the reasons just discussed, founder dispersal ('chance', or long-distance dispersal) is not employed.

DISPERSAL–VICARIANCE ANALYSIS

In Ronquist's (1997) method of dispersal–vicariance analysis, inferences of dispersal events are minimized as they attract a 'cost'. Extinction also attracts a cost but vicariance does not. It was not explained why this approach was taken and it appears to be based on a confusion of the two different concepts of 'dispersal'. Ecological dispersal in the sense of ordinary movement should not attract any cost in any model; founder dispersal would attract no cost in a traditional dispersalist model, but, in a vicariance model of speciation or evolution, it is rejected a priori.

'BASAL' GROUPS

Small (less diverse) sister groups are often described as 'basal' to their more diverse sister clades. The term is useful and is employed here, but it should not be interpreted as implying that the 'basal' group is more primitive than its sister or ancestral to it (Krell & Cranston, 2004). An ancestor would be basal in a phylogeny, but a basal group is not necessarily ancestral. Similarly, although the basal clade in a group is often interpreted as occupying the centre of origin for the group, this assumption is not valid, as indicated in the examples discussed below. Fossils, where available, can be incorporated in the analysis along with extant groups and the oldest fossil clade cannot be assumed to phylogenetically basal to the others. Morphological analysis may show that it is, but even then it cannot be assumed to be ancestral to the others; it may simply be an extinct sister group.

CASE STUDIES

Although molecular and morphological phylogenies may differ in individual groups, many of the broader biogeographic patterns indicated by molecular phylogeny were known to the early workers. Avise (2007) concluded that 'traditional non-molecular systematists generally seem to have done an excellent job in identifying and classifying salient historical discontinuities in the biological world'. He emphasized that intraspecific molecular phylogroups are nearly always allopatric and that their geographic distributions 'usually make biogeographic sense', as the spatial arrangements 'orient well' with known patterns. These comments also apply to many clades above species level.

The examples given below were selected from recent studies to illustrate common types of pattern found in molecular clades and the different ways of interpreting them. The same principles can be applied to interpreting morphological phylogenies. Distribution maps of Australian plants were retrieved from: <http://www.anbg.gov.au/avh>. Lists of plant taxa are available at: <http://www.anbg.gov.au/cgi-bin/apnii>. Ranges of Chilean plant genera are given in Moreira Muñoz (2007).

LOCALLY ENDEMIC GROUPS BASAL IN COSMOPOLITAN GROUPS: *AMBORELLA* (ANGIOSPERMS), *ACANTHISITIDAE* (PASSERINES), AND *NESTOR/STRIGOPS* (PARROTS)

The genus *Amborella* is basal in the angiosperms (Müller, Borsch & Hilu, 2006). It is restricted to the south-west Pacific, where it occurs only on the basement terranes of central New Caledonia (Fig. 1) (Heads, 2008). Despite appearances, this does not imply that New Caledonia was the centre of origin from which flowering plants have migrated. Instead, initial vicariance may have been between proto-*Amborella* on the basement terranes, originally dispersed across a broader region of the Pacific until they were juxtaposed and fused in the Jurassic, and the other angiosperms that occurred everywhere else. After the formation of New Caledonia, local overlap has occurred there as many angiosperm families (not all) have invaded the basement terranes, perhaps as Mesozoic weeds. Similar cases are seen in *Acanthisittidae* of New Zealand terranes, sister to all the other passerines, and the New Zealand–Norfolk Island parrots *Strigops* and *Nestor*, sister to all other parrots (Fig. 1) (Heads, 2009).

A REGIONAL ENDEMIC BASAL IN A COSMOPOLITAN GROUP: *NOTHOFAGUS* (BASAL FAGALES)

Southern beech or *Nothofagus*, the only genus in *Nothofagaceae*, dominates many cooler rainforests of

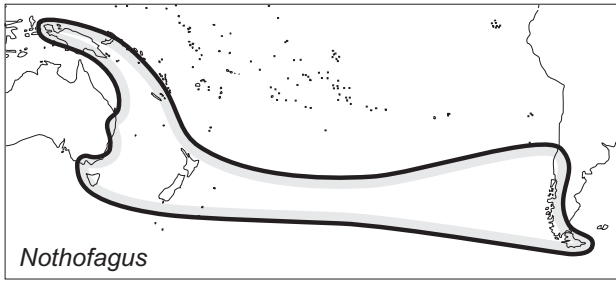


Figure 2. Distribution of *Nothofagus*, basal in the Fagales (cosmopolitan) (Stevens, 2009). (Extralimital macrofossils also occur in Australia and Antarctica).

the South Pacific (Fig. 2). Fossils extend the range to south-western Australia and Antarctica. The four subgenera (all known from Cretaceous fossils) have their respective centres of diversity in Chile south of Valdivia (basal); New Zealand; New Guinea/New Caledonia; and Chile north of Isla de Chiloé (Heads, 2006). The traditional analysis of a group such as this, ranging from New Guinea to Chile, would aim to locate its centre of origin in one part of the region or elsewhere by examining fossils and phylogeny. In fact, it is difficult to infer the origin of a group by looking at the group itself because most groups have come into existence together with at least one other group. To investigate the origin of a group means to examine its sister group and the broader phylogenetic context. In this case, *Nothofagus* is sister to the rest of Fagales (Stevens, 2009), a large group (seven families) found in most parts of the world in which *Nothofagus* does not occur. *Nothofagus* is allopatric with the other families, except for some secondary overlap with Casuarinaceae, a group centred in Australia. For example, *Nothofagus* is completely absent from the Bolivia–Venezuela arc and from the Borneo mountains, two major centres of diversity. There are no obvious ecological explanations for this and because the areas not occupied by *Nothofagus* are held by other Fagales (Fagaceae, Betulaceae, Myricaceae, etc.), the absences are probably phylogenetic. Much debate has focused on the trans-Pacific disjunction in *Nothofagus* but a more fundamental issue is the cause of the primary phylogenetic break in the order, between *Nothofagus* and the rest. Because *Nothofagus* is monophyletic, this break happened before the breaks within *Nothofagus*. There is no evidence for the range of *Nothofagus*, or any point in it, being the centre of origin for the genus or the order. Instead, a primary phylogenetic break has taken place between *Nothofagus* and the other Fagales. The geographic location of this break, which is around the margins of *Nothofagus* (i.e. the margins of the South Pacific basin), indicates the site of primary differentiation that is a

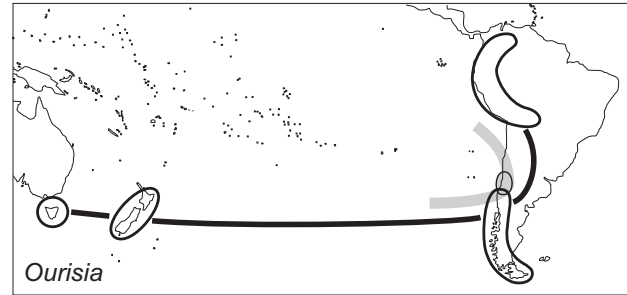


Figure 3. Distribution of *Ourisia* (Orobanchaceae), showing the two clades, subgen. *Suffruticosae* (fine line with grey) and subgen. *Ourisia* (thicker line) (Meudt & Simpson, 2006).

phylogenetic/biogeographic break or junction in a cosmopolitan ancestor, and not a centre of origin.

A LOCAL, BASAL GROUP WITH A WIDESPREAD SISTER GROUP: *OURISIA* (PLANTAGINACEAE)

Ourisia is a plant genus found mainly in the alpine vegetation of lands bordering the South Pacific. There are two main clades (Fig. 3) (Meudt & Simpson, 2006). One clade, subgen. *Suffruticosae*, includes three species of small shrubs found in the Coast Range of central Chile and also adjacent parts of the Andes. The Coast Range (Elórtegui Francioli & Moreira Muñoz, 2002) is lower and less well-known than the Andes, but has special importance for southern hemisphere biogeography. The other clade in *Ourisia*, subgen. *Ourisia*, is much more widespread than its sister group and includes 20 species of herbs in the northern Andes, southern Andes, New Zealand, and Tasmania. The two clades show minor overlap in central Chile. In Meudt & Simpson's (2006) analysis, the smaller (basal) group was taken to occupy the centre of origin. From central Chile, the genus dispersed south to the southern Andes, and from there north to the northern Andes (around or over the basal clade), and also west (against the prevailing winds) to New Zealand and Tasmania. However, although the small clade is 'basal', as indicated above, this only means that it is the smaller of two sister groups and the main differentiation in the genus involves the allopatry of the two clades. Rather than being an ancestor–descendant pair, the two sister groups can be interpreted as the result of simple vicariance. Figure 3 suggests one possibility: that they occupy two parallel arcs with extinction of offshore populations of the small clade. The endemism and diversity of the Coast Range biota is higher than that of the Andes at the same latitude and altitude (Smith-Ramírez, 2004; Smith-Ramírez, Armesto & Valdovinos, 2005). This diversity anomaly, together

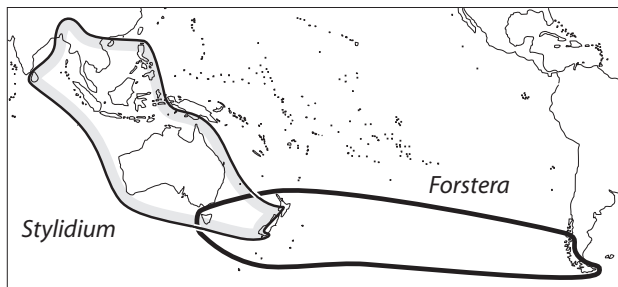


Figure 4. Distribution of Styliidiaceae, showing the two main clades *Styloidium* s.lat and *Forstera* s.lat. (Wagstaff & Wege, 2002).

with indications from geology that the Coast Range terranes are allochthonous (Moores, Wakabayashi & Unruh, 2002), suggests a tectonic origin for biota there.

SISTER GROUPS WITH REGIONAL OVERLAP:
STYLIDIUM AND FORSTERA (STYLIDIACEAE)

The plant family Styliidiaceae (Asterales) is sister to the cosmopolitan Campanulaceae (Bremer *et al.*, 2002) and comprises two genera, *Styloidium* (incl. *Oreostyloidium* and *Levenhookia*) and *Forstera* (incl. *Phyllachne*). These two are mainly allopatric, with *Styloidium* on the Indo-Australian plate and *Forstera* around the southern margins of the Pacific plate. However, the two show overlap around the margins of the Tasman basin (Fig. 4) (Wagstaff & Wege, 2002). Rather than focusing on this area as a centre of origin for the family, with subsequent long distance dispersal to Asia and South America, the pattern can be interpreted as the result of vicariance. There is interdigitation and overlap in Tasmania and New Zealand but, even here, the two clades show little real sympatry. *Styloidium* has a single, distinctive species in New Zealand, which occurs mainly in the west (in the east it extends north only to Mihiwaka; pers. obs.). *Forstera* is present in the west, but is also very common in the New Zealand subantarctic islands and along a strip through central New Zealand (on Torlesse terrane: north Otago, Canterbury, Marlborough, and eastern North Island), and, in both areas, *Styloidium* is absent. Within the potential area of overlap, *Styloidium* occupies several significant localities, mainly coastal, where *Forstera* is absent (Inch Clutha, Awarua Plain, Breaksea Islands off Stewart Island, and Borland Mire). Around the Westport area (Townson, 1906) and on Stewart Island (Wilson, 1987), *Styloidium* is replaced by *Forstera* at higher altitude and the altitudinal ranges do not overlap; in the Westport district, the mutual boundary occurs at approximately 2000 feet (600 m). Conversely, in Tas-

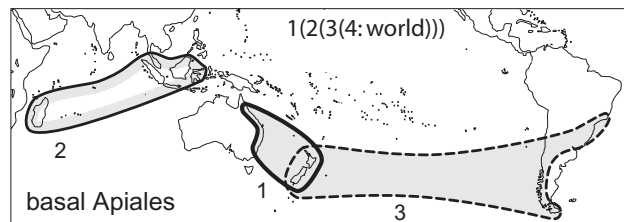


Figure 5. The three basal clades in Apiales: 1, Pennantiaceae; 2, Torricelliaceae (including *Melanophylla* and *Aralidium*); 3, Griseliniaceae. The nested sequence of numbers indicates the phylogeny (Stevens, 2009).

mania, *Styloidium* is widespread but *Forstera* is quite restricted, occurring only in the west. Thus, even at a local scale, microvicariance in ecology and distribution reflect old, intercontinental breaks in phylogeny and biogeography, and the two clades of Styliidiaceae do not show true sympatry. Overall, *Styloidium* is a warmth-loving Indian Ocean group, and *Forstera* is a cold-tolerant Pacific group.

SISTER GROUPS WITH REGIONAL OVERLAP:
BASAL APIALES

Apiales are cosmopolitan plants. They comprise three small clades found mainly in the southern hemisphere (Fig. 5) and one much more diverse clade (not shown on the figure) including Pittosporaceae (Old World trees), Araliaceae (pantropical trees), and Apiaceae (cosmopolitan herbs). The phylogeny given by Stevens (2009) is: Pennantiaceae [Torricelliaceae (Griseliniaceae + Pittosporaceae/Araliaceae/Apiaceae)]. Thus, assuming a worldwide ancestor, the sequence of differentiation is: Pennantiaceae (Tasman Sea region) and the rest, Torricelliaceae (Indian Ocean region) and the rest, and Griseliniaceae (South Pacific region plus south-eastern Brazil) and the rest, or, in short: Tasman basin, Indian Ocean basin, South Pacific basin, world. Apart from the overlap of *Pennantia* and *Griselinia* in New Zealand, the basal clades have remained allopatric after their formation, although there has been complete overlap with the cosmopolitan clade. Given the allopatry among the basal clades, this overlap is probably a result of a phase of range expansion by the cosmopolitan clade and, given the allopatry among many of its own subclades, this took place early in its history.

CLADES WITH SIGNIFICANT OVERLAP IN ONE AREA:
MARSUPIALS

In extant marsupials (Fig. 6), the Didelphidae, with 65 species from central Chile north to Mexico, and one in the eastern USA, form one clade. The other comprises the Caenolestidae (central Chile; northern

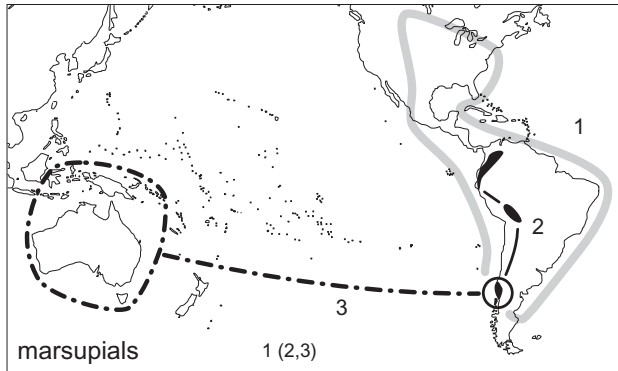


Figure 6. Extant marsupials: 1 (grey), Didelphidae; 2 (black), Caenolestidae; 3 (broken dotted line), Australidelphia. The circle indicates the distribution of *Rhyncholestes* (Caenolestidae) and of *Dromiciops* (Australidelphia). The nested sequence of numbers indicates the phylogeny (Beck, 2008; Beck *et al.*, 2008; Meredith *et al.*, 2008).

Andes) and its sister, all the remaining families (central Chile; Australasia) (Beck, 2008; Beck *et al.*, 2008; Meredith, Westerman & Springer, 2008). The vicariance of the last two clades does not involve a split in the South Pacific itself, but rather at a node in central Chile. Caenolestids are represented there with *Rhyncholestes*: Isla de Chiloé – Concepción, and adjacent Argentina. *Dromiciops*, of the otherwise Australasian clade, is endemic to an almost identical area. Didelphidae also reach their southern limit at a point between Isla de Chiloé and Concepción. The overlap of three clades here, at the southern end of the Coast Range, does not represent a centre of origin, but is significant for the biogeography of the group as an evolutionary fracture zone, at least between caenolestids and the mainly Australasian clade.

Although *Rhyncholestes* and *Dromiciops* have almost identical distributions, one has affinities with the northern Andes, the other with Australasia, and the two genera may well show phylogenetic or ecological differences within their range.

GROUPS WITH OUTLIERS NESTED IN THE PHYLOGENY: ARCTOTIDINAE (ASTERACEAE)

Many groups have several clades in one area, *a*, and may overlap there, but also have a disjunct population in another area, *b*, nested phylogenetically in the first group. The pattern is usually explained as the result of dispersal within the clade from *a* to *b*. However, the ancestor may have already been widespread in both *a* and *b* (Fig. 7A). Allopatric evolution around a node at *a* (Fig. 7B), secondary overlap there, and extinction of populations between *a* and *b* leads to the pattern described (Fig. 7C). The overlapping clades in area *a* often show slight but significant

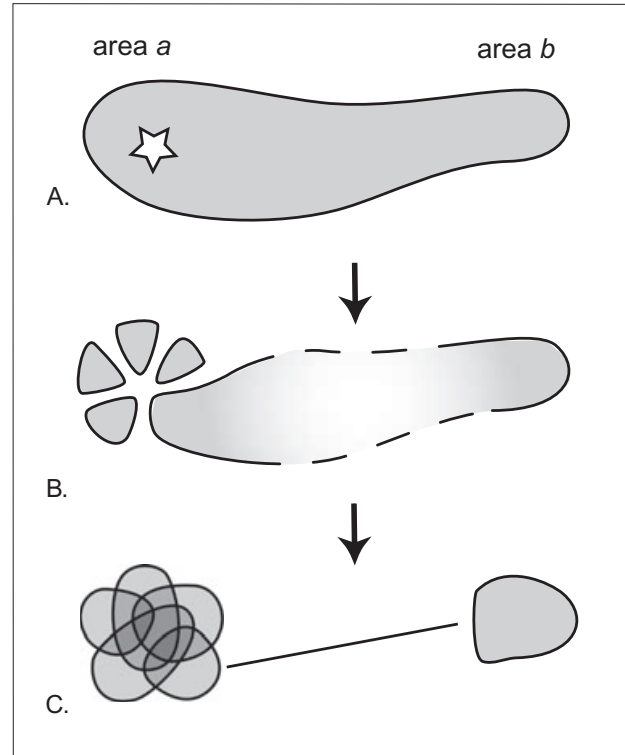


Figure 7. A hypothetical example of distribution. A, a widespread ancestor begins to differentiate around a node associated with, for example, formation of a mountain range or inland sea (star). B, the ancestor has differentiated into five allopatric clades, four with a narrow range and one widespread. Their ranges begin to overlap, whereas some of the populations of the widespread clade suffer extinction (broken line). C, the clades now overlap but the ranges still show traces of their original allopatry. After extinction of intermediate populations, the outlier may appear to be a secondary feature and the result of long distance dispersal.

differences in their distribution (Fig. 7C) and these may represent traces of the earlier phase of allopatry.

One example of this type of pattern, the Arctotidinae (Asteraceae) is made up of a basal grade of three southern African clades, and also *Cymbonotus* of southern Australia which is sister to two other southern African genera (Fig. 8) (Funk, Chan & Holland, 2007). The authors suggested: ‘given that the family is relatively young . . . it seems certain that *Cymbonotus* is the result of a long-distance dispersal event from Africa’. In fact, the age of the family itself (not just its fossil members) is unknown. On the evidence of the phylogeny, southern Africa is not a centre of origin and *Cymbonotus* is not ‘an endemic Australian genus embedded in a southern African clade’ as Funk *et al.* (2007) suggested, instead, it is an Australian genus embedded in a southern African–Australian

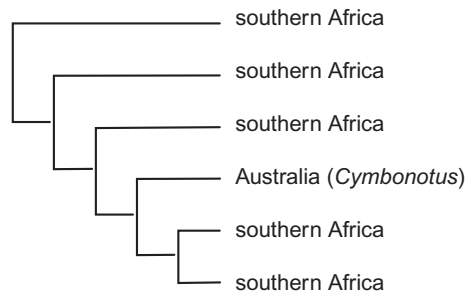


Figure 8. The phylogeny and distribution of clades in the Arctotidinae (Funk *et al.*, 2007). *Cymbonotus* is sister to a southern African clade and embedded in an Australian–southern African clade; it is not embedded in a southern African clade.

clade (Fig. 8). However, there is a point of fracture or node in the vicinity of south-eastern Africa around which the ancestral complex broke up. Among the most important Mesozoic events in this region were the Early Jurassic flexing and intense volcanism on the Lebombo monocline, a volcanic rifted margin, and the mid-Jurassic to Cretaceous breakup of Gondwana. Other disjunct Africa/Australia pairs in the same tribe as *Cymbonotus* (Inuleae) include *Delamerea* of East Africa and *Coleocoma* of north-west Australia, and *Adelostigma* of tropical Africa and *Eyrea* of Australia (Bremer, 1993).

GROUPS WITH BASAL CLADES OVERLAPPING IN ONE REGION AND WIDESPREAD DISTAL CLADES:
ASTERACEAE

Many groups have a pattern similar to that of the last example, with several phylogenetically basal groups clustered in one region. In Figures 7 and 8, the outlier clade has a restricted distribution. Other cases are similar but the distal clades are widespread groups, and not localized outliers. For example, in Asteraceae, the dandelion tribe Cichorieae (= Lactuceae) is a cosmopolitan group that has its basal clades and its sister group (Gundelieae) in the Mediterranean region (Funk *et al.*, 2005). This does not mean the Mediterranean basin was a centre of origin from which the tribe itself spread, only that it was an early centre for differentiation in an already global ancestral Cichorieae.

The Asteraceae as a whole, the largest plant family with approximately 24 000 species, is another example (Fig. 9). The phylogeny (Funk *et al.*, 2005; Panero & Funk, 2008) is: Barnadesioideae (Mutisioideae (Stiftoideae (Wunderlichioideae (Gochnatioideae + seven remaining subfamilies))). The sister group (Calyceraceae) and the five basal branches are small groups mainly found in southern South America. The most distal of the five basal clades, the South American

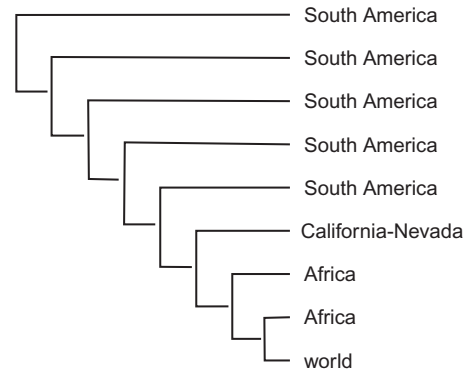


Figure 9. Phylogeny of Asteraceae (Funk *et al.*, 2005; Panero & Funk, 2008).

Gochnatioideae, is sister to the cosmopolitan sister group made up of all the other members of the family. Instead of a centre of origin in South America, the phylogeny may reflect evolution of a worldwide ancestor in which the modern groups differentiated at breaks in or around what is now southern South America. The process is the same as that shown in Figure 7, with South America equivalent to the area on the left. The clade in the bottom right hand corner of Figure 7 (equivalent to all the Asteraceae except the five basal clades) has subsequently expanded its range to include most of the Earth's nonpolar land area. Funk *et al.* (2005) wrote 'it appears incontrovertible' that the family itself had a centre of origin in southern South America, but there is no real evidence for this; there is no reason why the site of the split in the modern group should indicate the distribution of the ancestor and the authors did not consider the possibility of a globally widespread ancestor. After the five basal South American groups have diverged from the others, the monotypic *Hecastocleis* of California and Nevada (mountains in the Mojave Desert) is sister to the rest, within which a large grade of African groups is sister to the remaining, cosmopolitan clade. Funk *et al.* (2005) wrote that the South American differentiation followed by the African phase 'might suggest a Gondwanan origin for the family'. But again, the observed phylogeny could instead have developed from an ancestor that was already cosmopolitan. In this case, it was the early differentiation in the family, and not its centre of origin, that occurred (mainly) in Gondwana. Differentiation occurred first around phylogenetic/biogeographic nodes or breaks in or near South America, then California (composed of Pacific, not Gondwana, terranes), then Africa.

Funk *et al.* (2005) wrote that 'the few data from pollen records and geology seem to indicate a more recent [Cenozoic] origin for the family' and relied on this when deducing a series of intercontinental dis-

persal events. However, these are not necessary if the fossil pollen dates and calibrations are only minimum, not absolute dates, and if any mobilism took place in an ancestor, over an ancestral landscape, and not in the modern clades. As Funk *et al.* (2005) stressed, the general perception of ecology in Asteraceae as simply 'weedy' is incorrect. Some species are cosmopolitan and pantropical weeds, but the vast majority are restricted range endemics and the main clades have conspicuous geographic centres of diversity in different areas (e.g. Liabeae in Peru, Stiffioideae in eastern Brazil, Heliantheae *s.l.* in Mexico–north-west Andes, Calenduleae in South Africa, and Gundelieae around the Mediterranean). The extensive endemism means that, although the family is very large, there are relatively few global clades (several of the larger tribes and subtribes, a few large genera). Thus, through the history of the family as a whole, only a small number of widespread ancestors may have existed (groups such as Senecioeae and Astereae each require their own global ancestor). These few ancestors may have undergone a phase of active mobilism in the Mesozoic in which they occupied much of Earth's land surface, before settling down into a Cenozoic phase of immobilism and speciation. The modern species are often very narrow endemics, but many retain a weedy ecology within their local centres of endemism, occupying disturbed sites such as cliffs and rocky outcrops on steep mountain slopes.

ABROTANELLA (ASTERACEAE)

The distribution of many terrestrial groups around ocean basins (Figs 2, 3, 4, 5, 6) is incongruent with the traditional biogeographic regions, which are based on the main areas of land, the continents. Many patterns also deconstruct smaller geographic regions. One example is *Abrotanella*, a genus of alpine cushion plants in Australasia and Patagonia (Wagstaff, Breitwieser & Swenson, 2006). The three main clades are all present in Australasia and one is shared with South America (Fig. 10). Neither New Guinea, south-east Australia, Tasmania, nor New Zealand appear as monophyletic regions. The basal clade is in eastern Tasmania. The rest of the genus comprises a trans-Tasman group in western Tasmania, south-eastern Australia, New Guinea, and New Zealand, and its trans-Pacific sister in southern New Zealand (Stewart Island only), Juan Fernandez and southern South America. The last two groups show overlap only on Stewart Island. Here, the Tasman Sea clade is represented by *Abrotanella linearis* at lower altitude and *Abrotanella pusilla* on Mount Anglem, whereas the trans-Pacific clade is represented by *Abrotanella muscosa*, a mainly subalpine species. The specimen

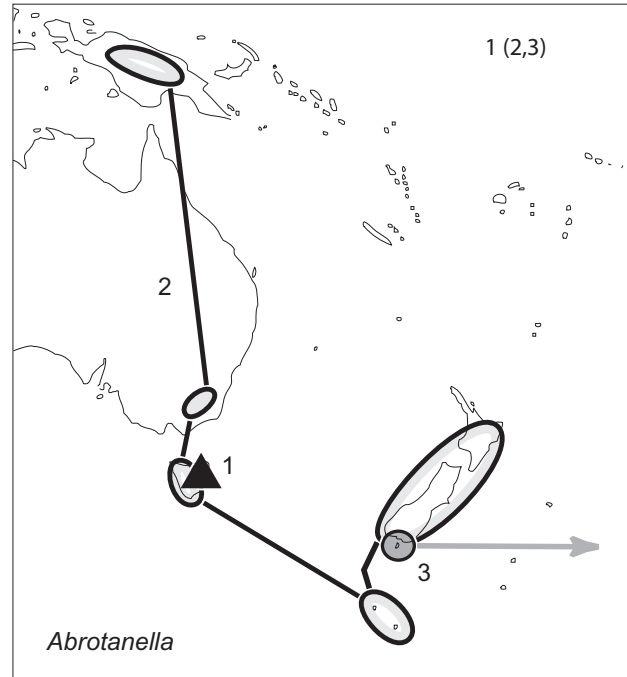


Figure 10. *Abrotanella* (Asteraceae), showing the three clades. The third clade also occurs in southern South America. The nested sequence of numbers indicates the phylogeny (Wagstaff *et al.*, 2006).

localities listed by Swenson (1995) indicate overlap between the two major clades at just one locality, the summit ridge of Mount Anglem, where *A. pusilla* and *A. muscosa* occur together. Overall, there is clear vicariance among the three main clades of *Abrotanella* and also within them. Tasmania 'dissolves' into eastern and western sectors that are not sister areas and are formed from different geological terranes (Heads, 1999). Stewart Island (part of the New Zealand Median Batholith) marks a biogeographic junction of intercontinental significance. The disjunctions across the Tasman and Pacific basins represent secondary fractures. Employing geographic areas such as Tasmania, New Zealand, and Stewart Island as units when in fact they represent phylogenetic composites, as in *Abrotanella*, can play havoc with biogeographic analysis.

PARALAMYCTES CENTIPEDES (HENICOPIDAE)

This genus also involves differentiation around the Tasman basin and again the clade distributions do not correspond with geographic areas. There are three main clades (Fig. 11): the basal group in Tasmania and at the McPherson–Macleay overlap; a clade based around the Indian Ocean and extending east to northern New Zealand; and its sister, a clade based around the South Pacific and extending west

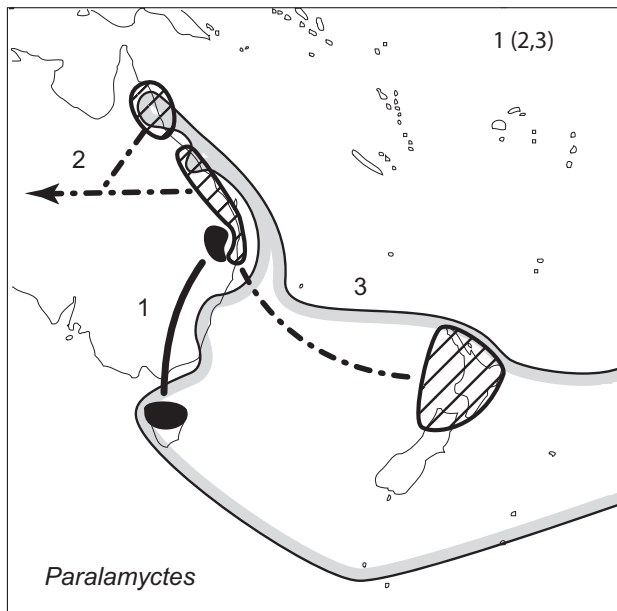


Figure 11. The centipede genus *Paralamyctes*, showing the three main clades and their distribution in the Tasman region. Clade 2 also occurs in southern India, Madagascar, Mozambique, and South Africa. Clade 3 also occurs in central and southern Chile, but note its absence from the McPherson–Macleay overlap where clades 1 and 2 meet. The nested sequence of numbers indicates the phylogeny (Edgecombe, 2001; Giribet & Edgecombe, 2006).

to Queensland, New South Wales, and Tasmania (Edgecombe, 2001; Giribet & Edgecombe, 2006). The two widespread clades show some secondary overlap in northern New Zealand and north-eastern Queensland, but the Indian Ocean clade is notably absent from Tasmania and most of New South Wales, whereas the Pacific Ocean clade is absent from the McPherson–Macleay overlap. The overall division is into eastern, central and western groups. However, the breaks do not correspond with the Tasman Sea, which appears to be a subsequent feature as it fractures the range of two of the groups.

DRACOPHYLLUM (ERICACEAE: STYPHELIOIDEAE)

Dracophyllum (incl. *Richea* and *Sphenotoma*) is another Tasman Sea group (Fig. 12). In these unusual ‘grass trees’ or ‘pineapple shrubs’ the leaf sheath is broader than the linear blade and often narrowed abruptly to it, as in many monocots. The five basal clades form a sequence: Tasmania; Western Australia; Queensland; Lord Howe I.; Tasmania (Wagstaff *et al.*, 2007). In the usual model, this sequence would be interpreted as the result of an epic, circum-Australian ‘tour’ involving four precise dispersal events, each comprising a leap of over 1000 km, starting and finishing in Tasmania. This is very unlikely and the

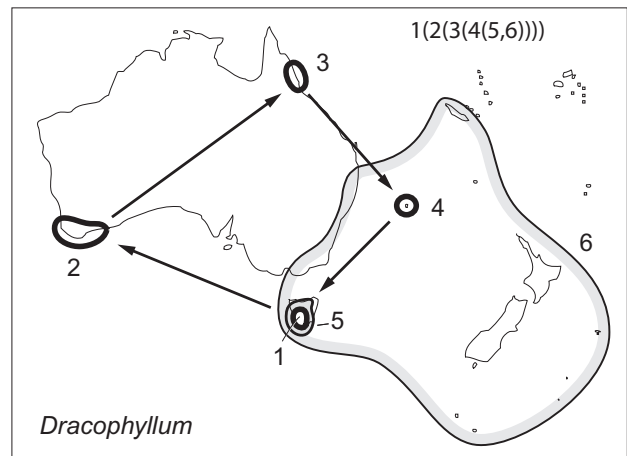


Figure 12. *Dracophyllum* (Ericaceae), showing the six main clades. The nested sequence of numbers indicates the phylogeny (Wagstaff *et al.*, 2007). The arrows indicate the phylogeny and the sequence of differentiation in a widespread ancestor, not a series of dispersal events.

phylogeny can instead be read as a sequence of differentiation in an ancestor already widespread over parts of Australia, New Caledonia, and New Zealand. In this approach, the distribution of a clade’s ancestor is broader, not narrower, than that of the clade itself.

It might be assumed from the distribution that *Dracophyllum* has simply died out in central Australia, perhaps with increasing aridity there. However, most of the remaining styphelioids (formerly Epacridaceae) are diverse in inland Australia and so the absence of *Dracophyllum* there may only be relative and a result of phylogeny, not extinction.

As indicated (Fig. 12), the first three clades to branch off from the rest of *Dracophyllum* are local taxa in the west of the genus range. Differentiation in the group then moves east, between clade 4 and 5 + 6, between 5 and 6, and finally within the diverse clade 6.

Dracophyllum clade 6 has three main subclades (Fig. 13). One occupies the western Tasman region: Tasmania–coastal south-east Australia–New Caledonia, one is in the western parts of central New Zealand, and one is widespread on the southern islands of the New Zealand Plateau, but is most diverse in the eastern South Island. The three groups are, again, largely vicariant, with secondary overlap along the west of New Zealand. In this area, there is ecological vicariance because the western New Zealand clade are forest trees, whereas the widespread New Zealand Plateau group are smaller shrubs, prostrate mats, and cushion-plants of open habitat, especially swamps and alpine vegetation. Within the western New Zealand clade, there is a disjunction along the Alpine fault, as in many other

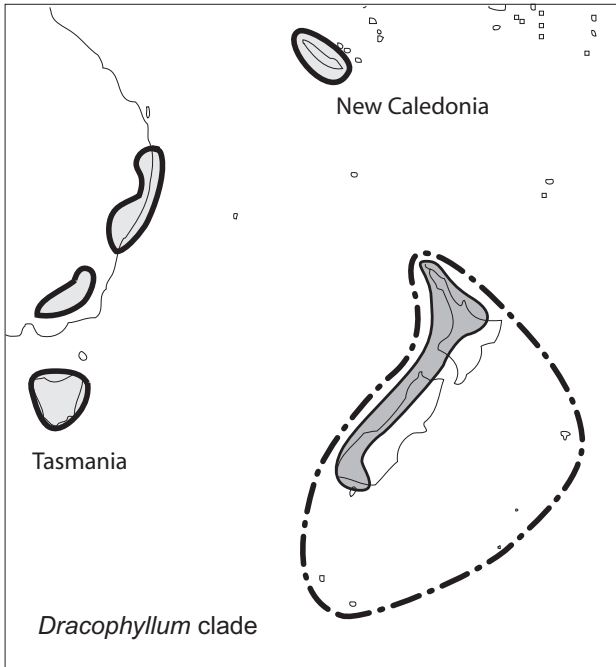


Figure 13. *Dracophyllum* clade 6 of Fig. 14, with three subclades (Wagstaff *et al.*, 2007).

taxa (Heads & Craw, 2004). In *Dracophyllum*, the break occurs between a clade that ranges north to Franz Josef Glacier (*Dracophyllum fiordense*/*Dracophyllum menziesii*) and its sister group which occurs from Mount Davy northwards (*Dracophyllum townsonii*/*Dracophyllum latifolium*). The 140-km gap is occupied by *Dracophyllum traversii*.

There is also vicariance within the New Zealand Plateau group (Fig. 14). This group has not yet been fully analysed, but the three preliminary clades are distributed in allopatric sectors of the plateau. The first clade occurs on mainland New Zealand, the Auckland Islands, and Campbell Island, with most diversity in east-central Otago. The second is on Campbell and Chatham Islands. The third clade shows an interesting biogeographic connection between the Chatham Islands and northern North Island that has also been found in molecular studies of ferns. *Asplenium flabellifolium* is widespread from south-western Australia to North Island, New Zealand (approximately 5000 km), but does not occur on The Poor Knights (20 km off north-eastern North Island) or Chatham Islands, where it is represented by its sister species, *Asplenium pauperequitum* (Fig. 15) (Perrie & Brownsey, 2005; Cameron *et al.*, 2006). The vicariance between the two species may have resulted from the juxtaposition of an Australian plate group (*Asplenium flabellifolium*) and its sister, a Pacific plate group (*Asplenium pauperequitum*). Perrie & Brownsey (2005) suggested *Asplenium pauperequitum*

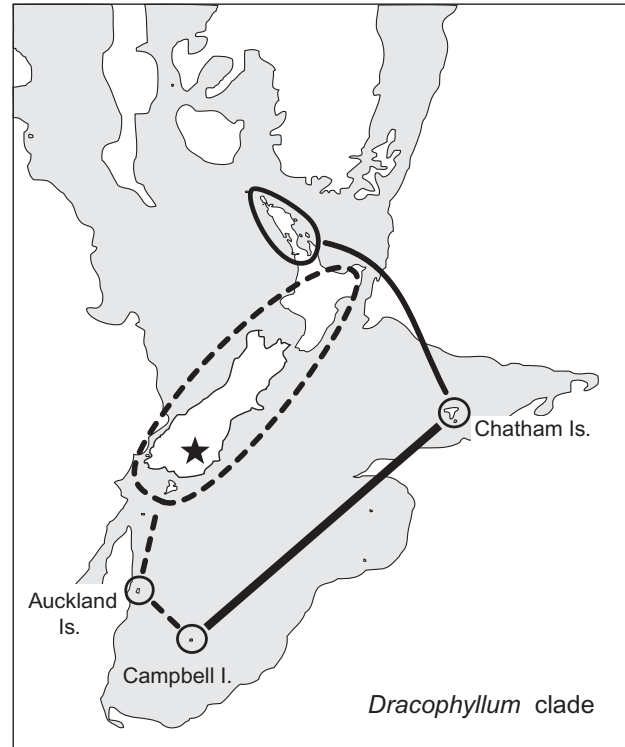


Figure 14. One of the three *Dracophyllum* subclades shown in Fig. 15. Broken line, *Dracophyllum longifolium* and allies; star, approximate region of maximum diversity for this clade. *Dracophyllum scoparium* on Campbell Island is closely related to *Dracophyllum paludosum* of the Chatham Islands (thick line). The thinner line indicates the affinity between *Dracophyllum arboreum* of the Chathams and *Dracophyllum adamsii*, *Dracophyllum sinclairii* and relatives of the northern North Island. Grey area indicates the New Zealand Plateau (3000 m isobath).

may be related to Pacific island species not yet sequenced. Rather than being a result of dispersal from New Zealand or extinction on the mainland (the usual explanations), the northern New Zealand–Chatham Islands groups may be relics of a biota once found widely over the former islands (now seamounts) of the Hikurangi Plateau and other terranes accreted to northern New Zealand (Heads, 2009).

Discussion of vicariance biogeography has often focused on the direct effects of plate tectonic rifting. But, the phylogenetic break in *Dracophyllum* at the Tasman Sea basin is secondary to differentiation between *Dracophyllum* and its relatives, the other Stypelioideae, which are widespread in inland Australia. If this primary differentiation already existed prior to the Late Cretaceous opening of the Tasman basin, it may have involved the Mesozoic seas that bisected the continent in Jurassic–Cretaceous times. These were epicontinental and not caused by rifting. Vast, shallow seas spread over large parts of all the

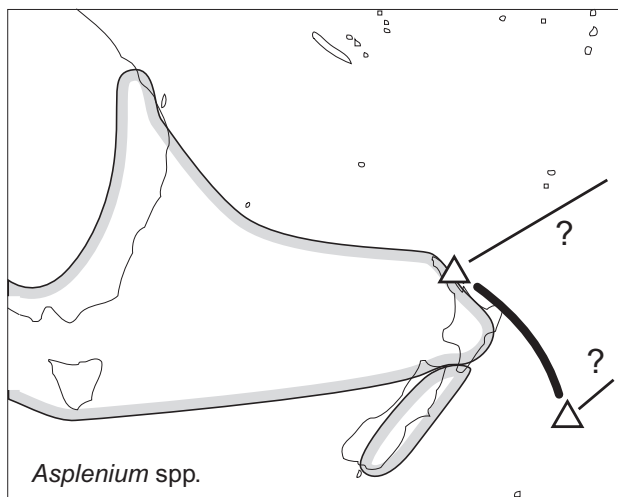


Figure 15. Two sister species in the fern genus *Asplenium*: *Asplenium flabelliforme* (grey line, also in south-western Australia) and *Asplenium pauperequitum* (triangles and black line). Possible vicariance between southern (octoploid) and northern (hexaploid) cytotypes of *A. flabellifolium* is indicated (Brownsey, 1977; Dawson *et al.* 2000). *Asplenium pauperequitum* may be related to Pacific island species not yet sequenced (lines with question marks) or to extinct species of former islands (now seamounts).

continents through the Mesozoic, before and approximately at the same time as the breakup of Gondwana. Examples include the Guaraní Seaway of central South America (northern Argentina to south-eastern Brazil) and the Sundance (Jurassic) and Western Interior (Cretaceous) Seaways of North America (Mexico to Alaska). The seas filled basins well-known for their role in forming and trapping deposits of oil, as in North America, and freshwater, as in the Guaraní aquifer in South America and the Great Artesian Basin of Australia. The latter, with its associated opal fields, marks the site of a Mesozoic inland sea and may be the Earth's largest aquifer. Some 60 000 km³ of fresh water are trapped beneath old seafloor. These long-vanished seas may have been the immediate cause of the primary vicariance in many intercontinental clades (Giribet & Edgecombe, 2006) and the origin of groups such as *Dracophyllum*.

OXYURA DUCKS

The ducks *Oxyura* and *Nomonyx* (Fig. 16) form a widespread clade with a phylogeny: America (America (America (Africa + Asia + Australasia))). McCracken & Sorenson (2005) inferred that the ancestral range of the group 'probably was lowland South America' because the two basal members occur there. But in fact, all three American clades are more or less allopatric, with some overlap in the Greater Antilles,

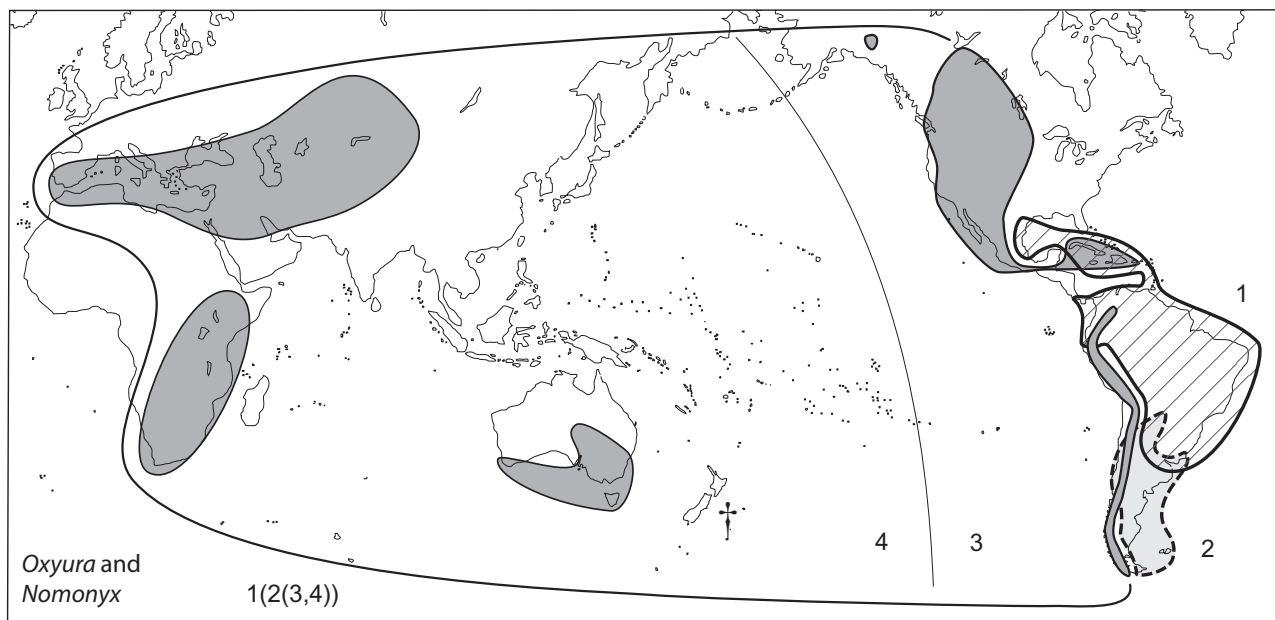


Figure 16. Distribution of the ducks *Oxyura* (two main clades in light grey and dark grey) and *Nomonyx* (diagonal lines). Breeding ranges only shown. *Oxyura jamaicensis* of the western USA is a seasonal migrant to the eastern USA, where there are also rare breeding records, but these are not shown here (see <http://www.massaudobon.org> and <http://www.natureserve.org>). The New Zealand fossil record of *Oxyura* (†) is cited in Worthy (2005). The nested sequence of numbers indicates the phylogeny (McCracken & Sorenson, 2005).

Colombia, and northern Argentina. The three Old World clades are also allopatric and so the simplest scenario, with a worldwide ancestor breaking up into six vicariant clades, is accepted here. Again, allocation of clades to a priori geographic areas, such as the continents, in the initial stages of biogeographic analysis can lead to incorrect assumptions of sympatry and centres of origin in these 'areas'.

Analysing 'America' into its components, the phylogeny for the *Oxyura* group is: {Brazil + Greater Antilles [Argentina (western North America + Greater Antilles + Andes) (Old World)]}. The first division is between Brazil-Greater Antilles (*Nomonyx*) and the rest of the world (*Oxyura*), with breaks around the Greater Antilles, Colombia/Ecuador, and northern Argentina. America does not appear as a monophyletic area, but as a composite of eastern and western sectors, each with endemic taxa that are not sisters. This is compatible with the tectonic division of the Americas into eastern (cratonic) and western (orogenic/accreted terrane) provinces. The second division in the phylogeny involves breaks in western Argentina, perhaps around the basins later incorporated in the uplift of the Andes. The third implies differentiation of the western North America–Antilles–Andes group and its Old World sister. Ducks are known from Cretaceous fossils, which give a minimum age for the group (Clarke *et al.*, 2005). In their account of *Oxyura* and *Nomonyx*, McCracken & Sorenson (2005) assumed a centre of origin in America and interpreted the phylogeny as a complex set of alternative intercontinental dispersal events. Yet, these are only needed if the location of the basal groups is assumed to be a centre of origin.

Oxyura species occur on lakes and in swamps, sometimes in brackish water (del Hoyo, Elliot & Sargatal, 1992; Kear, 2005). *Nomonyx* is also recorded in mangrove. In North America *Oxyura jamaicensis* breeds inland, mainly in the northern prairies and south into the intermontane basins and valleys of the western US, reaching the coast in southern California. In the northern Andes, *Oxyura jamaicensis andina* is at 2500–4000 m. These populations are now alpine, but they may have been derived from ancestral populations that lived in the mangrove swamps and lakes of the pre-Andean Cretaceous basins. With uplift in the Andean orogeny, which began in the Cretaceous, the birds were also lifted up, remaining more or less *in situ* (cf. Ribas *et al.*, 2007). The populations that differentiated in Brazil at some stage as *Nomonyx*, lay too far east to be caught up in the main Andean orogeny and remained in the lowlands.

OLD WORLD RATS AND MICE

This group (subfamily Murinae) occurs throughout the Old World. One of the Philippines clades (*Batomys* and

Phloeomys) is basal to all the rest (Steppan *et al.*, 2005). However, 'Whether the Philippine Old Endemics represent a relictual distribution from the periphery or the core of the ancestral range of the Murinae cannot be determined'. The Philippines archipelago is a geological composite, with some terranes having an Asian origin, whereas others had an original location further east in the central Pacific (Metcalf, 2005). The latter explains the strong biogeographic connection between the Philippines and northern New Guinea and its offshore islands. In Murinae, Steppan *et al.* (2005) described the relationship between another Philippine group and taxa in Australia–New Guinea as 'perhaps [their] most surprising finding'. It is possible that the two clades of Murinae are Indian Ocean (main clade) and West Pacific (basal clade) in origin, with secondary juxtaposition of the basal clade and others following accretion of Pacific terranes to New Guinea and the Philippines.

Steppan *et al.* (2005) suggested that the murines 'appear to have originated in Southeast Asia and then rapidly expanded across all of the Old World'. But this is only because 'three of the four basal branches . . . include taxa almost entirely restricted to South East Asia'. In fact, the four basal clades have quite different distributions, with one in the Philippines as discussed, one in the Philippines and New Guinea/Australia, one in tropical Asia, and its sister, the last main clade, mainly in Africa. Vicariance in a widespread Old World/Pacific ancestor and subsequent juxtaposition and range overlap in the Philippines, a region of tectonic accretion, account for the pattern.

BASAL LAURALES

Trees in the order Laurales are abundant and diverse in most rainforests (Fig. 17, basal clades only). There are three main clades: one in the north (basal), one in the south, and one (not mapped), which is widespread in warmer areas. The basal clade is a mainly northern hemisphere group, Calycanthaceae, but has its own basal clade, *Idiospermum*, in Australia (Stevens, 2009). Calycanthaceae are sister to the rest of the order, and there is secondary overlap between the two in parts of the northern hemisphere and in northeastern Queensland. The second split in Laurales is between three southern families, Siparunaceae, Gomortegaceae, and Atherospermataceae (Fig. 17) and the rest of the order (the pantropical Lauraceae, Monimiaceae, etc.; not shown). This implies later secondary overlap in the southern hemisphere between the three southern families and the pantropical group. Within the southern group, the first split is between Siparunaceae of tropical America and West Africa, and Gomortegaceae of central Chile (Coast Range) plus Atherospermataceae of southern Chile and Australasia (Renner, Foreman & Murray,

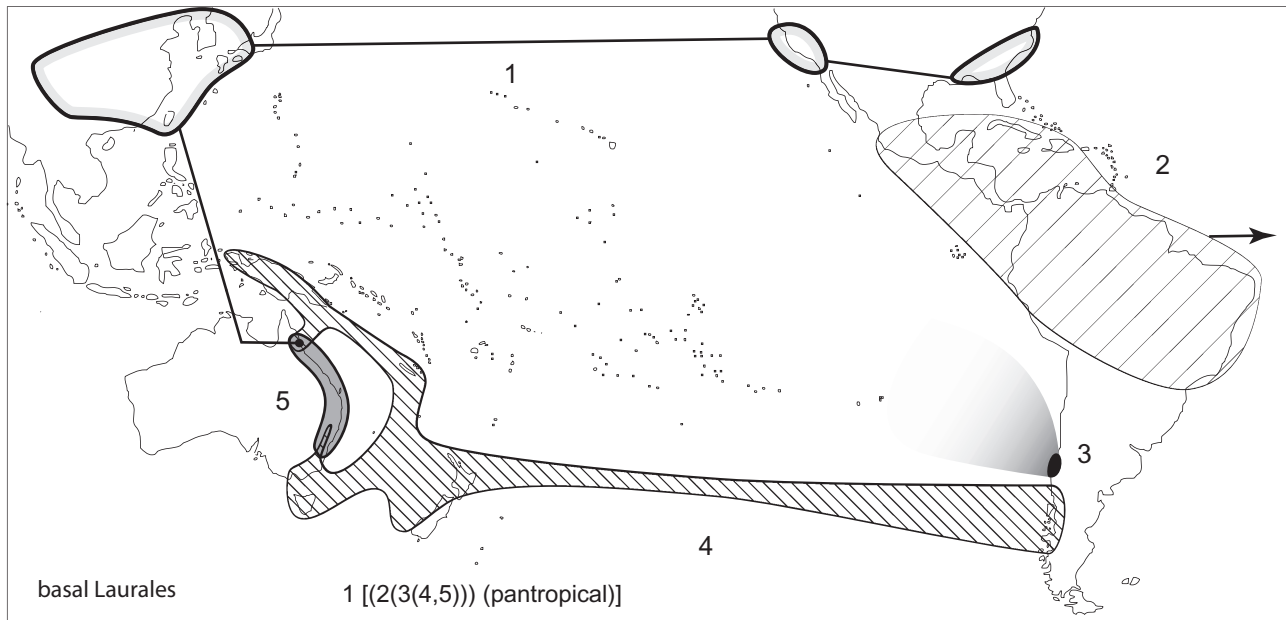


Figure 17. The two basal clades of Laurales (phylogeny *sensu* Renner *et al.*, 2000), distributions *sensu* Stevens (2009). 1, Calycanthaceae with an outlier in north-east Queensland (*Idiospermum*); 2, Siparunaceae, also in Cameroon; 3, Gomortegaceae; 4, the main clade of Atherospermataceae ranging north to the Barrington Tops (not north of the Macleay River); 5, the basal clade of Atherospermataceae (*Doryphora* and *Daphnandra*; both at the McPherson–Macleay overlap). The nested sequence of numbers indicates the phylogeny.

2000). Within Atherospermataceae, the main break is between a widespread group found from Chile to Tasmania and New Guinea, mainly in swamp forest, and a second, mainly vicariant clade in eastern Australia, for *Doryphora* and *Daphnandra*. Both these genera occur along the central part of the eastern seaboard of Australia. This region includes the important centre of endemism between the McPherson Range and the Macleay River, the McPherson–Macleay overlap (equivalent in part to the Gympie–Beenleigh terrane).

Within the southern group of families, the sequence of differentiation proceeds westward: from a node between Peru/Bolivia (Siparunaceae) and central Chile (Gomortegaceae/Atherospermataceae), to a node between central Chile (Gomortegaceae) and southern Chile (Atherospermataceae), to a node somewhere between the McPherson–Macleay overlap and the rest of the Tasman/Coral Sea region.

DISCUSSION

FOSSIL-CALIBRATED MOLECULAR CLOCK SUPPORT FOR DISPERSAL IS SPURIOUS

The examples shown above were selected to illustrate analytical principles, and not particular patterns. Nevertheless, the examples highlight certain phylogenetic and biogeographic nodes, such as the

McPherson–Macleay overlap in eastern Australia, central Chile, and South Africa/Madagascar. Although the Earth's biosphere is much thinner than the crust or mantle, it has a much more complex geographic structure and one of the clearest examples of this is the clumping of basal nodes in certain geographic regions. This and other patterns cannot be accounted for by chance. Although chance dispersal has been favoured in many studies using molecular clocks, earlier studies questioned the efficacy of means of dispersal and this problem has not been resolved; molecular clock workers often admit that the evident means of dispersal in the studied organism do not appear sufficient to explain the geographic pattern, but support chance dispersal anyway. Sometimes studies suggest that additional work is required to elucidate the means of dispersal, although the dispersal events suggested are very rare, one-off events that are not correlated with any others and it is hard to imagine how they could ever be studied empirically, whether by examining means of dispersal or anything else. Most studies inferring founder dispersal are discreet enough to avoid discussing the mechanics of the process at length. In this context, it is worth looking at *Abrotanella* again (Fig. 10) because it illustrates some important aspects clearly. Wagstaff *et al.* (2006) concluded that distributions in the genus 'undoubtedly' reflect a 'convoluted history of

dispersal'. This conclusion agrees with much recent work, although these analyses are based solely on a fossil-based chronology and are incompatible with the precise geographic allopatry of clades at intercontinental, regional, and local scales. The spatial evolution of *Abrotanella* could hardly be less convoluted than it is because it involves three almost entirely vicariant groups and vicariant species within them. The authors concluded that long distance dispersal across the South Pacific (10 000 km) must have occurred, although they did not even speculate as to how this could have actually happened. *Abrotanella* fruit do not have the pappus ('thistle-down') present in most Asteraceae.

Abrotanella is probably an old group. In the sample of Wagstaff *et al.* (2006), it is sister to a clade including the cosmopolitan *Senecio* (1500 species) and other genera, including *Blennosperma*. This last genus is disjunct in the east Pacific, where it is known only from California and central Chile: Valparaíso south to Concepción, and shows exact vicariance with *Abrotanella* further south: Australasia and southern Chile: Juan Fernandez Islands and Isla de Chiloé south to Fuegia (Heads, 1999). The vicariance occurs between Chiloé and Concepción (cf. marsupials, etc.). Funk *et al.* (2005) did not sample *Abrotanella* but found *Blennosperma* to be basal to the entire Senecioneae tribe, the largest in Asteraceae. The topology may be: (*Abrotanella* – South Pacific) (*Blennosperma* – east Pacific; Senecioneae – world).

Wagstaff *et al.* (2006) wrote that *Abrotanella* 'initially diverged during the Miocene', but this age was calculated using fossil-based clock dating and, as these authors noted, fossil dates (and any dates derived from these) give minimum ages. Thus, the genus diverged at some stage before the Miocene. Wagstaff *et al.* (2006) suggested that the disjunct distribution 'must reflect long-distance dispersal' and that the genus has a 'convoluted history of dispersal and extinction . . .', but only because the minimum *Abrotanella* date was transmogrified into a maximum age. This meant that Mesozoic vicariance was ruled out. Finally, Wagstaff *et al.* (2006) wrote that rates of molecular evolution calculated for the Juan Fernandez endemic genera *Dendroseris* and *Robinsonia* (Asteraceae) were 'only slightly slower' than the rates calculated for *Abrotanella* and that this corroboration was significant. However, the ages suggested for the Juan Fernandez genera are also likely to be underestimates because the genera were assumed to have differentiated from their respective ancestors only after the formation of the current islands.

In a similar case and in the same family, Asteraceae, McKenzie & Barker (2008) studied the Arctotideae of southern Africa and Australia that were discussed above (Figs 7, 8). They provided divergence

dates but emphasized that these must be 'interpreted with caution'. The 'poor fossil record' for the group means that obtaining 'reliable' calibration points is a 'widespread problem'. It is suggested here that fossils should not be used for clock calibration. Time calibration of phylogenies is best performed by taking advantage of the many obvious correlations between dated tectonic events and distributions of molecular clades.

McKenzie & Barker (2008) estimated that the Asteraceae were likely to have originated '*within the last 60 Mya based on the oldest fossil pollen evidence . . .*' [italics added], but oldest fossils only give a minimum age, not a maximum age. Again, minimum ages (fossil-based dates) for clades have been transmogrified into absolute ages. This illogical step leads to the conclusion that the clade is very young and that dispersal from southern Africa to Australia has taken place in the Pliocene. As admitted by McKenzie & Barker (2008), the fruits in Arctotideae lack the family's usual adaptations for long-distance dispersal (as in *Abrotanella*) and 'the mode of dispersal is difficult to envisage'. Nevertheless, they cited 'increasing evidence' for the importance of long-distance dispersal and their own 'evidence' will add to this, whereas their earlier discussion about using 'caution' in interpreting the 'poor fossil record' will be ignored. It is suggested here that the calculated clock dates do not constitute evidence, just logical extrapolations from faulty premises: the transmogrified fossil dates.

CONCLUSIONS

Molecular data provide a fabulous new source of information on biogeographic differentiation and evolution. However, satisfactory interpretation of the patterns has lagged behind their description. Methods of analysis often rely on the out-dated concepts of the 'modern synthesis', namely the centre of origin and chance dispersal. The sequence of branching in a phylogenetic tree can be read either as a sequence of dispersal, with taxa invading a new region, differentiating and then invading another region, or as a sequence of differentiation in an already widespread ancestor. The second process appears more likely and has been accepted for lizards in the Andes (Doan, 2003) and *Rhododendron* (Ericaceae) in Malesia (Brown, Nelson & Ladiges, 2006). Each split is assumed to be a vicariance event and the sequence of splits (each a phylogenetic and geographic node) forms a simple geographic sequence. Phylogenies indicate a sequence of divisions (nodes), and not a sequence of ancestors and descendants. Dispersalists have assumed the latter but this has only led to a long-lasting, unresolved debate as to whether 'advanced taxa' (Darwin, etc.) or 'primitive taxa' (Mayr, etc.) occur at the centre of

origin. In the model of evolution proposed here, there is no true radiation as there is no centre of origin. If the ancestor is already widespread before the differentiation of the descendant groups, the issue is no longer about how any of the modern groups reached a certain area, but instead where the breaks occurred that led to its differentiation. Once the spatial context is clarified, the question of timing should become more straightforward.

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