South Pacific biogeography, tectonic calibration, and pre-drift tectonics: cladogenesis in Abrotanella (Asteraceae)

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Abrotanella is the basal genus in the large tribe Senecioneae (Asteraceae) and has a disjunct distribution in Australasia and South America. A recent molecular phylogeny of the genus was used to investigate whether the main biogeographical patterns in the group could be related to the region’s tectonic history in a coherent way. The phylogenetic/biogeographical breaks and overlaps in the genus imply a series of vicariance and range expansion events. Each of these can be related to one of the main tectonic events in the region, including assembly of the New Zealand terranes, crustal extension, and magmatism in Gondwana that preceded seafloor spreading, opening of the Tasman and Pacific basins, and transcurrent movement on the New Zealand Alpine fault. The coincident sequence indicates that pre-drift tectonics and magmatism have been more important for the origin of trans-Tasman and trans-Pacific groups than the final rifting of Gondwana that led to their disjunction. For example, during the pre-drift phase of break-up, the Whitsunday volcanic province of Australia and the Median Batholith of New Zealand formed a large, active igneous belt. Its distribution is aligned with the break between New Zealand–south-eastern Australia clades, and New Zealand–New Guinea clades. © 2012 The Linnean Society of London, Biological Journal of the Linnean Society, 2012, 107, 938–952.


INTRODUCTION

Many biological groups are endemic to Australasia and southern South America, and have an approximately 9000 km disjunction across the South Pacific. One well-known example is the tree Nothofagus (Nothofagaceae: Fagales), and others include Abrotanella (Asteraceae), a genus of alpine subshrubs. The most obvious question is: what is the reason for the disjunction? In Abrotanella, it has been attributed to the Cretaceous breakup of Gondwana (Heads, 2011), although other studies have suggested this is impossible because it would imply that the Asteraceae are 1.5 billion years old (Swenson, Nylinder & Wagstaff, 2012). The present study examines the case of Abrotanella in more detail. A recent molecular phylogeny of the group is used to test whether the sequence of phylogenetic breaks in the genus corresponds with the sequence of main tectonic and magmatic events in the region.

CURRENT METHODS IN BIOGEOGRAPHY

Many current studies in biogeography rely on Bayesian dating analyses and on spatial analyses that use approaches such as DIVA (dispersal vicariance analysis; Ronquist, 1997) and DEC (dispersal–extinction–cladogenesis; Ree & Smith, 2008). If certain priors are selected, Bayesian dating analyses will support young clade ages, as outlined below, and this will support dispersal theory. Similarly, if a clade occurs in two areas, A and B, and has an area phylogeny: (A (A (A (A, B))))), methods such as DIVA and DEC will always find a centre of origin in area A and dispersal from A to B (Heads, 2009). A vicariance model, with an ancestor in A+B, followed by differentiation, and subsequent local overlap, in A, will always be ruled out.

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Implicit conversion of fossil-calibrated, minimum clade ages into maximum clade ages

Wagstaff, Breitwieser & Swenson (2006) accepted that ‘The first appearance [of a clade] in the fossil record imposes only minimum age constraints’ (p. 100). Nevertheless, they treated their fossil-calibrated dates for *Abrotanella* as maximum ages, concluding that the genus ‘initially diverged during [not before] the Miocene’ and that species radiations ‘occurred 3 million years ago’ (not ‘before 3 million years ago’) (p. 95). In this way, they were able to rule out earlier vicariance and conclude that the disjunct distributions ‘must reflect long-distance dispersal’ (p. 104), and that ‘radiations’ in the genus ‘undoubtedly reflect long-distance dispersal . . .’ (p. 95; emphasis added).

Conversion of fossil ages into maximum clade ages in a Bayesian framework

Many studies now depict fossil-calibrated phylogenies annotated with both minimum and maximum estimates of clade ages, given in the form of 95% credibility intervals. Fossil-calibrated ages have been converted from minimum into maximum estimates, with statistical support. In these studies, the transmogrification is carried out in a Bayesian framework, using software such as BEAST (Drummond & Rambaut, 2007). Prior probability distributions (priors) for the probability/age curves of clades are assigned to the calibrations before any analysis is carried out.

Drummond & Rambaut (2007) wrote that the priors ‘may represent other sources of knowledge such as expert interpretation of the fossil record’ (p. 4). Yet they can also introduce error, by incorporating the traditional, literalist interpretation of the fossil record. In this approach, the oldest fossil age can be used to provide the most likely clade age, and a study can stipulate that clade age can be no more than, say, 10 Mya older than the oldest known fossil. By selecting appropriate priors, young clade ages with narrow credibility intervals can be calculated. In their study of *Abrotanella*, Swenson et al. (2012) transmogrified fossil-calibrated dates (minimum ages) into maximum clade ages by using BEAST and specifying appropriate priors. The question for Bayesian analysis is: how are the priors selected?

Several studies have already noted the problem of the priors (Lee & Skinner, 2011; Wilkinson et al., 2011; Warnock, Yang & Donoghue, 2012). Parham et al. (2012) observed: ‘Most studies use a Bayesian framework for estimating divergence dates . . . but there is presently no practical way to estimate curve parameters [for priors] . . .’ (p. 352). They concluded: ‘the fact that a widely applied methodology is subjected to such ambiguous assumptions that have a major impact on results . . . is a major limitation of molecular divergence dating studies’.

Bayesian analyses that stipulate appropriate priors will provide ‘evidence’ for young clade ages, one of the corner-stones of modern synthesis biogeography. These clade ages can then be used to rule out earlier vicariance and support a centre of origin/dispersal model. As in traditional transmogrification, the age of the oldest fossil in a clade is converted from a minimum clade age into an estimate of maximum clade age before any analysis, and the credibility intervals provide an illusion of statistical support.

Using island age calibrations to corroborate Bayesian transmogrification

Wagstaff et al. (2006) and Swenson et al. (2012) compared their fossil-calibrated evolutionary rates in *Abrotanella* with rates estimated for the genera *Dendroseris* and *Robinsonia* (Asteraceae), which are both endemic to the Juan Fernández Islands. They found that the rates calculated for these genera corresponded quite closely to the rates calculated for *Abrotanella*. Nevertheless, the rates calculated for the Juan Fernández genera are probably overestimates because the genera were assumed to have differentiated from their respective ancestors only after the formation of the islands. This assumption may not be correct because other taxa endemic to Juan Fernández, such as the plant *Lactoris* (Aristolochiaceae), have fossils dated as Cretaceous (Gamerro & Barreda, 2008). Thus, the fossil-calibrated dates and the island-age calibrated dates for *Abrotanella* could both be underestimates of actual age and the corroboration between them is not convincing.

Tectonic calibration

Calibrating the age of clades with spatially-related tectonic events avoids the many problems in interpreting clade age using fossils and the method is being adopted in studies of groups that have a limited fossil record (Genner et al., 2007; Azuma et al., 2008; Cracraft & Barker, 2009; Irestedt et al., 2009; Allwood et al., 2010; Moyle et al., 2012; Bewick et al., 2012; Jønsson et al., 2012). The method has been developed in the light of new findings in sequencing studies, where one of the most striking general results is the deep geographical structure of the molecular variation seen in most groups. The dovetailing geographical structure of life is revealed in the molecular work even more clearly than in morphological studies. Typical examples include a group of Opiliones in which ‘geography is better than taxonomy in predicting phylogeny’ (Hedin et al., 2012) and the plant
genus *Mimosa*, in which ‘Clade W is taxonomically disparate and is better defined by its geographical distribution restricted to the Andes than any obvious morphological or classificatory coherence’ (Simon et al., 2011: 1221). The new gecko family Phyllodactylidae, sister of Gekkonidae, was never suspected in traditional morphological studies and the sole synapomorphy is a 3-bp deletion in one nuclear gene (Gamble et al., 2008). Yet it also has a standard, trans-Atlantic distribution pattern (in America, the Antilles, Macaronesia, and through the Mediterranean and West Africa to the Arabian Peninsula; Amphibinae have a similar range, see Heads, 2011). In a chance dispersal paradigm, there is no reason to expect such simple, clear-cut geographical structure, although the pattern is consistent with vicariance theory and makes novel predictions (e.g. that similar patterns will recur in different groups).

Most studies using tectonic calibration have calibrated a phylogeny with single tectonic events (such as the rise of the Panama isthmus), although this can lead to problems (Heads, 2005) and, in the approach suggested here, a phylogeny is calibrated with multiple tectonic events.

If tectonic calibrations are used, the phylogeny topology provides relative dates for the different nodes, whereas geology provides the sequence and absolute dates (with errors) for tectonic events. As discussed above, the problems associated with converting fossil age into maximum clade age are complex and perhaps insurmountable. Estimates of potential error are especially problematic. By contrast, tectonic and magmatic events have been assigned absolute dates using radiometric techniques and the error in these dates is much smaller (approximately 1% in many studies) than in the molecular clock dates.

An earlier biogeographical analysis of *Abrotanella* (Heads, 1999) was based on a morphological phylogeny (Swenson, 1995) and showed that the clad distributions revealed a simple structure with dovetailing allopatry. The molecular phylogeny (Swenson et al., 2012) provides even clearer and simpler patterns of allopatry.

**TECTONICS, BIOGEOGRAPHY, AND ABROTANELLA**

To decide whether a fossil-calibrated model or a tectonics-calibrated model works best in practice, both need to be tried out. Swenson et al. (2012) tested the fossil-based model and explained the distribution in the genus as the result of chance dispersal. They rejected a tectonic model of evolution in theory (relying on a clock model of evolution), although they only examined one tectonic break (seafloor spreading at 84 Mya, causing the trans-Pacific disjunction) and did not attempt to produce a general tectonic model for the genus. A more detailed test of tectonic/biogeographical calibration would be desirable. Is a coherent integration of evolution in *Abrotanella* with regional tectonics even possible? Such a model would not require the use of chance dispersal to explain repeated patterns, nor the dubious transformation of fossil-calibrated clad ages from minimum dates into maximum dates.

Swenson et al. (2012) contributed a molecular phylogeny of the genus *Abrotanella* but did not examine the distributions of the clades in any detail and did not map them. Tectonic/biogeographical calibration requires analysis of the distributions and so these are mapped in the present study; the species distributions (Swenson, 1995; Heads, 1999) are arranged into groups according to the phylogeny. The clades are mapped rather than being assigned to a priori, physiographical areas (‘New Zealand’, ‘Tasmania’, etc.) because these are polyphyletic and would confuse the analysis (Heads, 1999). Instead, the emphasis is on the geography of the clades and, in particular, the phylogenetic breaks.

**DIFFERENTIATION BETWEEN ABROTANELLA AND ITS SISTER GROUP**

The South Pacific disjunctions in *Abrotanella* (Fig. 1) are dramatic, although they are only one aspect of the distribution and they developed after the genus had already evolved. Seafloor spreading in the South Pacific has separated Australia, New Zealand, and South America from Antarctica and each other, and these well-dated events may explain the ruptures in the distribution of *Abrotanella*. However, they do not explain the overall distribution itself, with a western limit in Australasia and an eastern limit in southern South America. The rifting cannot explain why *Abrotanella* is absent from Africa or the northern Andes. Thus, even if the exact date of the disjunctions were known, this would only provide a minimum age for the origin of the genus.

Explaining the origin of any group requires comparison with the sister group. The South Pacific disjunct *Abrotanella* is sister to a diverse, cosmopolitan clade, the rest of the tribe Senecioneae (Felser et al., 2010). In the same way, the South Pacific disjunct *Nothofagus* (Nothofagaceae) is sister to a diverse, cosmopolitan clade, the other Fagales (Stevens, 2011). This pattern is repeated in many groups. For example, in monocots, the clade Rhipogonaceae (Australasia) + Philesiaceae (Chile) is sister to the cosmopolitan Liliaeae + Smilacaceae (Stevens, 2011). In frogs, Myobatrachidae (Australia and New Guinea) + Calyptocephalellidae (central and southern Chile) is sister to the global Hylidea (Hylidae, Bufo-
Figure 1. Distribution of *Abrotanella*, showing clades I (black), II (light grey), and III (dark grey). Phylogeny indicated with nested numbers (distributions from Swenson, 1995; phylogeny from Swenson et al., 2012). Whitsunday volcanic province/Median Batholith as dashed line (Mortimer et al., 2005; Campbell and Hutching, 2007).

Figure 2. Distribution of *Hebe* and allies (Plantaginaceae): 1, Leonohebe; 2, Detzneria; 3, Chionohebe and Hebejeebie; 4, Parahebe; 5, Hebe. Phylogeny indicated with nested numbers (phylogeny from Albach & Meudt, 2010).
nidae, etc.) (Pyron & Wiens, 2011). In birds, Pediono-
midae (Charadriiformes; south-eastern Australia) +
Thinocoridae (Patagonia to the Peruvian Andes) is
sister to a pantropical clade, Jacanidae + Rostra-
tulidae (Fain & Houde, 2007).

How old could these South Pacific groups and their
distributions be? Unlike the small cushion and mat
plants of Abrotanella, which produce minute amounts
of pollen, Nothofagus trees are forest giants, dominat-
ing forest over large areas and producing immense
quantities of pollen. It is not surprising that Abrota-
rella has no fossil record (as with many groups in its
family), whereas, in Nothofagus, all four extant sub-
genera are known from fossils dating back to the
Cretaceous. This gives a useful minimum date for
Nothofagus and may also apply to other groups that
share similar distribution patterns.

The South Pacific distribution (and not just the
later disjunction) is restricted to the Pacific margin
of Gondwana, comprising Australasia, western Ant-
arctica, and southern and western South America.
Is there any tectonic feature that corresponds with
this distribution? The region is a major orogenic belt
(the Australides) that does not include the core of
Gondwana (Western Australia, India, Africa and cra-
tonic, eastern South America). Active terrane accre-
tion and uplift took place along this belt from the
Neoproterozoic to the Late Mesozoic (Vaughan, Leat
& Pankhurst, 2005). One of the last, large-scale
events was the New Zealand Rangitata orogeny
(Jurassic to mid Cretaceous) and this, together with
related events in other parts of the Australides, may
have been involved in the origin of the South Pacific
groups. The timing is not well constrained, however,
because of repeated reactivation in the orogenic belt.

As already mentioned, the origin of Abrotanella is
related to the origin of its sister group. The tribe
Seneconeae is a diverse, cosmopolitan group that
includes approximately 3000 species. The basal node
in the tribe separates Abrotanella from the rest, and
subsequent nodes in the group may also shed light on
Abrotanella. A recent phylogeny of Seneconeae is
given below (Pelser et al., 2010, combined data set):

**Abrotanella:** Australasia and Patagonia.

**Capetio:** South Africa (south-western Cape region)

**Chersodoma:** South America (north-western
Argentina to northern Peru)

**All others:** cosmopolitan.

A dispersal model might infer a South Pacific centre
of origin, with subsequent dispersal across the Indian
Ocean to South Africa, then across the Atlantic to
South America, and from there to the world. Instead,
in a vicariance model, differentiation of an already
global ancestor occurred around the South Pacific,
then around South Africa, and then around the region
that began to rise as the Andes in the Late Jurassic
or Early Cretaceous. The three basal nodes are all
southern and allopatric. Subsequent overlap has
developed between the cosmopolitan clade and all
three basal clades, although the allopatry of the first
three could reflect their original vicariance.

The overlap of the fourth clade of Seneconeae with
the others may have occurred soon after the events of
the first three nodes, perhaps with epicontinental
flooding. If the overlap developed in mid-Cretaceous
time, it would be compatible with Late Cretaceous
riifting producing South Pacific disjunctions in both
Abrotanella and in the fourth, cosmopolitan, group of
Seneconeae. One of just three clades in the latter is the
Brachyglottis group, and, again, this has a stand-
ard, disjunct distribution in the southern hemisphere,
with the phylogeny (Pelser et al., 2010):

2. New Zealand, montane to alpine (South and
Stewart Islands): Dolichoglottis.
3. New Guinea (Papuacalia), New Zealand
(Brachyglottis, Haastia, Urostemon, Traver-
sia), south-eastern Australia and Tasmania
(Bedfordia, Centropappus), and central Chile
(Acrisione).

The break between the New Zealand Dolichoglottis
and its sister-group occurred before the trans-Pacific
and trans-Tasman disjunctions in the sister. If this is
correct, Dolichoglottis is much older than the Neogene
mountains it now inhabits, a conclusion which is
probably also true for Abrotanella.

If the overlap of the four main Seneconeae clades
occurred in mid-Cretaceous, the basal nodes, includ-
ing the origin of Abrotanella, could reflect Jurassic–
Early Cretaceous events. These include the Rangitata
orogeny, in which the New Zealand basement ter-
raines were juxtaposed, sutured, and uplifted.

**DIFFERENTIATION OF THE THREE MAIN CLADES
OF ABROTANELLA**

The three main clades in Abrotanella (I, II, and III;
Fig. 1) show almost complete allopatry. There is local
overlap in central Tasmania and on one mountain in
Stewart Island, southern New Zealand (Heads, 1999).
The two main breaks do not correlate with ocean
basins of today. Instead, one break (between clade I
and clades II + III) is located in Tasmania, whereas
the other (between clades II and III) is in Stewart Island.
The phylogeny indicates that these breaks occurred
before rifting in the Tasman disrupted clade II
and rifting in the Pacific split clade III. Thus, the
breaks are attributed to the Early Cretaceous pre-
drift extension and plutonism that developed in and
around Tasmania and Stewart Island (Allibone &

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Outside New Zealand, the break between the *pusilla* group and the *linearis* group corresponds to a large igneous province. This is a vast belt of magmatism comprising the Whitsunday volcanic province of Australia, the Median Batholith of New Zealand, and granites in West Antarctica (Fig. 1, dashed line; Antarctica localities not shown) (Rey & Müller, 2010). The Whitsunday volcanic province is made up of mid-Cretaceous silicic volcanics with a main period of eruption from 120–105 Ma (Bryan & Ernst, 2008). The last phase of Median Batholith magmatism occurred at the same time, with belts of granite batholiths emplaced from 125–105 Ma (Campbell & Hutching, 2007). This extension-related, pre-drift magmatism along the Gondwana margin followed a different line from the spreading centre that developed soon after and led to the opening of the Tasman and Coral Seas. The distribution of this pre-drift belt is aligned with the break or node between the *pusilla* and *linearis* groups, and also the break between clades II and III, at Stewart Island.

The *pusilla* and *linearis* groups (Fig. 3C, D) are allopatric in eastern South Island but overlap in western South Island, Stewart Island, and southern North Island. The overlap developed after the break between the two groups (attributed to mid-Cretaceous magmatism) but before Miocene displacement on the Alpine fault (discussed below). This period of time (i.e. Late Cretaceous and Paleogene) coincides with crustal extension, seafloor spreading, subsidence, and widespread marine transgressions in many parts of the New Zealand plateau (Zealandia). Thus, it appears likely that the high levels of environmental disturbance associated with marine transgressions facilitated the overlap.

Within the *pusilla* group (Fig. 3C), there is perfect allopatry among all three clades. The first node corresponds to the Bass Strait basins (most active in the Early Cretaceous). The other two clades, 2 and 3, form parallel arcs along western New Zealand, although there is a gap in the western clade 3 around the Haast River, and the Central Otago part of clade 2 connects with Mount Kosciuszko in southeastern Australia. Clade 3a connects Fiordland with the New Zealand subantarctic islands. Clade 2 (Abrotanella caespitosa group) and clade 3b (Abrotanella pusilla) are both disjunct along the Alpine fault zone, a transform fault zone that marks the boundary of the Pacific and Indo-Australian plates. Movement on the fault has a large strike-slip or horizontal component, with the displacement being dextral (i.e. the land on the other side of the fault from the observer has moved to the right). Displacement is thought to have begun in Miocene time and has been a major feature of New Zealand geology. One reconstruction of New Zealand Neogene history

Figure 3. Distribution of *Abrotanella* 'clade II'. A, the 'pusilla group'. B, the 'linearis group'. C, the 'pusilla group' in the South Island. D, the 'linearis group' in the South Island. The disjunct southern populations of *Abrotanella fertilis* are at the Copland Range and at Lake Sweeney, 2–3 km east of the Alpine fault (species distributions from Swenson, 1995, Heads, 1999; phylogeny from Swenson *et al*., 2012).
is shown in Figure 4. This illustrates the deformation of the continental crust and the development of the Alpine fault.

Within the *linearis* group (Fig. 3D), the three clades are mainly allopatric, with possible overlap in north-west Nelson (north-west South Island) and Westland. *Abrotanella fertilis* is disjunct along the Alpine fault.

Three of the four New Zealand clades in clade II are disjoint along the Alpine fault. This pattern, with the offsets having the same, dextral sense as the displacement on the fault, is documented in more than 100 other groups (Heads & Craw, 2004). Examples documented in molecular studies include clades of skinks (Fig. 5) and harvestmen (Fig. 6). In contrast with chance dispersal or ecological explanations, a vicariance model predicts that similar breaks will recur in different groups with different ecology and means of dispersal. Groups that are disjoint along the Alpine fault include alpine plants (*Abrotanella*), invertebrates from lowland forest (the harvestmen), and vertebrates that occupy open vegetation, from lowland to alpine elevations (the skinks).

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**Figure 4.** A model of Neogene deformation of mainland New Zealand (Musgrave, 2003). Black line, Dun Mountain-Maitai terrane (the Median Batholith lies west of this terrane).

**Allopatry and overlap in *Abrotanella***

One of the most obvious features in the biogeography of *Abrotanella* is the high level of allopatry seen throughout the phylogeny. There are also two important phases of regional overlap. The overall pattern can be summarized:

- Allopatry between the genus and the two other basal clades of Senecioneae. Complete overlap of these three by the remaining, diverse clade of Senecioneae.
- Allopatry among the three main clades of the genus (I, II, and III), at breaks in Tasmania and Stewart Island (Fig. 1). Minor local overlap.
- Allopatry in the widespread Tasman clade between the *pusilla* group and the *linearis* group (Fig. 3). Overlap in western South Island, Stewart Island, and southern North Island.
- Allopatry within the *pusilla* group (Fig. 3C). Perfect allopatry among all three clades.
- Allopatry within *linearis* group (Fig. 3D). Clades mostly allopatric; possible local overlap in north-west Nelson and Westland.
Four trans-oceanic clades of *Abrotanella* (Fig. 1) overlap in central New Zealand. These have their respective extra-New Zealand distributions in the subantarctic islands (clade 3a in the *pusilla* group); south-eastern Australia (clade 2 in the *pusilla* group); New Guinea (*linearis* group); and South America (clade III). The four clades also have different distributions within New Zealand. As already noted, a similar pattern is seen in clades such as the *Hebe* group (Plantaginaceae) (Fig. 2) and *Olearia* 'clade 2' (Asteraceae). It is also documented in morphological analyses of groups that have not yet been sequenced, such as *Euphrasia* (Orobanchaceae) (Heads, 1994). All these groups comprise trans-Tasman, trans-Coral Sea basin, and trans-South Pacific clades, and these overlap in New Zealand.

The traditional explanation for this pattern proposes a centre of origin in New Zealand or one of the other localities, followed by chance dispersal to the remaining four localities. In an alternative model, the distribution pattern can be explained by differentiation of a widespread Australasia–Patagonia ancestor into the modern clades. This occurred during pre-drift extension (late Early Cretaceous) in ‘New Zealand’ and elsewhere. This was followed by limited local overlap of the clades in New Zealand and rifting of the clades with seafloor spreading in the Late Cretaceous–Eocene (forming Bass Strait, Tasman Sea, Coral Sea, Southern Ocean, and Great South basins). Final rupturing of clades in New Zealand took place with Cenozoic strike-slip movement on the Alpine fault.

One interesting difference between the patterns in *Abrotanella* and in the *Hebe* group concerns the phylogeny. In *Abrotanella*, the trans-Pacific clade differentiates before the trans-Coral Sea and trans-Tasman clades, whereas, in the *Hebe* group, the trans-Tasman clade differentiates before the trans-Coral Sea and trans-Pacific groups. This incongruence might be attributed to chance dispersal or extinction, although other alternatives include approximately simultaneous developments in pre-drift tectonics. For example, in the last phase of Median Batholith magmatism, belts of granitic plutons were intruded. At the same time, east of the Median Batholith, pre-drift extension led to the exhumation of a belt of metamorphic core complexes across the South Island (Forster & Lister, 2003). The activity on both the granite belt and the metamorphic antiform through the mid-Cretaceous (Aptian-Albian) could have led to differentiation of trans-Tasman, trans-Coral, and trans-South Pacific clades in different groups, with similar distributions but different phylogenetic sequences.
**REGIONAL TECTONIC HISTORY AND PHYLOGENY IN ABROTANELLA**

The main tectonic developments in eastern Australasia since the mid-Mesozoic are listed below, with the age of the events, the tectonic regime in place, the nature of the tectonic events, and spatially related breaks in the *Abrotanella* phylogeny.

1. **Jurassic–Early Cretaceous. Compression.** Terranes spread along approximately 6000 km of the Gondwana margin (from New Guinea to Tasmania and possibly Antarctica) were translated along the margin, juxtaposed, and sutured to form proto-New Zealand (Rangitata orogeny). The timing and location of these events suggest that they could have been involved in the origin of *Abrotanella*. Events that occurred about the same time, or soon after, around South Africa and South America, caused the next breaks in the remaining Senecioneae.


3. **End of Early Cretaceous. Extension.** Pre-drift magmatism in Queensland (silicic volcanism) and New Zealand (granite intrusion). Break in clade II between the *pusilla* group and the *linearis* group.

4. **Mid–Late Cretaceous. Extension.** Seafloor spreading in Bass Strait, Tasman, and Great South Basins. Rifting in clade II.

5. **Late Cretaceous. Extension.** Seafloor spreading in the Southern Ocean separated New Zealand, Antarctica, and South America. Rifting in clade III.

6. **Cenozoic (Miocene). Oblique compression (transpression).** Strike-slip displacement on the Pacific/Indo-Australian plate margin at the Alpine fault. Rifting of three New Zealand groups in clade II along the Alpine fault.

7. **Miocene onwards. Transpression.** Uplift of the modern New Zealand mountains (Kaikoura orogeny), with the main divide running parallel with the Alpine fault and several kilometers east of it. Little obvious effect on the biogeography of *Abrotanella* apart from the uplift of many populations.

Together, the main tectonic events in the region account for the main phylogenetic and geographical breaks in the *Abrotanella* phylogeny. Thus, the main nodes in the phylogeny show a coherent, sequential pattern when related to the tectonic history. In addition, the main phase of overlap (between the *pusilla* and *linearis* groups, discussed above), occurred in the Late Cretaceous–Paleogene and coincided with marine transgressions. Other features of the biogeography that are not examined in the present study may also relate to tectonics (Heads, 1999). For example, in New Guinea, the northern boundary of the genus corresponds to the edge of the Australian craton; the group does not occur in the mountains of the accreted terranes, despite apparently suitable habitat there. In Patagonia, strike-slip disjunction occurs in *Abrotanella submarginata* along the margin of the South America and Scotia plates. Both of these patterns are repeated in many groups.

**DISCUSSION**

**DISPERAL LEADS TO OVERLAP, NOT ALLOPATRY**

One explanation for the precise, interlocking geographical structure in *Abrotanella* is chance dispersal. Based on their fossil-calibrated, post-Cretaceous dates for *Abrotanella*, Wagstaff *et al.* (2006) inferred a 'convoluted' history of long-distance, trans-oceanic dispersal. Yet the actual distribution patterns show a high degree of allopatry throughout the phylogeny and could hardly be less convoluted. The only dispersal events that are required in *Abrotanella* are the minor range expansions needed to explain local clade overlap, mainly in the western South Island. The mechanism for these range expansions could have been the normal, observed means of dispersal of the plants, and not the very unusual mechanisms required for one-off trans-oceanic dispersal events over thousands of kilometres. The local range expansions would have involved whole populations, not just single individuals.

Swenson & Bremer (1997) concluded: ‘... *Abrotanella* must have reached New Zealand by long-distance dispersal long after its separation from other continents... Possible long-distance dispersal events of *Abrotanella* are hard to envision, however, ... such occasions must be extremely rare, otherwise there would be a lot of distributional noise and we would not be able to perceive any general biogeographical pattern’ (p. 503). This is a crucial point. Indeed, the proposed chance dispersal events have not just been ‘extremely rare’, they have been unique in geological time: once across the Pacific, once between New Zealand and New Guinea, once across the Tasman, and once across the Great South Basin. Why have the different clades each crossed a different basin, and why have they each crossed their respective basin only once? This distinctive combination of phenomena also occurs in other groups. The overall pattern could be explained by vicariance and local range expansion, both caused not by chance but by geological or climatic changes affecting whole communities.

For two sister clades in two disjunct areas, dispersal theory proposes a single dispersal event between...
the two. The singularity of the event implies that the movement is not related to the organism’s usual means of dispersal, its normal means of survival. Proposed mechanisms for extremely rare dispersal events include, for example, tsunamis, megastorms or floating islands with living vegetation. These could have crossed the Tasman or Pacific and such very rare events might only occur once every 1000 years. Yet these would have occurred ~65 000 times since the Cretaceous (5000 times since the Miocene) and so would be much too frequent over geological time to explain simple allopatry. The proposed trans-Pacific, trans-Tasman, and other transport events in Abrotanella have each happened just once in the entire history of the genus, and, as Swenson & Bremer (1997) concluded, they are hard to envision. They are one-off events that occur at random and are not associated with any other factor, either physical or biological. Their probability is vanishingly small. Yet despite this, the same distinctive pattern seen in Abrotanella, with a trans-Tasman affinity, a trans-Coral Sea affinity, and a trans-Pacific affinity, recurs in many other clades, including the Hebe group, Olearia, and Euphrasia.

The many different meanings of ‘dispersal’ include annual migration, daily migration, normal ecological movement within a range, range expansion, and also the inferred process of ‘chance dispersal’. This last process, unlike the others, involves not only physical movement, but also genetic differentiation. The break or decrease in gene flow leading to founder speciation is caused not by environmental changes or intrinsic, genetic changes but, instead, by chance. This process is rejected in the model proposed in the present study, which is based on alternation between phases of vicariance and phases of overlap caused by range expansion. Range expansion differs from chance dispersal in several key ways: it does not involve dispersal across a barrier; it uses normal, observed means of dispersal; in itself, it does not lead to cladogenesis; it is not due to chance but, instead, to changes in the environment; and it leads to overlap, not to allopatry.

Overlap can be caused by dispersal (range expansion using normal means of dispersal) but, in theory, it could also be explained by sympatric speciation. In practice, however, most putative examples of sympatric differentiation involve an allopatric component: the species do not have the same distribution. This means that the limited sympathy probably results from allopatric differentiation followed by secondary overlap, rather than sympatric evolution. Molecular studies have indicated this in the forms of threespined sticklebacks (Gasterosteus aculeatus) of British Columbia, for example, that were previously accepted as a classic case of sympatric, ecological speciation (Taylor & McPhail, 2000). Limnetic and benthic forms in the same lake are not sister groups and, instead, are closer, respectively, to limnetic and benthic forms of other lakes.

For these reasons, secondary overlap is assumed to be the result of simple range expansion, and not sympatric speciation. Normal ecological movement and range expansion both proceed using the normal means of dispersal of an organism, as seen every day in the weeds that colonize a cleared garden. Phases of range expansion, as with phases of vicariance, are not a result of chance but, instead, environmental changes. For example, the last, great sea level maxima in the mid-Cretaceous, caused by a combination of tectonic and climatic factors, appear to have caused the last, great phase of overlap in groups of the Amazon and Congo basins (Heads, 2012) and also in groups around the Pacific, such as Abrotanella.

**IS EVOLUTION CLOCK-LIKE?**

The Australasia–southern South America distribution pattern is seen in many organisms with a wide range of means of dispersal and ecology, suggesting that these factors are not the explanation for the disjunction. It has long been known that the disjunction also occurs in groups with very different taxonomic rank, from species groups (Abrotanella), to families (Notofagaceae) and clades above family rank (e.g. Rhipogonaceae–Philesiaceae). This suggests that the component groups of the pattern show very different branch lengths and this probably also applies to all important disjunct patterns, such as trans-Tasman, trans-Atlantic, and trans-Indian Ocean.

Nineteenth century studies rejected an evolutionary clock model; for example, Hutton (1872: 250) concluded that: ‘differentiation of form, even in closely allied species, is evidently a very fallacious guide in judging of lapse of time’. Instead, Hutton accepted that a single geological event could cause lead to the evolution of endemics at different ranks in a region, at the same time. By contrast, Matthew (1915) and the authors of the modern synthesis assumed a dispersal model and an evolutionary clock. Groups with different branch lengths that belonged to a single biogeographical pattern were attributed to chance dispersal events in the different groups at different times. For example, Mayr (1931: 9) discussed the unusual avifauna of Rennell Island, in the Solomon Islands, and wrote: ‘The different degree of speciation suggests that the time of immigration has not been the same for all the species’. Similarly, for the birds of New Caledonia, Hawaii and other islands, he wrote that ‘Strikingly different degrees of differentiation indicate colonization at different ages’ (Mayr, 1944: 186).
Developing a critical approach to the molecular clock and branch length does not mean denying that branch length exists but investigating what it might represent. Is branch length simply related to time, or does it instead reflect, say, prior features of genome architecture that determine evolvability? If evolutionary rate shows extreme variation, for example, with rates dropping throughout large groups after a phase of differentiation, branch length might be a function of the time involved in a differentiation event, not the age of the event. As an alternative, branch length could be largely determined by prior aspects of genomic architecture alone. In this case, branch length would not be an accurate reflection of the time involved in the differentiation, or its age.

Swenson et al. (2012) suggested that a rifting explanation for the disjunction in *Abrotanella* is impossible, as it would imply that the Asteraceae are 1.5 billion years old. This deduction would be correct if a clock or relaxed clock model of evolution were accepted but, if evolution is not clock-like, the genus could have evolved in the Cretaceous and the family in, say, the Jurassic. In a nonclock, or very relaxed clock model, rapid changes in evolutionary rate can occur both within and between lineages, and most of the differentiation in a large group can happen over a short time. Studies using tectonic calibrations indicate that this is often the case.

**HIGH LEVELS OF GEOGRAPHICAL STRUCTURE IN MOLECULAR VARIATION**

Most modern studies date clades using the fossil record, the age of strata and islands, and single tectonic events such as the uplift of the Panama Isthmus. In this approach, there is no need to map clades. Yet molecular workers are now mapping clades anyway because the geographical patterns are often their most interesting results. As deep, intricate geographical structure, including precise allopatry, is reported in more and more molecular studies, chance dispersal becomes less likely. Deep geographical structure is reported in all groups, including, to the surprise of specialists, marine groups (Heads, 2005) and even microorganisms (Vyverman et al., 2007). This suggests that groups’ geographical distributions are much less fluid than was previously assumed and can be a direct result of phylogeny.

In the traditional model, distribution ranges develop after the phylogeny, with groups spreading out from their centre of origin. This model is supported by ecologists (Levin, 2000), palaeontologists (Eldredge et al., 2005), and systematists (Swenson et al., 2012). Instead, in a vicariance model, the distribution develops at the same time as the phylogeny, by simple allopatry, and a group may have already had a wide distribution at the time of its origin. Subsequent range expansion may or may not occur. In this model, distribution is much more closely related to phylogeny than in dispersal theory, and this is compatible with the geographical structure being discovered in so many phylogenies. In a vicariance model, many aspects of distribution represent inherited information. Accordingly, distribution data have potential applications in tectonics; for example, in the debate about whether or not the West Caledonian fault in New Caledonia exists (Heads, 2008).

**ESTIMATING SAMPLING ERROR IN THE FOSSIL RECORD**

Ho & Phillips (2009: 374) wrote: ‘By what period of time could we reasonably expect the age of a node to predate the age of the oldest fossil on either of its descendent lineages? Answering this question is an exceptionally difficult task . . . It is evident that estimating the level of uncertainty might simply be impossible for the majority of fossil calibrations’. Palaeontologists have estimated clade ages by assuming that the richer the fossil record of a group is, the less likely it is that the group is much older than its earliest known fossil. However, the actual numbers are difficult to estimate and the problem is confronted in the current debate about the assignment of priors (Heads, in press). In general, assessments of gaps (sampling error) in the fossil record that are made using the fossil record itself are not convincing, and so estimating realistic priors for clade ages based on fossils is, indeed, ‘exceptionally difficult’. If phylogenetic breaks are calibrated with tectonic/biogeographical breaks, and not with fossils, estimating the error in the fossil record with an external data set is possible. For example, one main phylogenetic break in primates (between lemurs and lorises) occurs at the Mozambique Channel, which rifted open at 160 Mya. A subsequent main break in the primates (between platyrhines and catarrhines) occurs at the Atlantic Ocean, with rifting at 120–130 Mya. Tectonic/biogeographical estimates of clade ages based on these events can be compared with the age of the oldest fossils in the clades to give an estimate of error in the fossil record (Heads, 2012). For example, lemurs have no pre-Pleistocene fossil record, indicating a gap in the fossil record of approximately 160 Myr. *Abrotanella* has no fossil record. Based on the fossil record of its family, Asteraceae, Swenson et al. (2012) estimated that the genus originated at approximately 38 Myr, and this suggests a gap in the record of *Abrotanella* of 38 Myr. The tectonics-calibrated analysis given above suggests instead that *Abrotanella* originated at approximately 120–145 Mya, indicating an equivalent gap in the fossil record.
CONCLUSIONS

The modern synthesis based evolutionary chronology on the fossil record and inferred that many groups, including many orders, evolved only in the Cenozoic. Distributions were explained by chance trans-oceanic dispersal. A modern synthesis view of evolution in Abrotanella relied on fossil calibration and proposed differentiation by trans-oceanic chance dispersal (Swenson et al., 2012). The idea of tectonic/biogeographical calibration was rejected, although without giving it a real test; the biogeography of the group was not examined and the clades were not mapped. Although Swenson et al. (2012) did not consider any tectonic events apart from the rifting of the New Zealand plateau from Gondwana, the main phylogenetic and geographical nodes in Abrotanella indicate that pre-drift tectonics (extension, volcanism, and plutonism) and post-drift tectonics (strike-slip displacement) are just as important as the break-up itself. Pre-drift evolution in the region has also been invoked for differentiation between Australia–South America groups and New Zealand–South America groups (Ribeiro & Eterovic, 2011).

In a growing number of cases, evolutionists are avoiding the use of fossils to give maximum clade ages and are instead using tectonic calibrations. Most of these studies still use only single tectonic calibrations that may be remote from the study group, in geography, phylogeny or both. One example concerns the birds of paradise (Paradisaeidae), a group found mainly in New Guinea. Irestedt et al. (2009) calibrated a phylogeny of the group by attributing the basal break in passerines to the rifting between Gondwana and New Zealand, where the basal passerine group is endemic. The results are already interesting but could be developed further by including the many tectonic/biogeographical calibrations that are possible in the family Paradisaeidae itself (Heads, 2002). This is the method used in the present study for Abrotanella; multiple nodes are dated using tectonics and this involves a broad engagement of tectonics with molecular phylogeny and biogeography. The model assumes that allopatry is caused by vicariance, and that overlap is caused by dispersal. Dispersal as range expansion is accepted (otherwise no clades would overlap) but chance dispersal as a mode of speciation is rejected.

There are two possible approaches in biogeographical analysis, as shown in the two models for Abrotanella. The first, chance dispersal, implies that rates do not show extreme changes, and that overall the fossil record is more or less accurate. It predicts no shared patterns; because of their different branch lengths, the components of a single biogeographical pattern are inferred to have developed the pattern at different times, not because of a single, causative event. The second option (i.e. phases of vicariance and phases of overlap) implies extreme rate changes in evolution (e.g. so that Asteraceae are not 1.5 billion years old) and implies that the fossil record of terrestrial life in general has massive gaps.

The pattern in Abrotanella, the Hebe group, Olearia, and others, involves several otherwise allopatric clades overlapping in New Zealand. This pattern could represent a species radiation from a centre of origin driven by chance dispersal and adaptation. Or instead, it could reflect the break-up of a South Pacific ancestor into allopatric sectors (and subsequent local overlap in New Zealand), with differentiation around belts of magmatism, spreading centres, and transform faults.

The second model predicts precise, highly-ordered patterns that are unlikely to be produced by chance dispersal. It also predicts that biogeographical patterns (i.e. patterns with no obvious ecological correlation) will repeat in different groups, even those with different means of dispersal. This can be investigated with more detailed field mapping of the clades and with comparative studies of other plants and animals.

Many contemporary studies can be described as ‘plug-and-play’ biogeography; they calculate: (1) a phylogenetic tree; (2) a time-course of the evolution, using software such as BEAST; and (3) a model of the spatial evolution, using DIVA or DEC. By specifying appropriate priors, BEAST can be used to support young ages for clades, while DIVA and DEC will infer a centre of origin at the location of a paraphyletic basal grade. Thus, it is not surprising that so many current studies still support the conclusions of the modern synthesis: 1. the fossil record is the best (or only) guide to the time course of evolution, modern intercontinental groups developed after the Mesozoic. 2. distribution is the result of chance dispersal from localized centres of origin by founder individuals. Although this approach is still current, the molecular revolution means that biologists no longer need to rely on fossils to calibrate evolutionary chronology. Instead, they can harvest a new, rapidly growing source of data: the distributions of the molecular clades. Distributions and distributional breaks can be integrated with regional tectonic events and the radiometric dates that have been proposed for them.

In this way, molecular biology can be combined with hard-rock geology to move beyond the modern synthesis and its reliance on chance to explain repeated patterns.

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