

Biogeographic relationships between Macaronesia and the Americas

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Abstract. A vicariance model is presented for the origin of Macaronesian endemics and their allopatric American relatives. Trans-Atlantic relationships are identified for 21 taxa in which an endemic Macaronesian clade either has a sister group in the New World or is part of a larger monophyletic group that includes representatives in the New World. Historical implications of this pattern are discussed in relation to current tectonic and geological models for the Central Atlantic and the Macaronesian Islands. The proposed vicariance model identifies a local origin for the Macaronesian endemics from ancestral distributions that already encompassed ancestral Macaronesia and parts of the New and Old World before formation of the Atlantic. The present-day existence of Macaronesian endemics is attributed to sequential colonisation of newly formed islands within the Atlantic from Mesozoic time.

Additional keywords: allopatry, dispersal, divergence, differentiation, evolution, geology, panbiogeography, tectonics, island biogeography, oceanic island, vicariance.

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Introduction

Vicariance would probably not be the first biogeographic thought that comes to mind for the island archipelagos collectively referred to as Macaronesia, and including the Azores, Salvages, Madeira, Canary Islands and Cape Verde. After all, the geological evidence shows that the present islands have never been connected with continents or with each other, and that they are all volcanoes (some including uplifted seafloor sediments) that emerged from the ocean floor (Juan *et al.* 2000; Cox *et al.* 2010). The only viable explanation for the origin of animals and plants on such islands would seem to be dispersal from the New World or Old World continents (Carlquist 1965; Cowie and Holland 2006; Fernández-Palacios *et al.* 2015). This is the general consensus for Macaronesian biogeography (e.g. Humphries 1979; Juan *et al.* 2000; Sjögren, 2000; Carine *et al.* 2004; Lledó *et al.* 2005; Whittaker *et al.* 2008; Fernández-Palacios *et al.* 2011, 2015; Caujapé-Castells 2013; Esteves *et al.* 2015; Borges *et al.* 2016).

Chance dispersal is the principal foundation of the model-based discipline that now dominates island biogeography as the successor to earlier, pattern-oriented approaches (Anderson *et al.* 2009; Salvo *et al.* 2010). Considering the scope and depth of this consensus, it is understandable that earlier Macaronesian vicariance models (e.g. Croizat 1965; Stock 1995) would be regarded as little more than historical footnotes. But the importance of chance dispersal is not an empirical biogeographic finding. It is an assumption built into model-based methods in which phylogenetic and molecular divergence data are taken to

represent empirical evidence of particular biogeographic processes. The following are additional assumptions made in dispersal studies of Macaronesia:

- (1) A sister-group phylogenetic relationship between Macaronesia and another locality is assumed to be the result of a single chance-colonisation event (e.g. Kim *et al.* 2008).
- (2) Two or more external relationships are assumed to be the result of two or more chance-colonisation events (e.g. Fuertes-Aguilar *et al.* 2002; Carine *et al.* 2004).
- (3) Nesting of mainland taxa within a Macaronesian group is assumed to be the result of 'reverse' chance dispersal from Macaronesia to the mainland (e.g. Carine *et al.* 2004; Caujapé-Castells 2013).
- (4) The higher frequency of Old World relationships is assumed to be the result of the higher frequency of chance dispersal from the Old World continents to Macaronesia (e.g. Carine *et al.* 2004; Carine 2005; Kim *et al.* 2008).
- (5) Molecular divergence is assumed to be the actual or maximum ages of Macaronesian colonisation.

These principles are widely accepted, but they are methodologically problematic because there are alternative ways of interpreting information on phylogeny, distribution and molecular divergence. These include the following:

- (1) Phylogeny and dispersal. Model-based approaches to Macaronesian biogeography assume that the sequence

of phylogenetic relationship reflects a sequence of chance dispersal. Although often cited as Hennig's progression rule, it is not a rule but an assumption that does not address the equal applicability of sequential differentiation across a widespread ancestor (Craw *et al.* 1999; Grehan 2011; Heads 2012). The progression rule also assumes that a 'basal' grade is located in the source region or centre of origin, but some Macaronesian clades are basal to large continental clades, and there are also clades with 'reciprocal monophyly' in which a diverse Macaronesian clade is the sister group to a diverse continental clade. These phylogenetic and geographic incongruities do not arise in a vicariance interpretation of phylogeny, because a basal clade or grade marks only the location of the initial phylogenetic break or breaks within a widespread ancestral range. This initial break may separate a localised distribution from a much larger sister-group range that is later subject to further differentiation. The result is a less diverse and more narrowly distributed 'basal clade' than a more diverse and widely distributed sister group (Heads, 2012). In this context, the higher number of Old World–Macaronesian relationships for Macaronesia is a consequence of a higher number of ancestral ranges shared between geographically proximate regions.

- (2) Chance dispersal and divergence. Model-based methods use chance dispersal to explain divergence and allopatry, and yet allopatric divergence requires isolation, which cannot exist if there is effective dispersal. Chance dispersal is also seen to be sufficient for successful colonisation over great distances (including entire oceans or continents) and yet insufficient to occur more than once for most taxa or to prevent isolation necessary for differentiation within small island archipelagos. Allopatry, either adjacent or disjunct, is a ubiquitous biogeographic characteristic of animal and plant distributions that is manifested by Macaronesian endemics and their nearest relatives in other regions. The contradiction between the need for localities to be accessible by dispersal and also isolated by divergence does not occur in a vicariance model, in which a formerly widespread ancestor differentiates into different descendants over different parts of the ancestral range. The vicariance model eliminates the contradiction between accessibility and isolation by recognising that dispersal (as movement) and divergence (as differentiation) are complementary phases of evolution. Under particular geological and climatic conditions, an organism's ability to move may result in range expansion (or contraction) during a time of mobilism, but does not lead to divergence. This phase alternates with periods of immobilism, in which the distribution range is geographically stable and allopatric differentiation may occur. Only during phases of immobilism can differentiation take place through geological or climatic isolation (Craw *et al.* 1999; Heads 2012).
- (3) Molecular-clock divergence estimates. Model-based methods, with rare exceptions, present molecular divergence ages as falsifications of early origins, at or before continental breakup, even though they are calibrated by fossils that can generate only minimal divergence dates. Although it is widely claimed that molecular-clock analyses generate evidence of dispersal (Sanmartín *et al.* 2008), molecular divergence

estimates artificially constrain the maximum age of taxa that may be much older than their oldest fossil or the age of the current island they occupy (Heads 2009a, 2012, 2014a, 2014b, 2016). Failure to recognise molecular divergence dates as minimal estimates has imposed an artificial boundary on the timing and origin of Macaronesian taxa and the evolution of their ecological communities (e.g. Kondrakov *et al.* 2015).

Chance dispersal has become the default interpretation for Macaronesian biogeography; however, reliance on a single working hypothesis may generate inflexible schemes that can actually hold up progress. To offset this problem, some research programs in geology and molecular biology emphasise the principle of 'multiple working hypotheses' (Heads 2012, p. 2). As noted by Williams and Ebach (2014), 'in order to understand any debate in any field, one needs to address and understand the many sides of the argument – for there are always many' (p. 175). In the current paper, I will present examples of relationships involving Macaronesia and the New World with respect to basal clades, sister-group allopatry and reciprocal monophyly, as evidence for an alternative vicariance hypothesis for the biogeography of Macaronesia. The vicariance implications will be assessed with respect to recent geological and tectonic models for the Macaronesian region. These biogeographic patterns challenge the frequent assumption that colonisation by chance dispersal is both necessary and sufficient to understand the origins of Macaronesian endemism.

Macaronesian geology

Integration between biogeography and geological history is a central theme of Macaronesian studies, but the common practice of subordinating biogeography to a particular geological reconstruction or to molecular divergence estimates is not really integration. Integration requires a comparison of independent sources of evidence – here, geology and the geographic relationships of phylogeny (Craw *et al.* 1999). Historical reconstructions of oceanic-island geology can be particularly daunting because of the difficulty of sampling submarine strata. Fragmentary insights may preclude a complete and sufficient historical model to account for biogeographic origins. This technical constraint is evident in the way new geological discoveries in Macaronesia have resulted in new historical models or have drawn attention to the ambiguous nature of current geological evidence.

The location of the Macaronesian islands within the Atlantic basin implies a shared historical relationship between the origin of these islands and Atlantic tectonics in general. The Atlantic basin formed through an extended tectonic process, beginning with continental thinning between Nova Scotia and Morocco between 203 and 190 million years ago, as indicated by formation of salt basins at that time. Magmatic intrusion was predominant between 190 and 177 million years ago, and this was followed by the formation of oceanic crust between 177 and 170 million years ago (Sibuet *et al.* 2012). Final separation of the New and Old World continents occurred between Brazil and West Africa in the late Albian at c. 104 million years ago (Heine and Brune 2014), although seas were already filling the rift valleys in the Central and South Atlantic by upper Aptian time, at c. 120 million years ago (Arai 2014). The North Atlantic

basin formed by a northward extension of the Central Atlantic combining with a separate rift extending southward in the vicinity of Iceland, with proposed separation of Greenland and Europe at *c.* 33–24 million years ago (Ellis and Stoker 2014) or earlier *c.* 52 million years ago (Torsvik *et al.* 2015).

As measured by dating of lava, the origins of the modern Macaronesian islands are recent compared to the age of the Atlantic basin (Geldmacher *et al.* 2001; Carracedo *et al.* 2015; Larrea *et al.* 2014). Estimated stratigraphic ages are as follows: Canary Islands–Lanzarote (*c.* 15 Ma), Fuerteventura (25 Ma), Gran Canaria (15 Ma), Tenerife (11 Ma), Gomera (12 Ma), La Palma (3–4 Ma), El Hierro (1 Ma); Madeira Islands (0–14 Ma); Salvagen Islands (29 Ma); Cape Verde: Sal (8.7–15.8 Ma), Mao (8–12 Ma), Santiago (2–6 Ma), Santo Antao (1–3, ?? Ma), Sao Vincete (4.4 Ma), Sao Nicolau (2.6–4.7 Ma), Fogo (>3 Ma), Azores: Corvo (0.7 Ma), Flores (2 Ma), Graciosa Terceira (<3.5 Ma) São Miguel (<4 Ma), Santa Maria (8 Ma), Pico (0.3 Ma), Fail (0.9 Ma) and São Jorge (1.3 Ma). In the absence of any earlier subaerial formation, these island ages would constrain the origin of Macaronesian endemics to the oldest island ages of each archipelago. However, geological evidence indicates the presence of older former islands within the Macaronesian region.

To the north-east of the Canary Island and Madeira archipelagos is a series of seamounts identified as paleo-Macaronesian islands, originating from two parallel hotspot tracks (Geldmacher *et al.* 2001, 2005). The Canary plume began near the Essaouira Seamount (dated at 68 million years ago) in the north and ends near El Hierro and La Palma (<4 million years ago), and the Madeira plume begins with the Ormonde Seamount (65–67 million years ago) and ends with Madeira (0–5 million years ago). Imperfect age relationships and the spatial position of some volcanic centres may indicate a role for interactions between plume and edge-driven convection processes (Geldmacher *et al.* 2005). Within the Canary archipelago, there are older Canary seamounts, with oldest ages of 142 Ma, that first came into existence when the North American and African continents were only 900 km apart (van den Bogaard 2013). Potential geological mechanisms for these islands include shallow mantle upwelling from Late Jurassic to Recent time, mantle plume and plate-related convection, multiple and successive mantle plumes, or a combination of Late Jurassic passive mantle upwelling near the Mid-Atlantic Ridge, with shallow edge-driven convection throughout the Cretaceous, followed by a deep-fixed plume in the Early Paleogene. The trend of the Cretaceous submarine volcanoes is almost orthogonal to the Canary and Madeira hotspot trends that show a curved age-progression from the oldest to the youngest islands mirroring the rotational movement of the African plate over the past 60 Ma. Recent geological assessments have argued that the eastern Macaronesian islands are the result of a mantle plume, whereas the Cretaceous seamounts represent an earlier, probably fracture-controlled magmatic episode (Troll *et al.* 2015; Zaczek *et al.* 2015). These reconstructions indicate the presence of islands off the coast of Africa from at least 140 million years ago.

Anguita and Hernán (2000) considered the potential role of tectonic processes in island formation, suggesting that in addition to volcanic activity from a mantle plume, the Canary

Islands were uplifted by transpressive shears. A tectonic connection between the Canary Islands and the Atlas Mountains was also suggested in the form of propagating fractures that have not yet been observed because of the thick sedimentary pile between the Canary Islands and Morocco. A shared geological mechanism for the Canaries and Cape Verde was suggested by Patriat and Labails (2006), with reference to a continuous basement ridge between the two archipelagos, the occurrence of Late Cretaceous uplift before the onset of the main volcanic phases, and the same pattern of sedimentary evolution and a very similar timing of volcanism and deformation in Fuerteventura (Canaries) and Maio Island (Cape Verde). Cretaceous sediments from Fuerteventura corresponding with a deep-water origin led Arthur *et al.* (1979) to conclude that no subaerial Canary Island Ridge existed during the Mesozoic. Similarities in the scale of seamounts in the Tore–Madeira Rise and Meteor Rise led Patriat and Labails (2006) to suggest that they may have formed at approximately the same time, and that the geological processes responsible for the Canary and Cape Verde islands may also be involved with the geological history of the whole eastern Central Atlantic region.

The Azores region has been subject to at least 85 Ma of hotspot activity, and the main volcanic ridges on the western platform may be the result of a combination of Mid-Atlantic Ridge magmatism and an overlapping hotspot plume. Between the Oceanographer and Pico–Gloria fracture zones, a continuous elevated rise links the Azores archipelago to the Great Meteor seamount group. Indirect estimates of seamount ages in the Great Meteor–Cruiser–Tyro–Atlantis complex are at least 65 Ma for the Cruiser group and 38–47 Ma for most of the other seamounts. Gente *et al.* (2003) suggested that the same, almost continuous, plume may be responsible for both the Great Meteor complex and the Azores Plateau Ridge over the past 85–90 Ma.

Materials and methods

Sampling

Twenty-one examples are presented to illustrate biogeographic relationships between Macaronesia and the New World. Groups were included in the present study if there was adequate systematic resolution of sister-group relationships, sufficient sampling of member taxa, adequate sampling of sister groups (a recognised problem in general for Macaronesian studies, Caujapé-Castells 2013) and adequate information on the geographic location of sister taxa. The quality of geographic information available for Macaronesian groups and their relatives varies widely, and accurate and precise distribution maps are not available for many groups.

Biogeography

In contrast to model-based methods, the approach used here is a ‘pattern-oriented exercise’ (cf. Salvo *et al.* 2010), in which the endemic Macaronesian taxa and their allopatric relatives are mapped. The underlying assumption is that phylogeographic patterns (phylogeny mapped geographically, Avise *et al.* 1987) are informative about historical origins (Croizat 1964; Craw *et al.* 1999).

The analysis presented here incorporates the following principle steps:

- (1) Identify the phylogenetic and distributional structure of taxa endemic to Macaronesia and their sister groups.
- (2) Identify the geographic location of phylogenetic breaks between sister clades.
- (3) Identify the geographic relationships between sister taxa using the minimum-distance criterion.
- (4) Evaluate the vicariance implications with respect to recent geological and tectonic models for the North Atlantic.

Geographic relationships are identified by the minimum-distance criterion, where all other factors are equal (i.e. there are no other contingent factors such as alternative phylogenetic relationships or geomorphology involved). The minimum geographic distance between distributions represents the geographic sector considered to be most likely responsible for a disjunction. For example, a sister-group relationship between a group in Macaronesia and one in America is attributed to a connection across the Atlantic, rather than, say, across Asia. Although this method has been criticised by both dispersal and vicariance biogeographers, it is in practice the most widely used criterion in biogeography and applied, at least implicitly, among

all schools of biogeography that relate biogeography to geological history.

Trans-Atlantic clades in Macaronesia

The following examples illustrate relationships between clades endemic to the islands of Macaronesia and their sister groups. The analysis includes examples of Macaronesian taxa, with immediate sister-group relationships involving the New World and Macaronesian taxa with Old World sister groups that are part of a larger pattern of allopatric distributions involving the New World. Allopatry *within* Macaronesia is described for one example (*Tarentola*), and it forms part of a larger allopatric pattern beyond Macaronesia.

(1) Biogeographic affinities of Macaronesian *Tarentola* (Reptilia: Gekkonidae)

Tarentola occurs in Cuba, Jamaica (extinct), Cape Verde, Salvage Islands, Canary Islands, equatorial to northern Africa and southern Europe. Phylogenetic analysis (Carranza *et al.* 2000, fig. 3) identified *T. americana* (Gray, 1831) of Cuba as the basal

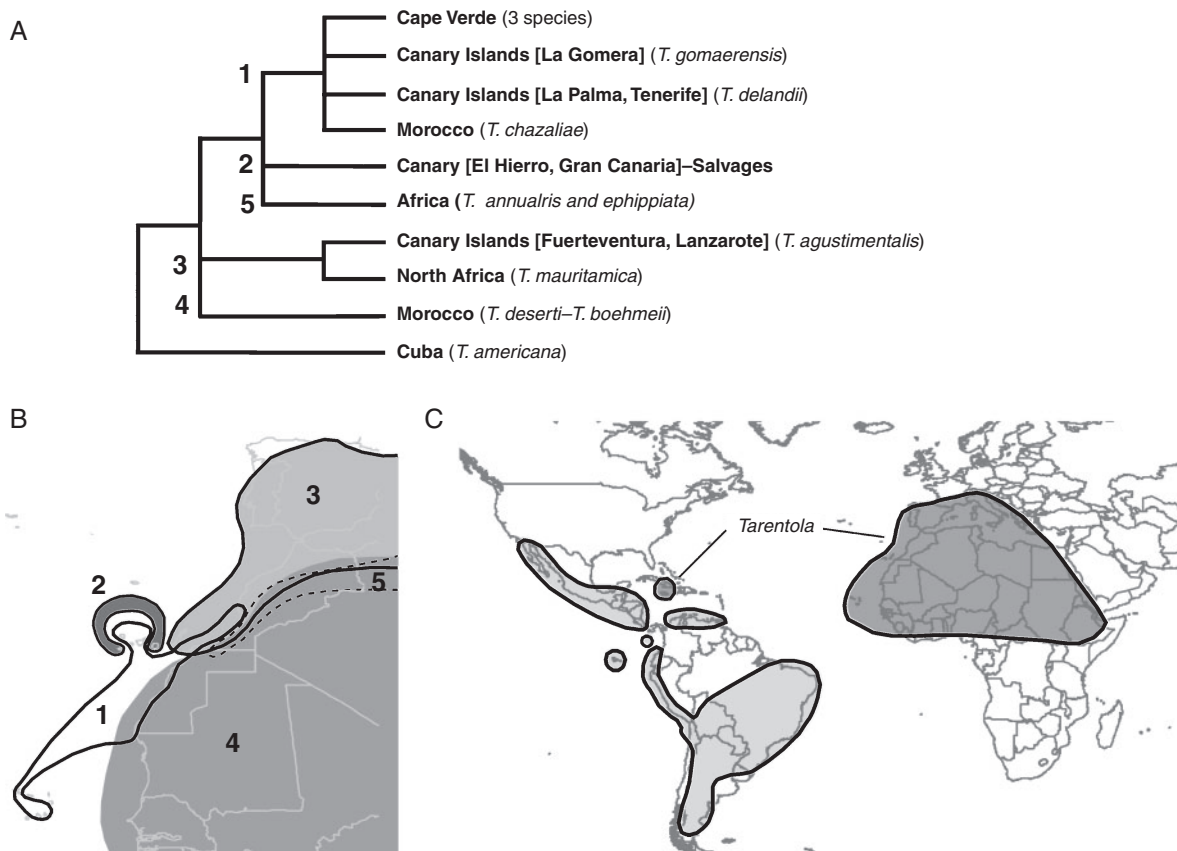


Fig. 1. Relationships of Macaronesian *Tarentola*. A. Phylogeny of Macaronesian relationships as a reduced-area cladogram (Carranza *et al.* 2000, fig. 3). B. Biogeography: of Old World *Tarentola* clades: Macaronesian Clade 1, Cape Verde–Canary–Morocco (clear, solid outline); Macaronesian clade 2, Canary–Salvages clade (dark shading); Macaronesian clade 3, Canary–Mediterranean (pale shading); Morocco–northern Africa clade 4 (*T. deserti*–*T. boehmei*, dashed outline); Africa clade 5, *T. annularis* and *ephippiata* (dark shading over Africa, northern boundary uncertain); C. Biogeography of *Tarentola* and New World sistergroup. Distribution data are from Joger (1984), Joger *et al.* (2006a, 2006b), Pellegrino *et al.* (2005), Gamble *et al.* (2011, 2012), Morando *et al.* (2014), Wilms *et al.* (2013) and <http://reptile-database.reptarium.cz/> (accessed 21 March 2017).

group, which was estimated to have diverged at 26 million years ago by Carranza *et al.* (2000, p. 645) and 10.6–17 million years ago by Carranza *et al.* (2002, p. 251). Separation of the Cuban and Old World species by plate tectonics was excluded by these authors because the divergence estimate post-dated the separation of Africa and South America. It was a ‘certainty’ that the ancestor of *T. americana* reached the Neotropics from an unspecified Old World centre of origin by trans-Atlantic colonisation. The basal position of *T. americana* also requires a successful return migration back across the Atlantic, but only once.

The molecular clock for *Tarentola* was calibrated by using an estimated geological age of 1.1 million years ago for El Hierro Island (Canary Islands) and assuming that endemics there were no older than the island. This approach has two problems, namely (1) the maximum age of the island is assumed to be correct, but this is uncertain, and (2) it assumes that the island inhabitants cannot be older than the island (i.e. that they could not have colonised El Hierro from older islands), although molecular studies often indicate that groups are older than the islands they are endemic to (Heads 2012). This latter possibility was rejected by Carranza *et al.* (2002, p. 248, 249) because the divergence between two El Hierro species would have required colonisation of the Canary Islands ‘many millions’ of years before their current formation.

The three Macaronesian clades (Fig. 1A) have the following distributions: Clade 1: Cape Verde–Canary Islands–Morocco; Clade 2: Canary Islands–Salvages; and Clade 3: Canary Islands–North Africa. The three clades are allopatric within Macaronesia, and two are partly sympatric in Africa (Fig. 1B). Of the remaining African *Tarentola*, Clade 4 (*T. annularis*

(Geoffroy, 1809) and *ephippiata* O’Shaughnessy, 1875) spans the northern half of Africa, whereas Clade 5 (*T. deserti* Boulenger, 1891 and *T. boehmei* Joger, 1984) occupies a boundary region between two other clades (Fig. 1B). Carranza *et al.* (2000, 2002) attributed the origin of Macaronesian *Tarentola* to multiple chance dispersals from Africa; however, this does not explain the allopatry within Macaronesia. The proposed chance dispersal led to successful landings in the New World and then back again in the Old World, but somehow did not obliterate this overall allopatry, especially among clades occupying multiple islands.

To account for the sister group of Old World *Tarentola* in Cuba, Gamble *et al.* (2012, p. 237) considered two ‘equally likely’ trans-Atlantic dispersal events. Either an Old World ancestor dispersed to America, or a single dispersal event resulted in the ancestor of *Tarentola* and its sister clades, followed by a ‘well established’ dispersal of a *Tarentola* species back to the Old World (Gamble *et al.* 2011, p. 238). In the same way that allopatric lineages within *Tarentola* are incongruent with the expectations of chance dispersal, so too is the allopatry of *Tarentola* and its New World sister group (Fig. 1C).

A vicariance explanation for *Tarentola* suggests that the allopatric clades are local products of a widespread ancestral distribution across much of northern Africa, at least eastern Macaronesia, and much of the New World. The phylogenetic sequence indicates initial vicariance between *Tarentola* and its American sister group, perhaps in the vicinity of what is now the Caribbean where both are present but allopatric. Divergence of the two groups may have occurred when the Caribbean oceanic plateau collided with the Great Arc of the Antilles (Hastie and Kerr 2010). The trans-Atlantic disjunction

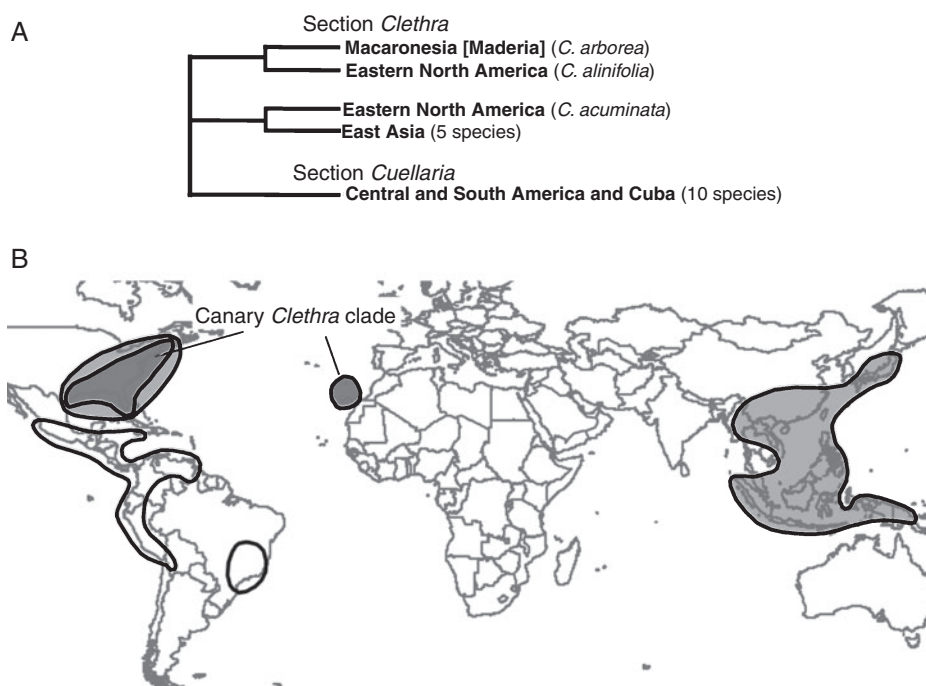


Fig. 2. Relationships of Macaronesian *Clethra*. A. Phylogeny of Macaronesian relationships (Fior *et al.* 2003, fig. 1). B. Biogeography of *Clethra*. (Distribution data from Fior *et al.* 2003).

can be dated to the opening of the Atlantic basin (Heads 2012, p. 416). The absence of living or fossil *Tarentola* from North America, and the occurrence of a single species complex mostly in southern Europe (Harris *et al.* 2004; Rato *et al.* 2012), may be consequences of the ancestral range being centred on or south of the Tethys Sea. The existence of three allopatric *Tarentola* lineages within Macaronesia suggests that the differentiation of each lineage encompassed multiple islands, rather than being generated by sequential chance dispersal among individual islands.

(2) *Biogeographic affinities of Macaronesian Clethra*
(Angiospermae: Clethraceae)

The Macaronesian *Clethra arborea* Aiton has been extirpated from the Canary Islands but survives on Madeira (Sjögren 2000) and, as an exotic introduction, in the Azores (Moniz and Silva 2004). Its sister group is *C. alnifolia* L. in eastern North America (Fig. 2A). The pair has an unresolved relationship with a North American–East Asian clade and another American clade (section *Cuellaria*; Fior *et al.* 2003, fig. 1) (Fig. 2B). This pattern is consistent with the Macaronesian species having evolved from a widespread ancestor present in both eastern North America and

Macaronesia. The ancestral range may have included Europe, as suggested by a fossil species there (*C. cimbrica* Friis, 1985). The presence of *C. arborea* on Madeira, despite the island's young age, and the absence of *Clethra* from the African mainland, were perplexing to Fior *et al.* (2003), but they did not consider possible prior occupancy of former islands or extinction in Africa.

(3) *Biogeographic affinities of Macaronesian Morella*
(Angiospermae: Myricaceae)

The geographic distribution of this genus is similar to that of *Clethra*, but *Morella* has additional species in East Africa and Madagascar. The pair of Macaronesian species has an unresolved relationship with an Africa–Madagascar group and a New World group (Fig. 3A). This clade is the sister group to two further species in the United States, followed by a group in eastern Asia (Herbert 2005, fig. 1). A vicariance origin could involve separation of a New World–Macaronesia ancestor or a New World–Old World ancestor, with subsequent vicariance between Macaronesia and the Old World mainland (Fig. 3B). Further phylogenetic resolution is required to determine whether

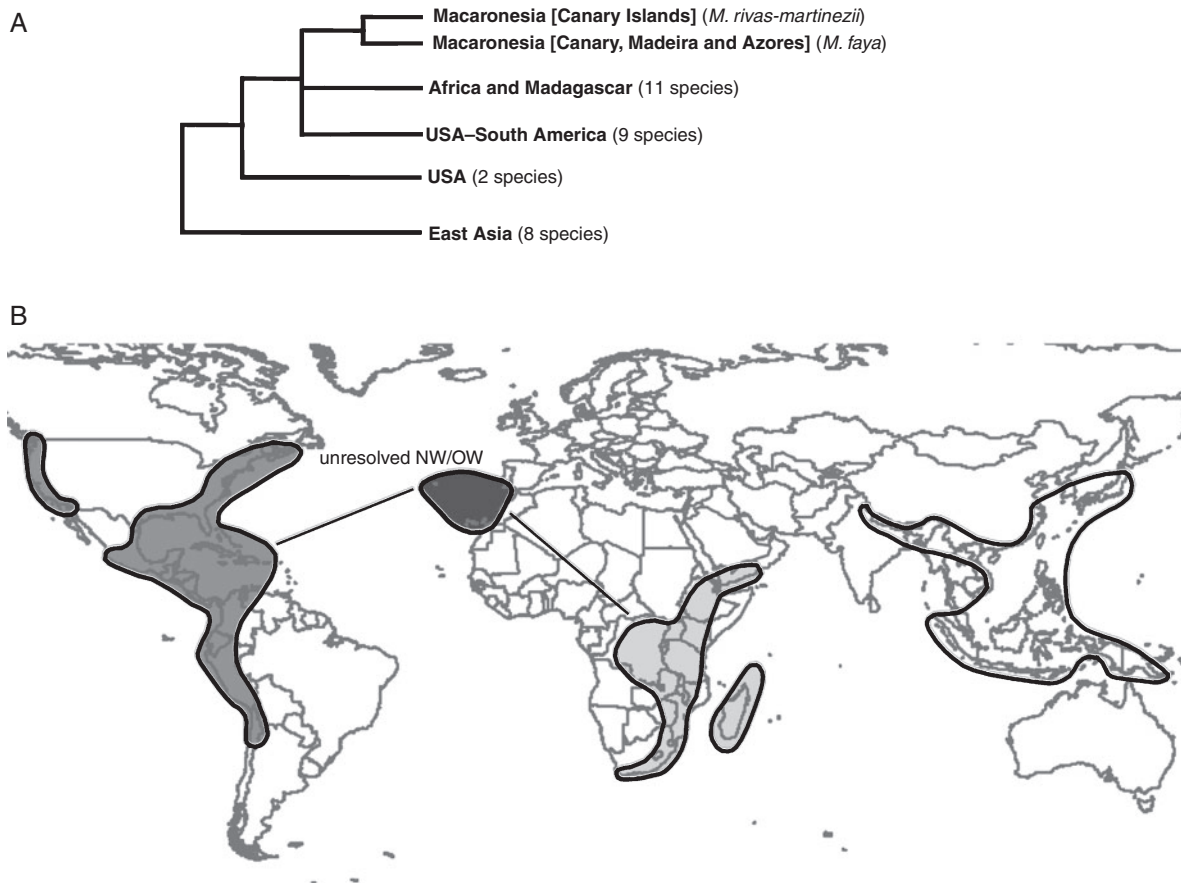


Fig. 3. Relationships of Macaronesian *Morella*. A. Phylogeny of Macaronesian relationships (Herbert 2005, fig. 1). B. Biogeography of *Morella*. Distribution data are from Herbert (2005).

the Macaronesian relationship with America is direct or also involves the East Africa–Madagascar clade.

(4) *Biogeographic affinities of Macaronesian Persea–Apollonias (Angiospermae: Lauraceae)*

The *Persea–Apollonias* clade occurs in America, Macaronesia and eastern Asia (Li *et al.* 2011). The monotypic Canary Island *Apollonias* is sister to species in southern Mexico and Guatemala, whereas the Azores–Canary–Madeira *P. indica* is sister to species in south-eastern United States and South America (Fig. 4A). Both clades display trans-Atlantic relationships (Fig. 4B), and together they are the sister group of an eastern Asian clade of ~36 species (Li *et al.* 2011, fig. 4; Fig. 4C).

Chance dispersal would require a complex series of migrations between Asia, Macaronesia and the New World that would somehow generate a geographic pattern similar to that of *Clethra* (Fig. 2B) and *Ilex* (see below). A vicariance explanation requires only a widespread ancestor connecting all three regions, followed by an initial split separating the Asian clade from the ancestor of the Macaronesian–American group and further vicariance within the latter. The Macaronesian–American groups may be historically correlated with opening of the Atlantic basin, whereas divergence of the Asian group may be related to closure of the Tethys Sea. It is also possible that the disjunction of the eastern North American and Andean

species is a consequence of the penetration of the Caribbean plate between North and South America (cf. Heads 2016).

(5) *Biogeographic affinities of Macaronesian Ilex (Angiospermae: Aquifoliaceae)*

Ilex (600 species) is distributed in tropical America, Macaronesia and Eurasia (Loizeau *et al.* 2005). There are two Macaronesian species, *I. canariensis* Poir, 1813 in the Canary Islands, and *I. perado* Aiton, 1789 with several subspecies in the Azores, Madeira, Canary Islands and southern Spain. Manen *et al.* (2010, figs 3, 4) identified the sister group of *I. canariensis* as either an American clade (nuclear DNA), or an eastern North American–Asian clade (plastid DNA; Fig. 5A). In contrast, *I. perado* is sister to the widespread European and North African *I. aquifolium* L. (Manen *et al.* 2010, fig. 4), and this pair is the sister group of western Asian clade (Fig. 5B).

The affinities of *I. canariensis* are trans-Atlantic (Fig. 5C), whereas *I. perado* has affinities in western Eurasia (Fig. 5D). The contrasting geographic patterns suggest an overlap between two ancestral lineages in Macaronesia, as part of a broad ancestral range encompassing both the New and Old Worlds. Geographic overlap between the two clades within Macaronesia may be the result of local dispersal. The geographic overlap between *I. perado* and its sister species in southern Iberia also indicates local range expansion of either or both species in that area. Fossil pollen records indicate that *Ilex* had already originated by the mid-Cretaceous (Loizeau *et al.* 2005).

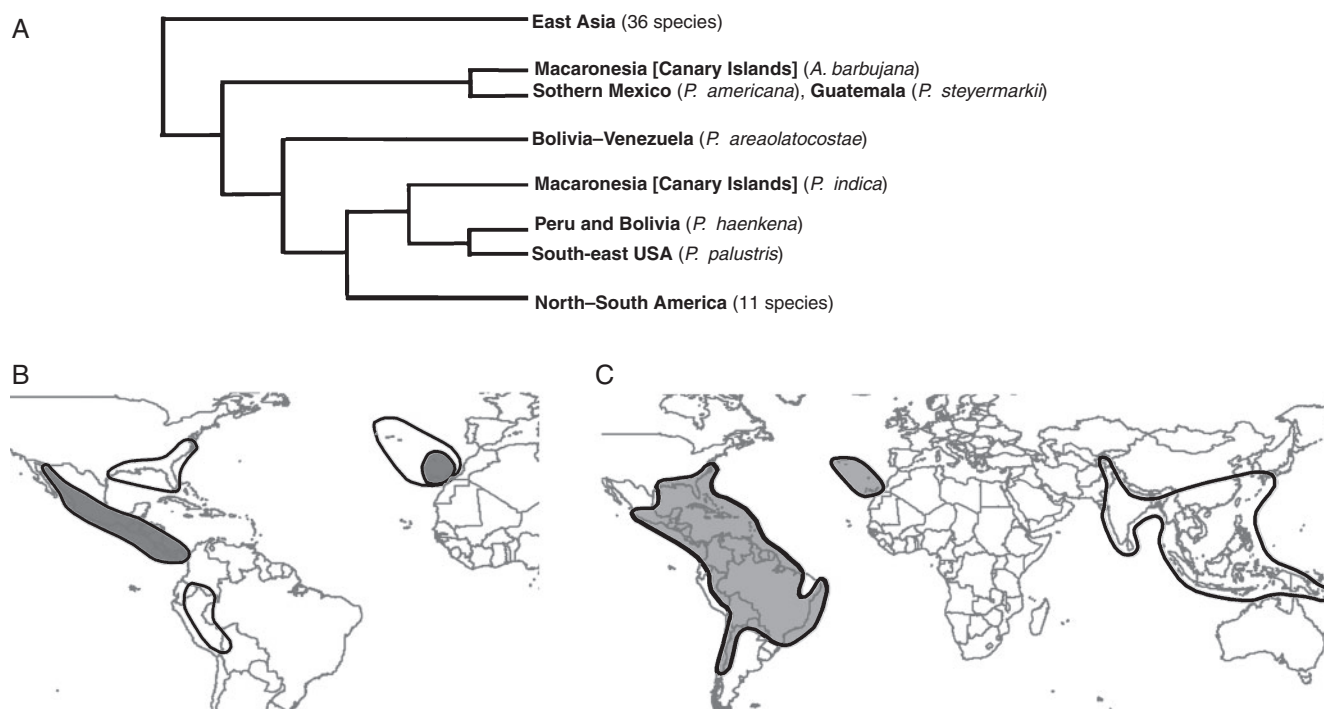


Fig. 4. Relationships of Macaronesian *Persea–Apollonias*. A. Phylogeny of Macaronesian relationships (Li *et al.* 2011, fig. 4). B. Trans-Atlantic biogeography of two Macaronesian *Persea* clades: *Apollonias* clade (shaded) and *Persea indica* clade (outline). C. Global biogeography of the *Persea–Apollonias* clade. Distribution data are from Seiler *et al.* (2016a, 2016b), Coder (2007), Smith (1966), Li *et al.* (2011).

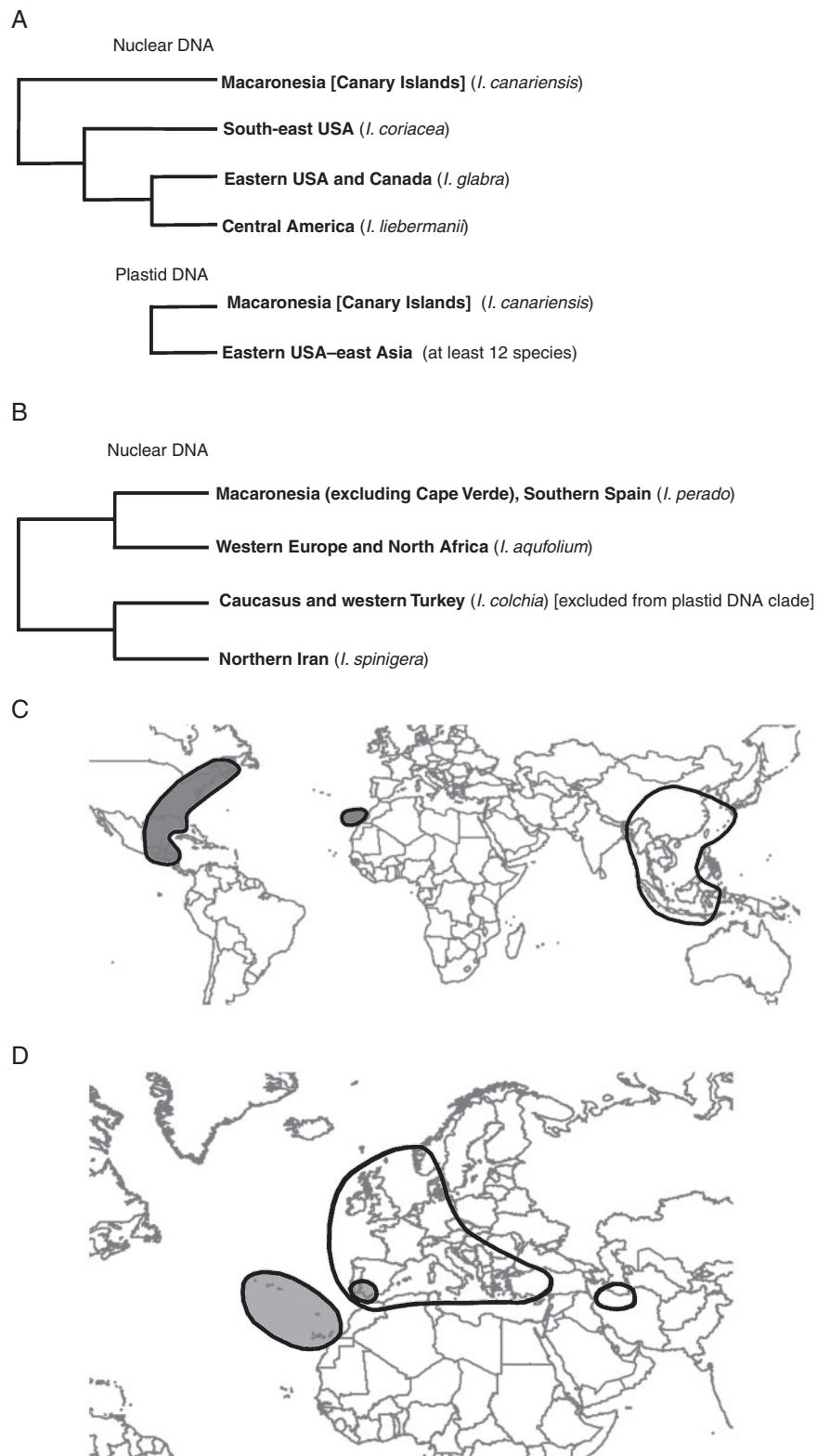


Fig. 5. Relationships of Macaronesian *Ilex*. A. Phylogenetic relationships of Macaronesian *Ilex canariensis* (Manen *et al.* 2010, figs 3, 4). B. Phylogenetic relationships of Macaronesian *Ilex perado* clade (Manen *et al.* 2010, fig. 4). C. Biogeography of *Ilex canariensis* clade: nuclear DNA clade (shaded), East Asia plastid DNA sistergroup (includes the North American species; outline). Distribution data from base.sp2000.cn/, gbif.org. D. Biogeography of *Ilex perado* (shaded) and sister taxa (outline). Distribution data are from Andrews (1984).

(6) *Biogeographic affinities of Macaronesian Roccella*
(Arthoniomycetes: Roccellaceae)

This genus of coastal fungi with 31 species includes a Macaronesian clade of four species that has its sister group in the New World (Fig. 6A; Tehler *et al.* 2010, fig. 16). Alternative chance dispersal and vicariance possibilities were considered by Tehler *et al.* (2009a), who contrasted the possibility of a single chance dispersal from somewhere in the Old World (probably the ‘ancient’ Macaronesian region) to the New World, with the idea of vicariance in an American–Macaronesian species group already distributed over an ancient region including parts of the New and Old World continents. For the latter model, Tehler *et al.* (2009a) suggested that the American and Macaronesian populations would have become increasingly isolated during the late Jurassic and fully separated in the late Cretaceous by formation of the South Atlantic. Tehler *et al.* (2009a) noted that the vicariance model ‘may seem somewhat inconceivable’ because it requires precursors to the genus to have evolved along the coasts of the western Tethys Sea over 200 million years ago. The Galapagos distribution was

regarded as evidence of dispersal playing an important role in the distribution of *Roccella* (Tehler *et al.* 2009b), but a vicariance origin involving former island arcs is also possible (cf. Craw *et al.* 1999; Grehan 2001; Heads 2016).

Only one of the four Macaronesian species is endemic within Macaronesia, namely, *R. elisabethae* Tehler, 2004 in the archipelagos of the Canaries, Madeira and Cape Verde (Tehler *et al.* 2004). This species has the basal sister group of *R. tinctoria* DC of Macaronesia (including the Azores) as well as the western Mediterranean and Atlantic coast between Portugal and Senegal, and *R. tuberculata* Vain with a similar range except for the Mediterranean. These species together are the sister group of *R. phycopsis* (Ach, 1810), also with a similar widespread range that extends to the entire Mediterranean (Fig. 6B). The disjunct Baja California, Galapagos, Peru and eastern Caribbean localities for the New World sister group highlight important distributional centres for this region (Heads 2016) and are comparable in particular to the general distribution centres for *Phyllodactylus* lizards (Grehan 2001). The allopatry between the New and Old World *Roccella* is consistent with vicariance of a widespread

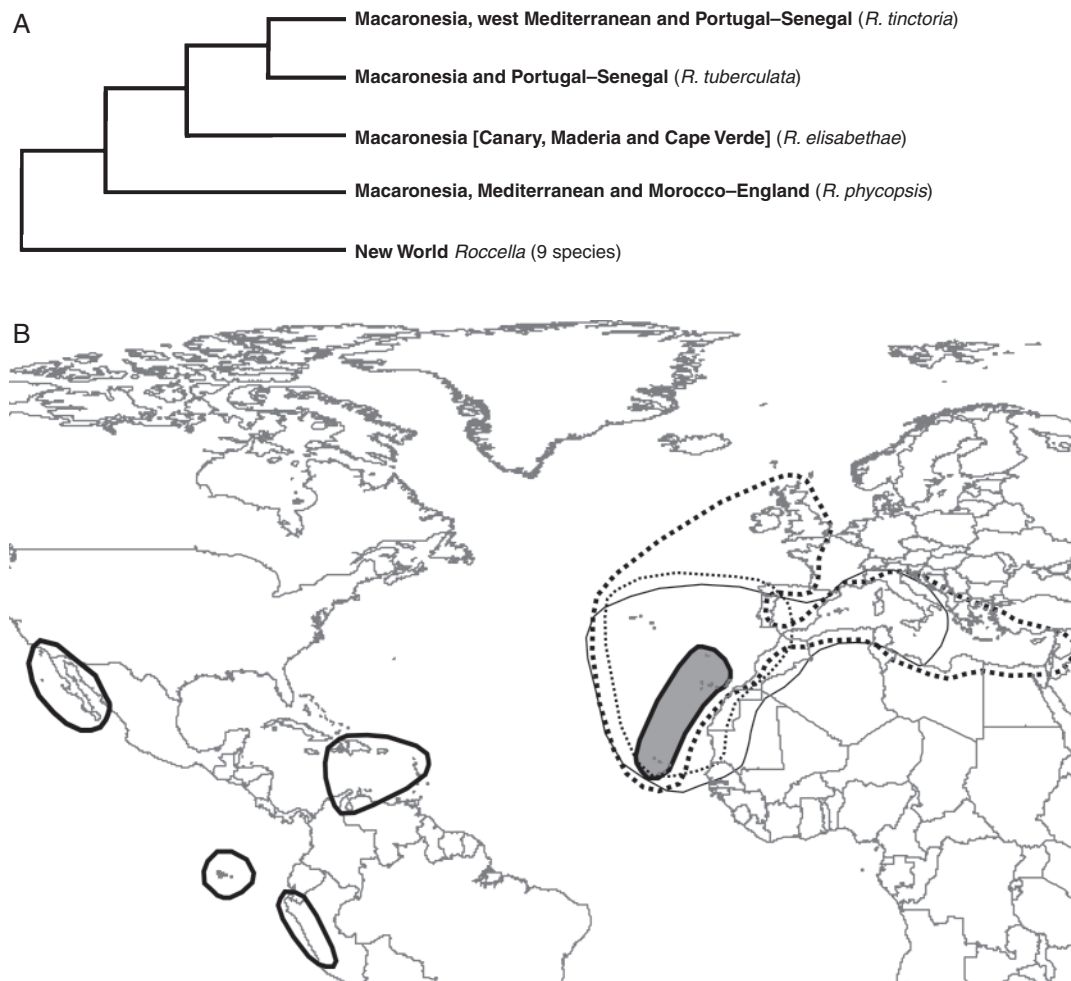


Fig. 6. Relationships of Macaronesian *Roccella*. A. Phylogenetic relationships of Macaronesian *Roccella* (Tehler *et al.* 2010, fig. 16). B. Biogeography: *R. elisabethae* (shaded), *R. tinctoria* (thin outline), *R. tuberculata* (dotted outline), *R. phycopsis* (dashed outline), and New World sister group (solid outline). Distribution data are from Tehler *et al.* (2004, 2009a, 2009b, 2010).

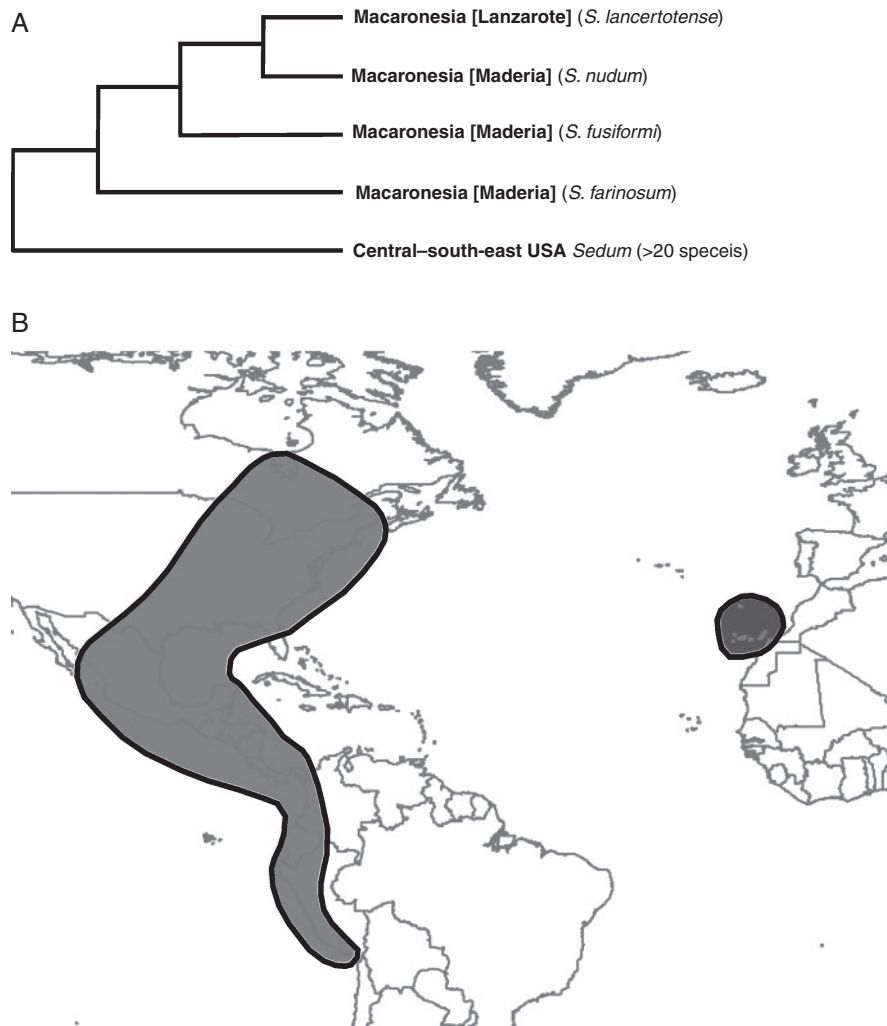


Fig. 7. Relationships of Macaronesian *Sedum* subclade. A. Phylogenetic relationships of Macaronesian *Sedum* subclade (Mort *et al.* 2001, fig. 2). B. Biogeography of *Sedum* subclade and New World sister group. Distribution data from International Crassulaceae Network (<http://www.crassulaceae.ch/>, accessed 21 March 2017).

ancestor distributed between the Galapagos hotspot and Macaronesia, followed by subsequent dispersal that has resulted in considerable (but not complete) sympatry of the Macaronesian species.

(7) *Biogeographic affinities of Macaronesian Sedum*
(Angiospermae: Crassulaceae)

Four Macaronesian species of *Sedum* are the sister group of 20 species in North and South America (Mort *et al.* 2001, fig. 2). The American range extends between eastern North America and Peru, but does not include the Caribbean. The trans-Atlantic disjunction may have resulted from vicariance of a widespread ancestor (Fig. 7). The Macaronesia–America clade does not have high bootstrap support, and Mort *et al.* (2002) cautioned that more phylogenetic work is needed to resolve the relationships.

(8) *Biogeographic affinities of Macaronesian Dirina*
(Arthoniomycetes: Roccellaceae)

The fungus *Dirina* is distributed between Peru and the United States, and across Europe, Africa and India (Tehler *et al.* 2013). A clade comprising *D. cretacea* (Zahlbr.) Tehler of the Mediterranean and its sister group in Cape Verde, Senegal and the Galapagos (Tehler *et al.* 2013, fig. 8; Fig. 8A) has a trans-Atlantic-Mediterranean relationship (Fig. 8B). Initial divergence separated the Mediterranean *D. cretacea* from the rest, and this was followed by differentiation in the Galapagos–Cape Verde–Senegal ancestor. Tehler *et al.* (2013, p. 434) thought the general distribution patterns of *Dirina* were best explained by vicariance, but they also suggested that long-distance dispersal was the only possible explanation for the Galapagos–Cape Verde clade. Tehler *et al.* (2013) accepted the fossil-calibrated dates for *Dirina* and *Roccella* (Section 6) at 20–30 million years ago as actual clade ages, and they concluded that long-distance dispersal is necessary

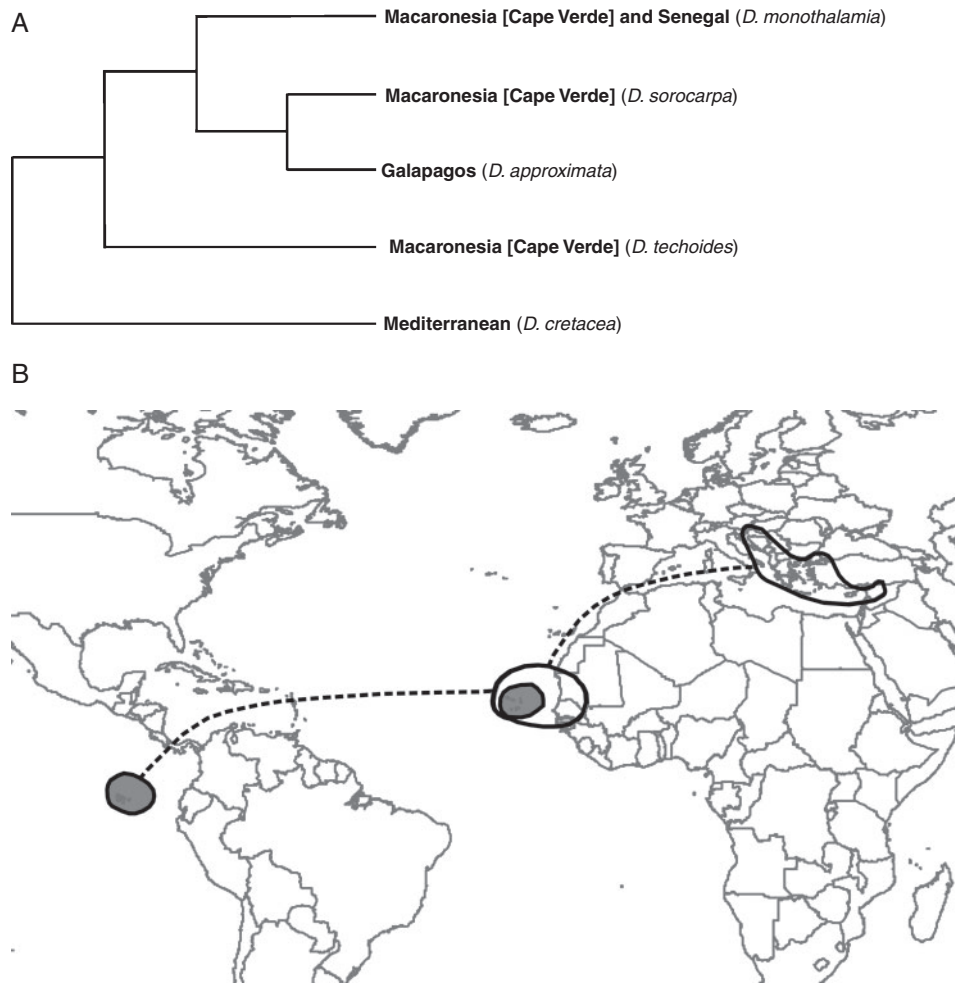


Fig. 8. Relationships of Macaronesian *Dirina*. A. Phylogeny of Macaronesian relationships (Tehler *et al.* 2013, fig. 8). B. Biogeography of Cape Verde *Dirina*: sister species *D. approximata* and *D. sorocarpa* (shaded), Cape Verde sister species and *D. cretacea* (outline). Hypothesised Tethyan links are indicated by dashed lines. Distribution data are from Tehler *et al.* (2013).

to explain the trans-Atlantic distributions. However, because molecular calibrations provide only minimal divergence dates, there is no evidence precluding an older vicariance history mediated by tectonics.

(9) *Biogeographic affinities of Macaronesian Morlockia* (Crustacea: Remipedia)

In the Remipedia, a single species lives in fully marine caves, whereas the rest inhabit anchialine caves fed by both terrestrial freshwater and oceanic seawater through subterranean channels. Two species from the Canary Islands (Fig. 9A) are nested in an otherwise Caribbean clade (Hoenemann *et al.* 2013, fig. 4). This whole group is sister to a species in Western Australia (Neiber *et al.* 2011; Hoenemann *et al.* 2013). The Macaronesia–Caribbean clade forms a trans-Atlantic relationship that may be part of a larger ancestral distribution associated with Tethys (Fig. 9B). Hoenemann *et al.* (2013) noted that the distribution of remipedes is compatible with the hypothesis that many widespread, disjunct, anchialine

species have descended from marine species in the Tethys Ocean, and that the disjunctions can be explained by seafloor spreading.

(10) *Biogeographic affinities of Macaronesian Metacrangonyx* (Crustacea: Metacrangonyctidae)

Of the 12 species of *Metacrangonyx*, two occur in Hispaniola and the remainder is in the Mediterranean basin, north-western Africa, and Macaronesia (Fuerteventura). Bauzà-Ribot *et al.* (2012, fig. 2) identified an ‘insular clade’ in which the Canary Islands species is sister to a pair from Hispaniola and the Mediterranean (Fig. 10A). Vicariance within this Atlantic clade would have separated the ancestor of the Macaronesian *M. repens* from the ancestor of the Caribbean and Mediterranean subclades before formation of the Atlantic (Fig. 10B). Bauzà-Ribot *et al.* (2012) estimated that the insular clade originated at 79 million years ago (95% HPD 60–108 million years ago), using a calibration based on separation of the Balearic Islands (16 million years ago), the Messinian Salinity Crisis

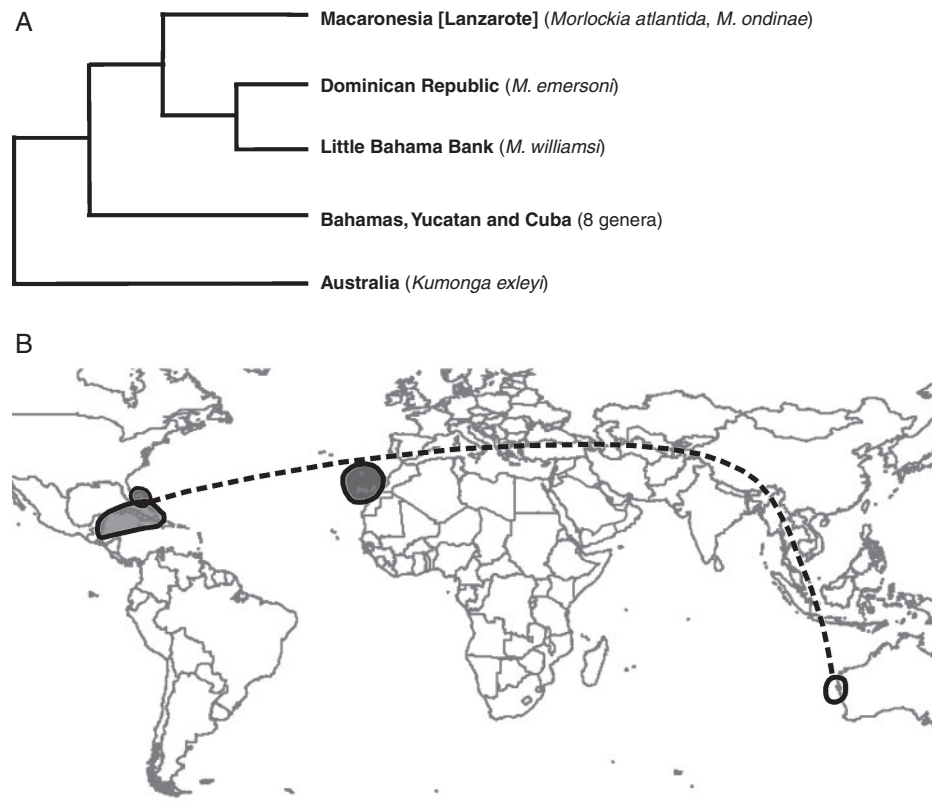


Fig. 9. Relationships of Macaronesian Remipedia. A. Phylogeny of Macaronesian remiped relationship (Hoenemann *et al.* 2013, fig. 4). B. Biogeography: Lanzarote–Bahamas subclade (dark shading), paraphyletic group of Caribbean species (light shading) and Australian sister species (outline). Hypothesised Tethyan link in indicated as a dashed line. Distribution data are from Neiber *et al.* (2011).

(5.5 million years ago) and uplift of the Marrakech High Atlas (37.2–25.0 million years ago). The authors regarded the divergence estimate as compatible with vicariance. At 79 million years ago, the Caribbean, the eastern Atlantic and western Mediterranean formed a continuous seaway, with their shores and islands much closer to each other than at present, and Bauzà-Ribot *et al.* (2012) suggested that the ancestor was a shallow-water marine species that populated shallow banks or strips of coast and possibly the earliest paleo-Macaronesian islands.

(11) *Biogeographic affinities of Macaronesian Hemidactylus*
(Reptilia: Gekkonidae)

This genus is widely distributed on islands and continents, and comprises 80 species, with three being endemic to Cape Verde (Carranza and Arnold 2006; Arnold *et al.* 2008). Analysis by Arnold *et al.* (2008, fig. 2) generated a sister-group relationship between a Cape Verde clade and a Kenya–São Tomé and Príncipe clade. Together, these two clades are sister to *H. brasiliensis* of Brazil (Fig. 11A). The Cape Verde group is part of a disjunct eastern Atlantic–East Africa group that has a trans-Atlantic relationship with an American group (Fig. 11B).

The São Tomé–Príncipe and East Africa–Madagascar affinity is a pattern repeated in other taxa, and the islands São Tomé and Príncipe also include other taxa with sister groups in America

(Heads 2014b). It is also evident within *Hemidactylus*, for a sister species relationship between *H. angulatus* Hallowell, 1854 of adjacent Bioko Island and *H. haitianus* Meerwarth, 1901 of Cuba that together belong to another Cape Verde–African group (Carranza and Arnold 2006, fig. 1: Clade 2). On the basis of the oldest exposed lavas, Príncipe is at least 31 million years old and São Tomé is at least 13 million years old. The islands are part of the Cameroon Volcanic Line (CVL), which is a line of magmatism that predates the individual volcanoes (including those on the African mainland). It has been episodically active since the end of the Cretaceous, with alkaline intrusive magmatism from 65 to 30 million years ago and volcanism recorded from at least 35 million years ago. The CVL connects to the Benue trough, which was active from the early Cretaceous and is associated with opening of the Atlantic basin (Heads 2012, fig. 5-2, 2014b). The locations and phylogenetic relationships in taxa such as *Hemidactylus* reflect this geological and tectonic history.

(12) *Biogeographic affinities of Macaronesian Chioninia*
(Reptilia: Scincidae)

The two species of *Chioninia* in Cape Verde are the sister group of *Trachylepis*, distributed across sub-Saharan Africa and Madagascar (Karin *et al.* 2016, fig. 1). These groups together comprise the sister group of *Mabuya* in southern Central America,

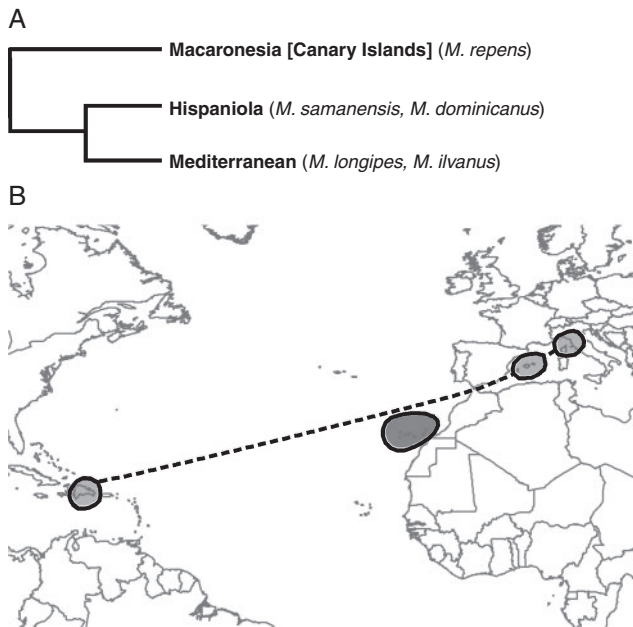


Fig. 10. Relationships of Macaronesian *Metacrangonyx* clade. A. Phylogeny of Macaronesian relationships (Bauzá-Ribot *et al.* 2012, fig. 2). B. Biogeography: Canary Islands *M. repens* (dark shading) and Hispaniola–Mediterranean sister group (light shading). Hypothesised Tethyan connection in indicated as a dashed line. Distribution data are from Bauzá-Ribot *et al.* (2012)

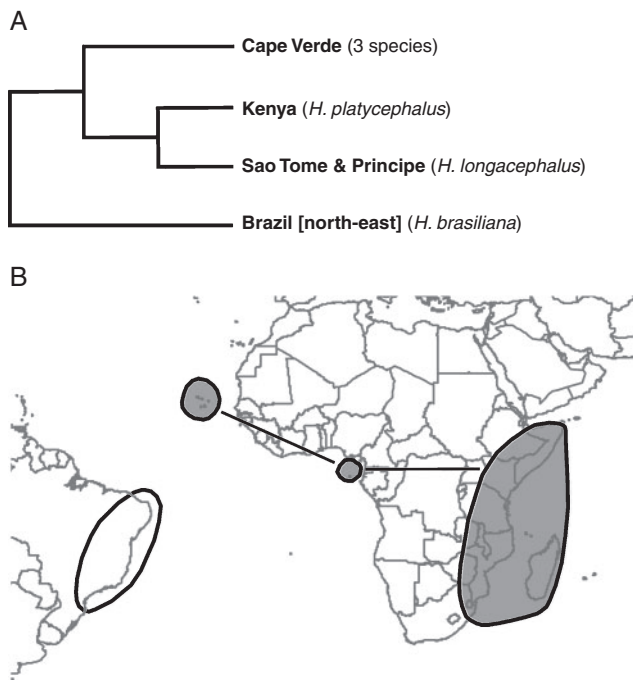


Fig. 11. Relationships of Macaronesian *Hemidactylus*. A. Phylogeny of Macaronesian relationships (Arnold *et al.* 2008, fig. 2). B. Biogeographic relationships of Macaronesian *Hemidactylus*: Cape Verde–Sao Tome & Principe–East Africa clade (shaded) and Brazilian sister species (outline). Distribution data are from <http://reptile-database.reptarium.cz/>, accessed 21 March 2017).

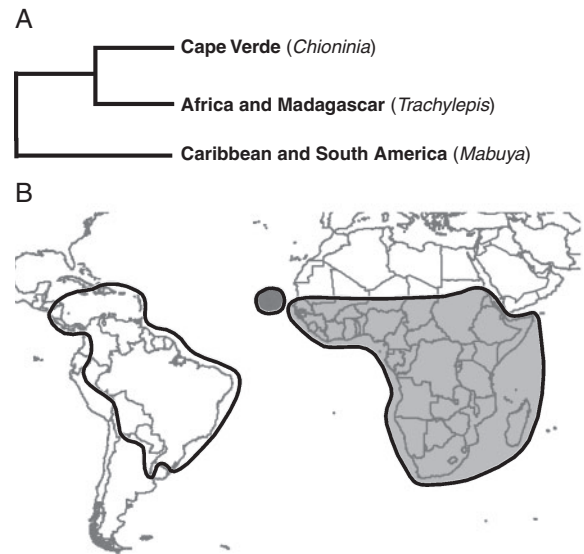


Fig. 12. Relationships of Macaronesian *Chioninia*. A. Phylogeny of Macaronesian relationships (Karin *et al.* 2016, fig. 1). B. Biogeography of Macaronesian relationships: *Chioninia* (dark shading), *Trachylepis* (light shading) and *Mabuya* (outline). Distribution data are from Karin *et al.* (2016).

the Caribbean, and northern South America (Fig. 12A). Karin *et al.* (2016, fig. 2) attributed the distributions of *Chioninia* and *Mabuya* to chance-dispersal events from Africa; however, this is contradicted by the basal position of *Mabuya*. The allopatric distribution (Fig. 12B) suggests a simple alternative, namely, that a widespread ancestor occupied America, Africa, Madagascar, and Cape Verde along with other island regions (Socotra, Comoros, Seychelles, São Tomé). The initial phylogenetic break, correlated with the opening of the South Atlantic, separated *Mabuya* from the Old World group, and this was followed by vicariance between *Chioninia* and *Trachylepis* in the Old World.

(13) Biogeographic affinities of Macaronesian *Ocotea* (Angiospermae: Lauraceae)

Ocotea is a widespread Old and New World group. The Macaronesian *Ocotea foetens* (Aiton) Baill. is the basal member of an Old World clade that is the sister group of a Mexico–South America clade (Fig. 13A) (Chanderbali *et al.* 2001, fig. 3). *Ocotea foetens* is most closely related to species in East Africa and Madagascar, although additional species in West Africa have not been sampled (Fig. 13B). The distribution is consistent with vicariance of a widespread ancestral range across much of the New World, Africa and Madagascar, in which *Ocotea* differentiated after formation of the Atlantic basin, and initial divergence within *Ocotea* occurred between Macaronesia and mainland Africa.

(14) Biogeographic affinities of Macaronesian Dryopteris (Pteridophyta: Dryopteridaceae)

The Canary Islands *D. oligodonta* (Desv.) Pic. Serm. is sister to *D. odontoloma* (Moore) C. Chr. of southern China, and the pair is sister to *D. pallida* (Bory) Fomin of Europe (Fig. 14A). This whole Eurasian clade is the sister group of another disjunct

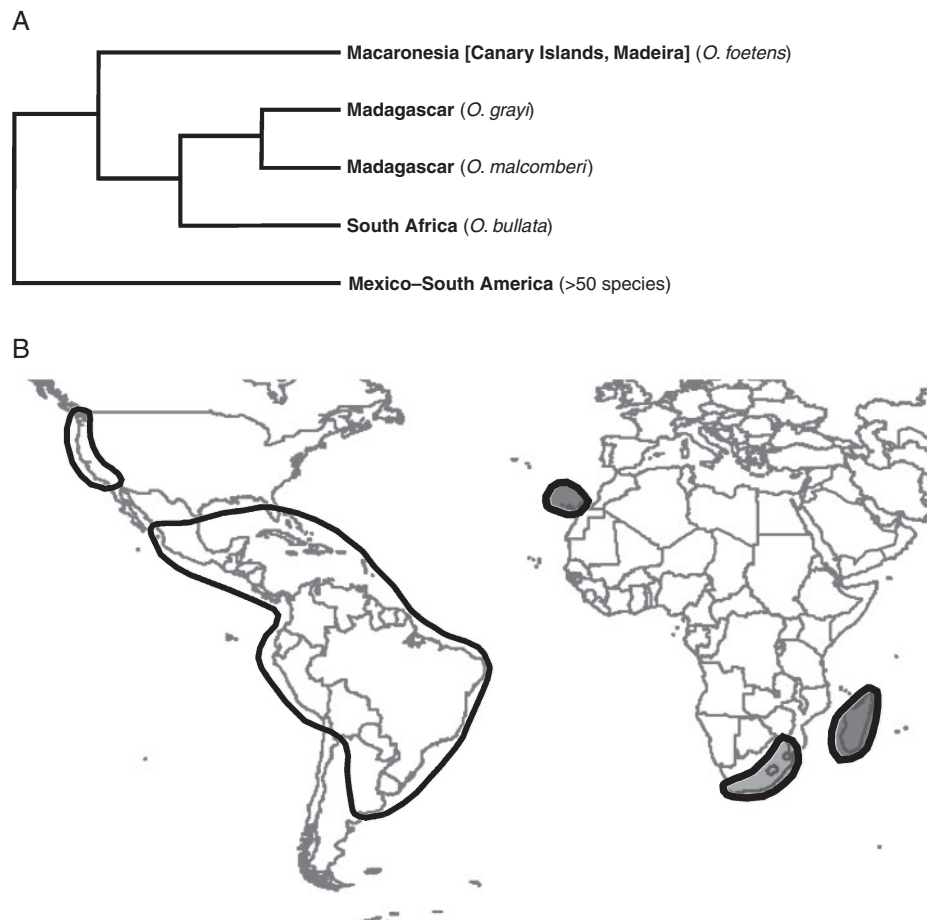


Fig. 13. Relationships of *Ocotea*. A. Phylogeny of Macaronesian relationships (Chanderbali *et al.* 2001, fig. 3). B. Biogeography of Macaronesian relationships: New World clade (outline), sampled Old World clade (shaded, thick outline) and unsampled species (shaded, thin outline). Distribution data are from Chanderbali *et al.* (2001), Williams *et al.* (2008) and World Conservation Monitoring Centre (1998).

species pair comprising *D. goldiana* (Hook. ex Goldie) A. Gray of North America and *D. monticola* (Makino) C. Chr. of Japan (Sessa *et al.* 2012, figs 3, 4).

Although the biogeographic origin of the Macaronesian species was not directly addressed, Sessa *et al.* (2012, p. 731) noted that, in general, long-range dispersal is the expected explanation for the biota of oceanic islands that have no physical connection to mainland source areas. But the disjunct affinity between the continental species *D. goldiana* and *D. odontoloma* was recognised as a well known pattern in other plants, and although long-distance dispersal could not be ruled out, the repeated ‘shared pattern of movement’ was thought to favour vicariance (Sessa *et al.* 2012, p. 744).

Allopatry within the *D. oligodonta* group (Fig. 14B) is consistent with the former existence of a widespread ancestor in Macaronesia, the rest of the Old World and the New World, that existed before differentiation of the modern species. Atlantic vicariance resulted in one group encompassing the New World and Old World (ancestor of *D. goldiana* and *D. monticola*) and another distributed between Macaronesia and eastern Asia. Subsequent vicariance in the Old World group resulted in the

differentiation between the Mediterranean *D. pallida* and the common ancestor of *D. oligodonta* and *D. odontoloma*. The latter differentiated into at least two species (both extant), followed by extinction across intermediate regions, a process that also explains the disjunction between *D. goldiana* and *D. monticola*.

(15) Biogeographic affinities of Macaronesian *Cneorum* (Angiospermae: Rutaceae)

The Macaronesian *Cneorum pulverulentum* Vent. has a Mediterranean sister species, and these two form the sister group of a south-eastern African clade (Fig. 15A). This group is sister to the largely allopatric *Harrisonia*, which is widespread in Australia and Africa (Appelhans *et al.* 2011, fig. 3). This whole group is sister to three genera in the Caribbean and South America (Fig. 15B). Using fossil-calibrated divergence dates, Appelhans *et al.* (2012) proposed a Late Cretaceous (78–58 million years ago) origin. Because this estimate post-dated the Atlantic separation of South America and Africa, the authors concluded that the group dispersed to South America at a time when the two continents were separated, but still quite close

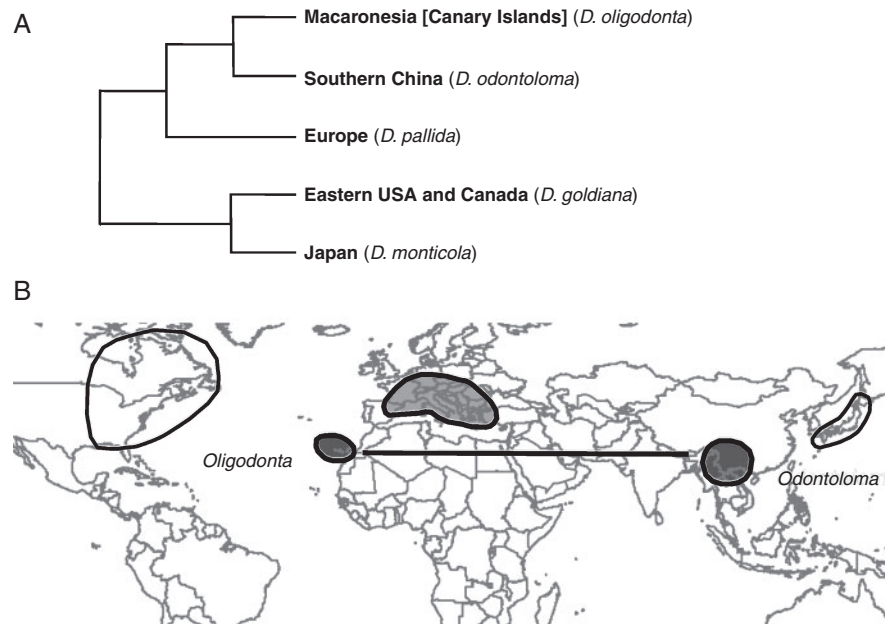


Fig. 14. Relationships of Macaronesian *Dryopteris*. A. Phylogeny of Macaronesian relationships (Sessa *et al.* 2012, figs 3, 4). B. Biogeography of Macaronesian relationships: *D. oligodonta* and *D. odontoloma* (dark shading) connected by track of hypothesised ancestral range; and sister clades *D. pallida* (light shading) and *D. goldiana*–*D. monticola* (outline). Distribution data are from Plants USDA (<http://plants.usda.gov/> accessed 21 March 2017), Flora Sicilia (<http://florasicilia.altervista.org/pagina-784937.html>) and GBIF (<http://www.gbif.org/>, accessed 20 March 2017).

to each other. Nevertheless, the authors accepted that fossil calibrations provide only minimal ages that do not preclude older vicariance. An estimated Miocene divergence of Canary Islands and Mediterranean lineages was seen to be consistent with a Canary Islands age of 20 Ma, but an older origin in north-western Africa or former paleo-Canary Islands was also acknowledged as a possibility. The predominant allopatry of *Cneorum* and its relatives suggests an origin of the Macaronesian *C. pulverulentum* by vicariance of a widespread ancestor, in which the initial break occurred with the Atlantic separation of the New and Old World clades. The Old World ancestor differentiated into *Harrisonia* and a Macaronesian–African ancestor. Extinction of northern African representatives resulted in a disjunction between the Macaronesian–Mediterranean ancestor and relatives in southern Africa, and subsequent dispersal has resulted in partial geographic overlap between this group and *Harrisonia*.

(16) *Biogeographic affinities of Macaronesian Ruta*
(Angiospermae: Rutaceae)

The immediate sister group of the Canary Islands *Ruta* clade is a Moroccan–Mediterranean species (*R. montana*), and these together are the sister group of a Mediterranean clade of five species (Salvo *et al.* 2010, fig. 2). This whole group is sister to *Thamnosma* in eastern Africa and western North America, and *Boenninghausenia* in Asia (Fig. 16A). The origin of the Canary Island species has been attributed to a single, long-distance dispersal event and the origin of the American *Thamnosma* to ‘possible’ migration across the Bering Land Bridge (Salvo *et al.* 2010, pp. 716, 717). The allopatric relationship between the

Canary Islands clade and its mainland sister group, along with the allopatry between *Ruta* and its sister taxa (Fig. 16B), supports vicariance of a widespread New and Old World ancestor, with the initial phylogenetic break occurring between the Macaronesian–Mediterranean ancestor and the *Thamnosma*–*Boenninghausenia* ancestor. Later, *Thamnosma* was fragmented by the opening of the Atlantic Ocean, whereas *Thamnosma*–*Boenninghausenia* was fragmented by the opening of the Indian Ocean. The only biogeographic evidence of dispersal is the sympatry between the Morocco–Mediterranean *R. montanus* clade and its Mediterranean sister.

(17) *Biogeographic affinities of Macaronesian Daucus*
(Angiospermae: Apiaceae)

A subclade of subfamily Scandiceae is present in Macaronesia, western Eurasia and America. In the Old World, the *Monzia*–*Melanoselinum* group of Madeira is sister to a group of a western Eurasian distribution including the Azores, Canary Islands, Mediterranean, Europe and western Asia. Within this group, the Azorean subspecies of *Daucus carota* L. and the Cape Verde genus *Tornabenea* form a clade with the European subspecies of *Daucus carota* (Fig. 17A) and this distribution is allopatric to *Cryptotaenia elegans* Webb ex Bolle, 1861 of the Canary Islands. This whole Old World complex is sister to a New World–Old World clade of *Daucus*–*Agrocharis* (Spalik and Downie 2007, fig. 2).

The clades overlap in the Mediterranean basin, in contrast to the allopatry of the clades within Macaronesia. This can be explained by overall vicariance followed by local dispersal causing geographic overlap of species in the Mediterranean

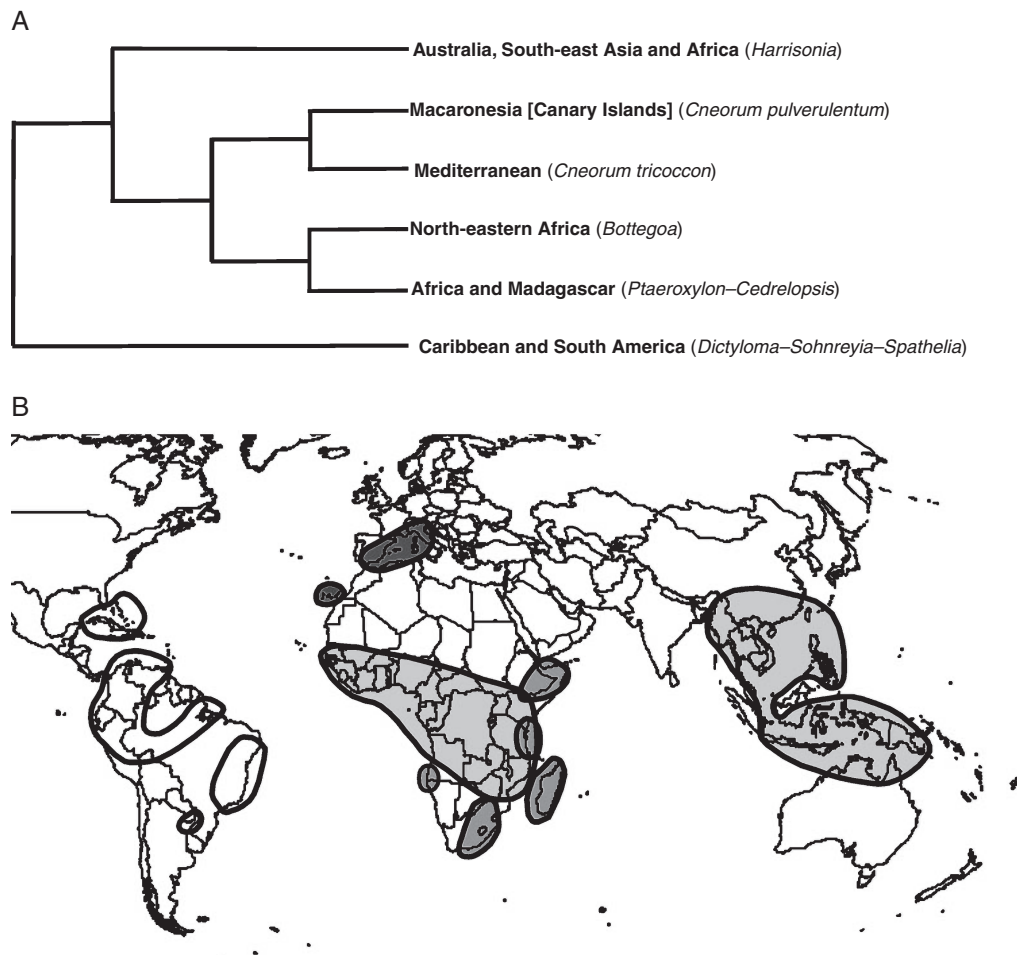


Fig. 15. Relationships of *Cneorum*. A. Phylogeny of Macaronesian relationships (Appelhans *et al.* 2011, fig. 3). B. Biogeography of Macaronesian relationships: *Cneorum* (dark shading), *Bottegoa* (Somalia–Ethiopia–Kenya), *Ptaeroxylon–Cedrelopsis* (south-eastern Africa–Madagascar; intermediate shading), *Harrisonia* (light shading) and *Dictyloma–Sohnreyia–Spathelia* clade (outline). Distribution data are from Appelhans *et al.* (2012) and African Plant Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php/>, accessed 20 March 2017).

(cf. *Tarentola* sympatry in North Africa). A vicariance origin for the group involves initial divergence between the southern New World–Old World *Daucus–Agrocharis* clade (Fig. 17B) and the ancestor of the remaining taxa, at least between Macaronesia and the eastern Mediterranean. Sequential vicariance of the northern ancestor generated the Madeira clade, the Canary Islands clade, and the Mediterranean–Azores–Cape Verde clade. The trans-Atlantic and trans-Indian Ocean disjunctions in the *Daucus–Agrocharis* group indicate that the ancestral range was at least as old as each ocean basin. The Atlantic and Indian Ocean range of *Daucus–Agrocharis* and the Macaronesia–Mediterranean clades parallel the distribution of *Ruta*.

(18) *Biogeographic affinities of Macaronesian Descurainia*
(*Angiospermae*: *Brassicaceae*)

The eight species of *Descurainia* in the Canary Islands comprise the sister group of *D. tanacetifolia* (L.) Prantl, 1892 in the Mediterranean, and this whole group is sister to New World clade of at least 37 species (Fig. 18A; Goodson *et al.* 2011, fig. 5).

The Macaronesian species might be attributed to chance dispersal from the Mediterranean, but this would not explain the trans-Atlantic sister group relationship. In addition, a dispersal narrative would require that the widespread New World clade (Fig. 18B) was able to disperse across the Atlantic only once, whether first to the Canary Islands or Mediterranean. A vicariance explanation requires only an initial divergence between the New and Old World clades caused by the formation of the Atlantic Ocean, and then vicariance of the Old World ancestor between Macaronesia and the Mediterranean. Absence of the New World clade from Central America and Caribbean may be the result of the intrusion of the Caribbean plate between North and South America (cf. Heads 2016).

(19) *Biogeographic affinities of Macaronesian Euphorbia*
subgen. Esula, section Paralias (*Angiospermae*:
Euphorbiaceae)

Euphorbia azorica of the Azores is the sister group of five Mediterranean species, and together this clade is sister to the

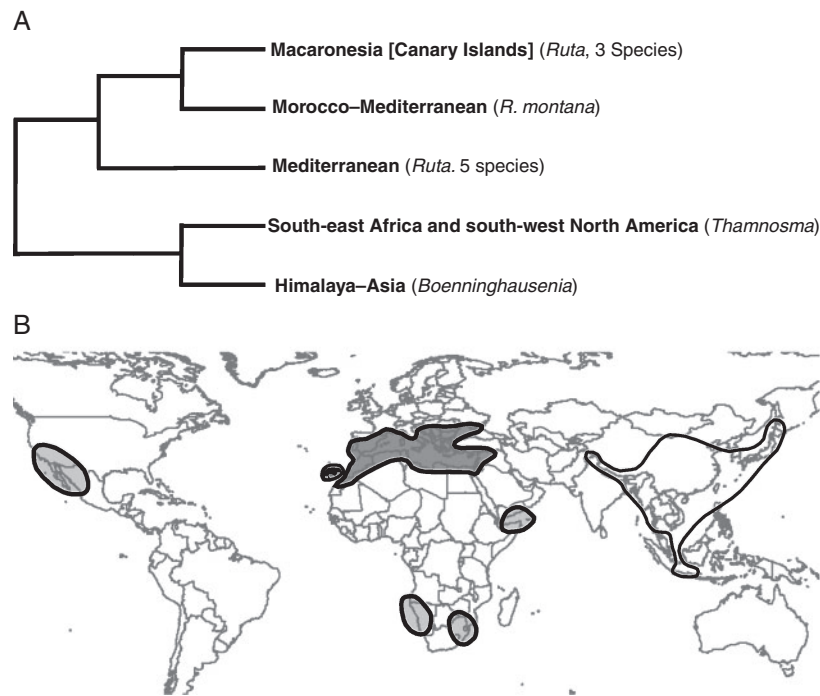


Fig. 16. Relationships of *Ruta*. A. Phylogeny of Macaronesian relationships (Salvo *et al.* 2010, fig. 2). B. Biogeography of Macaronesian relationships: Canary Islands *Ruta* (dark shading), paraphyletic sister species (intermediate shading), *Thamnosma* (light shading) and *Boenninghausenia* (outline). Distribution data are from www.gbif.org (accessed 20 March 2017), Salvo *et al.* (2010) and Thiv *et al.* (2011).

Caribbean *E. trichotoma* Kunth (Riina *et al.* 2013, fig. 5d; Fig. 19A). Riina *et al.* (2013) attributed the New World species to chance dispersal from Europe and the Mediterranean, and they noted that the Macaronesian species can be explained in the same way, as one of the ‘numerous examples of plant taxa that have diversified there following either single or multiple colonization events’ (p. 329). However, the phylogenetic and geographic pattern of the clade shown in Fig. 19B is compatible with an origin by simple vicariance of a widespread ancestor distributed in Macaronesia, Europe–Mediterranean and the Caribbean.

(20) *Biogeographic affinities of Macaronesian Fagonia*
(Angiospermae: Zygophyllaceae)

Fagonia has a ‘remarkably disjunct’ distribution in arid areas of the New World and Old World (Beier *et al.* 2004, p. 91). There are four principal clades (Beier *et al.* 2004, fig. 5), with the basal lineage in northern Mexico (Fig. 20A). The distribution (Fig. 20B) is explicable by vicariance of a widespread ancestor, with the initial break occurring in northern Mexico, followed by divergence of a Macaronesian–Mediterranean ancestor, and then Atlantic vicariance of a widespread New World–Old World ancestor. Axelrod (1970) regarded *Fagonia* and other dry tropical and subtropical plants as remnants of a dry flora that inhabited Gondwanaland before its breakup by seafloor spreading near the close of the Cretaceous. Beier *et al.* (2004, p. 104) attributed the New and Old World lineages to a Tertiary land bridge in the North Atlantic, whereas *Fagonia* in southern

Africa and South America were regarded as the result of chance dispersal. Neither the distribution nor the phylogenetic pattern is suggestive of a North Atlantic connection, whether this developed by vicariance or dispersal over a land bridge.

(21) *Biogeographic affinities of Macaronesian Vanessa*
(Lepidoptera: Nymphalidae)

The Macaronesian *Vanessa vulcania* Godart, 1819 is sister to a clade of five species in Southeast Asia, and this pair is sister to the Asian *V. indica* (Herbst), 1794 and *V. atalanta* L., 1758–*tameamea* Escholtz, 1821 (Fig. 21A; Wahlberg and Rubinoff 2011, fig. 1). The position of *V. vulcania* was not strongly resolved and may lie with either the Southeast Asian species or *V. indica*. All species of this group are largely or entirely allopatric, with some uncertainty regarding overlap of *V. atalanta* and *V. indica* in central Asia. Kostrowicki (1969, p. 282) suggested that the disjunct populations could be relicts of a former, much wider Tertiary range. Vane-Wright and Hughes (2007) considered this possibility but attributed the Macaronesian species to dispersal. The early Oligocene butterfly fossil *Vanessa amerindica* Miller & Brown, 1989 from Colorado, and an apparently extinct Newfoundland species (illustrated but unnamed) appeared to be closely related to the *V. indica* complex. Nevertheless, Vane-Wright and Hughes (2007) did not consider this to be sufficient evidence for the distribution of *Vanessa* being directly linked to the opening of the North Atlantic, because it would require the *V. indica* complex to be at least 70 million years old.

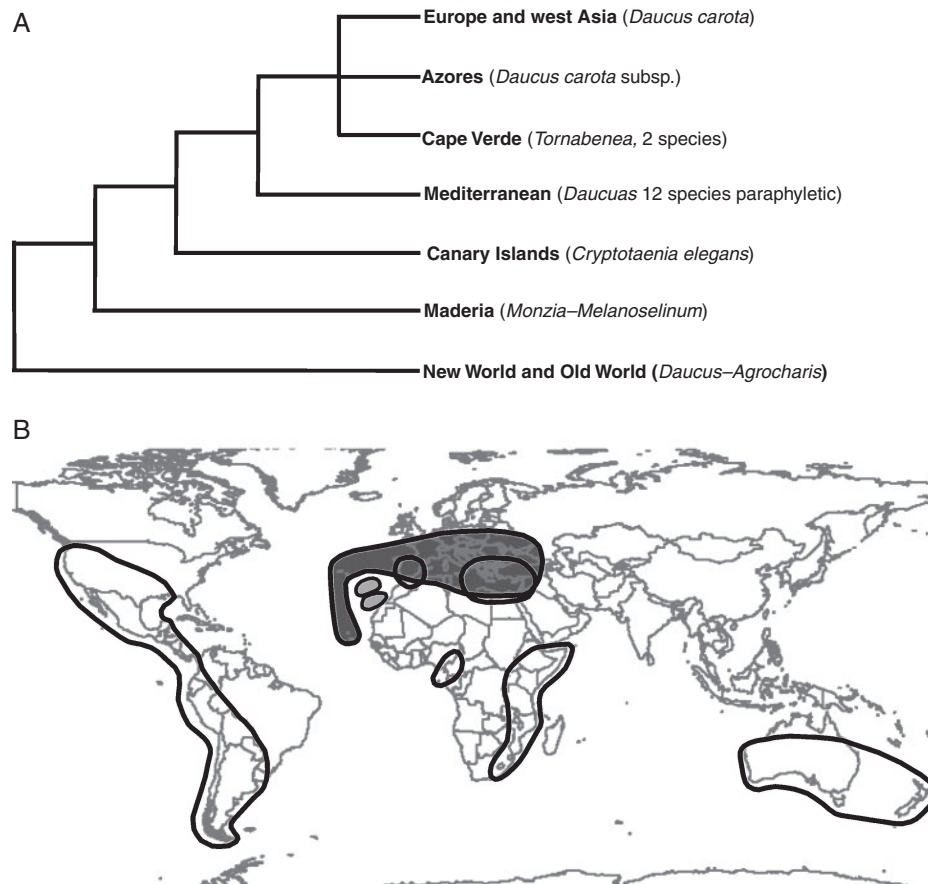


Fig. 17. Relationships of *Daucus*. A. Phylogeny of Macaronesian relationships (Spalik and Downie 2007, fig. 2). B. Biogeography of Macaronesian relationships: Cape Verde–Azores–Europe clade (dark shading), Canary Islands *Cryptotaenia elegans* and Madeira *Monzia*–*Melanoselinum* (light shading), and *Daucus*–*Agrocharis* (outline). Distribution data are from Spalik and Downie (2007).

Craw (1990) noted that although species such as *Bassaris itea* Fabricius, 1775 may occasionally migrate across the Tasman Sea and *V. atalanta* is a migrant (including colonisation of the Canary Islands), the phylogenetic and geographic relationships of *Vanessa* can be interpreted as a pattern of underlying vicariance and localised dispersal, resulting in marginal sympatry. A vicariance origin would involve fragmentation of a widespread New and Old World ancestor by the formation of the Atlantic (with *V. atalanta* possibly diverging only to subspecies level), and the disjunction of the *V. indica* subclade being caused by closure of the Tethys basin in the Old World. The origin of *V. vulcania* requires only a widespread ancestor between Macaronesia and Asia, followed by extinction of intermediary localities, perhaps across northern Africa or along the former Tethys (Fig. 21B). This vicariance model is also compatible with the ancestral range of the *V. indica* clade originally extending west of Macaronesia to include the Americas; this provides a parallel to the ancestral trans-Atlantic range of *V. atalanta*.

Integration of biological and geological data

The allopatric sister-group relationships discussed above permit the following two principal historical inferences: (1) the

trans-Atlantic sister groups evolved from widespread ancestral distributions that existed before the formation of the modern Atlantic, and (2) the endemic Macaronesian clades are local descendants of those widespread ancestors that occupied the Macaronesian region and continental habitats *together*. This is a conception very different from the chance-dispersal model in which occupation of the islands is from external sources, whether for current islands or former Macaronesian islands, as that proposed by Fernández-Palacios *et al.* (2011, 2015). The timing of ancestral differentiation may be assessed either by fossils (including molecular extrapolations) or tectonic–biogeographic correlation. Fossil data provide only the minimum known-age of taxa and fossils are often lacking for clades of interest to Macaronesia. In tectonic correlation, the estimate of clade age is more precise, because it refers to a particular, dated event, rather than a minimal (fossil-calibrated) age. There will always be an associated margin of error, but it is not usually as great as that proposed for fossil-calibrated divergence dates. The trans-Atlantic relationships of many taxa present in Macaronesia provide a biogeographic correlation for the time of origin of the groups and their mainland relatives. There is no single Atlantic separation event that can be automatically applied to the Macaronesian groups. Most

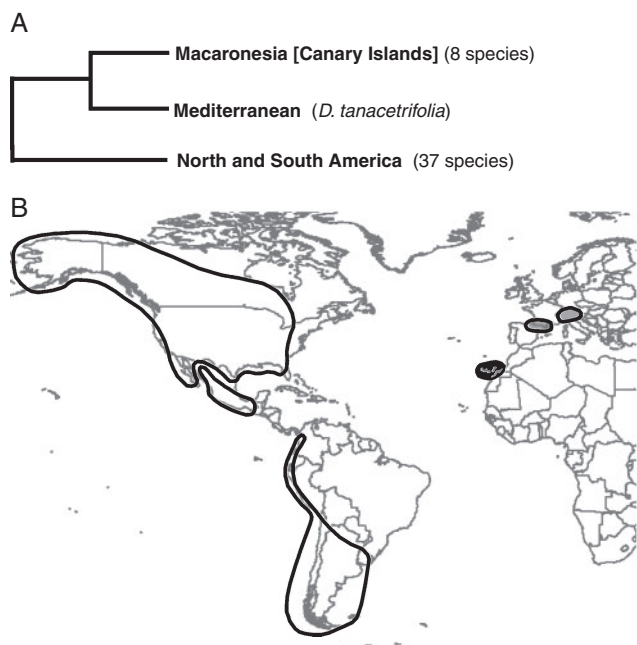


Fig. 18. Relationships of *Descurainia*. A. Phylogeny of Macaronesian relationships (Goodson *et al.* 2011, fig. 5). B. Biogeography of Macaronesian relationships: Canary Islands clade (dark shading), Mediterranean clade (light shading) and New World clade (outline). Distribution data are from Goodson *et al.* (2011).

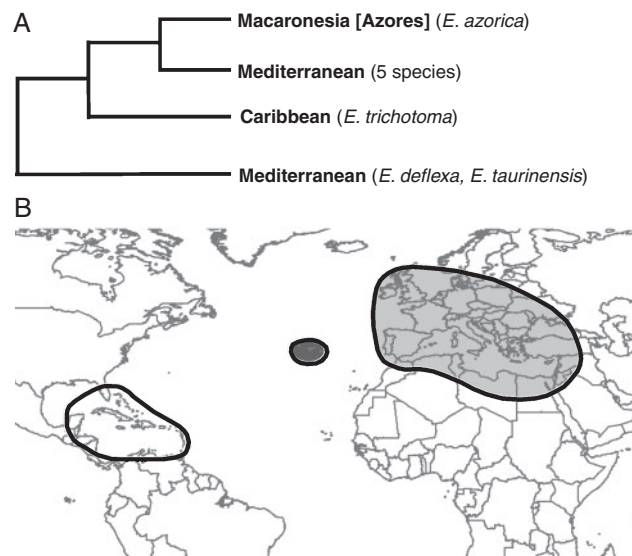


Fig. 19. Relationships of *Euphorbia* subgenus *Esula* section *Paralias*. A. Phylogeny of Macaronesian relationships (Riina *et al.* 2013, fig. 5d). B. Biogeography of Macaronesian relationships: *E. azorica* (dark shading), Mediterranean sister group (light shading), and basal sister species (outline). Distribution data are from Euro+Med PlantBase (<http://ww2.bgbm.org/EuroPlusMed/query.asp>, accessed 20 March 2017), GBIF (<http://www.gbif.org>, accessed 20 March 2017) and Tropicos.org (Missouri Botanical Garden, <http://www.tropicos.org/Name/12804971>, accessed 21 March 2017).

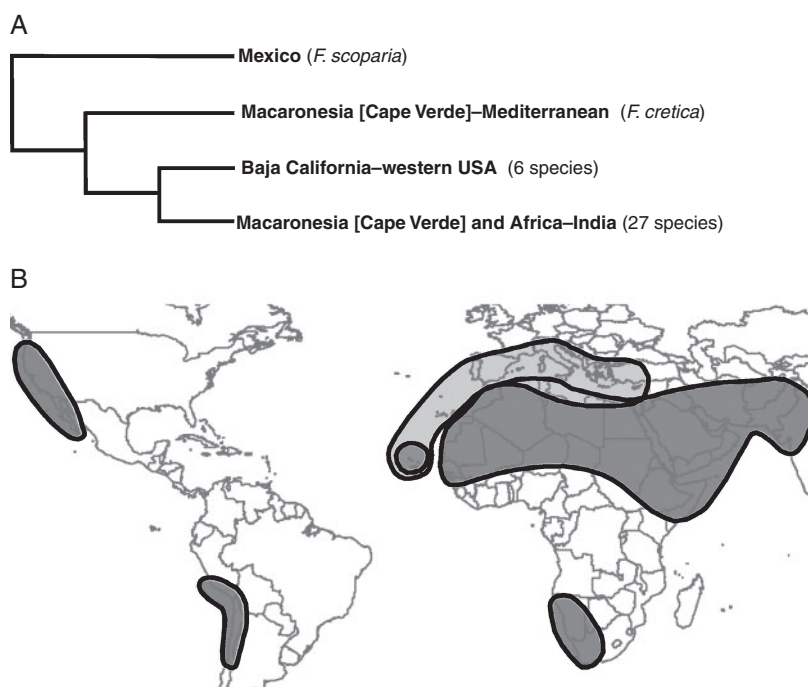


Fig. 20. Relationships of Macaronesian *Fagonia*. A. Phylogeny of Macaronesian relationships (Beier *et al.* 2004, fig. 5). B. Biogeography of Macaronesian relationships: Cape Verde–Africa–India clade and New World sister group (dark shading), Cape Verde Mediterranean clade (light shading) and basal clade (outline). Distribution data are derived from Beier *et al.* (2004).

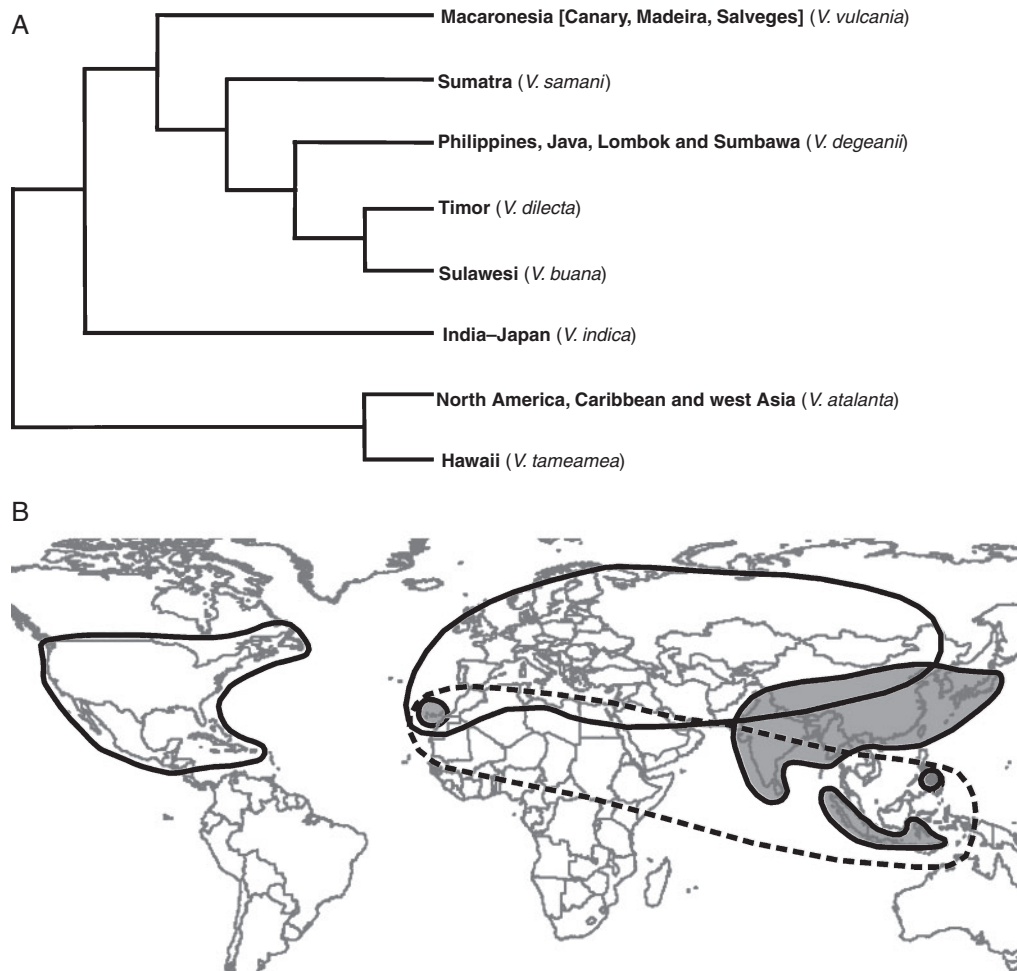


Fig. 21. Relationships of *Vanessa*. A. Phylogeny of Macaronesian relationships (Wahlberg and Rubinoff 2011, fig. 1). B. Biogeography of Macaronesian relationships: Canary Islands *Vanessa* clade (dark shading) and sistergroup (light shading), and basal North American-Eurasian *Vanessa atalanta* (outline). Hypothetical ancestral range of Canary Islands clade as dashed outline. Distribution data are from Kostrowicki (1969), Field (1971) and Hanafusa (1992, pp. 1–2, 7–8, 15–16).

Macaronesian taxa with relatives in eastern North America are also represented, in various combinations, in the Caribbean, Central America and South America, and some Macaronesian taxa (*Ilex*, *Tarentola*, *Esula*, *Apollonia*, *Roccella*) show direct relationships with the Caribbean. These distributions suggest that the ancestral ranges were not centred on the North Atlantic, but on a region corresponding to the modern Mediterranean and Caribbean sectors that finally broke up at c. 120–100 million years ago. Because fossil records and fossil-calibrated molecular divergence extrapolations do not preclude earlier origin, it is neither surprising nor problematic that the biogeographic divergence estimate for Macaronesian endemics may considerably predate their current fossil ages or molecular divergence estimates (see Table 1). However, the age of modern Macaronesian islands has been used to reject older molecular divergence estimates, such as the 40 million years old fossil *Crepetocarpon perkinsii* (Berry) Dilcher & Manchester that resulted in ‘too great an age for several Macaronesian taxa, so additional calibration points were inserted, based on maximum age for the Canary Islands of 20.6 Ma. . .’ (Bruyns *et al.* 2011, p. 1721).

Molecular clock-based dispersal approaches to Macaronesian biogeography all employ a model in which the island inhabitants are all derived from sources outside the region. The origin of oceanic island biotas is treated as the result of unlikely accidents of history, in which each island taxon has its own history and its own set of unique accidental movements that have nothing to do with any other organisms. In effect, the Atlantic of the present, including its geographically isolated islands, defines the Atlantic of the past. In contrast, the vicariance model recognises that the allopatric sister-group relationships are evidence that colonisation of Macaronesia occurred along with colonisation of the New World and Old World continental regions, rather than being a derivative of either. This biogeographic inference requires a different way of looking at the geo-biogeography of these oceanic islands.

The available geological evidence for the history and origin of Macaronesia is ambiguous and open to alternative interpretations; hence, the various debates over the causes and origins of islands. These constraints notwithstanding, the present evidence lends itself to the view that whereas the Atlantic

Table 1. Minimal ages of origin for Macaronesian clades or their inclusive taxon according to fossil and molecular divergence extrapolations

Taxon	Class/family	Fossil or molecular minimum age	Source
1. <i>Tarentola</i>	Reptiles/Gekkonidae	≥26–10 million years old <i>Tarentola</i> (molecular)	Carranza <i>et al.</i> (2000, 2002)
2. <i>Clethra</i>	Angiospermae/Clethraceae	≥14 million years old <i>Clethra</i> – fossil ≥93–86 million years old Clethraceae – sister group fossil	Friis <i>et al.</i> (2011) Martínez <i>et al.</i> (2016)
3. <i>Morella</i>	Angiospermae/Myricaceae	≥38 million years old Myrica – molecular	Wikström <i>et al.</i> (2001)
4. <i>Persea–Apollonia</i>	Angiospermae/Lauraceae	≥98–90 million years old Lauraceae – fossil	Crepet <i>et al.</i> (2004)
5. <i>Ilex</i>	Angiospermae/Aquifoliaceae	≥90 million years old <i>Ilex</i> – fossil	Loizeau <i>et al.</i> (2005)
6. <i>Roccella</i>	Arthoniomycetes/Roccellaceae	≥200 million years old Roccella – tectonic correlation	Tehler <i>et al.</i> (2013)
7. <i>Sedum</i>	Angiospermae/Crassulaceae	≥18 million years old Sedum – molecular	Wikström <i>et al.</i> (2001)
8. <i>Dirina</i>	Arthoniomycetes/Roccellaceae	≥200 million years old Roccella – tectonic correlation	Tehler <i>et al.</i> (2013)
9. <i>Morlockia</i>	Crustacea: Remipedia	≥300 million years old Remipedia – fossil	Neiber <i>et al.</i> (2011)
10. <i>Metacrangonyx</i>	Crustacea/Metacrangonyctidae	≥60–108 million years old	Bauzá-Ribot <i>et al.</i> (2012)
11. <i>Hemidactylus</i>	Reptilia: Gekkonidae	≥130 million years old Gekkonomorpha – fossil ≥92–45 million years old <i>Hemidactylus</i> – molecular	Conrad and Daza (2015) Bansal and Karanth (2013)
12. <i>Chionina</i>	Reptilia: Scincidae	≥74–66 million years old Scincoidea – fossil ≥209–176 Scincidae – molecular	Krause <i>et al.</i> (2003) Hedges and Vidal (2009)
13. <i>Ocotea</i>	Angiospermae: Lauraceae	98–90 million years old Lauraceae – fossil	Crepet <i>et al.</i> (2004)
14. <i>Dryopteris</i>	(Pteridophyta: Dryopteridaceae)	≥65–55 million years old <i>Dryopteris</i> – fossil	Sessa <i>et al.</i> (2012)
15. <i>Cneorum</i>	(Angiospermae: Rutaceae)	≥5–2.5 million years old <i>Cneorum tricoccon</i> – fossil ≥78–58 million years old Cneoroideae – molecular	Traveset <i>et al.</i> 2005 Appelhans <i>et al.</i> 2012
16. <i>Ruta</i>	(Angiospermae: Rutaceae)	≥78–58 million years old Cneoroideae – molecular	Appelhans <i>et al.</i> 2012
17. <i>Daucus</i>	(Angiospermae: Apiaceae)	≥26–13 million years old <i>Daucus</i> – molecular	Spalik <i>et al.</i> (2010)
18. <i>Descurainia</i>	(Angiospermae: Brassicaceae)	≥52 million years old Brassicaceae – molecular	Kagale <i>et al.</i> (2014)
19. <i>Euphorbia</i>	Angiospermae/Euphorbiaceae	≥40 million years old Crepetocarpon – fossil	Bruyns <i>et al.</i> (2011)
20. <i>Fagonia</i>	Angiospermae/Zygophyllaceae	≥45 million years old <i>Guaiacum</i> – fossil	Beier <i>et al.</i> (2004)
21. <i>Vanessa</i>	(Lepidoptera: Nymphalidae)	≥35 million years old Vanessa – fossil	Miller and Brown (1989)

continental margins are tectonically passive, the geological history of the Central Atlantic has been anything but. Geological evidence indicates that there has been sustained volcanic activity in the Central Atlantic for *at least* the past 140 Ma, and uplift of the seafloor has also occurred at different times during this period. These processes have resulted in a sequential series of island archipelagos in the Central Atlantic, particularly east of the Mid-Atlantic Ridge. This current geological understanding does not exclude the presence of land and terrestrial organisms in parts of the Atlantic basin throughout its existence. The presence of a dynamic system of ephemeral islands and island archipelagos, from the time of separation between the New and Old Worlds, allows for an early occupation of Atlantic islands during periods of ancestral mobilism encompassing islands and continents alike. This model is concordant with the trans-Atlantic relationships being the result of local differentiation within those ancestral ranges.

A biogeographic concept of colonisation is still applicable to allopatric Macaronesian clades, but with an important difference. This colonisation was not by a mainland ancestor, but from an ancestor distributed in regions that subsequently became 'island' and 'continental' habitats. This mobilism may have been affected by the tectonic formation of the Central Atlantic and its connection with Tethys. In this model, the geological processes of rift-valley formation, crustal thinning and associated volcanism created a dynamic geomorphology, resulting in the dispersion of particular organisms over a contiguous region of 'oceanic' and 'mainland' islands. This region was subsequently disrupted by the formation of the Atlantic, resulting in final vicariance of the ancestral distributions.

The vicariance model does not require continuous land connections or 'landbridges', either between archipelagos or between islands and mainland. However, the present geological evidence is suggestive of extensive former subaerial archipelagos within the Central Atlantic that reduce the current geographic distance between some of the extant island archipelagos and it is possible that this proximity contributed a Macaronesian ancestral range that diverged from 'mainland' relatives. However, it is not distance as such that is the only critical factor affecting faunal similarity, as suggested by Guerrero *et al.* (2005) for the lizard fauna of the Canary Islands, which are, as has been so often noticed, only 100 km from the African mainland. Despite this short distance, the Canaries support endemic taxa and include phylogenetic relationships that exclude Africa. This can be compared to the 70% difference between the bird faunas of New Britain and New Guinea, although they are separated by a sea strait only 72 km wide (Croizat 1958 vol. 2a, p. 602).

The concept of mobilism recognises that it is only under particular geomorphological and tectonic circumstances that taxa spread and establish new distribution ranges. These taxa may, subsequently, experience vicariance and local differentiation of descendants, whether these are in Macaronesia, America, Africa or Eurasia. As the Atlantic basin expanded, some taxa became extinct on the islands, whereas others became locally extinct (resulting in present-day disjunctions) or entirely extinct on the continents. The existence of endemic taxa encompassing multiple Macaronesian archipelagos suggests that although these islands are geographically separate and distinct in the present day, they had more in common geologically in the past. The different

patterns of geographic relationship between Macaronesian endemics and continental relatives are not due to the vagaries of chance dispersal, but are the result of different ancestral ranges that overlapped within the ancestral Macaronesia region (Fig. 22). The following biogeographic sequence (Fig. 23) is, therefore, proposed for the origin of Macaronesian endemics with New and Old World sister taxa:

- (1) Jurassic–Cretaceous ancestral distributions across a geographic region.
- (2) Initiation of the Mid-Atlantic Ridge generates a dynamic landscape of rift valleys and associated volcanoes that is

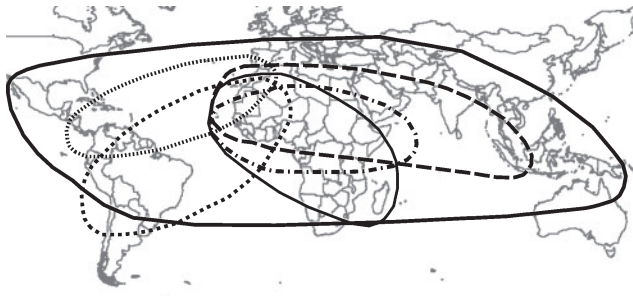


Fig. 22. Concept of Macaronesia as a region of intersecting widespread ancestral ranges in the region now called Macaronesia. Range polygons are generalised and conceptual.

- (3) As the Atlantic basin widens and subsides, volcanoes are transformed into islands, with biota becoming geographically isolated.
- (4) Island biota survives erosion and subsidence of island habitats by local dispersal onto newer volcanoes (it is this aspect that is recognised in various studies of Macaronesian inter-island relationships such as Fernández-Palacios *et al.* (2011)).

The proposed continuity of biological and geological evolution within the Atlantic basin provides a geologically integrated vicariance model for Macaronesian allopatry and trans-Atlantic relationships. It is also geologically and biogeographically consistent with the existence of ancient Macaronesian endemics such as the bryophyte genus *Alophosia* (Heads 2011). This has a minimal molecular-clock date of 253–207 million years ago and is sister to the rest of the globally distributed class Polytrichopsida (Bell and Hyvönen 2010). The allopatric affinities of Macaronesian clades with New World groups suggest that there have always been plants and animals around the region that is now the Central Atlantic, and that the present-day endemics represent their descendants (cf. Heads 2012 for the Pacific). This does not mean that all the inclusive taxa involved (e.g. the families of ferns, angiosperms, fungi, reptiles, arthropods) are of the same evolutionary age, but it does suggest that the ancestors of these various groups

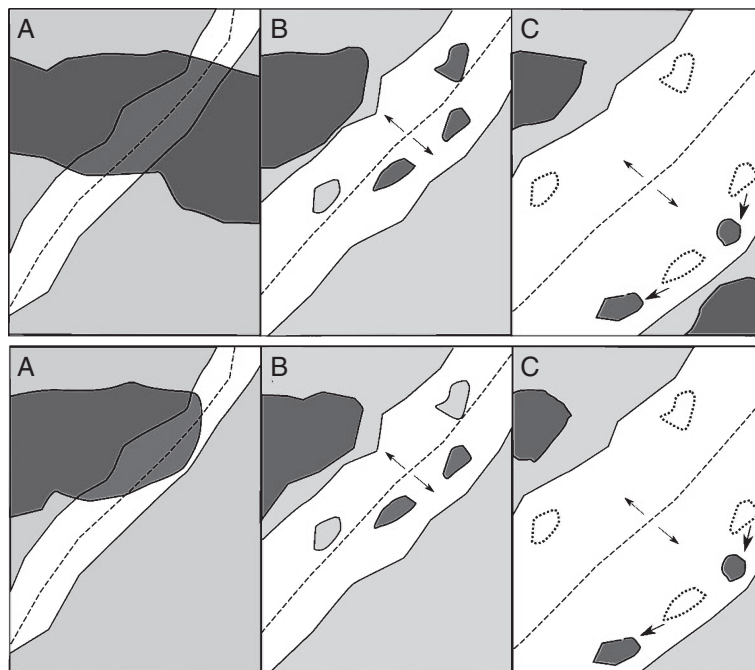


Fig. 23. A. Highly generalised model for the origin of endemic Macaronesian clades from Mesozoic ancestors as dark grey shading distributed over all (top row) or part (bottom row) of a complex rift valley formation, including spreading ridge (dashed line) and volcanoes. B. Descendants stranded on volcanoes now forming oceanic islands. C. Survival of descendants by colonisation (small arrows) of new volcanoes (dotted outline) as earlier volcanoes erode and subside.

did all exist before formation of the Mid-Atlantic Ridge. The tectonic correlations also suggest that the origin of many Macaronesian taxa predate their oldest fossil record or minimum fossil or island-calibrated molecular extrapolation (Table 1).

So long as a succession of new islands formed in association with earlier islands, these ancestral taxa were able to colonise, survive and persist into the present (Axelrod 1972). Populations on volcanic islands and atolls, and on their reefs, survive and evolve in the same way they do on any other recurring mainland habitat 'islands', such as termite mounds or forest gaps (Heads 2009b). As each habitat or island forms, it becomes available for colonisation, whereas former areas of occupation, whether within oceans or continents, may be lost. Because islands are constantly forming and disappearing at subduction zones, hotspots, and other long-term tectonic structures, each island receives its biota from earlier islands that are now submerged (Heads 2005, 2012, 2014a). In this way, species may persist more or less *in situ*, even though the originally colonised landscapes no longer exist. Biogeographically speaking, the Canary Islands are not simply 'oceanic islands' subject to a separate set of rules for dispersal, but represent isolated fragments of a larger biological and biogeographical world (Croizat 1965).

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