

Biogeography by revelation: investigating a world shaped by miracles

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Abstract. This article reviews the methods of biogeographic analysis in current use, as summarised by Alan de Queiroz, 2014 (*The Monkey's Voyage*, Basic Books, New York). The methods rely on molecular clock dates (the weakest part of molecular research) rather than analysis of the distributions of clades defined in phylogenies (the strongest part of the research). One of the main findings of the molecular work is the unexpected, high levels of geographic structure in clades, especially allopatry. The modern synthesis and many molecular clock studies suggest that allopatric speciation is caused by founder dispersal, whereas panbiogeography attributes it to vicariance. De Queiroz and many modern studies have accepted that panbiogeography ignores critical evidence, and that vicariance theory was dominant in the 1970s–1990s, but has since declined. Closer examination shows that these claims are incorrect. Other popular misconceptions include the ideas that fossils and fossil-calibrated molecular clocks provide maximum possible ages of clades, that vicariance theory rejects the fossil record and molecular clock dates, that DNA sequences ‘reveal’ long-distance dispersal, that distribution is chaotic, and that chance dispersal can generate repeated patterns. The conclusions of modern island biogeography, as discussed in detail by de Queiroz, are reviewed here for the following islands: São Tomé and Príncipe in the Gulf of Guinea, Madagascar, the Seychelles, New Zealand, the Chatham Islands off mainland New Zealand, New Caledonia, Norfolk Island, the Hawaiian Islands, the Falkland Islands and Fernando de Noronha off Brazil. Biogeographic analyses of particular groups are illustrated here with respect to ratite birds and primates. Finally, modern methods of ancestral-area analysis are reviewed. These make the unjustified assumption that the location of a basal paraphyletic grade represents a centre of origin.

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Introduction

The main theme of Alan de Queiroz's (2014) book is that a flawed approach, vicariance theory, dominated biogeography from the 1970s to the 1990s, but that a more reliable theory, chance dispersal, has since claimed the field. However, the reality is different; chance dispersal is not a recent theory, but has been the dominant paradigm in biogeography ever since the rise of the modern synthesis in the early 1940s. Despite the dominance of chance dispersal theory, the significance of vicariance began to be taken seriously in the 1970s. Since then, it has become much more widely accepted, despite its radical undermining of the traditional theory (Fig. 1).

None of the arguments in de Queiroz's (2014) book are new, and the book as a whole constitutes a readable account of modern dispersal theory. For this reason, its points of view on different topics are examined here in more detail, and when the name ‘de Queiroz’ is mentioned, this can be taken to stand for ‘modern dispersal theory’. Throughout this paper, ‘de Queiroz’ refers to his book, and numbers cited in parentheses refer to page numbers in it.

An earlier review of de Queiroz concluded: ‘as a history it is sadly incomplete...’, the author ‘takes most second-hand stories

at face value...’, and ‘the book takes a sometimes uncritical look at its subject’ (Morrison 2014). Modern biogeography often takes an uncritical attitude to fundamental questions; authors take a ‘plug-and-play’ approach, running their data through the latest popular program and accepting the results without question. Another reviewer, Mazza (2014) noted de Queiroz's ‘passionate endorsement’ of molecular dating, and observed that molecular clock dates were ‘the true basis for his theories’. Mazza was critical of de Queiroz's reliance on oversea rafting, and he concluded that ‘natural rafting certainly solves problems of distribution, but it raises many more questions than it answers’.

Biogeography without maps

De Queiroz's book glosses over any inconvenient evidence, and this is most obvious in the fact that there are so few distribution maps. In the first sentence, de Queiroz wrote that he recently put up a map of the world in his house for the children: ‘As something of a map hoarder... I appreciate a map made with care...’ (p. 1). The map he put up on his wall showed different groups (e.g. lions, kangaroos) in their respective areas. Some of the main evidence for vicariance theory consists of distribution patterns and their repetition in large numbers of groups, and distributions are best

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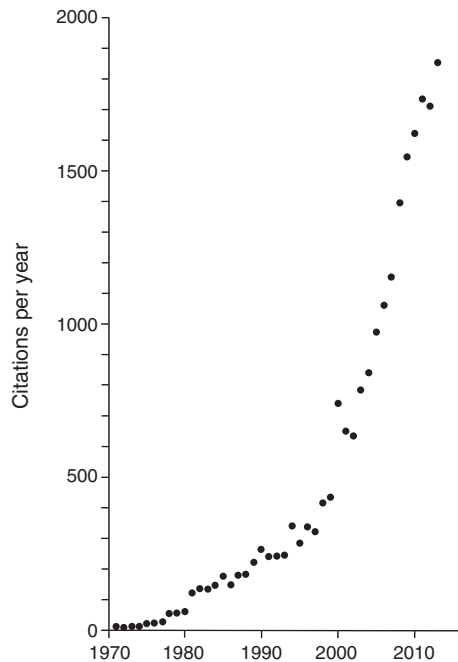


Fig. 1. Number of citations of 'vicariance' per year (Google Scholar, accessed 20 July 2014).

depicted in maps. The one that de Queiroz put up for his children is an excellent example. Nevertheless, despite his book including dozens of illustrations, for example, of famous people, organisms and phylogenies, there are only two distribution maps (fig. 1.2, showing a snake in northern Mexico, and fig. 3.2 showing ratite birds). Most of the book focuses on intercontinental distributions and affinities between continents and islands, so why are there no other maps showing the details of these? Maps, as graphs, allow the facts to speak for themselves, and sidelining them means that any serious engagement with the key evidence is diminished.

De Queiroz's book supported the idea that biogeography can be done with phylogenies and dating programs alone, and that maps are unnecessary. In practice, this is a standard approach. I review many manuscripts for the *Journal of Biogeography*, and in nearly all cases my main comment to the authors is something along the lines of 'your clades and their distributions are especially interesting, but you have not mapped them or even mentioned the precise allopatry between them'. A regional study of geology without maps is virtually inconceivable; why should it be any different for biogeography? A phylogenetic break on the western side of the Central Cordillera in Colombia or at the craton margin in New Guinea, for example, may not mean very much to a taxonomic specialist or an expert in phylogeny reconstruction, but for a biogeographer it provides key evidence.

Vicariance and dispersal

As de Queiroz accepted, two concepts of dispersal are often confused (p. 10). *Normal dispersal* is seen every day in the weeds that colonise a garden, or in an albatross crossing the Pacific, and takes place by normal, observed means of dispersal. This sort of dispersal does not lead to speciation.

Table 1. The differing explanations for allopatry and overlap in dispersal theory and panbiogeography theory

Theory	Explanation for allopatry	Explanation for overlap
Dispersal theory	Chance dispersal	Normal dispersal
Panbiogeography	Vicariance	Normal dispersal

The second sort of dispersal is *chance dispersal* or founder dispersal. (This is sometimes called 'long-distance dispersal' (LDD), although it is proposed to take place at many spatial scales.) This process is an inferred mode of speciation that involves one-off dispersal events 'across a barrier' by a founder. It may occur only once in the entire history of a lineage, and it does not rely on the group's normal means of dispersal; these are 'not informative in the context of LDD (Higgins *et al.* 2003). Chance dispersal from a centre of origin is the primary concept in modern dispersal theory. (The term LDD, *as used by ecologists*, refers simply to normal dispersal over long distances, with no implication of speciation; *as used by biogeographers and systematists*, LDD refers to a mode of speciation, as described above.)

Another key concept is *vicariance*. In this process, allopatric forms evolve following the development of a *new* geographic barrier within the range of a widespread ancestor. This contrasts with allopatric speciation by the chance dispersal of a founder across a *prior* barrier. In a vicariance event, the origin of the descendant clades does not involve their range expansion, although this may, or may not, occur later. Vicariance was a basic concept of Croizat's panbiogeography, a synthesis of biology and geology that gave rise to modern vicariance theory.

Dispersal theory and panbiogeography attribute allopatric speciation to chance dispersal and to vicariance respectively, but they agree that overlap is caused by normal dispersal (Table 1). (De Queiroz did not repeat one myth that is often cited: the idea that vicariance theory denies dispersal; see Heads 2014b) In a key document of dispersal theory, Darwin (1859, p. 352) admitted that:

Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle.

Ten years later, Darwin (1869, p. 467) emphasised this view in the 5th edition of his book, arguing

... that not only all the individuals of the same species, but that allied species, although now inhabiting the most distant points, have proceeded from a single area, – the birthplace of their early progenitor.

Of course, all groups originate in a particular area. But in dispersal theory, all species have had a localised centre of origin and have attained their observed distribution by dispersing from there. If a species (or a higher-ranked group) occurs in two places,

it must have dispersed from one to the other (p. 27). Matthew's (1915) influential review supported Darwin's model, and a century after Darwin's book was published, Mayr (1965a) wrote that 'Quite obviously, except for a few extreme [i.e. local] endemics, every species is a colonizer because it would not have the range it has, if it had not spread there by range expansion, by 'colonization', from some original place of origin.' (p. 203). Later, Mayr (1982a, p. 601) wrote that although some textbooks showed 'a widespread species cut in half by a geographical barrier [i.e. vicariance]', 'more detailed studies... suggest a different solution', namely speciation by founder dispersal. The widely used text book by Stebbins (1966, fig. 5-1) applied the same ideas to plant speciation. It accepted that allopatric differentiation developed solely by migration and ecological differentiation; there was no mention of the appearance of new barriers. In other popular text books, Grant (1971, 1981, 1985) included many maps of allopatric forms, but did not mention geographic change and barrier formation as a cause of this.

In contrast with the modern synthesis text books of earlier decades, most text books on evolution written after 1980 cite vicariance as one of the main modes of speciation. As de Queiroz (p. 13) wrote, 'The rise of vicariance biogeography in the 1970s was a big deal within the discipline, to put it mildly'. De Queiroz described how vicariance theory put differentiation of clades by the fragmentation of environments (rather than founder dispersal) at the front of people's minds; it also provided a simple explanation for patterns shared by many groups.

Areas of high species diversity, such as central New Guinea or the Andes, are often located in areas with many potential barriers between populations. In dispersal theory, ancestral founders have dispersed over what are otherwise barriers; this has led to the differentiation of new species. In this model, Earth and life do not evolve together. In vicariance theory, the barriers have developed by uplift, subsidence, climatic change and so on. This has divided ancestral complexes that were already widespread in the region, leading to the formation of new species. In this model, Earth and life evolve together. In vicariance theory, range expansion is also caused by geographic change, such as alterations in climate or sea level, not chance events in individual clades.

Modern authors such as Eldredge *et al.* (2005) have continued to accept a centre of origin, arguing that if novel forms are to become widespread, they 'must spread beyond their site of origin...'. But in the case of, say, a world-wide group differentiating into northern hemisphere and southern hemisphere clades, both groups are already widespread at the time of their origin.

De Queiroz followed the modern synthesis approach and assumed that all groups have spread out from a centre of origin. In the case of the sundew, *Drosera*, for example, he wrote that 'Over millions of years, members of the genus obviously have moved great distances, as their world-wide distribution indicates...' (p. 153). *Drosera* is sister to *Dionaea* (eastern United States) and *Aldrovanda* (Old World, but absent from most parts of Africa, Asia and Australasia) (Rivadavia *et al.* 2003). Thus, if *Drosera* originated by simple vicariance with its sister group, it could have already been widespread globally at the time of its origin, and absent only from the eastern United States and parts of the Old World.

As de Queiroz (p. 13) wrote, vicariance biogeography emphasises vicariance events. But it is obvious that vicariance cannot be the only process leading to distribution; vicariance on its own would result in every small area on Earth having only one, endemic clade. During phases of mobilism, groups expand their range by normal dispersal and as the result of geological or climatic change (not chance), and this leads to clade overlap. During a phase of general population immobilism, groups can undergo vicariance, resulting in allopatry. De Queiroz seems to have understood this, and he cited phases of immobilism and mobilism (p. 81). Despite this, he finished every chapter by citing observations of animals or plants moving long distances, as if this indicated chance dispersal. He argued that 'we know that long-distance dispersal occurs because people have actually seen it happen' (p. 228). But the observed dispersal is 'normal dispersal' (without speciation), which often takes place over very long distances, as in sea birds, migrating birds, sharks and others.

A critical feature of vicariance is that the development of a barrier, such as a new seaway or mountain range, will not affect just a single taxonomic group, but many groups in the community. Thus it is a potential explanation for standard biogeographic features, such as geographic-phylogenetic break-zones, or nodes. These are repeated in many groups and so are not easily explained by chance dispersal.

In addition to vicariance and normal dispersal, the process of extinction contributes to distribution patterns. In practice, many accounts ignore extinction in favour of chance dispersal. For example, the wattles are the species of *Acacia s.lat.* (Fabaceae) that bear phyllodes (these species are now treated as *Acacia s.str.*). They extend from Réunion island (near Madagascar) via Australia to Hawaii, a standard pattern (cf. *Myoporaceae*; Heads 2014c, p. 139). *Acacia heterophylla* of Réunion is phylogenetically nested among populations of *A. koa* of Hawaii, and so Le Roux *et al.* (2014) inferred a single dispersal event from Hawaii to Réunion, a distance of 18 000 km. Nevertheless, they did not consider the possibility of extinction in Australia, and this was also overlooked in a commentary on their paper (Marris 2014). Widespread extinction in Australia following Miocene aridification is well documented; however, instead of accepting this normal process, or even mentioning it, dispersal theorists propose a unique event for which there is no known mechanism.

Seven myths about biogeography

De Queiroz began his book with the following epigraph from Popper (1963): 'Science must begin with myths, and with the criticism of myths.' (p. 50). Yet, although de Queiroz accepted many myths about biogeography, he did not subject them to any critical analysis. Seven of the key myths that modern biogeography and de Queiroz accepted are discussed next.

The myth that panbiogeography ignores critical evidence

De Queiroz (p. 277) wrote that 'When I asked Steve Trewick why the panbiogeographers, once prominent in New Zealand, had been 'exiled', he replied, 'They were seen for what they are, a group of fundamentalists who have refused to engage with other thinkers or other evidence.'. In fact, the panbiogeographers were exiled, not for failing to engage with the establishment, but for

engaging with it and disagreeing with it. Panbiogeographers have always engaged with other biogeographers, including Trewick himself (Heads and Craw 2004).

In contrast, dispersalists have often failed to engage with panbiogeography. For example, although de Queiroz himself cited many papers published in 2013, he did not mention my 2012 book (Heads 2012b). Thus, he cited Goswami and Upchurch's (2010) 'rebuttal' of my ideas on fossil age v. clade age (p. 322), but not my response (Heads 2012b, p. 132). Likewise, he cited Ali and Huber's (2010) suggestion that ocean currents explain dispersal to Madagascar (p. 248), but did not mention my critique of their paper (Heads 2012b, p. 117).

De Queiroz (p. 277) also claimed that there is 'other evidence' that the vicariance has ignored, but what is this evidence? My 2012 book (Heads 2012b) alone cited more than 1000 papers. Panbiogeography has not ignored evidence, but it does disagree with the traditional interpretations of it. The dispersalists in turn have responded to our critique, not by engaging with panbiogeography, but by ignoring the issues it raises or objecting to the 'editorial and review processes [that] continue to allow this misleading approach to be promulgated' (Waters *et al.* 2013). It is well documented that the dispersalists' own strategy for dealing with vicariance theory was to ignore it. For example, a symposium volume edited by Kubitzki (1983) carefully skirted around the controversial new approaches of panbiogeography and vicariance. A review of Kubitzki's volume noted that 'The conflicts [vicariance v. dispersal] are almost completely killed by silence... is it an alternative to avoid methodological discussions...?' (Nordal 1985, p. 14). Avoiding any discussion of vicariance in this way was still a standard approach to the topic in the 1980s. This approach continued until it was no longer possible. For example, Mayr did not mention Croizat's work at all until 1982 (Mayr 1982a, 1982b), 24 years after the publication of '*Panbiogeography*' (Croizat 1958).

Trewick (pers. comm. in de Queiroz, p. 277) claimed that panbiogeographers are fundamentalists, and Waters *et al.* (2013) compared us with creationists. But it is dispersal theory, not panbiogeography, that accepts centres of origin (cf. Eden and Ararat), 'design' and 'purpose' in nature, chance dispersal as 'revealed', and Earth as 'a world shaped by miracles' (p. 281). Thus, it is the dispersalists, not the advocates of vicariance, whose thinking resembles that of fundamentalist creationism.

The myth that vicariance theory was dominant in the 1970s–1990s

Dispersal from a centre of origin has been the dominant explanation for biogeographic patterns for at least the past 2000 years. Vicariance theory was referred to in the 18th, 19th and early 20th centuries, but was more or less eliminated from discussion by Darwin and the authors of the modern synthesis (especially from 1940 to 1980), and started to be accepted only in the past few decades (Fig. 1).

De Queiroz argued instead that dispersal theory in the modern era is an edgy, new idea that has challenged the establishment view, vicariance. Thus, dispersal is a 'new story' (p. 18) and 'turns biogeography on its head' (p. 16). This is incorrect. Vicariance began to be discussed in the 1970s and interest in the idea has

grown steadily, but dispersal theory has remained the official view. For example, de Queiroz cited Susanne Renner, currently one of the most prominent dispersal theorists. She was taught dispersal theory at the University of Hamburg in the 1980s by Klaus Kubitzki, a well-known dispersalist (p. 170). Dispersal, not vicariance, was the dominant viewpoint then, as seen in Kubitzki (1983). Likewise, for the 1990s, de Queiroz (p. 170) cited the large, edited volume '*Biological relationships between Africa and South America*' (Goldblatt 1993). This collection of papers, published by Yale University Press, was an authoritative study on the topic, and is a typical example of biogeography in the early 1990s. De Queiroz admitted that most of the contributing authors 'hadn't absorbed the message' of vicariance (p. 170), and instead 'invoked ocean crossings' (the contributions by Bauer and Gentry were exceptional in supporting vicariance).

Contrary to his thesis, de Queiroz admitted (p. 100) that vicariance 'never came to thoroughly dominate historical biogeography...', but suggested (p. 100) that 'in New Zealand it came fairly close'. What is the evidence for this view? He (p. 101) 'asked several New Zealand biologists what people there were thinking at the time, roughly from the mid-1970s to the early 1990s, and they all had the same memory: vicariance had taken over as the paradigm for biogeography.'. Yet, the three people that he asked, namely, Dallas Mildenhall, Mike Pole and Steve Trewick, were all dispersalists, and they have a vested interest in portraying themselves as independent, critical thinkers.

In fact, from the 1960s until the late 1980s, the New Zealand biogeographical establishment was led by a prominent dispersalist, Sir Charles Fleming (1916–1987). Fleming's major work (Fleming 1979) was an influential book on dispersal theory published in 1979, when New Zealand had supposedly been taken over by vicariance. Fleming's supporters included all the senior government scientists in the field, such as R. M. McDowall, D. C. Mildenhall, M. S. McGlone, and N. Hornibrook, as well as university academics such as D. G. Lloyd, and all of these were ardent dispersalists. Discussing McDowall's work, de Queiroz (p. 227) even suggested that 'It wasn't easy being a dispersalist in the mid-1970s', but, in fact, *all* biogeography published in New Zealand at that time was dispersalist, except Craw (1978) (cf. Fig. 1).

As an aside, it is interesting to note de Queiroz's suggestion that 'Bob McDowall never wavered from his old-fashioned, dispersalist viewpoint' (p. 227). This is not correct; after McDowall retired and 1 year before he died he confessed that (McDowall 2010, pp. 1, 2, italics added):

I am not as ready as some to say 'goodbye' to Gondwana and to attribute the entire biota to dispersal derivations (McGlone 2005; and see Wallis and Trewick 2009). *This might seem surprising for a life-long dispersalist...* It is possible that there was an ancient role for Gondwana in the freshwater fish fauna... a few elements in the freshwater fish fauna may reflect ancient Gondwanan origins, e.g. perhaps the species of the non-diadromous 'pencil galaxias' complex (a group of small, subalpine species...).

However, this was much later.

During the 1970s and early 1980s, the only advocates of vicariance in New Zealand were PhD students (R. Craw, J. Grehan, I. Henderson and myself). In 1984, we were joined

by a National Museum zoologist, F. Climo, who organised a symposium at the museum in 1989 (Matthews 1990). Papers on vicariance were also contributed by two other PhD students, R. Gray and R. Page.

Following the publication of the contributed papers (Matthews 1990), there was an immediate reaction from the establishment; the panbiogeographers employed in New Zealand lost their jobs (Craw and Climo), whereas the graduating PhD students had to find work overseas (Grehan, Heads and Page), or they stayed in New Zealand but never wrote about vicariance again (Henderson and Gray). Following the 1989 conference, no funding proposal for vicariance research ever succeeded in New Zealand, and no vicariance work has been accepted for publication, in either the government or the Royal Society journals.

Thus, de Queiroz's suggestion (p. 117) that in the early 1990s 'New Zealand was like a nation polarized into two warring political parties' is fallacious, as is the idea (p. 160) that Pole's (1994) dispersalist paper 'bucked the tide of vicariance thinking'. De Queiroz's promotion of the idea that vicariance dominated biogeographic research in New Zealand is contradicted by his admission (p. 277) that the New Zealand panbiogeographers who introduced vicariance theory to New Zealand were exiled.

The effective suppression of panbiogeography in New Zealand that began in 1990 has continued, and senior New Zealand academicians have recently called for panbiogeography to be banned (Waters *et al.* 2013). (This is despite, or perhaps because of, the large numbers of panbiogeographic studies that are now being published, especially in Latin America.)

The myth that fossils and fossil-calibrated molecular clocks provide maximum possible ages of clades

As already noted, Morrison (2014) and Mazza (2014) concluded that de Queiroz's book is uncritical, and that the argument against vicariance and for chance dispersal relies on the dating of the nodes in molecular phylogenies. If groups are too young, vicariance is ruled out.

...A critical look at the data, then, would involve questioning the molecular dating procedure. For example, if the true dates of the branches are older than the current estimates, *then the evidence* [for dispersal] *begins to melt away*. De Queiroz makes only a half-hearted attempt to address this issue... A more critical view of dating suggests two potential sources of underestimation of divergence ages... [Morrison 2014, p. 848, italics added]

As Morrison (2014) wrote, '...hybridization and introgression events ... will hamper any attempt to identify the original divergence events, and will lead to underestimates of the associated dates' (p. 848). (The other issue that Morrison cited is a more technical problem that is not considered here).

There are also many other problems with the molecular clock ages. Traditionally, dispersalists assumed that the oldest fossils of a clade provide the oldest possible age of that clade, rather than the youngest possible age. This was accepted even when the oldest

fossils are already quite modern in their appearance, suggesting that they had a long existence before the fossil was formed.

In modern dispersal theory, Bayesian methods are used for dating the nodes on a phylogeny and calibrating the molecular clock. In this method, it is admitted that fossils provide only minimum clade ages, but these are converted into maximum clade ages by a statistical sleight-of-hand. In Bayesian dating programs, before any analysis is carried out, authors stipulate as a 'prior' that a clade can be only a certain number of years older than its oldest fossil. The authors can choose any number they like, on the basis of their 'expert knowledge'. If authors choose a small number, the method is guaranteed to produce young clade ages, and this is what is usually done in practice. Unless a group has an exceptional fossil record, this methodology automatically rules out early clade ages and vicariance. It would be much less deceptive to use fossils for calibration and to accept that the calculated clade ages are minimum ages only. The 'problem of the priors' and studies in which authors have used small priors to rule out vicariance are discussed elsewhere (Heads 2012a, 2014c).

De Queiroz referred to the 'thorny but critical issue of whether we should trust molecular dating studies' (p. 119), and concluded that we should, although he did not mention the problem of the priors. He admitted that clocks are 'critical but controversial' (p. 15), and that 'many scientists still have doubts about the validity of molecular clock analyses'. He also quoted an unnamed evolutionary biologist, a 'moderate and reasonable' colleague, who described the clock dates as 'bullshit' (p. 130).

De Queiroz admitted that the fossil record is very incomplete, and that fossils give only minimum ages for clades (p. 136; cf. p. 110). He agreed that this is a 'fundamental weakness' of the clocks (p. 137), but despite this, he argued that molecular clocks must be calibrated with fossils, and that the calculated dates for clades can be treated as maximum ages.

De Queiroz also admitted that placing a fossil on a phylogeny is difficult. For example, allocations of primate fossils to positions on phylogenies 'remain controversial (as they often are with fossils)' (p. 287). This, along with the problems cited by Morrison (2014) and the problem of the priors, is another source of underestimates of clade ages. Several authors have acknowledged the tendency to put fossils at basal nodes, and in a stem group (a paraphyletic complex of fossil members basal to the extant members) rather than a crown group (the youngest clade including all extant members of a group). For example, Heads (2014c, p. 43) stated the following:

Many Cenozoic fossils are probably closer to extant clades than is often acknowledged, and the clades themselves are correspondingly older. Pennington *et al.* (2004) noted 'a tendency in many studies' to assign fossils to the stem of the clade to which they belong. As they emphasised, this will lead to underestimates of divergence times. Smith *et al.* (2010, p. 5897) also described 'the default practice of assigning fossils to the stem of the most inclusive crown clade to which they probably belong, thereby possibly biasing estimated ages (possibly throughout the tree) to be younger'. There is no evidence that many fossil groups assumed to be basal or even ancestral just because they are 'old' have such a special status. A typical example concerns the geckos (*Gekkota*) and their oldest fossil, the

mid-Cretaceous *Cretaceogekko*. Studies in Australia (Pepper *et al.* 2011) and New Zealand (Nielsen *et al.* 2011) have used this fossil to calibrate the base of the gecko tree. Nevertheless, while *Cretaceogekko* is the oldest gecko fossil, the only study of the genus (Arnold and Poinar 2008) gave no indication that it is basal in the group.

Although de Queiroz admitted that, in theory, there are problems with the clock dates, he argued that we should believe them anyway. Clock dates are good enough to give ‘ballpark estimates’ of (absolute, maximum) clade ages (p. 88). But what exactly is a ‘ballpark estimate’? Just how big is the potential error? How would you know? How much older than its oldest fossil can a lineage be? De Queiroz did not mention this critical issue.

De Queiroz (p. 134) quoted personal communications from Michael Donoghue, as follows: clock analyses are ‘mostly pretty suspect’, he’s ‘sort of appalled’ as a lot of it is ‘pretty sloppy stuff’. Nevertheless, Donoghue thought that we must accept the dates, and that ‘the vicariance people are crazy to ignore the molecular dating evidence’. But vicariance workers do not ignore them; they just do not use them to establish *maximum* possible clade ages.

De Queiroz also quoted personal communications from Matt Lavin on the ages of some legume clades. These were all calculated to be too young for vicariance: ‘We tried to bias ‘em and make them old ... putting the fossil on the crown instead of the stem node ... or taking the oldest possible minimum age that the fossil could be, if that makes any sense ... [but] we could not make them older than 20 million years or something’ (pp. 157, 158). Despite this suggestion, if it is accepted that fossils give a minimum age for their clade, they do not place any limit on the maximum possible age of the clade.

The myth that vicariance theory rejects the fossil record and clock dates

De Queiroz wrote that vicariance biogeographers are ‘notably disinterested in using fossils to place ages on evolutionary groups’ (p. 117); we think the fossil record is ‘basically worthless’ (p. 119) or ‘essentially worthless’ (p. 87). Likewise, we regard fossil-calibrated clock dates as ‘basically worthless’ (p. 273) and we ‘completely discount’ them (p. 88); we ‘dismiss the whole practice’ of molecular clock dating and we are ‘anti-dating’ (p. 146).

All this is a myth, a straw-man. Fossils and fossil-calibrated clock dates are valuable, and panbiogeographic work uses them constantly, but only to give minimum clade ages, not maximum or actual ages. For example, vicariance theory will often claim that a group’s fossils indicate it is *too old* to have originated with some younger event, *x*. Dispersal theory instead takes fossils to indicate maximum ages, and often writes that fossils show groups are *too young* (p. 118) to have been influenced by some older event, *y*.

As de Queiroz noted, ‘...some vicariance biogeographers continue to argue vehemently against the [molecular clock] timetree approach’ (p. 277). Yet workers in other fields, for example, geneticists such as Morrison (2014), quoted above, have also noted problems with the approach.

De Queiroz (p. 137) suggested that only ‘good’, ‘reliable’ parts of the fossil record should be used to calibrate clocks. But how can one know which part of the record is good (in an absolute sense, not just better than other parts)? De Queiroz (p. 137) wrote that ‘What qualifies as ‘especially good’ and ‘reliable’ is subjective, but there are some cases that do seem convincing.’ As an example, he cited the bird–crocodile split. The crocodile lineage is known from fossils dating back to 240 million years ago (Ma) (*Arizonasaurus*). At 245–250 Ma, there are no fossils of the bird–crocodile lineage, therefore, ‘conservatively’, the bird–crocodile branching point could not have occurred earlier than 250 Ma; this is ‘reasonable’ and the approach ‘should give accurate ages’ (p. 144). In fact, this is not a conservative estimate; conservative palaeontologists accept that the fossil record indicates minimum clade ages.

Discrepancies between fossils and fossil-calibrated clock dates

Molecular clock dates imply vast gaps in the fossil record, and so palaeontologists who read clade ages directly from the fossil record are often very critical of the clock dates (Mayr 2013). De Queiroz overlooked this major disagreement, and instead claimed (p. 146) that ‘The overall agreement between molecular age estimates and good fossil-based ones indicates that the approach is reasonable in general...’. However, in many groups there is no ‘overall agreement’. For example, whereas oldest fossils indicate an origin for primates (Euprimates) in the Paleocene, at *c.* 56 Ma, fossil-calibrated molecular clocks calibrated with fossils from other groups suggest that the group originated in the Cretaceous, at 86 Ma (Murphy and Eizirik 2009) or *c.* 90 Ma (Janečka *et al.* 2007). The oldest fossils of passerine birds are Early Eocene, *c.* 50 Ma (Mayr 2013), whereas molecular clock dates give an origin in the Late Cretaceous, at 97 Ma (van Tuinen 2009). A recent, detailed survey concluded the following (Ksepka *et al.* 2014, p. 1, italics added):

Major disparities are recognized between molecular divergence dates and fossil ages for critical nodes in the Tree of Life, but broad patterns and underlying drivers remain elusive. We harvested 458 molecular age estimates for the stem and crown divergences of 67 avian clades to explore empirical patterns between these alternate sources of temporal information. *These divergence estimates were, on average, over twice the age of the oldest fossil in these clades.*

Tectonic calibration

According to de Queiroz (p. 143), vicariance theory insists that tectonic events ‘must be used to calibrate molecular clocks’. This is not correct, as vicariance analyses also incorporate fossil dates; these are used to provide valuable minimum clade ages. But are fossils essential for dating?

De Queiroz (p. 135) wrote that ‘one usually needs fossils’ for calibration, but this is not correct; a survey of 613 papers published 2007–2013 showed that only half (52%) used fossil calibrations (Hipsley and Müller 2014). Tectonic calibration is often used, and de Queiroz (p. 142) cited an example in which the

break between African and American clades of amphisbaenian squamates was attributed to the opening of the Atlantic Ocean and was used to calibrate a phylogeny. De Queiroz (p. 143) wrote that ‘An even more egregious example comes from Michael Heads, who has stated explicitly that tectonic and other fragmentation events should be used as calibration points in place of what he sees as horribly unreliable fossil calibrations.’. Again, vicariance theory has never suggested that *only* tectonic events should be used. Data from the fossil record, where available, must also be incorporated to establish minimum ages. In any case, the use of geological calibration is not ‘egregious’, as many studies utilise this method (sometimes well, sometimes badly), mainly to avoid relying on the fossil record to give maximum clades ages. Hipsley and Müller (2014) found that 15% of 613 dating studies published between 2007 and 2013 used geological calibrations.

To summarise, dispersal theory uses what is generally acknowledged as the weakest part of the molecular program, namely, the dates, to establish young clade ages and rule out vicariance. Vicariance theory exploits the strongest part of the molecular program, namely, the delimitation of clades and their spatial distribution, as the basis from which to infer clade ages.

The myth that DNA sequences ‘reveal’ long-distance dispersal

Long-distance dispersal is often regarded as ‘revealed’ by theoretical studies (Matzke 2014) and analyses of DNA sequences (e.g. Schaefer *et al.* 2009; Susanna *et al.* 2011; Antunes Carvalho and Renner 2012; Takayama *et al.* 2013; Gruenstaedl *et al.* 2013; Lo *et al.* 2014; Voelker *et al.* 2014; Daniels *et al.* 2015; Müller *et al.* 2015). De Queiroz (p. 160, italics added) accepted that Susanne Renner, for example, has carried out many dating studies that ‘*reveal* many dozens of ocean crossings by plants’. Nonetheless, the revelation of long-distance dispersal is not evidence; it is an inference, an interpretation that is based on certain prior assumptions and extrapolations. These include the conversion of a fossil age into a clade age. In modern biogeography, a centre of origin and a dispersal route are ‘revealed’ by running particular computer programs with particular settings.

The myth that distribution is chaotic

De Queiroz (p. 82) cited:

serious weaknesses in Croizat’s argument. . . First, his claim that there are very few fundamental tracks was misleading. The tracks of individual lineages on New Zealand, for instance, run all over the place – to New Guinea, New Caledonia, South America, Australia, Tasmania, and Southeast Asia, among other places.

It is obvious that, if the affinities of any biota are traced far enough, all areas will eventually connect with all other areas. Yet, with respect to direct, phylogenetic connections, there is a common one linking New Zealand to north-eastern Australia, but not to north-western Australia; to Madagascar, but not to India; to southern Africa and East Africa, but not to West Africa, and so on. De Queiroz also cited direct affinities of Hawaiian groups linking the islands with different parts of the Pacific margin. However, in contrast, there are no standard tracks linking Hawaii with Europe,

India or Madagascar, for example, and all of these would be within the range of chance dispersal (cf. the 18 000-km dispersal event proposed from Hawaii to Réunion in phyllodine acacias, cited above).

In addition, it is well-known that phylogenetic and biogeographic breaks do not show a chaotic distribution, but are concentrated in particular areas. Wallace’s line is perhaps the most famous, and acts as the boundary for many, high-level groups. Other nodes are of more local significance and involve fewer, lower-ranked groups.

If it were true, as de Queiroz argued (p. 82), that distribution patterns ‘ran all over the place’ and were chaotic, there would be no point in studying them. This is, in fact, the conclusion of dispersal biogeography; it is a nihilist approach that has led to the surprising lack of distribution maps in many biological ‘monographs’ (in contrast with geological monographs). The nihilistic approach to distributions and the interpretation of distribution as ‘shaped by miracles’ (p. 281) effectively short-circuit a science of biogeography; for any distribution, an author simply concludes ‘it must have been caused by a miraculous event of chance dispersal achieved by unknown means’. The approach requires little work, because there is no need to understand the geology of the area, which is often complex, or to compare the distribution with a large number of others in the same area to assess whether or not it conforms to a standard pattern.

The myth that chance dispersal can generate repeated patterns

As a second weakness with Croizat’s argument, de Queiroz (p. 82) wrote that:

The fact that unrelated organisms with different means of dispersal share the same track doesn’t necessarily argue against long-distance dispersal; it is possible for rare, chance dispersal events to collectively produce a clear pattern. . .

Linkem *et al.* (2013) also argued that the high level of precise geographical structure in molecular clades is proof of the great powers of chance dispersal.

‘Chance’ in this ancient sense of ‘luck’ or ‘factors beyond our understanding’ can be used to explain any pattern, anywhere; chance dispersal can happen in any direction, at any time (cf. p. 86), and it does not depend on normal, observed means or any other factor. But if ‘chance’ is used in the modern, statistical sense of ‘calculated probability’, ‘chance dispersal’ refers to a normal, observed process, based on observed dispersal distance and calculated probabilities. This everyday, ecological dispersal cannot explain the patterns though. The shrubs of the *Hebe* complex (*Veronica s.lat.*: Plantaginaceae) that inhabit alpine New Zealand and Australia provide a good example. At least 10 of the species have a hygrochastic capsule that opens when moistened by rain. Raindrops that then fall into the open capsules splash droplets out, taking the seeds with them. Close observations on five of the species indicated that the average distance of seed dispersal was 13 cm, and the greatest distance covered by a single dispersal event was 1.1 m (Pufal and Garnock-Jones 2010). This is valuable primary data on observed dispersal. In contrast, on the basis of a molecular phylogeny, the authors also *inferred* that two

species in the complex (*V. ciliolata* and *V. densifolia*) have dispersed ~1700 km from New Zealand to Australia, against the prevailing winds. Thus ‘chance dispersal’ operates over metres in one model, over hundreds of kilometres in another.

De Queiroz (p. 155) wrote that ‘even when no obvious mechanism presents itself, nonetheless we often must infer that long-distance dispersal did occur. Rare, mysterious and miraculous things do happen...’. Of course, extremely rare events that occur only once in the entire history of a lineage do occur, but they do not explain distribution patterns that are repeated in many different groups with different means of dispersal and very different ecology.

Analyses of areas

De Queiroz (p. 172) suggested that ‘the history of life is extremely serendipitous and unpredictable’, but it is easy to demonstrate that distribution patterns are repetitive. A common pattern can, in turn, be examined with respect to the historical geology of the region, to see whether there is any tectonic or paleogeographic feature that coincides spatially with the pattern. In the following sections, different interpretations suggested by dispersal theory and vicariance are considered for some of the areas that de Queiroz discussed, starting in Africa and moving east.

São Tomé and Príncipe

One biogeographic case study that de Queiroz discussed concerns the amphibians of São Tomé and Príncipe, two of the four volcanic islands in the Gulf of Guinea (Fig. 2). De Queiroz (p. 178) wrote that São Tomé and Príncipe ‘are true oceanic islands, meaning that, since their emergence from the ocean –

some 31 Ma in the case of Príncipe and ~13 Ma for São Tomé – they have never been connected to the mainland’. Nevertheless, these dates give only the ages of the oldest exposed lavas, and different authors have stressed that these provide only a *minimum* age for the islands (Measey *et al.* 2007; Frolov 2013). Likewise, all the exposed lavas on Mount Cameroon, part of the same volcanic line as the islands, are less than 1 million years old, with the mountain built up on much older lava flows.

Because São Tomé and Príncipe are currently surrounded by deep water, Measey *et al.* (2007) suggested that they provide an ‘indisputable example of dispersal of amphibians over a marine barrier’. Instead, it is suggested here that the amphibians’ ancestors (not the modern species) were always in the region, before the islands were formed and even before the Atlantic opened.

De Queiroz (p. 178) wrote that the ‘deep history’ of the islands ‘begins with a series of volcanoes, called the Cameroon Line’. However, the Cameroon volcanic line (CVL) is more than just the present volcanoes; it is a line of magmatism that predates the individual volcanoes seen today. The CVL is an intraplate hotline, not a plate margin, and is unique in having volcanic centres in both continental and oceanic crust. Mount Cameroon is the best-known volcano along the CVL, and it has been active during this century. From Cameroon, the CVL extends as far as Annobón (Pagalu), and perhaps even to Saint Helena near the mid-Atlantic Ridge (Meyers *et al.* 1998).

The volcanoes along the CVL do not show a linear age sequence, and so the line is probably controlled structurally rather than by plate movement over a hotspot. It has been active in episodes since the end of the Cretaceous, with alkaline intrusive magmatism from 65 to 30 Ma and volcanism

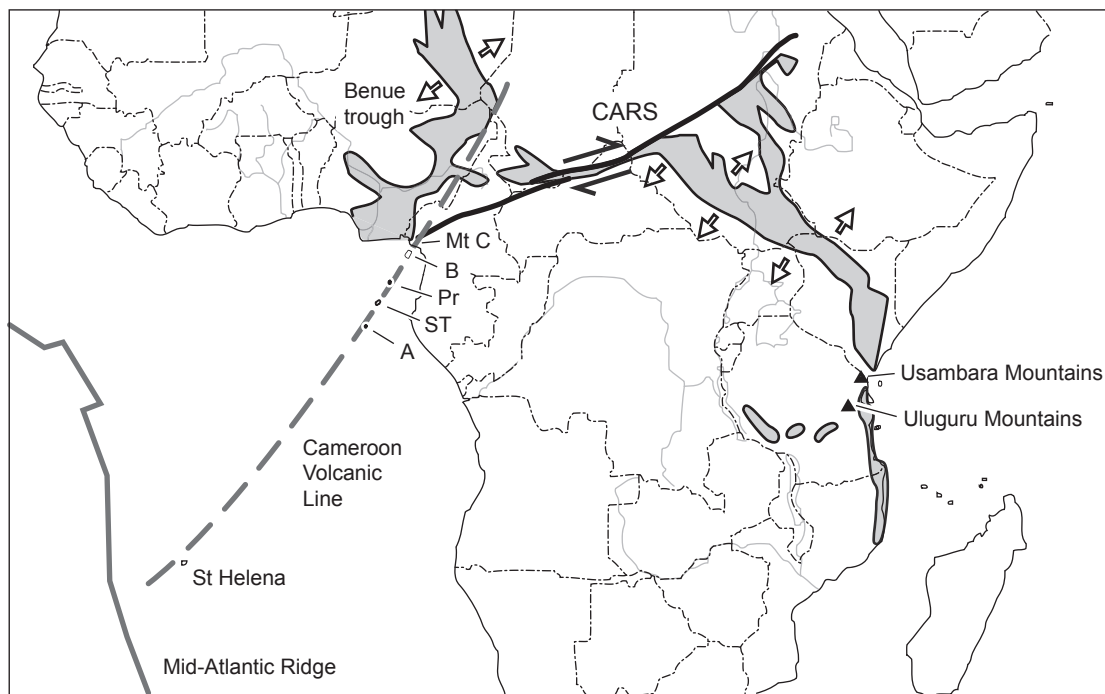


Fig. 2. The Gulf of Guinea islands and their tectonic context (Meyers *et al.* 1998; Heads 2012b). Mt C, Mount Cameroon; B, Bioko; Pr, Príncipe; ST, São Tomé; A, Annobón; CARS, Central African Rift System. Gray, CARS and related rifts.

from 35 Ma to the present. No older magmatic rocks are exposed in the area, but the CVL abuts a major rift, the Benue trough, that was active from the early Cretaceous and was associated with the opening of the Atlantic basin (Heads 2012b, fig. 5-2). Before that, the region was occupied by the continental crust of what became Africa and South America. Thus, the history of the region now occupied by the CVL islands and their biota predates the islands themselves and even the structure, the CVL, that produced them. It is not surprising that a lizard endemic to Annobón (*Afroablepharus annobonensis*) has been dated as ~10 million years old (a minimum age based on a fossil-calibrated rate), older than the oldest exposed rocks on the island (4.5 million years old; Jesus *et al.* 2007). The authors wrote that 'it is extremely difficult to explain these results' (Jesus *et al.* 2007, p. 911), but many young islands host much older endemics, and this is consistent with prior islands having existed in the same area (Heads 2011).

De Queiroz (p. 178) argued that the amphibians on São Tomé and Príncipe had to cross a saltwater barrier to get to the islands, because the islands 'have never been connected to a continent' (p. 180). Thus, he (p. 180) suggested that the amphibians are 'an affront to vicariance biogeographers'. In fact, amphibians on oceanic islands do not constitute a problem for vicariance theory, and they can be analysed in the usual way. Croizat (1958) introduced his treatment of Polynesian biogeography by discussing the frogs of Fiji (*Platymantis* and *Cornufer*, now treated together as *Platymantis s.lat.*), but these were not mentioned by de Queiroz. Although the individual islands of Fiji are young and have never been connected to any continent, the structure producing them, the Pacific subduction zone, originated by a mainland. The subduction zone has been producing islands continuously since it migrated away from the mainland of Gondwana (Australia) in the Cretaceous (Schellart *et al.* 2006). Thus, for biogeography, the history of individual islands is much less important than the history of the structure producing them, such as the Pacific subduction zone or the CVL trough. In other words, tectonics is more important for biogeography than is stratigraphy.

São Tomé and Príncipe harbour a diverse amphibian fauna, comprising six frogs and one caecilian, all being endemic to the islands. One of the frogs is *Ptychadena newtoni* (Ptychadenidae), known only from São Tomé. Its sister-group does not occur on the adjacent mainland of Africa, but in eastern Africa (Egypt, Uganda, Kenya and Tanzania). To explain this, Measey *et al.* (2007) inferred a centre of origin in eastern Africa, followed by an epic voyage down the Congo River (across major waterfalls and rapids), out to the Atlantic, and then north to São Tomé; the frogs have not colonised anywhere along the way. Measey *et al.* (2007) suggested that the dispersal could have taken place by means of floating rafts or even islands. De Queiroz (p. 195) accepted this and included a painting of a large, floating island that bears substantial forest and even large cliffs. He wrote (p. 192) that 'I have to admit that these stories sometimes do sound ridiculous', but they are 'necessary'. Nevertheless, they are necessary only if there is no alternative.

The São Tomé and Príncipe–eastern Africa pattern is a common pattern. In addition to *Ptychadena*, two of the other frogs of São Tomé and Príncipe show a similar disjunction; *Phrynobatrachus dispar* (Phrynobatrachidae) on Príncipe and

P. leveleve on São Tomé form a clade with *P. mababiensis*, which is widespread in eastern Africa (Zimkus *et al.* 2010).

The frogs *Hyperolius molleri* of São Tomé and Príncipe and *H. thomensis* of São Tomé (Hyperoliidae) form a clade that is sister to *H. cinnamomeoventris* on the adjacent mainland of Gabon–DR Congo (Bell *et al.* 2015).

The sixth frog on the islands is *Leptopelis palmatus* (Hyperoliidae) of Príncipe (Drewes and Stoelting 2004). *Leptopelis* comprises 49 species and is found through sub-Saharan Africa, but no molecular or phylogenetic analysis including *L. palmatus* appears to have been published.

The last of the São Tomé and Príncipe amphibians, and the only caecilian there, is *Schistometopum thomense*. It is endemic on São Tomé and has its only congener in eastern Africa, possibly west to eastern Congo. (Measey *et al.* (2007) cited one specimen 'most probably collected from eastern Congo', but no further details were given.) Measey *et al.* (2007) and de Queiroz accepted that, as with *Ptychadena newtoni*, *S. thomense* dispersed down the Congo River and then to São Tomé. Nevertheless, a study of *S. thomense* populations in São Tomé demonstrated that 'these animals have deep genetic divisions over very small areas in accordance with previous speculations of low dispersal abilities' (Stoelting *et al.* 2014, p. 1).

De Queiroz (p. 193) concluded: 'Let us now imagine the whole story...'. Yet, at this point, he had considered only the most superficial aspects of the geology in the São Tomé and Príncipe area, and only a very small fraction of the biota, namely, two of the amphibians (*Ptychadena newtoni* and *Schistometopum thomense*). There is no need to 'imagine a story', when analysis of a larger sample of the biota is possible.

By jumping to 'the story', de Queiroz overlooked the important fact that the São Tomé and Príncipe–eastern Africa disjunction evident in clades of *Ptychadena*, *Phrynobatrachus* and *Schistometopum* is a general pattern that is repeated in many groups with many different means of dispersal. Did each group result from a separate, unrelated event of miraculous dispersal, with the repetition of the pattern caused by chance? Or was there a single, ecosystem-wide event (such as a vicariance event) that accounts for all the individual cases? The repetitions in the following examples suggest the latter.

- In birds, the flycatcher *Terpsiphone atrochalybeia* (Monarchidae) of São Tomé is most similar in its appearance to *T. corvina* of the Seychelles (north of Madagascar; see illustrations in del Hoyo *et al.* 2006). A molecular study instead found *T. atrochalybeia* to be sister of *T. mutata* of Madagascar, but did not sample *T. corvina* (Fabre *et al.* 2012). In either case, the São Tomé birds are closest to Indian Ocean species, whereas the mainland African species of *Terpsiphone* form a separate group. Fabre *et al.* (2012) gave the phylogeny of sampled *Terpsiphone* as: north-eastern and South-east Asia (Mascarenes (southern Asia (Madagascar + São Tomé (Africa mainland))).
- A genus of swifts, *Zoonavena* (Apodidae), comprises *Z. thomensis* (São Tomé and Príncipe), *Z. grandidieri* (Madagascar and Comoros) and *Z. sylvatica* (southern India to Nepal and Myanmar). It is absent from mainland Africa. The genus belongs to tribe Chaeturini, in which three other genera are all widespread through mainland Africa, but absent

- from São Tomé, Príncipe and Madagascar. The birds are *Telecanthura* (Senegal to Zimbabwe), *Rhaphidura* (Sierra Leone to Kenya, including Bioko, also Myanmar to Borneo and Java) and *Neafrapus* (Sierra Leone to South Africa). Chaeturini also includes *Mearnsia* (Philippines and New Guinea), *Hirundapus* (needletails; India to Australia) and *Chaetura* ('swifts'; Americas) (del Hoyo *et al.* 1999).
- The bird *Prinia mollerii* (Cisticolididae) of São Tomé has the song and nest of *Prinia* (the genus is widespread in Africa), but it also shows plumage affinities with *Artisornis* of eastern Tanzania (Usambara, Nguru, and Uluguru Mountains; Fig. 2) and northern Mozambique (Njesi Plateau) (sometimes placed in *Orthotomus*), as well as *Orthotomus* (India to the Philippines) (del Hoyo *et al.* 2006). Molecular study of *P. mollerii* is needed.
 - In squamates, preliminary evidence suggests that *Mabuya* skinks from São Tomé are most closely related to eastern African clades (Jesus *et al.* 2005).
 - In landsnails, *Bocageia* comprises subg. *Petriola* known from São Tomé and the Comoros, off Madagascar, and subg. *Liobocageia* known only from Mount Ruwenzori (Gascoigne 1994). *Rhysotina* of São Tomé resembles *Plegma* of the Mascarenes (Gascoigne 1994).
 - In the Diptera (Edwards 1934) and Lepidoptera (Meyrick 1934) of the Gulf of Guinea islands, Gascoigne (1994) cited similar, disjunct affinities with eastern Africa.
 - In plants, *Melchiora mannii* (Theaceae) of São Tomé is related to a species of eastern Congo, and the Usambara and Uluguru Mountains. *Afrocarpus mannii* (Podocarpaceae) of São Tomé is related to eastern African species (Figueiredo *et al.* 2011). *Mesogyne insignis* (Moraceae) is known only from São Tomé and eastern Tanzania (Figueiredo 1994; Figueiredo *et al.* 2011; GBIF 2014).

Disjunction across the Gulf of Guinea

Groups on São Tomé and Príncipe are also involved in other, large-scale disjunctions. In many cases, distribution 'cuts the corner' across the Gulf of Guinea, missing large areas such as Nigeria and Ghana. Examples include the following:

- The grey parrot, *Psittacus erithacus*, comprises two subspecies. *P. e. timneh* occurs from Guinea to the Ivory Coast, and is disjunct on Príncipe; and *P. e. erithacus* is widespread from the Ivory Coast to Angola and Kenya, including Príncipe (Melo and O'Ryan 2007). *P. e. timneh* is disjunct 1400 km across the Gulf of Guinea, from Príncipe to the Ivory Coast, with the gap in Ghana, Togo, Benin and Nigeria filled by its relative.
- The ibis *Bostrychia olivacea* occurs in Sierra Leone and Liberia, and from there it is disjunct 1700 km across the Gulf of Guinea to São Tomé, Cameroon, Gabon, and east to Kenya–Tanzania (del Hoyo *et al.* 1992). This bird lives in dense lowland forest, including swamp forest and mangrove, in western Africa, and at montane elevations in eastern Africa.
- The pigeon *Columba* (or *Aplopelia*) *larvata* is in Sierra Leone and Liberia, and is disjunct to south-eastern Nigeria, Bioko, Príncipe, Annobón (not São Tomé), also eastern Africa. *C. simplex*, related to *C. larvata*, is endemic on São Tomé (del Hoyo *et al.* 1997).

- Another *Columba* species, *C. iriditorques*, is widespread in western and central Africa, but skips 300 km in south-eastern Nigeria, and is replaced on São Tomé, Príncipe and Annobón by *C. malherbi*, which is endemic there (del Hoyo *et al.* 1997).

Biota of the CVL in general

Groups distributed elsewhere on the CVL show patterns similar to those of São Tomé and Príncipe. For example, the plant *Mitriostigma* (Rubiaceae) from Bioko and adjacent parts of Cameroon is disjunct in south-eastern Kenya, eastern Tanzania (Usambara Mountains), eastern coast of Mozambique and eastern coast of South Africa. (The Usambara species – far from the Congo – is keyed with the Cameroon–Bioko species; Sonké *et al.* 2009). *Mitriostigma* appears to be closest to *Oxyanthus*, which is widespread through Africa from Senegal to South Africa.

A study of the tree composition of tropical African forests indicated that four of the six types recognised had their boundaries at the Benue trough–CVL (wet–moist western African and dry western African forest types had their eastern limit at the Benue trough–CVL, whereas western central African and upland eastern African forest types had their western limit there; Fayolle *et al.* 2014). Eastern African upland forest had a western outlier on Bioko, giving the usual disjunction between the CVL and the central African lakes.

All these disjunctions from the Gulf of Guinea islands to eastern Africa and Indian Ocean islands could be the result of extinction on mainland Africa, rather than long-distance dispersal. This is the standard explanation usually given for the pattern (although it was not mentioned by de Queiroz), and climatic change is often cited as a cause. However, the pattern includes groups with a wide range of ecology, and so marine incursions in the Congo basin (Heads 2012b, fig. 5-2) might be a more likely explanation for extinction. Another alternative is possible, because the São Tomé and Príncipe + eastern Africa groups all have close relatives on mainland Africa. This suggests simple vicariance, with eastern and western groups having been connected to the north (perhaps via the central African rift system; Heads 2012b, fig. 5-2) or the south.

These explanations do not account for the disjunction between the CVL and Liberia–Sierra Leone, across the Gulf of Guinea. This is possibly involved with the trans-Atlantic disjunction described next.

Biogeographic links between the CVL and America

Several groups of the CVL exhibit closer links with America than they do with mainland Africa. Examples include the following:

- The plant *Utricularia mannii* (Lentibulariaceae) of São Tomé and Príncipe, Bioko and Mount Cameroon is a member of the *Orchyllium* group, which is otherwise restricted to America (Taylor 1964).
- The tree *Hernandia* (Hernandiaceae) is disjunct between America, São Tomé and Bioko, and South Africa to Polynesia (Michalak *et al.* 2010). The authors inferred dispersal from America to Bioko.

- The scarab genus *Stenosternus* is endemic to São Tomé, and is placed in a tribe, Aegidiini, that is otherwise restricted to America (Frolov 2013).
- Many coastal, shallow-water fishes of São Tomé and Príncipe have their closest affinities in the western Atlantic (Wirtz *et al.* 2007).

These suggest that the biota of the CVL dates to before the opening of the Atlantic.

The CVL–Benue trough region is one of the most important biogeographic nodes in the world. It is a major centre of endemism, an important zone of disjunction, the major phylogenetic break in the African tropical rainforest, and the site of many other anomalies. For example, in a study of island avifaunas worldwide, plots of percentages of endemic species *v.* island area showed three parallel curves, with one for ‘solitary, well isolated islands’, one for ‘single islands, near mainlands or large archipelagos’, and one for ‘islands in the Gulf of Guinea’ (Mayr 1965*b*). The Gulf of Guinea avifaunas showed the highest levels of endemism per unit area. A detailed biogeographic analysis of actual distribution patterns in the region (free of any assumptions about chance dispersal) would be of great interest.

Madagascar

In the traditional view, all the groups of plants and animals in Madagascar have been derived by chance dispersal (Matthew 1915). Matthew accepted the idea of an evolutionary clock, which proposes that the degree of differentiation of groups is proportional to the time since their origin (Heads 2012*b*, Chapter 2). This concept had been rejected in the 19th century, but following Matthew’s work, it was reinstated in the modern synthesis. When applied to molecular differentiation, it formed the basis of the molecular clock. Matthew (1915, p. 203) concluded that the differing degrees of differentiation of the Malagasy mammals ‘point to a number of colonizations of the island by single species of animals at different times’. All biogeographic patterns include groups with a wide range of degrees of differentiation, but evolutionary rates differ in different groups (and in the same group at different times), and so a single pattern can be the result of a single vicariance event. Nevertheless, de Queiroz (p. 248, italics added) wrote that ‘Recent studies *show* that the traditional, dispersalist view of the Madagascan biota is correct.’. The recent evidence comprises molecular clock dates, as reviewed by Yoder and Nowak (2006). Yet, as Morrison (2014) indicated, if the clock dates are incorrect, the evidence for dispersal ‘begins to melt away’.

Yoder and Nowak (2006) reviewed many clock studies, most of which used fossil calibrations and treated the clock dates, illogically, as maximum clade ages. The actual clade ages could be much older, but the clade ages were accepted by Yoder and Nowak (2006) as absolute dates. This meant that a vicariance history for Madagascar groups caused by the opening of the Mozambique Channel could be eliminated (because it was too old), and chance dispersal could be invoked. The one clock study in their review that did not use fossil calibrations supported vicariance. So although Yoder and Nowak (2006, p. 416) concluded that the importance of dispersal ‘cannot be denied’, the only thing that their review really indicated was the

importance of the calibration method (see Heads 2012*b*, Chapter 3, for more details).

The Seychelles

These islands are located north-east of Madagascar and are formed from old granite (continental crust). De Queiroz (p. 251) suggested that ‘most Seychellian species are in the same genera or even the same species as taxa found elsewhere, indicating that they arrived fairly recently by overwater dispersal’. (This reasoning is, again, based on Matthew’s (1915) idea of an evolutionary clock, in which the taxonomic rank of a group is proportional to its age.) Nevertheless, the frog *Sooglossus* of the Seychelles is sister to *Nasikabatrachus* of India, and in caecilian amphibians, *Praslinia*, *Grandisonia* and *Hypogeophis* of the Seychelles are sister to *Gegeneophis* of India (Zhang and Wake 2009). Although de Queiroz admitted that these affinities were too old to be the result of trans-oceanic dispersal (they are probably the result of pre-drift, intra-continental rifting), he did not discuss them further, arguing that they are ‘intriguing but no longer part of the main theme’ (p. 251). In fact, they are typical examples of the well-documented Seychelles–India connection.

New Zealand

New Zealand played a key part in de Queiroz’s argument, and was cited in his book more than any other area. De Queiroz considered a sample of common New Zealand plant genera, such as, for example, *Celmisia* and *Coprosma*, and argued that ‘*taken at face value*, the fossil record indicates that not a single one is a Gondwanan holdover. They all seem to have arrived by crossing the sea’ (p. 105, italics added). This can be compared with a palaeontologist’s view, namely that ‘the fossil record provides direct evidence. . . *but it cannot be taken at face value*’ (Smith 2007, p. 731, italics added).

De Queiroz (p. 226, italics added) concluded that the vicariance view ‘*clearly* does not hold up for the flora of New Zealand’. This is because the fossil pollen record ‘*clearly* indicates the late arrival of many New Zealand plant lineages’ (p. 106, italics added). Fossil-calibrated clock dates also indicate dispersal (p. 162), and so New Zealand plant families ‘*must be explained by oceanic dispersal*’ (p. 319, italics added).

Despite these assertions, de Queiroz (p. 110, italics added) admitted that ‘. . . it is well known that the fossil record is incomplete. . . Everyone agrees that New Zealand’s plant fossil record is far better than its vertebrate fossil record, but that *doesn’t necessarily mean the plant record is reliable in an absolute sense*. One possibility is that many lineages persisted during certain periods only in small refugia where they were unlikely to leave any trace in the fossil record.’. This idea of species surviving as metapopulations in multiple microrefugia has long been accepted in vicariance models of New Zealand biogeography (Heads 1993).

Chance dispersal does not make any predictions, whereas vicariance theory predicts that New Zealand could not have been completely submerged in the Cenozoic. Some geologists have argued that it was (Landis *et al.* 2008), and the idea received a lot of publicity because it would falsify vicariance. Nevertheless, geologists have now found substantial evidence for exposed

land in many parts of New Zealand at the height of the marine transgression, in the late Oligocene (Bassett *et al.* 2014).

Chatham Islands

The Chatham Islands are located east of the New Zealand mainland, and are the only emergent portion of the continental Chatham Rise. De Queiroz discussed the Mesozoic, Gondwanan biota on the islands (fossils of terrestrial groups are known) and asked the following question (p. 240): ‘Did any of those Gondwanan lineages persist to the present? The rocks tell us the answer is ‘not likely’.

On the basis of stratigraphic evidence from the Chatham Islands (in particular, the young age of the highest-elevation rocks) geologists have inferred complete submersion of the Chatham Islands between Late Cretaceous and Early Pliocene, with uplift of the present islands beginning at *c.* 4 Ma and leading to emergence at 2 or 3 Ma (Campbell 2008; Campbell *et al.* 2008, 2009). Many studies have accepted this as the oldest age of any islands in the region. For example, Landis *et al.* (2008, p. 191) concluded that ‘there is certainty that the entire Chatham Islands biota (before the arrival of people) is derived from long-distance dispersal, all within the last two million years’.

Nevertheless, the existence of other, prior islands in the vicinity of the Chathams is suggested by the buoyancy of the Chatham Rise continental crust, the repeated phases of volcanism, the many flat-topped seamounts in the area, complex faulting within the islands, older molecular clock dates for several groups, and the endemism and phylogenetic relationships of the living taxa. These are discussed next.

Repeated phases of volcanism around the Chatham Islands and seamounts

Precise paleogeographic data are not usually available for large areas that are now submerged, but in the Chatham Islands region there are already many indications as to where land could have existed in the past. The Chatham Islands are an emergent, volcanic part of the Chatham Rise, itself formed from Jurassic continental basement (Chatham Schist), and this is exposed in the northern part of the main island.

Exposures of mid-Cretaceous sandstone dated at 100 Ma occur on Pitt Island, and since the Late Cretaceous there have been repeated phases of volcanism (Campbell *et al.* 2008). Widespread eruptions at 80–70 Ma formed the main southern part of Chatham Island, now much eroded.

De Queiroz (p. 240) cited marine strata in the islands, ‘Suggesting that the Chathams were completely submerged’ through the Cenozoic until 6 Ma. Nevertheless, sporadic but widespread eruptions at 63–55 Ma (Red Bluff tuff) ‘may have formed an island’ (Campbell 2008, p. 38). Eruptions at 42–34 Ma produced Mount Chudleigh (which ‘may have formed a small island’), and further eruptions occurred at 6 Ma and 5–3 Ma.

These eruptive phases are only those whose products are exposed on the present islands; other signs of former eruptions have either been eroded away, are buried, or lie out to sea. Rowden *et al.* (2005) mapped 812 seamounts on the submerged part of the New Zealand plateau and these included ~40 located around the rim of the Chatham Rise, with a strong concentration south-east of the Chatham Islands.

Multibeam bathymetric surveys east of the South Island showed numerous submarine volcanoes on the Chatham Rise and evidence of submarine erosion on its southern margin (Collins *et al.* 2011). The largest volcanic cones are ~2000 m in diameter, and some stand as high as 400 m above the surrounding seafloor. The tops of most of the volcanic cones are flat, indicating that they have been eroded to sea level. Other submerged features on the Chatham Rise that were probably former islands include the flat-topped Mernoo Bank, currently only 51 m deep at its highest point. Holdaway *et al.* (2001, p. 151) wrote that ‘The former presence of islands between the South Island and the Chathams, where the Veryan and Mernoo banks now stand, show that not all [Chatham Islands] species would necessarily have had to cross the present distance from the mainland.’ Yet, rather than simply being stepping-stones for dispersal from the mainland, the former islands (Veryan Bank and nearby Mernoo Bank) could have hosted their own biota, including endemics. These would have colonised new land at the Chatham Islands, and when Veryan and Mernoo Banks were submerged, the clades would be left as endemics on the Chathams. Given the active volcanism and the normal means of dispersal of plants and animals, it is likely that the biotas of many other former islands (now flat-topped seamounts) around the Chathams underwent the same process.

Tectonism in and around the Chatham Islands

Apart from the volcanism and subsidence around the Chatham Islands, several cryptic faults have been active within the archipelago. These mean that stratigraphic evidence for submersion from one area, such as the young marine sediments at the highest point, may not apply to the region as a whole for any one period of time. For example, one major fault must be responsible for the uplift of the basement schist in northern Chatham Island, although the fault is not exposed (Campbell 2008). Displacement on other large-scale faults in the region would have also led to differential uplift and subsidence. Holt (2008) recorded considerable variation in uplift rates across Chatham Island and over very short distances (including 10-fold differences in rates over just 400 m), and these variations ‘cannot yet be fully explained’. Again, they could reflect activity on the basement fault between the Chatham Schist to the north and younger rocks to the south. Uplift rates are higher in the north and south, and less in the central parts. Holt (2008, p. 139) described the ‘Poor understanding of the characteristics and history of tectonics and uplift of the Chatham Islands area. . . Chatham Island tectonic history is not resolved . . . the tectonic history may be quite complicated. The northern, central, and southern regions of Chatham Island behave differently in terms of deformation.’ This localised tectonism (found throughout Zealandia) means that the evidence for submergence of part of the Chatham Islands does not require that the whole archipelago was submerged.

The Hikurangi Plateau

The Hikurangi Plateau is a large plateau (much larger than New Zealand mainland), that crashed into the eastern mainland and Chatham Rise after arriving from the central Pacific. Originally, it formed part of the Ontong Java–Hikurangi–

Manihiki plateau that was erupted, at least in part, in subaerial conditions and includes fossil wood (Heads 2014c). This megaplateau was later rifted apart. The Hikurangi Plateau includes many guyots (flat-topped seamounts), and its history is likely to explain the affinities of the Chatham Islands groups that have sister-groups in the central Pacific. For example, the Chatham Islands endemics *Hebe chathamica* and *H. dieffenbachii* (Plantaginaceae) are most closely allied *H. rapensis* of Rapa Island (south-eastern Polynesia) (Bayly and Kellow 2006), and the Chathams beetle *Rhantus schauinslandi* (Dytiscidae) is more closely related to species such as *R. vitiensis* of Fiji than to New Zealand mainland species (Ordish 1989).

Molecular clock dates of Chatham Islands groups

As noted above, young marine strata occur at what is currently the highest point of the Chatham Islands, and geologists have concluded that the present-day Chatham Islands were completely submerged from 6 until 3 Ma (Campbell 2008; Landis *et al.* 2008; Campbell *et al.* 2008, 2009). Nevertheless, several plants endemic to the Chatham Islands have been dated as older than 3 million years old (Heenan *et al.* 2010), including the following:

- *Hymenanthera chathamica* (Violaceae): 3.6–4.7 million years old,
- *Embergeria grandifolia* (Asteraceae): 3.5–7.8 million years old,
- *Sporadanthus traversii* (Restionaceae): 5.2–5.9 million years old, and
- *Myosotidium hortensium* (Boraginaceae): 7.0–14 million years old.

There are also several animal clades on the Chatham Islands that are dated as older than 3 Ma. An endemic clade of beetles (*Geodorcus capito* + *G. sororum*: Lucanidae) was dated at 6 million years old (Trewick 2000). The widespread New Zealand beetle *Brachynopus scutellaris* (Staphylinidae) includes an endemic Chatham Islands clade with an estimated age of 10.17 Ma (0.95 credible intervals: 4.67–16.27 Ma) (Buckley and Leschen 2013). The endemic skink *Oligosoma nigriplantare nigriplantare* was dated at 5.9–7.3 million years old (Liggins *et al.* 2008a).

The phylogenies of these plants and animals (apart from that of *Brachynopus*) were calibrated either with fossils, which give minimum clade ages, or by using the ages of islands in the region (Norfolk: 3 Ma; Lord Howe: 7 Ma; and Kermadec Islands: 2 Ma) to date endemics there that are related to Chatham Islands taxa. This latter procedure assumes that island-endemic taxa can be no older than their islands, although the ages that Heenan *et al.* (2010) calculated for the four Chatham Islands species listed above contradict this principle. Also, with respect to groups endemic to Norfolk and Lord Howe Islands, such as the skink *Cyclodina*, have been shown to be much older (25 million years old) than their islands (Chapple *et al.* 2009). This means the island-endemic plants there used for calibration could have survived in the area long before their current islands existed, on prior islands.

Thus, Heenan *et al.* (2010, p. 105) correctly emphasised that ‘Because the majority of the molecular divergence ages given here are based on independent calibration points such as the geological age of islands or the fossil record, they should be considered as minimum ages.’. This means that many other Chatham Islands endemics with younger dates, in addition to those listed above, are likely to be older than the current islands. It also undermines de Queiroz’s (p. 241) conclusion: ‘The idea that species on the Chathams evolved only recently from ancestors that lived elsewhere has been confirmed by extensive molecular studies...’.

Heenan *et al.* (2010) suggested that the clades dated as older than 3 Ma (listed above) mean that there could have been emergent land in the Chatham Islands before 3 Ma, formed by some of the eruptions, or on the Chatham Rise. (They did not mention the guyots on the Hikurangi Plateau.) This contradicts the conclusions of the geologists, but is supported here, and the principle also applies to earlier times in the Cenozoic, when it is even harder to deduce paleogeography from geological evidence alone. The Chatham Islands region has a long history of volcanism, dating back to the Mesozoic, and so it is possible that plants and animals have survived in the region since before Gondwana breakup.

Affinities of Chatham Islands groups

Several Chatham Islands groups are basal to (not nested in) groups that are diverse and widespread on the New Zealand plateau, and so deriving the Chatham Islands forms from the mainland requires extra, *ad hoc* hypotheses that are not needed in a simple vicariance model. To cite just two examples, the parakeet *Cyanoramphus forbesi* of the Chathams is sister to the six remaining New Zealand species, which range from Macquarie Island to Lord Howe and the Kermadec Islands (Boon *et al.* 2001), and the duck *Anas chathamica* (formerly *Pachyanas*) of the Chatham Islands (extinct by the 19th century) is sister to a diverse clade (brown teals) that is widespread through New Zealand from the Auckland and Campbell Islands to the northern North Island (Mitchell *et al.* 2014a).

Summary on the Chatham Islands

De Queiroz did not mention the following: the continued phases of volcanism in the Chatham Islands; the many guyots surrounding the islands; the evidence for major local tectonism that would have raised or lowered different parts of the islands; the Hikurangi Plateau (with its many guyots) that crashed into the Chatham Rise after arriving from the central Pacific; the affinities between many Chathams groups and relatives in the central Pacific; the clock ages of Chathams endemics that pre-date the current islands; and the many Chatham Islands groups that are basal to diverse complexes on mainland New Zealand. Thus, de Queiroz suppressed all the relevant evidence except for fossil-calibrated clock dates, and he treated these, illogically, as maximum clade ages. Only in this way was he able to conclude (p. 242) that ‘there is no evidence whatsoever of Gondwanan relict species on the Chathams’. In fact, there is a wide range of evidence consistent with the direct ancestors of the current species having lived in the area before the islands that currently host them existed, and before Gondwana breakup.

New Caledonia

New Zealand and New Caledonia are parts of the same block of continental crust, termed Zealandia. Close biogeographic links between the two areas are well known (Hutton 1872), and the pattern can be attributed to vicariance. Nevertheless, de Queiroz rejected this close relationship and, in support, cited (p. 165) a centre of origin study (Sanmartín and Ronquist 2004) that was ‘significant for its generality, reminiscent of Croizat’. De Queiroz seems to have believed the reports (from dispersalists) that described Sanmartín and Ronquist’s study as ‘a comprehensive meta-analysis of austral biogeography’ (Waters and Craw 2006, p. 354), but this assessment is not correct. Unlike Croizat’s (1958) work, which cited a large amount of supporting evidence, the study by Sanmartín and Ronquist (2004) relied on a very small sample size (54 animal groups, 19 plants). It concluded that ‘None of the animal or plant area cladograms show the sister-group relationship between New Zealand and New Caledonia predicted by the geological scenario (p. 231). . . Our results, therefore, do not support the notion of a common relict late Cretaceous Gondwanan biota in the two landmasses’ (p. 240). This result is an artefact caused by the statistical problem underlying the study, and many groups not examined by the authors show a sister-group link between the two areas (e.g. Heads 2014c, p. 267).

De Queiroz (p. 242) wrote that some geologists ‘now think that New Caledonia was entirely underwater from ~37 to 70 million years ago. . .’. This is the same argument proposed for New Zealand, the Chatham Islands, Hawaii (below) and other areas. Yet, to prove this, there would need to be marine strata of the same age completely covering the New Caledonian archipelago, and nothing like this exists. In areas such as New Caledonia, New Zealand and the Chatham Islands that have undergone differential uplift and subsidence at local scales, it is impossible to rule out small areas of land. In addition, even if the present islands of New Caledonia were submerged, it is known that areas of now-subsided land existed nearby, for example, on the Norfolk Ridge (see below).

De Queiroz discussed Mesozoic groups in the region and suggested (p. 343) that there is ‘little evidence to show that they’ve been riding on a New Caledonian ark ever since then. . .’. However, there is *no* evidence to show they occurred anywhere else. For example, the plant *Amborella* is sister to all other angiosperms and is endemic to New Caledonia. It is obviously much older than the Cenozoic, and there are no records, either living or fossil, from anywhere but the Paleozoic–Mesozoic basement terranes of the New Caledonian mainland (Heads 2014c).

Norfolk Island

Norfolk Island is a small island on the Norfolk Ridge, a strip of continental crust that extends between New Zealand and New Caledonia. The island’s biota includes many interesting endemics, such as the Norfolk pine, *Araucaria heterophylla*. De Queiroz pointed out that the island is a volcano that arose from the sea at only 3 Ma, and so the ancestors of *A. heterophylla* ‘*must* have arrived by oceanic dispersal’, with New Caledonia being ‘the closest likely source’ (p. 108, italics added). Nevertheless, there is now excellent evidence for a former, large, long-lived

Cenozoic island lying adjacent to Norfolk Island (Heads 2014c, fig. 7.2). The island has been obliterated by extension, but Meffre *et al.* (2006) illustrated a well-preserved leaf fossil from seafloor rocks in the area.

Hawaiian Islands

Many authors have assumed that because the Hawaiian Islands were never joined to a continent, the ancestors of the Hawaiian biota must have come from either Asia or North America (e.g. Wilson 2001). De Queiroz also accepted this; because islands such as Hawaii ‘originated and persisted as *remote and isolated* bits of land, native lineages . . . *must* have reached them by long-distance, overwater dispersal’ (p. 79, italics added). The Hawaiian Islands are remote and isolated *now*, but the groups endemic there could have evolved on former islands in the vicinity and colonised the present islands by normal dispersal.

De Queiroz argued that Hawaiian groups could not have survived on the Hawaiian–Emperor chain throughout the Cenozoic, because there was a period between 33 and 29 Ma when there were no emergent islands in the chain (Clague 1996; Clague *et al.* 2010). Therefore, groups ‘*must* have reached the [Hawaiian islands] by natural long-distance dispersal’ (p. 75, italics added). Nevertheless, the method that Clague (1996) and Clague *et al.* (2010) used to calculate the former heights of what are now submerged seamounts in the Hawaiian chain underestimated the heights of the present volcanoes (Table 2), and so it is also likely to have underestimated the former heights of the seamounts.

In any case, even if the Hawaiian endemics did not survive within the Hawaiian chain itself, the archipelago is surrounded by former islands. These include, for example, the Musicians Seamounts to the north (Heads 2012b), and the Necker Ridge, Horizon Guyot and Mid-Pacific Mountains to the west (Gardner *et al.* 2013).

De Queiroz considered the example of the bristletails (Archaeognatha), a widespread group that occurs on Hawaii, ‘2400 miles from North America and even further from any other likely continental source area’ (p. 260). ‘Bristletails are supposed to be inept at crossing ocean barriers, because they’re flightless and delicate and have a tendency to jump in a completely random direction when disturbed, presumably not the best thing to do on a raft shaken by waves’ (pp. 260, 261). So, what is the evidence that they did undergo trans-oceanic dispersal? The evidence is simply that they occur in Hawaii. De Queiroz (p. 261) stated that ‘their presence in Hawaii suggests that their voyaging capabilities have been underestimated. . .’. (As mentioned above, under the

Table 2. Actual heights of volcanoes on Maui and Hawaii, and maximum heights predicted by Clague (1996)

Volcano	Actual height (m)	Clague (1996) estimate (m)
East Maui	3055	2180
Kohala	1670	1740
Hualalai	2521	1040
Mauna Kea	4205	3050
Mauna Loa	4170	3050
Kilauea	1277	1040

heading Vicariance and dispersal, the actual, observed means of dispersal of a group bear no relationship to its inferred chance dispersal; in dispersal theory, a group inferred to have jumped thousands of kilometres across open ocean may have excellent means, or no apparent means.)

The closest relative of the Hawaiian bristletails is found along the western coast of North America. De Queiroz wrote that ‘the *obvious interpretation*’ of this affinity is that the Hawaiian bristletails originally came from North America. Yet although the closest relative *now* inhabits North America, de Queiroz’s inference overlooks possible former populations on what are now submerged seamounts. De Queiroz (p. 263, italics added) suggested that dispersal event was ‘presumably by rafting’ from America to Hawaii, or (because the North American species is nested in the Hawaiian ‘group’) from Hawaii to North America. In any case, de Queiroz assumed an unbroken, long-distance dispersal between Hawaii and North America, because there are no islands between the Americas and Hawaii to use as waystations (p. 262).

There are no current islands between Hawaii and North America, but de Queiroz’s conclusion overlooks prior islands there. Maps of the ocean floor are far from complete and we have better topographic maps of the Moon and Mars (Koppers 2009). Of a possible total of ~200 000 seamounts more than 1 km high, only ~15 000 have been mapped (Wessell 2009), and only a few hundred have been sampled. Nevertheless, many seamounts have already been mapped between Hawaii and California (Etnoyer *et al.* 2010). The seamounts are now submerged, because the seafloor has subsided by thousands of metres through the Cenozoic as it has moved away from the spreading ridge that produced it and cooled (Heads 2012*b*). This large-scale subsidence is overlooked in modern dispersal theory; however, new seafloor subsides ~1000 m in the first 10 million years of its existence (as it spreads away from the ridge and cools), and at a slightly slower rate after that. This relationship is shown in the well-known age *v.* depth curve for seafloor (van der Pluijm and Marshak 2004, fig. 16.26). Zhong *et al.* (2007, fig. 1*a*) depicted the depth of the Pacific seafloor (with the spreading ridge, the East Pacific Rise, in light brown) and this can be contrasted with the age of the seafloor (Zhong *et al.* (2007, fig. 1*d*). The seafloor between California and Hawaii has dropped thousands of metres (light brown to light blue in fig. 1*a*, Zhong *et al.* 2007), as it has aged. The plate is subducting in the west Pacific; where the seafloor is oldest and deepest.

De Queiroz based his idea of direct dispersal between North America and Hawaii solely on the absence of present islands there, and wrote (p. 266) that ‘we’re [dispersalists] all just doing what scientists are supposed to do, namely, focusing on the evidence’. But the dispersalists are also suppressing other evidence, such as evidence for prior islands, that does not fit their narrative. Even the great dispersalist Ernst Mayr accepted former, sunken islands between Hawaii and North America (Mayr 1982*a*, p. 453). However, he viewed them as possible stepping stones for dispersal, rather than as simply providing habitats for widespread, ancestral metapopulations in the eastern Pacific as proposed in vicariance theory.

There are many ancient lineages endemic to islands that are much younger (Heads 2011). De Queiroz (p. 244) cited the examples of *Hillebrandia* on Hawaii (dated at 50 Ma), and

Bolyeriidae snakes on the Mascarene Islands, dated at 70 Ma. De Queiroz (p. 244, italics added) wrote that these groups ‘*must* have colonized their young, volcanic island homes by overwater dispersal, subsequently becoming extinct in the source areas’. All fresh lava is colonised from somewhere, but this source may have been very close to the lava flows, on the same island or possibly on *former* land, and not necessarily from what is *currently* the closest mainland. *Hillebrandia* is sister to the rest of the family Begoniaceae (a diverse, pantropical group), and the Mascarenes Bolyeriidae are sister to Xenophidiidae of Borneo (Pyron *et al.* 2013). This Mascarenes–Borneo distribution of the sister-groups suggests a ‘probably ancient Gondwanan distribution for their shared common ancestor’ (Lawson *et al.* 2004, p. 291).

Falkland Islands

The Falkland Islands, off the southern tip of South America, are formed from a block of continental crust derived from Gondwana. McDowall (2005) thought that the Falklands block was initially part of Africa and later drifted across the South Atlantic after it opened, ending up attached to South America. This was based on geological work published up until 1996. De Queiroz accepted this idea (citing geological work up until 1999) and wrote (p. 233) that ‘Anyone who understood vicariance biogeography and knew that the Falklands had once been part of Africa might have expected to find a significant African–Gondwanan element in the islands’ biota.’. In fact, McDowall (2005) found that most of the Falklands groups had their closest relatives in America. This finding falsifies *either* a vicariance history *or* the accepted geology, but McDowall and de Queiroz considered only the former possibility.

By assuming that vicariance could be rejected, McDowall (2005) (and de Queiroz) missed an opportunity to question the accepted geology and make a novel prediction about the subject, one that was subsequently proposed by geologists; Martin (2007, p. 245) concluded that the Falklands block was ‘initially attached to southern Patagonia/West Antarctic Peninsula’, and that southern Patagonia and the Falklands block subsequently broke up as the result of ridge jump, backarc extension or both. Before Gondwana breakup, the Falklands block was *also* connected by continental crust to what became Africa, but this was before the Atlantic formed. Martin (2007) showed that ever since the beginning of breakup, it has been attached to South America.

McDowall (2005) and de Queiroz (p. 323) both assumed that the geological work on the Falkland Islands from the 1990s was the final word on the subject. Thus, de Queiroz (p. 251, italics added) concluded that ‘The rock of the Falkland Islands may be ancient, but the biota, as a continuous entity, *definitively* is not.’ This might be reasonable if earlier geological analyses are accepted, and geological work from the 21st century is ignored; however, geology (unlike dispersal biogeography) moves on, as a progressive research program, and generates bold, new, testable ideas. According to de Queiroz (p. 252), the most interesting aspect of McDowall’s (2005) work on the Falklands was ‘the demonstration that the Croizatian dictum that ‘Earth and life evolve together’ does not have general application...’. Yet the model proposed by Martin (2007) and overlooked by de Queiroz corroborates Croizat’s dictum.

Fernando de Noronha

Fernando de Noronha is an archipelago 354 km off north-eastern Brazil. The skink *Mabuya atlantica* is endemic there and is sister to African species of *Mabuya*, not to the South American ones that are much closer geographically. De Queiroz (p. 205) accepted the conclusions of Carranza and Arnold (2003) that the ancestor of *M. atlantica* 'must' have reached Fernando de Noronha from Africa. The lizards 'must have travelled at least 1800 miles overwater. . .'; 'the DNA studies . . . show that *M. atlantica* came from Africa' (p. 205, italics added). Nevertheless, de Queiroz did not consider the possibility that the species' ancestors could have dispersed from former islands in the vicinity, or be derived from ancestral, generalised forms of *Mabuya* that were already in the region before the opening of the Atlantic.

The idea that *M. atlantica* arose when Africa and South America were already widely separated by the Atlantic Ocean, and that the ancestor must have made very long transoceanic journeys, depends entirely on the calculated age of *M. atlantica*, namely, 7–9 Ma (Carranza and Arnold 2003). This in turn depends on the calibration that was used, and this assumed that three lizard clades endemic to El Hierro island in the Canary archipelago could be no older than the age of the island (1.1 Ma). Nevertheless, a recent study of the Canary Islands and their neighbours suggested that this is not justified. Fernández-Palacios *et al.* (2011, pp. 226, 228) wrote that large and high islands may have been continuously available in the region for very much longer than is indicated by the maximum age of the oldest current island (27 Ma) – possibly for as long as 60 million years. They concluded that:

Consistent with previous work on the Hawaiian system . . . and the Galápagos . . ., there is now increasing evidence of a significant history of Macaronesian landmasses extending back in time beyond the age of the oldest currently emergent islands, and probably providing a considerably longer continuous insular history of large islands than for either of these classic evolutionary systems. . .

This means that the evolutionary rate estimated from the El Hierro lizards would be much too fast, and so the date that

Carranza and Arnold (2003) calculated for *M. atlantica* (7–9 Ma) would be a minimum, not a maximum age.

De Queiroz (p. 205) wrote that 'The ancestors of *M. atlantica* apparently made their transatlantic voyage within the past 3.3 million years (the maximum estimate for the age of Fernando de Noronha)', but he did not consider the underlying structure that has produced the islands. This has usually been inferred to be a hotspot, with the South American plate moving westward over it and producing Fernando de Noronha, along with older seamounts located to its west. Nevertheless, the hotspot idea has been questioned, and a genetic link between Fernando de Noronha and the oceanic fracture zones has been proposed instead (Knesel *et al.* 2011). In either case, older islands have existed in the vicinity of Fernando de Noronha before the emergence of the present islands.

Analysis of two groups: ratite birds and primates

De Queiroz's ideas on dispersal can be examined with respect to two groups that he discussed, ratites and primates. Clades in both groups show high levels of allopatry, as well as some areas of overlap.

Ratite birds

Ratites (Fig. 3) are sister to all the other extant birds. Extant ratites comprise four main clades with the following phylogeny (Mitchell *et al.* 2014b):

- (1) **Africa** and (fossil) **Eurasia**, east to China: ostriches (Struthionidae).
- (2) **South America** south of the Amazon: Rheas (Rheidae).
- (3) **Trans-Pacific basin**: moas (Dinornithidae) of New Zealand (extinct in historical times), and tinamous (Tinamidae) from South America and north to Mexico.
- (4) **Trans-Indian Ocean basin**: elephant birds (Aepyornithidae) of Madagascar (extinct in historical times) and kiwis (Apterygidae) of New Zealand; emus of Australia (Dromaiidae) plus cassowaries of New Guinea and Queensland (Casuariidae).

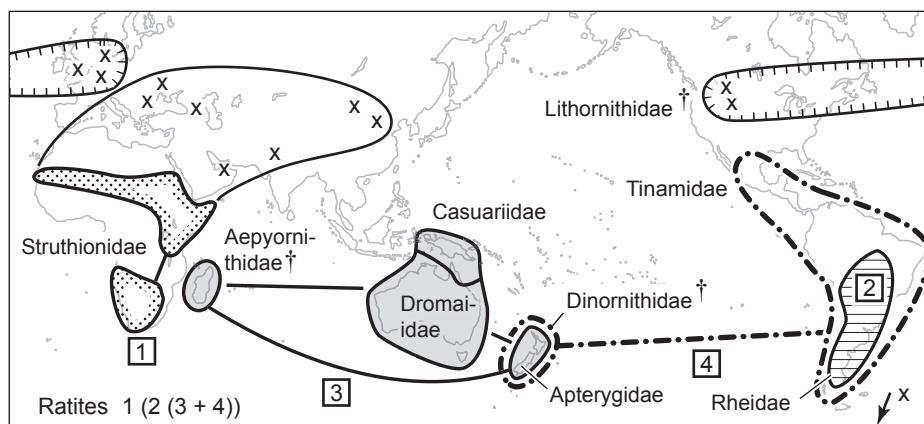


Fig. 3. Distribution of ratite birds (Heads 2014c; Mitchell *et al.* 2014b).

There are also allopatric, fossil clades in the north, notably Lithornithidae in Europe and North America; however, as with many fossil groups, their affinities are controversial. (Lithornithids are sometimes linked with Tinamidae.)

Neither the recent molecular studies (Phillips *et al.* 2010; Mitchell *et al.* 2014b) nor de Queiroz mentioned the most striking aspect of the distribution, namely, the global allopatry of the four main clades and the fossil lithornithids everywhere except New Zealand and South America (Fig. 3). This high level of allopatry is consistent with an origin of the clades by vicariance of a widespread, global ancestor, followed by local dispersal leading to clade overlap in New Zealand and South America.

Within the extant and subfossil groups (the only ones for which molecular information is available), the primary break is between Africa and Madagascar (Middle Jurassic rifting), between China and New Guinea, and in the Atlantic Ocean (Early Cretaceous rifting). The break between Pacific basin and Indian Ocean basin clades lies somewhere in the New Zealand region, and coincides spatially and temporally with the pre-drift intra-continental rifting that took place there in the mid-Cretaceous. A more detailed study of the group (Heads 2014b) showed that if the group started as a worldwide complex, the distributions of the individual clades can be explained by the following vicariance events:

- (1) Break between ostriches in Africa and their Indo-Pacific sister group. Opening of Mozambique Channel at 160 Ma (Late Jurassic).
- (2) Break between rheas and Clades 3–5. The last pulse of Chon Aike volcanism (138–157 Ma, latest Jurassic–earliest Cretaceous).
- (3) Break between the Indian Ocean clade (3) and the Pacific clade (4). Rangitata orogeny and earlier phases of the Whitsunday–Median batholith igneous province at *c.* 130 Ma (Early Cretaceous).
- (4) Break within the Indian Ocean clade (3), between the Madagascar–New Zealand group and the Australia–New Guinea group. Seafloor spreading around India, plus continued activity in the Median batholith, at *c.* 130 Ma (after Node 3, but before separation of Madagascar–India from Antarctica–New Zealand, especially after *c.* 120 Ma) (Early Cretaceous) (Reeves 2014).
- (5) Break between emus and cassowaries. Last active phases of magmatism in Whitsunday volcanic province at *c.* 100 Ma (mid-Cretaceous).
- (6) Break within the Pacific clade (4), between the moas of New Zealand and the tinamous of South America. Opening of basins around New Zealand at 84 Ma (Late Cretaceous).

The overlap of moas and kiwis in New Zealand occurred after their origin, but before strike-slip displacement on the Alpine fault, starting in the Miocene, caused species-level differentiation in each; the overlap of rheas and tinamous developed at some stage following their origin, but has not been studied.

De Queiroz (p. 245), following Phillips *et al.* (2010), wrote that ‘A pure vicariance scenario for ratites now seems unlikely because of the lack of agreement between the branching order in the ratite evolutionary tree and the sequence of breakup of the Gondwanan fragments.’ Mitchell *et al.* (2014b) also relied on this

argument. Nevertheless, continental breakup is not the only large-scale geological event, and is not the only mode of vicariance. It is true that the pattern cannot be the result of ‘pure vicariance’, because kiwis and moas overlap in New Zealand, and rheas and tinamous overlap in southern South America, and overlap is explained by normal dispersal. Nevertheless, the main clades are allopatric and this is consistent with vicariance. De Queiroz and Mitchell *et al.* (2014b) rejected it because they assumed, incorrectly, that Gondwana breakup is the only possible mode of vicariance. The ratite pattern is easily explained instead by vicariance caused by breakup and also pre-breakup, intra-continental rifting. De Queiroz (p. 245) suggested that a vicariance model for ratites was contradicted by fossil-calibrated molecular-dating studies. Nevertheless, these give only minimum ages, and ‘molecular dating provides limited power for testing hypotheses about ratite biogeography’ (Mitchell *et al.* 2014b, p. 899).

De Queiroz concluded that ratite birds and southern beeches (*Nothofagus*) ‘clearly haven’t held up as pure examples of vicariance’ (p. 269), and that ‘...evidence for the vicariant origins of ‘obvious’ Gondwanan groups like the ratites and southern beeches has fallen apart’ (p. 246, italics added). But for ratites, he did not mention, let alone explain, the most striking and well-supported evidence for vicariance, the distributions of the molecular clades, the location of the breaks and the phylogenetic sequence.

Nothofagus (Nothofagaceae) is a tree found in Australasia and South America. Sauquet *et al.* (2012) studied the timeline of its evolution, and showed that using different calibrations led to estimates for the crown group age of *Nothofagus* that varied from 13 to 113 Ma. This indicates that fossil data alone cannot resolve the problem of dating, even in a group such as *Nothofagus* that has a rich, well-studied fossil record. Using younger, more safely identified fossil calibrations gave young ages consistent with previous molecular dating studies. These studies inferred that the geographic disjunctions in *Nothofagus* were caused by long-distance dispersal rather than vicariance. In contrast, when older, more ambiguous fossils were used for calibration, the estimated ages were compatible with vicariance.

Sauquet *et al.* (2012, p. 307) wrote that several alternative explanations could weaken the inferences of long-distance dispersal that have been made in previous studies of *Nothofagus*. ‘First, the maximum age constraint of 125 Ma on the root [the eudicot clade] might be an incorrect assumption. . . [this is very likely; cf. Smith *et al.* 2010; Heads 2014c, p. 67]. Second, there might have been systematic changes in the rates of evolution, with generally higher rates of evolution early in the diversification of the group than at later stages. Third, the risky fossils might have provided a more accurate calibration of the phylogeny.’

Primates

De Queiroz (p. 210) cited a vicariance model for primate evolution (Heads 2010, 2012b), and concluded that this could be rejected because ‘the timing is all wrong’. But the timing is controversial. Fossil dates suggest that primates are Cenozoic; fossil-calibrated molecular clock dates suggest that they are Cretaceous (see above); tectonic calibrations suggest that they are Jurassic. The last date assumes that vicariance has caused

the allopatric differentiation between euprimates and the plesiadapiformes to their north, between New World and Old World monkeys, and between lemurs of Madagascar and lorises of Africa. De Queiroz (p. 218) instead supported chance dispersal and argued that ‘Timetrees and fossils rule out alternative hypotheses. . .’. However, as usual, they only provide minimum clade ages that do not rule out earlier vicariance.

Why are haplorhine primates in America but not Madagascar, while members of the sister-group, strepsirrhines, are in Madagascar but not America? Why have no primates at all crossed Salween Strait (20 km across) from Sulawesi to Australasia (although monkeys introduced in New Guinea have thrived)? Why is the phylogenetic diversity of strepsirrhines concentrated in eastern Africa, that of haplorhines in western Africa? These and other distributional phenomena constitute critical evidence, and are explained simply in a vicariance model without invoking ‘chance’, but none was mentioned, let alone explained, by de Queiroz, who relied entirely on age estimates. He (pp. 213, 214) concluded that for primates, ‘reasonable’ clock methods give a ‘reasonable’ age estimate, and for dispersal theory a ‘reasonable’ age estimate is one that rules out vicariance.

Ancestral-area analysis

Modern studies support dispersal theory with two main kinds of calculations. The first involves dating. As already discussed, young clade ages can be generated by treating fossil ages as more or less equivalent to clade ages, or by converting fossil-calibrated minimum clade ages into maximum ages by stipulating very narrow priors. The results of this approach form the conclusions of many case studies cited by de Queiroz.

The second type of evidence used to support dispersal theory is generated by ‘ancestral-area analysis’. This uses programs such as DIVA (Ronquist 1997) and DEC (implemented in LAGRANGE; Ree and Smith 2008) to find a centre of origin, and this approach is used in many current studies. The programs are based on the illogical assumption that a paraphyletic basal grade indicates a centre of origin.

De Queiroz made only a brief mention of ancestral-area analysis. In one example, concerning the sundew, *Drosera* (Droseraceae), he (p. 153) wrote that ‘two species found in the eastern US fall within a group of South American species, indicating that their ancestors dispersed from that continent’. Representing South America by SA, the phylogeny has the form SA (SA (SA (SA (SA, eastern US))). Here the South American species do not form a group; they are a paraphyletic complex or grade. In this case, ancestral-area programs will always find a centre of origin in South America, because of the basal grade there. Nevertheless, the phylogeny is just as compatible with a widespread ancestor already present in both South America and the eastern US, followed by differentiation events at breaks in and around South America, and then local overlap there (Hedges 2012b, figs 1–6).

In a second example, de Queiroz (p. 263) suggested, without justification, that North American populations of the bristletail *Neomachilis halophila* ‘might actually fall, in an evolutionary sense, within the Hawaiian bristletail group’, because the Hawaiian species form a basal paraphyletic grade within the

Hawaiian–North American clade. De Queiroz suggested that this would indicate dispersal from Hawaii to North America. He also cited (p. 325) ‘DNA-based phylogenetic evidence for at least one Hawaii-to-mainland dispersal by *Scaptomyza*’, and this is based on the same, flawed reasoning.

In a final example of deducing a centre of origin from a phylogeny, de Queiroz cited the work of Song *et al.* (2013) on the locust genus *Schistocerca*. The genus comprises one Old World species and ~50 in the New World. The authors studied a sample of species and proposed the following phylogeny:

Old World: *S. gregaria*.

Galapagos: three *Schistocerca* species.

Continental New World: 17 *Schistocerca* species.

Song *et al.* (2013, p. 659) wrote that ‘Regarding the origin of the desert locust *S. gregaria*, our four-gene analysis clearly points to the Old World origin because of its basal placement in the phylogeny of *Schistocerca*’. However, this is an elementary mistake; *S. gregaria* and its sister-group, present in the Galapagos and continental America, are equally basal.

With respect to timing, Song *et al.* (2013, p. 658) reasoned that ‘Considering when the Galapagos Islands became available for terrestrial colonization (3–4 Ma; Peck 2001), *Schistocerca* as a whole appears to be a very young genus’. Nevertheless, this overlooks recent studies showing that prior islands existed in the Galapagos region long before the current islands formed. Werner and Hoernle (2003) sampled rocks of the volcanoes along the Galapagos hotspot tracks between the Galapagos and central and South America (Cocos, Carnegie, Malpelo and Coiba ridges). They found guyot-shaped seamounts, palaeo-beach or intertidal wave-cut platform deposits and other features, indicating that islands have existed continuously above the Galapagos hotspot for at least the past 17 million years. This gives a minimum date for the existence of islands in the area; the hotspot itself has been active since the Cretaceous (Hauff *et al.* 1997; Nerlich *et al.* 2014).

Many authors now accept that Galapagos clades differentiated *in situ*, long before the current islands existed. For example, the marine iguana (*Conolophus*) and its sister, the endemic land iguana (*Amblyrhynchus*), are both endemic to the Galapagos and are thought to have differentiated at 10 Ma (Parent *et al.* 2008). A clade of six *Phyllodactylus* lizard species endemic to the Galapagos is thought to ‘have colonized the [ancestral] archipelago at 13.2 Ma, when the islands currently above water had not yet emerged’ (Torres-Carvajal *et al.* 2014, p. 1883). (These clade ages are fossil-calibrated, and so are minimum dates.)

De Queiroz did not discuss Galapagos biogeography, but he repeated the inferences of Song *et al.* (2013) without question, stating that (p. 279) ‘. . . within the past several million years, they [*Schistocerca* locusts] successfully dispersed across the Atlantic from Africa . . . and very rapidly gave rise to some 50 New World species’. In this way, flawed conclusions based on logical errors and neglect of the literature were promulgated and perpetuated.

Conclusions

As discussed above, de Queiroz accepted the myth that long-distance dispersal is ‘revealed’ by sequencing studies (p. 160).

At the end of his book he increased this apocalyptic tone, citing plagues of locusts (p. 280) and ‘a world shaped by miracles’ (the title of the last chapter). For de Queiroz, dispersal operates by miracles, and this is the only possible view: ‘...it *must* be that the living history of the entire planet has been deeply influenced by ocean crossings and other long-distance colonizations. That is an *inescapable* conclusion ... Chance colonizations have had *clear* and profound effects. ...’; ‘By now it should be *clear* that, for a large number of [transoceanic disjunctions] ... the primary explanation of the vicariance biogeographers – ...drifting tectonic plates – was the wrong explanation’ (p. 281, italic emphasis added). Yet all these conclusions rely entirely on the clock dates (and on treating these as maximum ages), and if they are wrong, the evidence for the miracles melts away.

For de Queiroz, the basis of biogeography is a mystery and a miracle, the unanalysable chance event that, given enough time, becomes a certainty. Of course, extremely rare events do occur, but in vicariance theory, it is the norms and averages of biological and geological processes that have shaped the world, not miracles. One of the problems with miracles is that they can be invoked to explain anything at all. Chance dispersal events are not related to any other physical or biological phenomena. In contrast, normal dispersal follows laws of probability, related to physical parameters such as wind and currents, and biological parameters such as a group’s observed means of dispersal.

Panbiogeography has been criticised for being concerned with general patterns and not accepting the lawless, one-off events of chance dispersal (Trewick and Wallis 2001; McDowall 2008). Likewise, powerful theologians such as Bossuet (1627–1704) criticised the early scientists for their dangerous belief in ‘general laws’ of nature, as this contradicted the existence of miracles. The importance of miracles had become well established by the middle ages, when, as in modern dispersal theory (Le Goff 2001, p. 329),

There was proof by miracle as well as proof by authority. ... What made medieval minds agree to believe in something was not what could be observed and proved by a natural law or by a regularly repeated mechanism. On the contrary, it was the extraordinary, the supernatural or at least the abnormal. Science itself was more willing to take as its subject the exceptional, the *mirabilia*...

Since the 1970s, several components of vicariance theory have become much more widely accepted. From the 1940s to the 1980s, one of its key concepts, vicariance, was almost completely suppressed by authors such as Mayr (1965a, 1982a), Stebbins (1966) and Grant (1971, 1981) in their widely used text books. Thanks to the work of Croizat *et al.* (1974), vicariance was introduced to the mainstream, and by now it is well established (Fig. 1). Associated concepts of vicariance theory – for example, that Earth and life evolve together, that orogeny causes uplift of communities, that fossils only provide minimum ages, and that many species are older than the Pleistocene – have also become familiar. In contrast, other aspects of vicariance theory, such as the rejection of chance dispersal as a mode of speciation, have not yet been accepted. However, the retention of chance dispersal is largely based on conservative prejudice and hold-overs from the Mayrian approach. These are incorporated in ‘ancestral-area’ programs

that automatically find a centre of origin (at the locality of a basal paraphyletic grade), and in the illogical treatment of fossil-calibrated clock dates as maximum clade ages or close to them.

De Queiroz (p. 269) admitted that vicariance theory is ‘inherently attractive’ and ‘seductive’, and this is supported by much of the evidence that he cited. He also admitted that random dispersal is ‘ugly’ (p. 272). This is because it relies on a literal reading of the fossil record, on molecular studies that illogically convert minimum clade ages into maximum ages, on the suppression of critical evidence (such as distribution maps), and on the use of chance and ‘miracles’ to explain clear-cut patterns that are repeated in many groups with different means of dispersal.

Despite making these admissions, de Queiroz argued that dispersal theory is not only corroborated, but is the final answer for biogeography; although the debate between chance dispersal and vicariance has been a long one, de Queiroz (p. 268) concluded that ‘...we’re finally getting it right’. Molecular dating is ‘the final step that might finally produce a paradigm in historical biogeography’ (p. 276), and ‘it strains credibility to simply dismiss it [molecular dating] as some sort of misguided intellectual fashion... Certainly, many mainstream scientists now see the rejection of the molecular clock as irrational’ (p. 277). Yet, no other published work has ever regarded the clock dates as being ‘proven’ in this way. Many mainstream scientists (such as Morrison 2014, quoted above) have instead given reasons to suspect that molecular clock dates could be seriously flawed.

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