

Jurassic primates, immobile ducks and other oddities: a reply to Heads' review of *The Monkey's Voyage*

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Abstract. In *The Monkey's Voyage*, I focused on the issue of disjunct distributions, and, in particular, on the burgeoning support from molecular-dating studies for long-distance dispersal over vicariance as the most reasonable explanation for many (but by no means all) distributions broken up by oceans. Michael Heads' assessment of the book is founded on his long-standing belief, following Croizat, that long-distance dispersal is an insignificant process and, therefore, that disjunctions are virtually always attributable to vicariance. In holding to these notions, Heads offered a series of unsound arguments. In particular, to preserve an 'all-vicariance' perspective, he presented a distorted view of the nature of long-distance dispersal, misrepresented current applications of fossil calibrations in molecular-dating studies, ignored methodological biases in such studies that often favour vicariance hypotheses, repeatedly invoked irrelevant geological reconstructions, and, most strikingly, showed a cavalier approach to evolutionary timelines by pushing the origins of many groups back to unreasonably ancient ages. The result was a succession of implausible histories for particular taxa and areas, including the notions that the Hawaiian biota is almost entirely derived from ancient (often Mesozoic) central Pacific metapopulations, that the disjunctions of extremely mobile organisms such as ducks rarely, if ever, result from long-distance dispersal, and that primates were widespread 120 million years before their first appearance in the fossil record. In contrast to Heads' perspective, a central message of *The Monkey's Voyage* is that explanations for disjunct distributions should be evaluated on the basis of diverse kinds of evidence, without strong *a priori* assumptions about the relative likelihoods of long-distance dispersal and vicariance.

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Introduction

Explaining disjunct distributions is a central and contentious issue in historical biogeography. In my book, *The Monkey's Voyage* (de Queiroz 2014), I described some of the history of thought about disjunctions, especially those involving distributions of terrestrial organisms broken up by oceans. I focused especially on the surge of molecular dating (=timetree) results that, when coupled with evidence about the timing of fragmentation of areas, frequently have supported relatively recent long-distance dispersal (LDD) as an explanation for disjunctions, including many cases that previously had been ascribed to more ancient vicariance events resulting from tectonic processes. This molecular evidence, I argued, has shifted historical biogeography towards a more balanced view, in which vicariance is not assumed to be the default explanation for disjunctions, and both LDD and vicariance are acknowledged as major factors in shaping distributions.

In his review of *The Monkey's Voyage*, Heads (2014a) is pointedly critical, taking issue with my depiction of the history of the field and, at greater length, with the evidence presented and conclusions reached concerning the causes of disjunctions (unless otherwise noted, 'Heads' refers to Heads 2014a). Heads is among a minority of biogeographers who believe, on the one

hand, that LDD is not an important process, and, on the other hand, that all or nearly all disjunctions must be explained by some form of vicariance (Heads 1985, 2005, 2009, 2010, 2011, 2012a, 2014b). In Heads' case, these beliefs derive directly from the panbiogeography of Croizat (1958, 1962), and, especially, the claim that an objective examination of distribution patterns reveals the dominance of the fragmentation and conglomeration of areas as biogeographic processes. Tellingly, Heads once wrote (in an email message to me in 2010), 'Apart from Croizat I don't think there has been much development [in biogeography] over the last 50 years' (de Queiroz 2014, p. 274). However, my argument here is not against Heads' Croizatian views in general, but, rather, against the idea that LDD is an insignificant process in biogeography, an idea that has been expressed not only by Heads and other panbiogeographers (e.g. Craw 1979; Grehan and Schwartz 2009) but also by scientists not labelled as such (e.g. McCarthy 2003; Parenti 2006; Nelson and Ladiges 2009; Mazza 2014). (A related point is that not all researchers who use the panbiogeographic approach of track analysis dismiss LDD as insignificant; e.g. see Page and Lydeard 1994; Morrone 2015.)

Regarding the opposing views at the heart of the present paper, it is important to correct from the start an inaccurate impression given by Heads. Specifically, Heads cast myself and others who

disagree with his perspective as ‘dispersalists’; he went so far as to use ‘de Queiroz’ to stand in for ‘modern dispersal theory’ (Heads, p. 282), which gave the impression that we believe LDD explains all or nearly all disjunctions. This representation is clearly misleading; I am not aware of any historical biogeographer who claims that vicariance is insignificant. Biogeographers such as the botanist Susanne Renner or the zoologists Steve Trewick and Miguel Vences, who Heads would surely label as ‘dispersalists’, have published multiple papers that support vicariance explanations (e.g. Trewick *et al.* 2000; Renner *et al.* 2010; Tolley *et al.* 2013). Similarly, the fact that I referred to only a few specific well supported cases of vicariance in the book reflects only my emphasis on establishing the importance of LDD, not a disbelief in the significance of fragmentation events. Just among publications from the past 10 years, I have seen scores of studies that present compelling evidence for vicariance, and I believe that thousands more such cases remain to be discovered.

This distinction between Heads’ perspective, entailing a wholesale rejection of long-distance colonisation as a significant process, and the more balanced views of those he is criticising, should be kept in mind in evaluating his review of *The Monkey’s Voyage*. As I will illustrate below, in case after case, the arguments he uses to support vicariance hypotheses and to cast doubt on LDD explanations strain credibility. Many of the points I raise here have been made by others in assessments of Heads’ work (e.g. Goswami and Upchurch 2010; O’Grady *et al.* 2012; Swenson *et al.* 2012; Lohman and Tsang 2014; Matzke 2015; McGlone 2015), or in general critiques of panbiogeography (e.g. Cox 1998; Briggs 2007; Waters *et al.* 2013), but I add to the deconstruction of Heads’ perspective through new arguments as well as discussions of many examples not considered elsewhere. In fact, my main purpose here is to use an abundance of detail, both in terms of pointing out diverse logical flaws and describing many case histories, to illustrate the problems with the anti-dispersal approach espoused by Heads.

My response is divided into five main sections. The first addresses Heads’ criticisms of my description of the history of the vicariance–dispersal debate, especially with respect to the situation in New Zealand since the early 1970s. In the second section, I evaluate his arguments against molecular-dating analyses. I argue that his conclusion that such analyses are extremely biased towards favouring LDD is based on mischaracterisations of the use of calibration points, lack of recognition of biases *against* LDD explanations, and an unsupported assumption about the mindset of investigators. In the third section, I describe several other specious arguments made by Heads in his review or in other relevant papers, including the erroneous inference that studies of normal dispersal demonstrate the implausibility of LDD events, and a misinterpretation of the relationship between LDD and speciation by genetic revolutions. The fourth section critiques Heads’ specific analyses of areas and of primates and ratite birds; these cases illustrate his unrealistic assumptions about the ages of groups and his repeated references to irrelevant or unsupported geologic reconstructions.

As I argued in the book, estimating divergence ages is critical to progress in historical biogeography; not having this

information when trying to decipher the history of taxa is something like trying to make sense of events in human history, such as the Great Depression or the Vietnam War, without knowing when they occurred. In the fifth and final section, I turn from criticism of Heads’ arguments to more constructive thoughts about this central issue of timing. In particular, I briefly describe some of the key, often surprising, conclusions that have emerged from timetree studies with respect to distributions of terrestrial taxa broken up by oceans.

In the interest of space, I have not attempted to address every point raised by Heads in his review. For instance, I do not specifically go through his seven supposed ‘myths about biogeography’ (although I deal with most of them at least indirectly) and I do not examine all the analyses of areas that he critiques. Nonetheless, the many cases evaluated here should make clear the pattern of misleading claims and unjustified inferences that characterise Heads’ arguments, and, in doing so, illustrate why the conclusions he draws, about *The Monkey’s Voyage* and about historical biogeography in general, are deeply flawed.

Some historical revision, especially concerning beliefs of New Zealand scientists

Before getting to the heart of this reply, I briefly address what I consider Heads’ most nearly legitimate criticism of the book, namely, that I inaccurately claimed that biogeography in the 1970s through much of the 1990s was dominated by the vicariance viewpoint and that this was especially true in New Zealand. There is some truth to this criticism, although Heads’ alternative description of the situation in New Zealand is clearly incorrect, as I will show.

For the field in general, I did claim, in the book’s Introduction (p. 15), to be telling the story of the shift ‘from a view dominated by vicariance to a more balanced outlook.’ I admit that this is an overstatement; I think it is more reasonable to say that, while the importance of vicariance as a process became very widely accepted, the view that it is the dominant explanation for disjunctions, although common, was less widely held. It is easy to find statements from biogeographers during this period that are not in line with the view of vicariance as dominant (e.g. Mayr 1982; Brown and Gibson 1983; Goldblatt 1993).

A more accurate and nuanced perspective comes out in other sections of the book, somewhat contrary to that claim in the Introduction. For example, in Chapter 7, I noted that many botanists continued to believe in the importance of long-distance colonisation, especially because of the relative ease of seed dispersal. I specifically pointed to the botanist Susanne Renner as someone who never wavered from believing in the great importance of LDD. And in Chapter 11, I stated that vicariance biogeography ‘never came close to being universally embraced’ (p. 276); in fact, in that chapter, I used the observation that the vicariance view did *not* take over the field as part of my argument that historical biogeography has been in a ‘pre-paradigm’ state for the past 150 years. Those statements more accurately represent my views of the situation in the 1970s through most of the 1990s than does the statement in the book’s Introduction.

For the purposes of the book, the key, in any case, is not that the vicariance viewpoint became thoroughly dominant, but that many disjunctions, such as those involving the ratite birds, southern beeches, baobabs, and many lesser-known examples, were typically interpreted as products of area fragmentation, without strong supporting evidence. This reflected a belief, even among scientists who did not hold an extreme vicariance worldview, that range fragmentation was the default explanation for disjunctions involving areas that had been connected in the past.

With respect to what people thought in New Zealand, I think the situation was less extreme than either Heads' description or mine indicated, although I argue here that my view was slightly inaccurate whereas Heads' view was grossly so. I said (p. 100) that, in New Zealand, the vicariance worldview came 'fairly close' to dominating historical biogeography, 'not in the consistent use of cladograms or Croizat's tracks, but in the belief that an ancient vicariance event was the key to understanding the biota.' In contrast, Heads claimed that in the 1970s and early 1980s, the only advocates of vicariance in New Zealand were he and three other PhD students and, a bit later, the National Museum zoologist F. Climo. Heads further argued that my claim that the vicariance view was dominant is contradicted by the fact that the New Zealand panbiogeographers were exiled by being fired or shut out from obtaining jobs in that country.

A part of the discrepancy here might be that Heads considered only panbiogeographers as having a vicariance viewpoint, whereas, as just noted, I included anyone who believed that Gondwanan breakup was a key to understanding the New Zealand biota. From the latter perspective (which has to be considered 'correct,' because the discussion is framed by how I defined the issue), Heads' claims are clearly misleading. During the period in question, many scientists in New Zealand, other than those identified by Heads, expressed the view that its biota was made up substantially of Gondwanan relict lineages. For instance, Skipworth (1974), in a paper titled 'Continental drift and the New Zealand biota', argued for the Gondwanan origins of many taxa, including plants in the Podocarpaceae, Winteraceae, Proteaceae and Restionaceae, *Sophora* and *Hebe*, and, among animals, *Peripatus*, chironomid midges, *Leiopelma* frogs, the tuatara (*Sphenodon*) and the ratites. Cooper and Millener (1993) considered many of those same groups to be Gondwanan hold-overs in New Zealand, and added to the list geckos, skinks, wetas, some spiders, terrestrial gastropods, the kauri (*Agathis australis*), and many ferns, lycopods and other 'lower' plants. Along the same lines, Daugherty *et al.* (1993, p. 437) noted that New Zealand differs strongly from oceanic islands such as Hawaii and the Galápagos 'because of the ancient continental origins of both the landmass and the biota.' All six of the authors of those three papers were New Zealand scientists.

This Gondwanan-relict view even influenced C. A. Fleming, who Heads (p. 285) described as 'a prominent dispersalist,' and the leader of the New Zealand biogeographical establishment from the 1960s to the late 1980s. By the mid-1970s, Fleming (1975) had accepted that New Zealand was once part of Gondwana and that the origins of some New Zealand taxa traced back to that early continental history. In particular,

Fleming interpreted some taxa in his 'paleo-austral' group as being Gondwanan hold-overs.

Furthermore, there were well known, vicariance-oriented technical papers written by scientists and others outside of the country but dealing with New Zealand taxa, as well as popular works that considered the origins of the country's biota, and it is reasonable to assume that these influenced scientists within New Zealand to adopt the Gondwanan-relict view. Some of the prominent papers included Brundin (1966), Raven and Axelrod (1972), Cracraft (1974), Nelson (1975), Humphries (1981) and Melville (1981), and the books included Enting and Molloy's (1982) *The Ancient Islands*, Flannery's (1994) *The Future Eaters* and, especially, Bellamy *et al.*'s (1990) *Moa's Ark: the Voyage of New Zealand*, which was also a popular documentary television series.

In light of this evidence for widespread acceptance of the idea that a large number of New Zealand taxa are Gondwanan relicts, the exiling of Heads, Craw and others, to the extent that it was related to their scientific views, should be seen, not as an attempt to squash the idea of vicariance in general, but as an indictment of the specific shortcomings of panbiogeography. (See McGlone 2015 for a more detailed discussion of the fate of the New Zealand panbiogeographers.)

In developing the argument that my description of biogeography in New Zealand was totally wrong, Heads (p. 285) also suggested that the three scientists who told me that the vicariance viewpoint was dominant in New Zealand, namely Dallas Mildenhall, Mike Pole and Steve Trewick, 'were all dispersalists, and they have a vested interest in portraying themselves as independent critical thinkers.' (I should point out that Mildenhall noted that neontologists tended to hold the Gondwanan-relict view whereas palaeontologists did not.) However, the references cited above, especially those that were written by New Zealand scientists, suggest that the memories of Mildenhall, Pole and Trewick are substantially correct. Could it be that Heads' own vested interest has drastically influenced *his* recollections and interpretations of those times?

From the above, it should be clear that Heads' depiction of the situation in New Zealand from the 1970s into the 1990s is grossly inaccurate. Nonetheless, I do not want to claim that everything I wrote in the book about this period was completely correct. In particular, there were a fair number of New Zealand scientists who maintained a belief through this time in the great (and, for some of them, dominant) importance of LDD. I recognised that fact in the book, mentioning Fleming, Mildenhall and Robert McDowall in that context, but I also de-emphasised their continuing influence through the period in question. Still, the works written at the time, given above, as well as perceptions of recent developments (Winkworth *et al.* 2002; Didham 2005; McGlone 2005; Waters and Craw 2006; Goldberg *et al.* 2008; Giribet and Boyer 2010; Trewick and Gibb 2010) indicate that, contrary to Heads' claim, historical biogeography within New Zealand *has* undergone a major shift away from vicariance and towards dispersal explanations for the origins of the biota. It has not been a case of 'dispersalism' simply maintaining dominance the whole time, as Heads would have us believe.

The key issue of estimating divergence ages

I emphasised in my book the significance of molecular divergence-date studies in promoting a shift away from vicariance explanations and in favour of dispersal explanations for many disjunctions. Heads argued, as he has in other publications (e.g. Heads 2005, 2009, 2012b), that estimates from these molecular studies, when calibrated with fossils, provide only minimum ages for groups (or, more accurately, nodes in a phylogeny), and that these age estimates, therefore, are often gross underestimates. As a result, he claimed that support from these studies for recent LDD over ancient vicariance is illusory.

The problem of calibrations and, more generally, of accurately estimating ages using molecular data are certainly real and are widely recognised. However, Heads presented a distorted view of the problems; he mischaracterised the current practice of how calibrations are chosen and used, ignored biases or deliberately conservative practices that work against the acceptance of recent LDD, and mistakenly assumed that a longstanding bias favouring LDD pervades the field. I will deal with these issues in turn.

Mischaracterising the choice and use of calibrations

Many recent molecular studies have used Bayesian methods to produce timetrees (trees with age estimates for nodes). For each calibration, these methods use the age of the oldest fossil of a group in applying a calibration prior, that is, a probability distribution for the age of the node in question, with the fossil age as the minimum bound. Heads focused on the fact that authors can choose a prior that extends only a small number of years older than this minimum age. According to Heads (p. 286), 'If authors choose a small number, the method is guaranteed to produce young clade ages, and this is what is usually done in practice', with the result that 'Unless a group has an exceptional fossil record, this methodology automatically rules out early clade ages and vicariance.'

However, this criticism focused on studies that 'choose a small number' for the range of the calibration prior. However, use of very narrow priors is not the current standard practice for timetree analyses. This is readily apparent in examining the extensive Fossil Calibration Database (Ksepka *et al.* 2015) in which the span between the minimum age of a node (the lower bound for the age of the fossil as indicated by stratigraphic, radiometric or other evidence) and the maximum age is often large in both an absolute sense (several tens of millions of years or more) and as a proportion of the minimum age. A perusal of recent timetree studies shows that such large ranges for calibration priors have become commonplace (e.g. Bell *et al.* 2010; Clarke *et al.* 2011; Meredith *et al.* 2011; Joyce *et al.* 2013; Rota-Stabelli *et al.* 2013; Prum *et al.* 2015). Further, many investigators use 'soft maxima' (Yang and Rannala 2006), which means that the prior probability distribution for the age of a node actually extends past the nominal maximum, albeit with a low probability density. In short, Heads' claim about the use of narrow priors is misleading and does not apply to the most sophisticated recent timetree analyses.

On a related point, Heads assumed that the fossil record places no limit on the maximum age of any group. This is

apparent from his extension of the age of many nodes to depths far beyond those considered reasonable by both palaeontologists and neontologists who specialise on the taxa in question (e.g. Heads 2005, 2010, 2012c). Heads' claim amounts to saying that the cumulative, and massive volume of palaeontological work provides no clues (other than minimum ages) for when any group appeared on the planet.

That claim is untenable given a simple observation, namely, that the appearance of groups in the fossil record is often significantly correlated with the branching order within phylogenetic trees (Norell and Novacek 1992; Benton *et al.* 2000; Smith *et al.* 2006; Marjanović and Laurin 2007). (Even before the wide acceptance of evolution, a similar relationship was known, namely, the increasing resemblance of fossil taxa to living ones with a decreasing age of the fossils.) It is true that the correlation does not exist for many groups, but these tend to be ones for which divergence-age studies are absent or are viewed as especially tentative (Wills 2002; Smith *et al.* 2006; Sohn *et al.* 2015). Indeed, if there were no such correlation for any group, it is doubtful that fossil calibrations would ever have been widely adopted in timetree analyses.

This correlation is very broadly acknowledged, so much so that it forms a standard part of educational curricula on evolution. It seems likely that, if no such correlation existed, the idea of evolution would not be so widely accepted. In fact, creationists recognise the importance of the correlation, which is why they have tried to undermine it by claiming, for instance, that human footprints have been found in the same strata as non-avian dinosaur fossils. And, on the other side, J. B. S. Haldane supposedly quipped that his belief in evolution would be shattered if a Precambrian rabbit were discovered. Seen in this light, Heads' view that the fossil record provides no information about the maximum ages of groups is extraordinary and, for an evolutionist, truly mystifying. His arguments imply that we should *not* be surprised at the discovery of Cretaceous humans, or of Precambrian lagomorphs, especially if their distributions could be explained by vicariance!

The relevance of the correlation between first appearances and branching order for inferring maximum ages of taxa can be appreciated if one considers the consequences of pushing ages for particular nodes to extreme depths, as Heads has done frequently. In a striking example of this, Heads (2012c) assumed that the separation of the New Zealand *Abrotanella muscosa* (Asteraceae) and its South American sister group, *A. submarginata*, occurred when the land connection between those areas was broken, c. 80–84 million years ago. Using this as a calibration point in a molecular-dating analysis, Swenson *et al.* (2012) estimated the age of crown-group Asteraceae as 1.456 billion years (95% HPD, highest posterior density: 0.77–2.36 billion years), which they rightly pointed out is absurd given the fossil record, not only of Asteraceae, but of land plants in general. This age estimate is implausible because even its lower bound predates the known fossil record of all land plants and, thus, renders coincidental the relationship between fossil first appearances and branching order for various major land-plant groups and major lineages of angiosperms. Under the scenario implied by Heads, Asteraceae was already an old group at the time of the first fossil appearances of land plants, bryophytes, lycopsids, ferns, gymnosperms and all branches

deeper than Asteraceae within angiosperms (Silvestro *et al.* 2015); thus, the facts that fossils representing early branches within land plants are hundreds of millions of years older than the first angiosperm fossils, and that fossils of many deep branches within angiosperms are tens of millions of years older than the first fossils of Asteraceae become completely irrelevant, unrelated to the actual sequence of evolution. Emphasising the implausibility of Heads' approach even further, Swenson *et al.* (2012, p. 530) noted that the point estimate derived from the tectonic calibration for *Abrotanella* places the origin of Asteraceae 'at a time when the biosphere was nearly exclusively populated by microscopic marine organisms.'

Similarly, Heads' scenario for the historical biogeography of primates (Heads 2010, 2012a; see Goswami and Upchurch 2010 for a detailed critique) assumes that crown-group primates are c. 180 million years old, more than 120 million years older than the oldest fossils for the group (O'Leary *et al.* 2013; Benton *et al.* 2015), and this, again, renders the correlation between first appearance and branching order for primates and deeper branches coincidental. For instance, in Heads' scenario, the fact that several early branches in the mammalian tree, such as monotremes and marsupials, are represented by fossils much older than any primate fossil has nothing to do with the actual ages of the involved groups, because all of them were already in existence at the time.

None of this is to say that calibration points and calibration priors currently in use are unproblematic; virtually everyone who uses molecular divergence dating recognises that fossil calibrations are prone to substantial error, and that there is a degree of arbitrariness to the form of prior probability distributions (e.g. Clarke *et al.* 2011; Parham *et al.* 2012; Warnock *et al.* 2014). The recent emphasis on compiling calibration points and ranges (Benton *et al.* 2015; Ksepka *et al.* 2015), evaluating the effect of using different calibration points (Near and Sanderson 2004; Schaefer *et al.* 2009; Clarke *et al.* 2011; Rota-Stabelli *et al.* 2013; Garzón-Orduña *et al.* 2015) and developing new methods for incorporating fossils more fully within a probabilistic framework (Pyrón 2010; Wilkinson *et al.* 2011; Ronquist *et al.* 2012; Heath *et al.* 2014; Claramunt and Cracraft 2015) reflects a general belief that the choice of fossils and their integration in timetree analyses are in need of improvement. Nonetheless, it does not seem an egregious leap of faith to assume that the first known fossils of a group do not grossly underestimate the actual age of the group, if the stratum containing those fossils is followed by younger strata in which the group is increasingly common, and is preceded by well sampled, geographically relevant strata not much older than contain close relatives of the group, but no members of the group itself. Couple such judicious choice of fossil calibrations with the practice of using many such calibration points, as well as evaluating sensitivity to using different samples of calibration points, and the effect of errors ought to be strongly reduced. Provisionally accepting the results of such analyses, while continuing to seek refinements through improved methods and new molecular and palaeontological data, seems far preferable to pushing the origin of primates into the Early Jurassic or the origin of sunflowers into the Proterozoic.

Conservative bias with respect to inferring long-distance dispersal in timetree analyses

Heads repeatedly insisted that the use of fossil calibrations biases timetrees towards young ages and, therefore, inflates the evidence for LDD. However, he conveniently ignored evidence that many such analyses may be biased to estimate ages of biogeographic events as too *old*, and might thus be more likely to fail to reject explanations based on ancient vicariance.

First, molecular estimates for many relatively deep divergences within mammals (Meredith *et al.* 2011; dos Reis *et al.* 2012), birds (Jetz *et al.* 2012; Jarvis *et al.* 2014; Mitchell *et al.* 2014a) and flowering plants (Bell *et al.* 2010; Zeng *et al.* 2014) typically are much older than the oldest known fossils of the groups in question (Friis *et al.* 2010; Mayr 2013; O'Leary *et al.* 2013). These groups have been key ones in debates over the importance of continental breakup *v.* overwater dispersal, so potential biases in estimations of their ages are clearly relevant to the issue at hand. Although the reasons for the age discrepancies remain controversial, plausible arguments have been made that molecular analyses have been biased to produce older divergence ages because of unrealistically old calibration priors (Mayr 2013; Prum *et al.* 2015), among-lineage rate heterogeneity (Magallón 2014; Beaulieu *et al.* 2015) and inadequate taxon sampling (Beaulieu *et al.* 2015). In any case, the key point here is that these examples are more likely to represent bias against rather than in favour of LDD explanations.

A second, possibly more widespread source of bias has to do with the logic of interpreting divergences between taxa in disjunct areas. Specifically, if the divergence between such taxa is old enough to have been caused by vicariance, then that explanation often is accepted (because, even today, vicariance is frequently treated as the default explanation). However, as pointed out by Poux *et al.* (2006) and others, such a divergence age provides only a maximum age for the existence of the taxa in both areas. Therefore, even if the estimated age is consistent with an ancient vicariance event, it may provide only weak support for that explanation.

Consider, for example, the divergence between the kauri (*Agathis australis*) of New Zealand and its living sister group in Australia. The molecular dating analyses of Knapp *et al.* (2007) gave an age for this split that is consistent with *Agathis* persisting in both areas since the opening of the Tasman Sea, some 80–84 million years ago (also see Wilf and Escapa 2015). However, because *A. australis* is the only New Zealand species in this clade, there is no evidence from these molecular studies for a deep divergence *within* New Zealand, and, thus, no strong support from this work that the lineage has been present in Zealandia since its separation from Australia. The fossil record also provides no clear evidence that *Agathis* was present soon after the separation; the earliest definitive New Zealand *Agathis* fossils are from the late Oligocene (Lee *et al.* 2007; Pole 2008). A plausible alternative is that the ancestors of *A. australis* dispersed from Australia to Zealandia after those landmasses separated, but that the Australian lineages closest to *A. australis* subsequently became extinct (Biffin *et al.* 2010).

In his 'Analyses of areas' section, Heads repeatedly assumed that the divergence age between an island lineage and its relatives elsewhere implies existence on the island or nearby

prior land since that time, thus inflating the evidence for the involvement of ancient events. For example, he stated that the skink *Afroablepharus annobonensis*, endemic to the Gulf of Guinea island of Annobón, ‘has been dated as ~10 million years old’ (Heads, p. 290), and used this information to argue for the long existence of this lineage on Annobón or on nearby islands that no longer exist (and are, it should be pointed out, hypothetical). However, the 10-million-year estimate is for the divergence between *A. annobonensis* and its relatives on the islands of São Tomé and Príncipe, not within Annobón. The cited study (Jesus *et al.* 2007) found no sequence divergence at all within *A. annobonensis*, and, thus, no clear evidence for long persistence there or on those hypothetical prior islands. Similarly, *all* of the divergence ages Heads cited for the Chatham Islands are for splits between Chathams taxa and related groups elsewhere, not divergences *within* the Chathams (see section below on the Chathams). I am not aware of any studies that show divergences within the Chathams significantly greater than 3 million years old (the age I gave in the book for the emergence of the current islands).

To reiterate the general point, interpreting between-area divergence ages as clear indications of persistence since that time in the areas in question produces a bias favouring the involvement of ancient events. Many investigators, not just Heads, have interpreted divergences in this way (e.g. Ericson *et al.* 2002; Nagy *et al.* 2003; Vences *et al.* 2003; Allwood *et al.* 2010; Heenan *et al.* 2010). Thus, as with the probable bias of molecular methods to overestimate the ages of divergences in birds, mammals and flowering plants, this logical error, if anything, has led to *underestimating* the importance of LDD. Fortunately, estimating both maximum (between-area) and minimum (within-area) divergence ages is becoming more common. Nonetheless, the collective body of evidence that Heads claimed is heavily biased against vicariance, has actually suffered from a widespread bias in the other direction.

Heads also ignored the fact that some investigators have intentionally biased timetree analyses towards older ages, with the specific intention of rendering the results conservative with respect to supporting LDD. For example, in the book, I mentioned that Matt Lavin and colleagues had run analyses for woody legumes in which fossils thought to predate crown groups were treated as crown-group fossils, which should push estimates towards deeper ages. For the same reason, de Queiroz and Lawson (2008) treated fossils that might be stem-group gartersnakes (*Thamnophis*) and watersnakes (*Nerodia*) as members of crown groups. Similarly, Renner (2004) used a possible stem-group fossil as the calibration for crown-group Myrtaceae. It is also common for investigators to use different sets of calibration points or ranges, and to accept biogeographic interpretations only if they are supported by all analyses (e.g. de Queiroz and Lawson 2008; Schaefer *et al.* 2009; Hedges and Conn 2012, Springer *et al.* 2012). That practice does not specifically bias results to favour ancient events, but it makes interpretations conservative in general, by widening the estimated age ranges in both directions.

In summary, Heads’ claim of a consistent underestimation of divergence ages in timetree studies is refuted by consideration of (1) the likely overestimation of such ages for certain key taxa, (2) a widespread bias tied to the use of divergence ages between (rather

than within) areas, and (3) intentionally conservative practices employed in many cases.

Is there a widespread investigator bias favouring long-distance dispersal?

Heads erroneously claimed that there is a strong *a priori* tendency among those who study historical biogeography to discount vicariance and favour LDD. For instance, he painted investigators as ‘dispersalists’ when, as I have shown above, these scientists generally have no problem favouring vicariance explanations when the evidence supports such hypotheses. In fact, as I described in the book, some of these investigators have admitted that they were initially biased to prefer vicariance explanations, but changed their beliefs because of evidence indicating that LDD also is extremely important. For example, Matt Lavin, who was studying woody legume taxa on both sides of the Atlantic Ocean, and Miguel Vences, working on amphibians in the Indian Ocean region, both started out focused on vicariance, but were convinced by timetree results that most of the involved disjunctions came about through LDD. Such personal histories call into question Heads’ (p. 300) statement that ‘the retention of chance dispersal is largely based on conservative prejudice and hold-overs from the Mayrian approach’. If these scientists have now come to agree with much (although certainly not all) of what Mayr and other ‘dispersalists’ believed, it is because the evidence made them reject the vicariance view on which they had been raised.

Further, one could make the case that the attributes of widely used biogeographic models, rather than indicating a dispersalist bias, suggest just the opposite. In particular, the models DIVA and DEC (Ronquist 1997; Ree and Smith 2008) do not specifically incorporate speciation by founder-event LDD, and are biased to support vicariance explanations for disjunctions (Matzke 2014, 2015).

If there is no pervasive investigator preference for LDD and if, as I have argued above, timetree analyses have not been consistently biased to favour that explanation, then we are left with the conclusion that I reached in the book, namely that evidence from many molecular-dating studies, coupled with fossil data, and geological reconstructions of landmass histories, point to the great importance of LDD in explaining disjunct distributions.

A trio of specious arguments against long-distance dispersal

In his review of my book and elsewhere, Heads incorrectly characterised the nature of chance, long-distance dispersal as envisioned by myself and many others, and also argued erroneously that population genetic studies refute the validity of speciation by small founding populations, as is assumed to occur in most cases of long-distance colonisation. These subjects provide more evidence of how Heads’ wholesale rejection of LDD and, thus, his critique of *The Monkey’s Voyage*, is based on specious arguments.

Concerning the nature of dispersal, Heads (p. 288) claimed that LDD as usually conceived involves ‘factors beyond our understanding’ and that such dispersal ‘can happen in any direction, at any time’. He went on to suggest that such rare

dispersal events 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' (Heads, p. 289).

If LDD were conceived to be *completely* random with respect to routes and timing of colonisation, then Heads would have a legitimate point here; fully random dispersal would invalidate the claim, made by myself and many others, that LDD is expected to produce general patterns of linkage among areas. However, those arguing that LDD is important do not view it as even close to completely random. For instance, with respect to dispersal of land organisms over sea barriers, the probability of colonisation should decrease with increasing distance between areas, patterns of colonisation by rafting should be influenced by prevailing ocean currents, and, for many taxa, routes with stepping-stone islands should be used more than those without stepping stones. It is from such considerations that expectations of repeated patterns produced by LDD emerge.

A significant point here is that, although *specific* LDD events are not predictable, this does not mean that LDD in general is beyond all understanding and provides no expectations about the phylogenetic connections among biotas. Such expectations arise from considering the *collection* of possible dispersal events. This is a straightforward point that comes out of probabilistic thinking, but it is worth emphasising in the present context.

In the same section, Heads also made a flawed argument about what can be inferred about long-distance dispersal from studies of normal dispersal. He focused on the case of New Zealand *Veronica* shrubs, for which observations found an average seed-dispersal distance of 13 cm and a maximum distance of 1.1 m (Pufal and Garnock-Jones 2010). From these results he suggested that the inference, from the occurrence of conspecific populations in New Zealand and Australia, that two *Veronica* species dispersed over the Tasman Sea is implausible; when normal, observable, ecological dispersal operates only over metres, Heads argued, it is untenable to posit chance dispersal over hundreds of kilometres. More generally, this argument implies that dispersal distances much greater than those that have been observed can be discounted.

Superficially, it might seem reasonable to posit, for any particular taxon, only the kinds of dispersal events that have been documented for that group. However, many other observations have indicated that such an assumption is unrealistically restrictive. For example, natural rafts often have been observed far out at sea (Van Duzer 2004), providing a mechanism of chance, long-distance dispersal for many kinds of land organisms, and rafting colonisation by large iguanas has even been witnessed (Censky *et al.* 1998). Diverse plant seeds, as well as some small arthropods and molluscs, can become attached to birds and might disperse great distances in this way (McAtee 1914; Carlquist 1974; Aoyama *et al.* 2012). Many seeds and at least some snails also can survive in the digestive tracts of birds (Proctor 1968; Sousa 1993; Nogales *et al.* 2012; van Leeuwen *et al.* 2012), and there is direct evidence of dispersal of seeds by this mechanism over hundreds of kilometres of ocean (Viana *et al.* 2016). Beginning with Darwin (1859), investigators have shown that many kinds of seeds remain viable after extended exposure to seawater (Carlquist 1974; Guja *et al.* 2010; Aoyama *et al.* 2012), which would allow seeds inundated on rafts or even floating free in the ocean to colonise distant areas. Furthermore, explicit

modelling of dispersal events, based on measurable physical and biological parameters, has validated the existence and importance of LDD (e.g. Nathan *et al.* 2008; Viana *et al.* 2013). The general point here is that plausible LDD mechanisms exist for a great diversity of taxa, even though direct observations of LDD have been made for only a few groups.

With respect to the *Veronica* shrubs cited by Heads, there is no good reason to believe that seed dispersal must be limited to distances similar to those seen in a study entirely focused on the standard dispersal mechanism, that is, raindrops displacing seeds out of the seed capsules. In fact, the authors of the study cited by Heads (Pufal and Garnock-Jones 2010) suggested that the lightweight seeds of *Veronica* might be carried long distances by strong winds and that, because the seeds become mucilaginous when wet, they might also be dispersed attached to the feet or feathers of birds. More generally, dispersal ecologists (who are mostly little concerned with the dispersal v. vicariance issue) have concluded that LDD events probably often occur by vectors that the species in question do not normally use (non-standard vectors), such as strong winds connected to extreme meteorological events, animal-mediated dispersal in organisms not adapted for such dispersal, and rafting (Berg 1983; Nathan *et al.* 2008; Viana *et al.* 2013). It follows that studies showing that standard vectors generate very short dispersal distances do not refute the occurrence of much longer-distance events. In short, Heads' notion that measured normal dispersal shows that LDD explanations are implausible is based on an insupportably narrow view of the evidence for LDD.

Heads' unrealistic rejection of LDD is also illustrated by his argument (Heads 2009, 2010) relating to founder effect speciation. Heads claimed that this mode of speciation, in which reproductive isolation is achieved partly through strong genetic drift tied to small founding population size, is not validated by experimental and other studies. He then went on to argue that the lack of support for founder effect speciation constitutes an argument against the occurrence of chance, long-distance colonisation by small numbers of individuals.

The importance of founder effect speciation remains controversial (Butlin *et al.* 2012), and, in fact, there is experimental evidence indicating that very small founding population size can promote reproductive isolation (Templeton 2008; Matute 2013). However, even if it were true that founder effect speciation is unimportant, this would provide no reason to reject colonisation of areas by small founding groups. Whether or not genetic drift leads to genetic revolutions and speciation, if founding populations persist in isolation, they are likely to become differentiated from source populations and, eventually, to become distinct species. For example, a small founding group might rapidly expand to a point at which genetic drift is relatively unimportant; however, this would not preclude divergence from the source population by natural or sexual selection. The logical flaw in Heads' argument is conflating a particular mode of speciation that *requires* small founding populations and strong genetic drift with *any* kind of speciation that *involves* small founding populations. It is telling that Jerry Coyne, who Heads cited for doubting the existence of founder effect speciation (Coyne and Orr 2004), accepts the importance of colonisations by LDD (Coyne 2009).

To summarise this section, Heads presented flawed arguments about (1) the nature of LDD and its relationship to repeated patterns, (2) the range of LDD events that can be inferred from normal dispersal, and (3) the connection between population genetic studies of founder effect speciation and the plausibility of long-distance colonisation by small founding groups. As with much else in his review and other work, these arguments show a mindset bent on denying the importance of LDD.

Ancient islands, ancient monkeys

Much of Heads' review was devoted to critiquing cases I presented involving continental and oceanic islands, as well as the historical biogeography of two taxonomic groups that I discussed in some detail, namely primates and ratite birds. These sections of Heads' review demonstrate how his refusal to place limits on the maximum ages of groups is connected to unrealistic interpretations of evolutionary history. More generally, they indicate, once again, a biased evaluation of the evidence for alternative explanations of geographic distributions.

Several of the islands or island groups on which Heads focused are either purely volcanic (e.g. the Hawaiian Islands) or are volcanic in the sense that the emergence of the current islands is thought to have been caused by vulcanism, but the islands are composed partly of continental rock (e.g. the Chatham Islands). The standard explanation, and the one I followed in the book, is that the native land biotas of these islands are derived from long-distance, over-water dispersal. In contrast, Heads believes that the ancestors of current species existed on prior land in these areas and that they reached the modern islands by normal dispersal. If one accepts either timetree results or a straightforward argument about the separation of conspecific lineages (see below), Heads' posited scenarios for these cases typically involve movements from land areas that are too ancient to have been involved in the origins of most or all of the taxa in question. Furthermore, for the majority of these cases, the earlier land areas emerged in the ocean as volcanic islands and were probably distant from other landmasses; thus, even if Heads were correct that these earlier land areas contained the progenitors of many species on the current islands, his scenarios beg the question of how those earlier areas were colonised.

In responding to Heads' criticisms, I focus here on the two island groups that he considered in the greatest detail, namely São Tomé and Príncipe, and the Chatham Islands. I then briefly discuss some of the other island cases, to establish more generally the flaws in Heads' analyses of areas. A key distinction between our views is that I consider scenarios untenable if they strongly conflict with the molecular divergence-date results, whereas, obviously, Heads does not constrain his argument in this way. (His major constraint is very different, namely, that LDD is not a viable explanation.) In my view, most of the geological evidence that Heads presented for ancient direct land connections or stepping-stone routes is irrelevant in the face of the timetree results, as I will indicate below.

São Tomé and Príncipe

São Tomé and Príncipe are volcanic islands in the Gulf of Guinea, respectively 255 and 220 km from the West African coast. They form part of the Cameroon Volcanic Line, a series

of volcanic swells, some on the African continent and others arising from the ocean floor. It is generally believed that São Tomé and Príncipe have never been connected to the mainland, which has led to the belief that their biotas originated through over-water dispersal, mostly of the chance variety, but also, for organisms that can disperse easily over sea barriers, by normal dispersal. In the book, I described, in particular, the arguments of Measey *et al.* (2007) for long-distance colonisation of these islands by several lineages of amphibians, especially *Ptychadena* frogs, organisms for which a sea barrier even a few kilometres wide probably would be surmounted only rarely and with difficulty.

Heads argued, in contrast, that few if any of the native species of São Tomé and Príncipe arrived there by LDD, but instead reflect former land connections or stepping-stone routes by which normal dispersal could have taken place. He suggested that 'the amphibians' ancestors (not the modern species) were always in the region, before the islands were formed and even before the Atlantic opened' (Heads, p. 289). Here, and for the ancestors of oceanic island taxa in general, Heads (2011, 2012a) envisioned ancestral metapopulations in which the individual populations may be on separated islands, but are connected to each other by normal dispersal. When islands become too widely separated, for example, because of submergence of some of them, metapopulations are fragmented and the now truly isolated parts are free to diverge. The process is therefore a vicariant one. For São Tomé and Príncipe, Heads cited not only the opening of the Atlantic *c.* 100 million years ago, but also alkaline intrusive magmatism along the Cameroon Volcanic Line from 65 to 30 million years ago, as well as more recent volcanic episodes, and he implied that all these geological events could have been directly involved in the origins of the biotas of the islands.

Obviously, the geological history of the region must be considered in studies of historical biogeography. However, the ages of evolutionary events for which explanations are sought are also critical; geological events that occurred long before the divergences in question are not relevant, at least not as processes that directly influenced those divergences. For the *Ptychadena* frogs of the Gulf of Guinea islands, the 16S rRNA sequence difference between the island species and the closest known relatives on the mainland suggests a divergence age of between 5.6 and 18.6 million years (Measey *et al.* 2007). Because the taxon sampling in Measey *et al.*'s (2007) study was limited (see Bell *et al.* 2015), it is possible that the actual closest mainland relatives were not included, which would make the estimate too old. (Recall also that divergences between islands and other areas are inherently biased high as estimates of the time of residence on the islands.) The only other Gulf of Guinea amphibian lineage for which an explicit divergence-age estimate is available is *Hyperolius*, with an estimated age of Pleistocene, based on the within-archipelago divergence, to late Miocene, based on the divergence between the island forms and their closest relative on the mainland (Bell *et al.* 2015). Additionally, Gulf of Guinea *Phrynobatrachus* are perhaps Miocene in age (Zimkus *et al.* 2010).

As far as I know, the only evidence of possible prior land in the Gulf of Guinea in the Miocene or later is the existence of two seamounts along the Cameroon Volcanic Line, one between

Bioko and Príncipe and one between São Tomé and Annobón (Njome and de Wit 2014). It is unclear whether these volcanic structures were ever subaerial. However, even if they were, they likely would have formed islands that *still* would have required colonisation by chance (not normal) dispersal by amphibians.

Of course, it is possible that geological evidence will emerge that indicates stepping-stone islands (which would have to be very closely spaced to allow normal dispersal by amphibians) or an actual land connection to Africa that could explain the existence of *Ptychadena*, *Hyperolius*, *Phrynobatrachus* and other amphibians on the Gulf of Guinea islands, without involving LDD. However, agreeing with Darwin, 'it shocks my philosophy to create land' (Burkhardt and Smith 1989, p. 344) without any evidence. The fact that volcanic or other magmatic processes were occurring in the area is not a compelling argument without any specifics. Thus, it seems premature to invoke such hypotheses to account for the occurrence of amphibians on São Tomé and Príncipe.

In his section on São Tomé and Príncipe, Heads also suggested that similar 'prior land' hypotheses can account for all amphibian occurrences on oceanic islands, citing as an example *Platymantis* frogs on Fiji. 'Although the individual islands of Fiji are young and have never been connected to a continent,' Heads (p. 290) noted, 'the structure producing them, the Pacific subduction zone, originated by a mainland.' I am not aware of any biogeographic studies that have dealt with the origins of Fijian *Platymantis*; however, it is worth noting that herpetologists have hypothesised that the ability of *Platymantis* and other ceratobatrachids to persist and reproduce without standing fresh water has facilitated their colonisation of islands (Brown *et al.* 2015). In any case, there is now evidence from timetree analyses for many instances of over-water dispersal by amphibians, including colonisations of Madagascar, many Caribbean islands, Sulawesi, the Maluku, the Lesser Sundas, the Philippines, the Seychelles, the Comoros, the California Channel Islands, North America, South America, South Asia and Australasia, the latter possibly involving dispersal across the entire Pacific from South America (de Queiroz 2014 and references therein; Pyron 2014). Given this body of examples, over-water dispersal to São Tomé, Príncipe and Fiji is hardly disconcertingly unique.

Furthermore, it is worth noting that the amphibian timetree as a whole indicates, as one would expect from the dispersal abilities of these animals, that the large-scale, continental distribution of amphibians is mostly well explained by the breakup of Laurasia and Gondwana (Bossuyt *et al.* 2006; Pramuk *et al.* 2008; Zhang and Wake 2009; Pyron 2014). In other words, the various over-water dispersal events are inferred within a time frame that generally supports a plausible history of vicariance, in line with much geological evidence. This result will come as no surprise or affront to modern 'dispersalists,' who are all perfectly accepting of vicariance as an important process. However, Heads must reject the molecular-dating results and rely on unsupported scenarios of prior land to preserve the notion that LDD is insignificant for amphibians (and in general).

Heads also presented lists of disjunctions that he believes argue strongly for vicariant origins for the biotas of São Tomé and Príncipe. These involve cases where the apparent closest

relatives of São Tomé and Príncipe taxa are found in areas very distant from these islands, including eastern Africa, the Indian Ocean region, areas well north and west of São Tomé and Príncipe (e.g. Sierra Leone and Liberia), and the Americas. However, this argument is fraught with problems in the data themselves and, even more so, in their interpretation.

First, these lists of disjunctions are made up primarily of cases based only on taxonomy rather than phylogenetic analyses, so their reliability can be questioned on that basis. Also, deciphering the relationships of São Tomé and Príncipe taxa to those in other areas is compromised by the fact that many African taxa have been poorly studied. Both Heads and I noted the connection of some São Tomé and Príncipe taxa to eastern African groups, but I now wonder whether this link is, at least partly, an artefact of limited sampling for some taxa, as suggested by Bell *et al.* (2015) for amphibians. An obvious potential bias is that, for political reasons, eastern African species are more likely to have been collected and described than those from central and western Africa.

Even assuming that the connections that Heads listed are real, they do not make a strong case for vicariant origins. First, these lists do not suggest that any of the distant geographic connections he mentions make up the *dominant* pattern for São Tomé and Príncipe taxa. If it could be shown, for instance, that the eastern Africa connection is the most common one among the taxa of these islands, that would be significant and would warrant re-evaluating the origins of the biotas of the islands (although it would not necessarily require a vicariant explanation). However, no such compilation has been made.

On the other side of the coin, the fact that São Tomé and Príncipe taxa show connections to various different areas, some of them distant from the islands, does not argue against origins by LDD. Although one would expect that many São Tomé and Príncipe taxa originated from the nearby African mainland, chance dispersal from other areas should not be ruled out, especially given the relatively great age of these two islands compared to most volcanic islands. For instance, as I described in the book (following Measey *et al.* 2007), an eastern Africa to Gulf of Guinea route is plausible by rafting via the Congo River, and would have been more likely when the climate was wetter. Also, extinction on the mainland is expected to produce greater geographic separation of some São Tomé and Príncipe taxa and their closest relatives than was true at the time of colonisation.

By analogy, native Hawaiian taxa show connections to many different areas, all of which are very distant from those islands, but this is not a reason to invoke vicariant origins for the Hawaiian biota (Cowie and Holland 2008; Gillespie *et al.* 2012). (Of course, Heads did exactly that, but his inferences for Hawaiian taxa require, among other things, rejecting the evidence that these taxa are young, see below.) Heads seems to think the fact that different, unrelated taxa show the same pattern of disjunction indicates an ecosystem-wide vicariance event, but such patterns for Hawaii (and other oceanic islands) indicate that this is not a logical conclusion.

Heads' discussion of São Tomé and Príncipe also highlights, once again, how far he is willing to strain the evolutionary timeline to avoid explaining distributions by LDD. This is especially evident in his suggestion that disjunctions with the

Americas, involving two marine fish species, a beetle, and two flowering plants, reflect the opening of the Atlantic, more than 100 million years ago. These examples have generally been interpreted as cases of trans-Atlantic dispersal, because the taxa are thought to be far too young to have been affected by the opening of the Atlantic (Wirtz *et al.* 2007; Michalak *et al.* 2010; Frolov 2013). For the two plant species, that age assumption has been validated by molecular dating. The Lentibulariaceae, the family that includes the disjunct *Utricularia*, is estimated to have split from its nearest relatives tens of millions of years after the separation of Africa and South America (Schäferhoff *et al.* 2010), and the divergence of interest within *Utricularia* must be far younger still. Similarly, the divergence of the Gulf of Guinea *Hernandia* from their New World relatives is estimated to have occurred within the past 15 million years (Michalak *et al.* 2010).

In summary, Heads' vicariance-only view of the origins of the biota of São Tomé and Príncipe relies on assumptions about land connections or close stepping-stone islands that lack any clear geological support, the erroneous notion that repeated connections to distant areas imply vicariance, and rejection of estimates for the ages of taxa. The idea that chance, over-water colonisation is significant for islands that have existed for at least 31 million years (Príncipe) and 13 million years (São Tomé) within several hundred kilometres of a continent, and are in the path of prevailing ocean currents from that continent, hardly seems surprising, yet Heads seems to view such colonisation events as next to impossible.

The Chatham Islands

The Chatham Islands, which lie some 850 km east of New Zealand, are composed partly of Gondwanan continental rocks, and contain Late Cretaceous fossils of typical Gondwanan groups such as theropod dinosaurs, *Nothofagus*, and podocarp conifers (Stilwell *et al.* 2006; Campbell and Hutching 2007). Clearly, the Chathams have a geological connection to Gondwana. However, the current islands are generally believed to have emerged through volcanic activity within the past several million years (Campbell and Hutching 2007; Stilwell and Consoli 2012). The flora and fauna of the Chathams are in keeping with the hypothesised young age of the current islands (as subaerial land); in particular, molecular-dating studies of various plant and animal groups (see below), and the observation that there are few endemic genera (Holdaway *et al.* 2001; Emberson 1998; de Lange *et al.* 2011) argue against ancient origins of the biota. In fact, most Chathams populations are classified as conspecific with ones found elsewhere (Emberson 1998; Holdaway *et al.* 2001; Heenan *et al.* 2010; de Lange *et al.* 2011).

Not surprisingly, Heads argued against origins of Chathams groups by LDD, and instead raised supposed evidence for vicariant origins of the biota. However, his arguments suffer from the same kinds of flaws as those he made regarding São Tomé and Príncipe. Specifically, he relied on geological reconstructions that are poorly supported or irrelevant in terms of refuting LDD, and he rejected all young ages of taxa estimated using molecular data or other evidence. In addition, his discussion of molecular-dating studies for the Chathams suffers from multiple errors and misinterpretations.

With respect to possible prior land in the region that could have contained the ancestors of current Chathams taxa, Heads mentioned numerous seamounts on the Chatham Rise and the Hikurangi Plateau, and islands associated with the Mernoo and Vryan Banks. However, none of these possible former islands indicate vicariant origins for the Chathams biota. Regarding the seamounts on the Chatham Rise, if one assumes, incautiously, that all of the known seamounts were subaerial at some point, and that they overlapped in time to provide stepping-stone paths to the Chatham Islands, the positions of these structures still indicate significant ocean gaps that, for many land organisms, would likely have required chance crossings (see Rowden *et al.* 2005, fig. 1). Within the Hikurangi Plateau, the volcanic activity that formed the current guyots is thought to have occurred some 89–99 million years ago or even earlier (Davy *et al.* 2008), and is thus irrelevant to the origins of the much younger biota of the Chathams. Finally, parts of the Mernoo and Vryan Banks did become emergent land during recent glacial periods (Heenan *et al.* 2010), but these islands were much closer to the main islands of New Zealand than to the Chathams; thus, if Chathams ancestors lived on these intermittent islands, LDD would still have been required for them to colonise the Chathams. In short, the geological 'evidence' cited by Heads for the Chathams suggests few if any routes of normal dispersal, which is the type of dispersal required by vicariance scenarios.

Heads' portrayal of the molecular evidence for the Chathams is also strongly misleading. A general problem is that he wrongly interpreted divergence ages between Chathams lineages and those elsewhere as minimum ages for the existence of these groups in the area of the Chathams. However, as pointed out above, minimum ages are given by divergences *within* the area in question. The lineage ages that Heads referred to as being older than 3 million years *all* refer to divergences between Chathams taxa and those elsewhere. Furthermore, the oldest divergence age cited by Heads, namely 7–14 million years ago for the borage *Myosotidium hortense*, was described by the cited authors (Heenan *et al.* 2010, p. 107) as being possibly 'a significant overestimation due to incomplete taxonomic sampling and/or extinctions', and they raised the possibility that such problems might apply to other cases as well. (In fact, overestimation of the relevant age because of incomplete sampling is often a possible problem.) It should also be pointed out that, even if these divergence ages were taken as minimum ages for occurrences of taxa in the area, they would suggest only that former islands were colonised, not that LDD was unimportant in the colonisation process.

Heads (p. 294) also claimed that '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 Chathams Islands forms from the mainland requires extra, *ad hoc* hypotheses that are not needed in a simple vicariance model.' However, the examples of *Cyanoramphus* parakeets and *Anas* ducks that he cited, far from suggesting vicariance, again indicate long-distance colonisation. It is true that one of the endemic Chathams *Cyanoramphus* parakeets, *C. forbesi*, is estimated to be sister to a clade including lineages occurring on the North and South Islands of New Zealand and various smaller islands in the area, but the other Chathams endemic,

C. novaezelandiae chathamensis, is deeply nested within that larger clade, a pattern that does not suggest a deep split between the Chathams and other areas (Chambers *et al.* 2001). Furthermore, *C. forbesi* is estimated to have diverged from its sister group less than 0.5 million years ago, and these together are estimated to have split from New Caledonian relatives less than 0.6 million years ago. Chambers *et al.* (2001) rightly interpreted these results as indicating recent over-water colonisation of the Chathams.

Similarly, although the extinct Chatham duck (*Anas* [formerly *Pachyanas*] *chathamica*) is estimated to be the sister of a clade of three species in the New Zealand area, the estimated age of this split is 0.69–1.80 million years (95% HPD interval; Mitchell *et al.* 2014b), which is much too recent to be accounted for by any plausible vicariance event. Furthermore, these four are inferred to have diverged from the Madagascar teal (*Anas bernieri*) only 1.78–3.97 million years ago (95% HPD interval; Mitchell *et al.* 2014b), which implies a dispersal event (or events) over the Indian Ocean.

For both the parakeets and the ducks, it is worth emphasising that the ‘extra, *ad hoc* hypotheses’ required by LDD explanations amount to several over-water colonisation events by highly mobile birds. The phylogenetic relationships within parrots and dabbling ducks, and their occurrence on many volcanic islands indicate numerous oceanic dispersal events in both groups, a conclusion reached by investigators even without reference to molecular timetrees (Johnson and Sorenson 1999; Schweizer *et al.* 2010). Given a choice between accepting the reality of such dispersal events *v.* wholesale rejection of timetree results and a reliance on *ad hoc* and implausible hypotheses of prior routes for normal dispersal, namely, routes that would have to encompass not only the Chathams, but several other islands distant from the main islands of New Zealand where the parakeets or ducks are or were found, I see no problem in choosing the dispersal explanation.

In summary, none of the geological or molecular evidence that Heads brought up refutes the notion that the biota of the Chathams has been derived by recent long-distance, over-water colonisation. Geological ‘evidence’ for prior land that can plausibly explain the biota of the islands by normal dispersal and vicariance amounts to wishful thinking, and molecular phylogenetic results, far from countering origins by LDD, collectively provide strong support for that explanation (Trewick 2000; Chambers *et al.* 2001; Heenan *et al.* 2010; Mitchell *et al.* 2014b).

Other islands

Heads’ discussions of other islands likewise suffer from wholesale rejection of evidence for the ages of taxa and reliance on unsupported or irrelevant geologic reconstructions of prior land, among other problems. Detailed deconstructions of Heads’ views on all these islands are possible, but here I will simply describe ‘highlights’ for some of these areas, to give a sense of the pervasive weakness of his arguments.

Madagascar

Heads’ primary argument against LDD origins is that the timetree results indicating origins of Malagasy lineages after the

separation of this island from other Gondwanan landmasses could be incorrect. However, for most of these taxa, the point estimates for divergence ages between Malagasy lineages and those elsewhere (which, as noted above, bias origins towards older dates) would have to be more than doubled to be consistent with a Gondwanan fragmentation hypothesis (Yoder and Nowak 2006). Given my arguments above regarding bias in divergence-age estimations, such strong, pervasive errors seem unlikely. Furthermore, although Gondwanan vicariance predicts that Malagasy taxa should have closest relatives in India, the Seychelles or the Mascarenes, the sister groups of Malagasy lineages are much more commonly African, which is expected if most of them arrived by over-water dispersal (Yoder and Nowak 2006).

The granitic Seychelles

I argued that the fact that most Seychellian lineages are congeneric or conspecific with taxa found elsewhere indicates that most are not ancient hold-overs, but instead arrived recently by over-water dispersal. Heads discounted this argument because it assumes that taxonomic rank is proportional to age. However, the assumption in this case is not a very stringent or controversial one; I was merely positing that most species and genera do not extend back to the time of the most recent separation of the Seychelles from other landmasses (i.e. from India, some 65 million years ago). Furthermore, several molecular-dating analyses cited in the book give divergence ages for Seychellian taxa that are far too young to be explained by Gondwanan breakup (Vences *et al.* 2003; Austin *et al.* 2004; Daniels 2011; Guo *et al.* 2012).

The Hawaiian Islands

Heads’ key claim is that the native Hawaiian biota in general could be derived from ancestral metapopulations that inhabited former land in the area. Such prior land could have existed or, in some cases, definitely did exist as parts of various volcanic formations, including the Hawaiian chain itself, which, as is well known, long predates the modern islands. In Heads’ view, colonisation of the current Hawaiian Islands did not require chance dispersal, but could have occurred by normal, ‘garden variety’ dispersal from these areas.

As I noted in *The Monkey’s Voyage*, divergences within some endemic Hawaiian clades predate the emergence of the current islands (e.g. *Megalagrion* damselflies, Jordan *et al.* 2003; *Mecaphesa* crab spiders, Garb and Gillespie 2009; lobeliads, Givnish *et al.* 2009; drosophilid flies, Russo *et al.* 2013; *Hyposmocoma* moths, Haines *et al.* 2014), suggesting that these groups colonised islands that are now submerged. These findings represent an important contribution of molecular timetree studies to knowledge of the history of the Hawaiian biota. However, they do not support the scenario envisioned by Heads. First, most of the areas of possible prior land in the region, i.e. the bulk of the Mid-Pacific Mountains, the Necker Ridge, the Hess Rise and the Musicians Seamounts, are estimated to have formed in the Cretaceous and are likely to have been submerged by the end of that period or in the early Tertiary (Thiede *et al.* 1981; Vallier *et al.* 1983; Kalnins and Watts 2009; Gardner *et al.* 2013). Thus, if ancestors of Hawaiian lineages

occurred in these old areas, the divergence ages of current Hawaiian taxa from continental relatives (which should be more distantly related than those hypothetical mid-Pacific ancestors) should, minimally, fall in that same time frame. However, the old Hawaiian groups just mentioned are estimated to have separated from continental relatives between 10 million years ago and 30 million years ago (Garb and Gillespie 2009; Givnish *et al.* 2009; Russo *et al.* 2013; Haines *et al.* 2014), thus refuting the involvement of Mesozoic or Early Tertiary islands. Heads (2011, 2012a) also invoked terranes accreted to or subducted beneath North America, but these areas are substantially older than even those just mentioned, and, thus, are even less plausibly tied to the current Hawaiian biota.

A key point is that the nearby former lands that are the appropriate age to account for the origins of these various old Hawaiian lineages are much fewer and farther between than Heads (2011, 2012a, 2014c) would have people believe. These possible source areas include the older islands in the Hawaiian chain, the Line Islands, and hypothetical islands within the formations mentioned above that formed after the main volcanic events had created the bulk of those formations.

In addition, and critically, these potential source areas all were volcanic islands, and, thus, one has to wonder how *they* were colonised by normal dispersal in the first place. Heads' scenarios require, at some point, colonisation from areas other than oceanic islands, which would necessitate a sequence through deep time of emerging land areas, with each subsequent one close enough to prior land to allow normal dispersal by a diversity of organisms. However, as just noted, the ages of the geologic formations in the region suggest that such a set of closely spaced islands relevant to the origins of the Hawaiian biota is unlikely.

Furthermore, most Hawaiian native lineages probably colonised the area within the past 5 million years, as indicated by timetree analyses (Price and Clague 2002; Bennett and O'Grady 2013; Roy *et al.* 2013) or by very limited anatomical divergence from non-Hawaiian relatives (e.g. the owl *Asio flammeus sandwichensis*, the stilt *Himantopus mexicanus knudseni*, and the convolvulaceous vine *Jacquemontia ovalifolia*, among others, are all classified as conspecific with populations elsewhere). These findings suggest that most Hawaiian lineages colonised the current high islands, not former land in the area, and that they must have crossed wide expanses of ocean to reach the archipelago.

Heads is correct in pointing out that the mapping of seamounts is far from complete (Kim and Wessel 2011; Sandwell *et al.* 2014), and many researchers studying the history of island biotas would no doubt be excited at the prospect of obtaining accurate maps of seamounts, and, especially, knowledge of when some of these were islands. But it is a major leap from the reasonable assumption that many such islands existed to the extreme conclusion that such former lands housed metapopulations from which all or nearly all native lineages of the Hawaiian archipelago are derived by normal dispersal, especially given the apparently young ages of most taxa on these islands. Interestingly, Zimmerman (1947) long ago suggested that the Hawaiian biota might have been partly derived from former islands in the region, but, nonetheless, he

found no reason to reject origins of the biota by LDD. New geological information has changed the details regarding former land in the area, but Zimmerman's basic conclusion is still sound.

Fernando de Noronha

In my book, I described the case of the skink *Trachylepis* (= *Mabuya*) *atlantica*, and I followed Carranza and Arnold (2003) in concluding that the ancestors of this species had arrived from Africa by crossing the Atlantic. Heads noted that Carranza and Arnold's timetree analysis used a potentially highly erroneous calibration that assumed that the ages of several lizard clades endemic to El Hierro in the Canary Islands must be no older than the age of that island. He claimed that this calibration is likely to have inflated the age estimate, and that the Fernando de Noronha skink could 'be derived from ancestral generalised forms of *Mabuya* that were already in the region before the opening of the Atlantic' (Heads, p. 297). However, other estimates of skink divergence ages, using different sets of calibrations, all strongly refute a Mesozoic origin for *T. atlantica* (Pyrn 2010; Gamble *et al.* 2011, their supplementary fig. 3; Mulcahy *et al.* 2012; Hedges *et al.* 2015, with data accessed from <http://www.timetree.org/>; except for the estimate from Hedges *et al.* (2015), these estimates are highly conservative because they involve deeper divergences that subsume all those within *Trachylepis*). Also, Carranza and Arnold (2003) noted that the rate of substitution in *Trachylepis* would have to have been more than 10 times slower than the rate calculated for other scleroglossan lizards to be accounted for by the opening of the Atlantic. In short, Heads has misleadingly focused on one possibly faulty calibration point and has, therefore, missed seeing that the conclusions regarding *T. atlantica*'s origins do not depend on that calibration.

Ratites and primates

In *The Monkey's Voyage*, I followed most recent researchers in explaining the distributions of ratite birds and primates partly by oceanic dispersal (e.g. Poux *et al.* 2006; Mitchell *et al.* 2014a), including the inference that monkeys colonised the New World from Africa by rafting across the Atlantic. In contrast, Heads argued that vicariance alone, involving only normal dispersal, explains the distributions of these groups.

For the ratites, Heads (p. 298) suggested that the striking allopatry within the group 'is consistent with an origin of the clades by vicariance of a widespread, global ancestor'. However, it is, in the first place, unclear why this case represents 'striking' allopatry because, as Heads himself admitted, the group shows considerable sympatry; specifically, tinamous are broadly sympatric with rheas in South America and kiwis and moas were broadly sympatric in New Zealand. Furthermore, it is also unclear why the degree of allopatry seen in ratites cannot be explained at least partly by LDD. In particular, rare chance dispersal events should often produce allopatric distributions, especially if some form of competitive exclusion is operating, such that early colonists decrease the likelihood of establishment by later ones (Mitchell *et al.* 2014a).

In the case of primates, Heads (p. 299) wondered 'Why are haplorhine primates in America but not Madagascar, while

members of the sister-group, strepsirrhines, are in Madagascar but not America?’ and also ‘Why have no primates at all crossed Salween Strait (20 km across) from Sulawesi to Australasia (although monkeys introduced in New Guinea have thrived)?’ He suggested that these distributional facts are inexplicable under LDD explanations, but, again, his logic is faulty. In fact, Heads perhaps provided part of a dispersal answer to the first question himself; he noted that haplorhines are more diverse in western Africa, whereas strepsirrhines are more diverse in eastern Africa, which suggests that the potential source pools could explain why haplorhines successfully dispersed across the Atlantic and strepsirrhines crossed the Mozambique Strait. In any case, given that primate dispersal across any significant body of water is expected to be rare, a more relevant question would be ‘Why, under LDD, would one expect both haplorhines and strepsirrhines to have successfully colonized both the New World and Madagascar?’ The answer is ‘You wouldn’t.’

Similarly, the fact that primates have not been able to colonise Australasia from Sulawesi should not come as a huge surprise given that (1) Sulawesi has not always been so close to Australasian land (Stelbrink *et al.* 2012), and (2) the primates (macaques and tarsiers) of the island might have arrived there only within the past 3 million years (Ziegler *et al.* 2007; Driller *et al.* 2015, their fig. 1e). In short, Heads seems to assume that, under the view that LDD is important, it is inexplicable that monkeys have not dispersed the short distance between Sulawesi and islands to the east; however, that is an overly simplistic view of the probabilities involved. This case, rather than illustrating the implausibility of LDD, emphasises the need for modelling dispersal probabilities, taking into account variables beyond the present distance between areas.

However, the greatest weakness in Heads’ arguments regarding ratites and primates is that they rely on vicariance tied to geological events that are far too ancient to be relevant for these groups. For example, to explain the divergence of ostriches from other ratites, Heads invoked the opening of the Mozambique Channel 160 million years ago, which is some 65 million years earlier than even a high-end estimate for the evolutionary split in question (i.e. the upper limit of the credibility interval given in Jarvis *et al.* 2014), and also predates estimates for the earliest crown-group birds, whether estimated from molecular data (Jarvis *et al.* 2014; Ksepka and Phillips 2015; Prum *et al.* 2015) or purely from fossils (Lee *et al.* 2014). On the more recent end of the spectrum, Heads explained the emu–cassowary divergence by volcanic activity that occurred c. 100 million years ago, an age that has been strongly refuted by recent molecular studies, which have placed that divergence some 70–90 million years later (Mitchell *et al.* 2014a; Prum *et al.* 2015).

Similarly, Heads’ (2010) vicariance-only scenario for primates requires the existence of crown-group primates in the early Jurassic, c. 180 million years ago, and invokes the opening of the South Atlantic c. 120–130 million years ago to explain the distribution of monkeys. These ages are far older than even the high end of recent, data-rich estimates for the corresponding nodes, being c. 80 million years and 60 million years too old respectively (Fig. 1). Also, under Heads’ scenario, monkeys have been in South America for at least 120 million

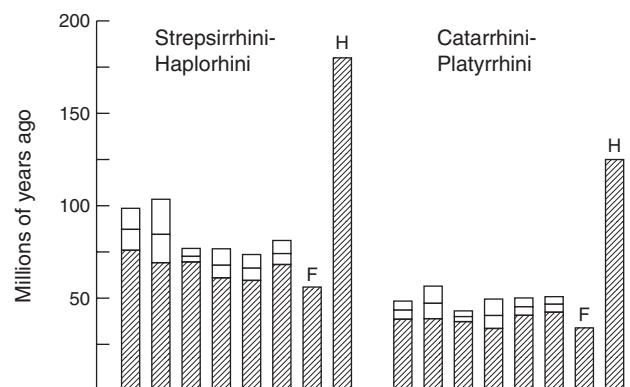


Fig. 1. Estimated divergence ages within primates (Strepsirrhini–Haplorhini and Catarrhini–Platyrrhini) conflict strongly with the ages for these nodes proposed by Heads (2010). For each set, the first six bars are age estimates based on recent molecular studies (in order Perelman *et al.* 2011; Wilkinson *et al.* 2011; Jameson *et al.* 2011; Springer *et al.* 2012; Finstermeier *et al.* 2013; Pozzi *et al.* 2014), with the unhatched part of each bar indicating the posterior mean estimate and 95% credible interval. ‘F’ indicates the age of the earliest known fossil of the group in question (i.e. crown Primates and crown Anthropoidea; ages from Benton *et al.* 2015), and ‘H’ is the divergence age according to Heads’ (2010) scenario for primate biogeographic history. The molecular studies involve different sets of genetic regions, different calibrations and different analytic methods, including one that attempts to quantitatively account for the degree of completeness of the fossil record (Wilkinson *et al.* 2011).

years, yet the oldest known monkey fossil from that continent is no more than c. 36 million years old and appears to be closely related to similarly young fossil anthropoids from Africa (Bond *et al.* 2015). Furthermore, Heads’ suppositions require that primates not only existed but also were widespread by the early Jurassic, making their absence from some 120 million years of the fossil record even more mystifying (Goswami and Upchurch 2010).

Summary of Heads’ area and taxa critiques

Heads’ critiques of my discussions of island biotas, and of ratites and primates show his persistent use of unsound arguments in an attempt to deny the significance of long-distance dispersal. The most obvious manifestation of this predilection is his straining of the timelines for groups, such that, although some events might be too young to explain the divergence between two lineages, they can never be too old. This results in a series of implausible inferences, including, among many others, the opening of the Atlantic, more than 100 million years ago, causing the divergence of the Fernando de Noronha skink from African relatives (estimated by molecular data to have occurred in the Oligocene or later), the relevance of Mesozoic volcanic islands in the central Pacific to the origins of the Hawaiian biota (despite the widely accepted inference that Hawaiian lineages mostly separated from relatives elsewhere within the past 5 million years), and the separation of Africa from Madagascar at c. 160 million years ago producing the divergence of ostriches from other ratites (although molecular timetree and fossil data indicate that ratites did not exist until at least 65 million years later). This lack of constraint on the

maximum age of geological or other events that might be relevant to specific lineage divergences seriously compromises the validity of Heads' approach. As illustrated by the examples of ratites and primates, in particular, inferences about biogeographical history devolve, under this approach, into a game of finding a series of fragmentation events in the right order and in roughly the right areas, regardless of absolute age.

Heads' bias is also shown in other kinds of unjustified conclusions drawn from divergence-age, distributional, and phylogenetic data. He repeatedly equated the divergence age between an island lineage and relatives elsewhere as the minimum age for existence of the lineage on the archipelago in question, but it is actually the divergence *within* the archipelago that provides that minimum age. He erroneously assumed that allopatry within a clade indicates vicariance, despite the fact that rare, chance dispersal is also expected to produce allopatric distributions. He assumed that phylogenetic connections between areas that are repeated in many different taxa preclude origins by chance dispersal, a belief that reflects a misunderstanding of dispersal processes (see section above on a trio of specious arguments).

In short, Heads' discussions of specific areas and taxa strongly reinforce the notion that his critique of *The Monkey's Voyage*, and his views on historical biogeography in general, are based, not on a measured evaluation of new information, but on adherence to prior beliefs regardless of evidence.

Concluding remarks

At the core of *The Monkey's Voyage* is the recent explosion of molecular timetree results, and their use in tests of historical biogeographic hypotheses. This development is widely seen as a crucial one. Thus, for example, Donoghue and Moore (2003) described the incorporation of timetree results as a logical step in the evolution of historical biogeography as an integrative science, similar to the earlier assimilation of phylogenetic branching-order evidence. Likewise, Crisp *et al.* (2011) viewed timetrees as a key aspect of a more hypothesis-driven, as opposed to narrative, historical biogeography, and Sanmartín (2012) described the critical role of such information in the elaboration of parametric biogeographic methods (also see Ree and Smith 2008; Ronquist and Sanmartín 2011). A general outcome of this integration of timetree evidence, also widely recognised as a crucial development, is the validation of LDD as a frequent cause of disjunctions, including many cases that had previously been attributed to vicariance (de Queiroz 2005; McGlone 2005; Gibbs 2006; Sanmartín 2012; Wen *et al.* 2013).

Obviously, Heads, holding to the belief that vicariance is the dominant cause of disjunctions, does not accept any of these positive views of timetrees, and he does not believe that such timing information indicates a multitude of LDD events. His general views, and the more specific arguments attached to them, are shared to a significant extent by some others. For example, his practice of pushing lineage divergences back to unrealistically deep ages, making these splits consistent with ancient vicariance, has been used by several other authors as well (McCarthy 2005; Grehan 2006; Cavalcanti and Gallo 2008; Costa 2013). Similarly, Heads' criticisms of molecular dating, especially the idea that clocks calibrated with fossils can provide

only minimum ages for branching points, have been echoed by other authors (Grehan 2006; Nelson and Ladiges 2009; Parenti and Ebach 2013). Perhaps most strikingly, his habit of invoking unsupported scenarios of geologic history is also seen in the work of others who dismiss timetree results and the importance of LDD, as with McCarthy's (2003) promotion of an expanding-Earth hypothesis (critiqued in Briggs 2004), and Nelson's (2006) suggestion of former land connections between Kauai and Oahu, and between Maui Nui and Hawaii (critiqued in Holland and Cowie 2006). These extreme views expressed by Heads and others are increasingly seen as insupportable (e.g. Briggs 2007; Goswami and Upchurch 2010; Renner 2010; O'Grady *et al.* 2012; Swenson *et al.* 2012; Waters *et al.* 2013; Matzke 2015; McGlone 2015), and, optimistically, one can anticipate that they will eventually fade away. My hope is that the present reply will, through its extensive detailing of flaws in Heads' criticisms of my book, make people further question the legitimacy of such views.

Having dwelled at great length on the negative, I would like to end on a more positive note, by emphasising that these are exciting times for historical biogeography, and that much of the progress being made revolves around incorporating the results of molecular-dating analyses. In particular, I highlight here the following six important and diverse conclusions that have emerged from timetree studies, with respect to distributions of land taxa broken up by oceans:

- (1) The biotas of ancient continental islands, such as New Zealand and Madagascar, typically include some lineages that are continental hold-overs, reflecting ancient vicariance, but these biotas seem to be dominated by lineages that arrived by over-water dispersal (Goldberg *et al.* 2008; Grandcolas *et al.* 2008; Samonds *et al.* 2012; de Queiroz 2014). This conclusion emphasises the biotic turnover on such islands, and debunks the popular notion that they are 'lands that time forgot.'
- (2) A substantial number of oceanic island radiations predate the current islands, indicating colonisation of prior land in the area (e.g. Rassmann 1997; Torres-Carvajal *et al.* 2014; Bradler *et al.* 2015; see Hawaiian section above). These findings indicate the potential complexity of island-colonisation histories, especially where many former islands existed. They also highlight two points on which Heads and I can agree, namely, the need for more complete and reliable reconstructions of the distribution of past oceanic islands, and the problematic nature of calibrating molecular clocks using the ages of current islands (Heads 2011).
- (3) Emerging taxonomic patterns of LDD, although often in agreement with intuitive expectations, include some surprises. For instance, current evidence indicates that birds as a whole are more constrained by ocean barriers than one might expect and, thus, disjunctions within this group are surprisingly often a result of vicariance (Claramunt and Cracraft 2015). In contrast, amphibians have been unexpectedly effective at surmounting modest sea barriers (see above), and burrowing reptiles have apparently crossed oceans on several occasions (Vidal *et al.* 2010; Longrich *et al.* 2015). Furthermore, some groups, such as mabuyine skinks (Carranza and Arnold 2003; Hedges and Conn 2012; Lima *et al.* 2013) and

cucurbit plants (Schaefer *et al.* 2009), have colonised areas by long-distance over-water dispersal an astonishing number of times. None of these examples is so inexplicable that it calls into question biogeographic methods, but they do suggest a need to rethink how particular organismal features influence dispersal probabilities.

- (4) It often is assumed, reasonably, that abiotic factors, such as the directions of wind and ocean currents, and the freshening of sea-surface waters by the output from large rivers, influence probabilities of successful long-distance colonisation. Tests of possible relationships between such factors and patterns of LDD through time are few, but show great promise. For instance, colonisations of Madagascar by animals that probably required rafting for over-water dispersal occurred less frequently after the Mid-Miocene, when paleocurrent models indicate that the prevailing current shifted from an Africa-to-Madagascar pattern to the reverse (Ali and Huber 2010; Samonds *et al.* 2012).
- (5) Overseas colonisations have had a deeper effect on continental biotas than is generally assumed. A case in point is the vertebrate fauna of South America, which contains hundreds of species that are likely to have been derived from such events, including large groups such as platyrrhine monkeys, caviomorph and sigmodontine rodents, *Rhinella* toads and xenodontine snakes (de Queiroz 2014 and references therein). Another indication of this effect is that many continental species used by humans owe their existence to overseas dispersal by their ancestors (de Queiroz 2014).
- (6) Plausible explanations for the distributions of widespread groups that show multiple disjunctions often involve a combination of vicariance and LDD (e.g. Renner *et al.* 2010; Gamble *et al.* 2011; Krosch *et al.* 2011; Simonsen *et al.* 2011; Springer *et al.* 2012; Thomas *et al.* 2014; Pyron 2014; Thornhill *et al.* 2015). In fact, such results are so common that the default expectation for disjunctions in such taxa might be that they are not fully explained by either pure vicariance or pure LDD scenarios.

This list highlights the importance of long-distance colonisation, but it also shows that the practitioners of molecular dating are not simply using this approach to support hypotheses of recent dispersal. In many cases that has been the outcome, but, in numerous others, ancient vicariance events have been supported (Points 1, 3 and 6). I raise that point here to emphasise that neither *The Monkey's Voyage* nor the present paper should be interpreted as an argument that timetrees show the dominance of relatively recent LDD as an explanation for disjunctions. It seems clear that long-distance over-water colonisation has been highly significant in shaping the history of life, and that claim is only strengthened by the unrealistic assumptions that are required to reject it. However, I view the relative importance of dispersal v. vicariance as secondary to a more fundamental message that hopefully comes through in the book, namely that biogeographers, and scientists in general, should evaluate the evidence with open minds rather than accepting a cherished hypothesis *a priori* and then bending (or discarding) contrary evidence to preserve their views. In fact, although it is something of an inside joke, the title *The Monkey's Voyage* was meant to be

a double entendre, referring to the literal dispersal of platyrrhine ancestors across the Atlantic and to the intellectual path taken by scientists, some of whom had to overcome their initial prejudice against such seemingly improbable journeys.

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