Points of View

Old Taxa on Young Islands: A Critique of the Use of Island Age to Date Island-Endemic Clades and Calibrate Phylogenies

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The age of a clade has been estimated by using the age of its oldest fossils, the age of islands or strata that the clade is endemic to, and the age of tectonic events that are spatially related to the clade's geographic distribution (Heads 2005a). These dates can be used to calibrate a phylogeny and to calculate the ages of other related clades. This paper focuses on the use of islands in calibration, but the two other methods are also discussed briefly.

The Use of Fossils to Date Clades

Donoghue and Benton (2007) wrote that: "directly or indirectly, all molecular clock analyses rely on paleontological data for calibration . . . molecular clocks require fossil calibration" (p. 424). Although countless textbooks portray the time course of evolution with reference to the fossil record, many modern clock studies, including most of those discussed below, do not use fossils at all. Forest (2009) wrote "There is general consensus that the fossil record provides by far the best information with which to transform relative time estimates into absolute ages" (p. 790). But the authors who have calibrated molecular phylogenies using tectonics and island age instead of fossils have all accepted that these alternative methods provide better means of calibrating the time course of evolution than the fossil record does.

Without further manipulation, the oldest fossils of a clade only give minimum ages, rather than absolute ages, for a clade. Forest (2009) suggested that "the age of a fossil is generally treated as a minimum constraint in calibration procedures" (p. 791). Although a growing number of authors do accept this in theory, in practice many do not. Authors often treat fossil age as a minimum at the start of a paper, but through the course of the paper, this minimum date and the dates derived from it (also minimum dates) are quietly and mysteriously transformed into maximum dates. A minimum date can only rule out later events as relevant, not earlier ones. But if it is transmogrified into a maximum, then it can then be used to rule out earlier events such as Mesozoic vicariance.

In one example, Richardson et al. (2004) calibrated trees based on fossil material and early in their paper "emphasized that all timings are therefore minimum ages." Nevertheless, following transmogrification, they were able to conclude that "most lineages within Annonaceae are too young to have had their distribution patterns influenced by break-up of previously connected Gondwanan landmasses . . . long-distance dispersal appears to have played a more significant role . . . than had previously been assumed." A subsequent study of New Caledonian Annonaceae by Saunders and Munzinger (2007, p. 502) accepted the transmogrification. The authors wrote that "The exceptionally young age of only 3.6–4.8 (±1.5) Myr recently postulated for *Goniothalamus* by Richardson et al. (2004) clearly indicates that the genus cannot represent an ancient lineage derived before the separation of New Caledonia from Australia."

For Malvaceae on Madagascar, Koopman and Baum (2008) used fossil calibrations to give minimum dates. By transmogrifying these, they were able to conclude that "our molecular dating analyses support a radiation of Hibisceae in the early to mid-Miocene (ca. 19.5–15.5 Ma) which is too late to be explained by vicariance (p. 372; the phrase *too late* indicates the transmogrification).

A study of danthonioid grasses in Africa, Australasia, and South America (Pirie et al. 2009) ruled out vicariance and instead inferred a complex series of dispersal events. Although the nature of the calibration was crucial, it was not mentioned in the paper and this is a common problem. The calibration was derived from Christin et al. (2008), who in fact used fossils. Christin et al. admitted that "Unfortunately, fossils only give a lower bound (i.e., minimal age)" (p. S1), but in practice they used fossils to set both lower and upper bounds. Pirie et al. (2009) were only able to rule out vicariance by using this transmogrified date.

As Donoghue and Benton (2007) noted, fossil calibrations are frequently used as actual rather than minimum dates "out of computational expediency" (p. 425). They also described some of the attempts that have been made to estimate error in the fossil record and to

extrapolate back to likely maximum ages of clades. But attempts to do this made on the basis of the fossil record itself, rather than by using an external set of evidence, are not convincing.

Calibrating a phylogeny with fossils is an explicit, logical, and testable approach. A problem only arises when the minimum dates are transmogrified into maximum dates. In some cases, the fossil record is excellent—in certain geographic areas, at certain times, some organs of some taxonomic groups of certain habitat types can be beautifully preserved. But the fossil record cannot be expected to give a detailed account of a lineage through long periods of time, and it should not be read literally. For example, cichlid fishes, like many groups, have their oldest fossils in the Eocene but show major Gondwanan and other disjunctions. In a literal reading of the fossil record, Eocene origins of these groups are accepted and so transoceanic dispersal, not vicariance, is proposed. However, Genner et al. (2007) concluded instead that the "dispersal implied by the cichlid fossil record may be due to its incompleteness" and supported earlier vicariance (as did Azuma et al. 2008). In practice, most groups have a fossil record that is poor to nonexistent and most groups with a "good" fossil record are only good in comparison with these.

The implicit faith many molecular biologists seem to have in the identifications and phylogenies of fossils is surprising as molecular studies have shown that the morphological classification of countless living groups is untenable. Despite this, molecular workers rely on morphological classifications of fossil clades—much more poorly understood than living groups—to assign fossils to nodes for calibrating molecular clocks. Taxonomists have often been biased by biogeographic preconceptions. For example, it has been assumed that island populations of coastal sea-dispersed taxa "cannot" be distinct species, whereas populations in montane habitats of widely disjunct islands "must" be distinct species (Heads 2006). In the same way, fossil taxa are often assumed to be basal to extant groups, and so the appropriate characters may be selected for phylogeny reconstruction. It is possible that many fossil groups assumed to be basal or even ancestral simply because they are "old" do not have such a special status. Different authors have concluded that controversial fossil groups, such as the adapiform and omomyiform primates, have been misinterpreted in this way (Heads 2010).

The Use of Island Age to Date Clades

In order to avoid the problems of interpreting the fossil record, many biologists have looked elsewhere for a means of calibrating the time course of phylogenies. Ho and Phillips (2009, p. 307) suggested that "Biogeographic and geological events, such as the formation of islands, can offer plausible instances of maximum age bounds, but these bounds must be chosen carefully." Vanderpoorten et al. (2010, p. 14) agreed, writing that: "In view of the scarcity of the fossil record in bryophytes, one promising solution [for establishing chronology] is to use instances of island neoendemic speciation to provide geographic calibration points."

At first sight, this seems reasonable, but can the age of islands really give maximum ages for clades that are endemic there? Some molecular studies do suggest that clades are younger than their islands, but many others indicate that island endemics can be much older than their islands, and examples are cited below. Due to the calibrations used, the calculated dates are conservative estimates only and the true ages of the taxa may be much greater than suggested.

The endemic taxa that are older than their island may have survived on former nearby islands that have been submerged or on a mainland, later going extinct there. Whatever the case, using the age of islands to date the endemic taxa there will often give unreliable results with unpredictable and sometimes massive errors. This is widely acknowledged, at least in theory, for individual islands in "conveyor belt" hotspot systems, such as the Hawaiian and Galapagos Islands, but will also apply to islands in other tectonic settings, such as the Solomon Islands (an island arc complex) and Barbados (an uplifted part of an accretionary wedge).

Southwest Indian Ocean

The plant *Monimia* (Monimiaceae) was dated in clock studies at 52 Ma (Renner 2004) but is endemic to the Mascarene Islands of Mauritius (oldest rocks 8 Ma) and Réunion (oldest rocks 3 Ma). Renner suggested that *Monimia* or its direct ancestors formerly survived on Madagascar. The palm *Hyophorbe* is also endemic to the Mascarene Islands and Cuenca et al. (2008, p. 772) concluded that the estimated age for the crown node of the genus in combination with data on the geology of the Mascarene Islands "suggest that the radiation of *Hyophorbe* may have taken place on islands in the Indic Ocean now submerged predating the creation of the present day Mascarene archipelago."

The Mascarene Islands have been interpreted as the southernmost and youngest rocks on a Réunion hotspot track that extends north along the Mascarene Plateau to older rocks (64 Ma) near the Seychelles (Sheth et al. 2003), and so former islands on the hotspot track and on the plateau may have permitted the survival of ancestors. Among the many other Mauritius endemics is the snake family Bolyeridae, comprising *Bolyera* and *Casarea*. The family has a potential sister relationship with *Xenophidion* of Borneo, a pattern that "presents an unusual and probably ancient Gondwanan distribution for their shared common ancestor" (Lawson et al. 2004, p. 291).

Indonesia

The passerine family Pachycephalidae occurs in Southeast Asia, Australia, and the Pacific islands. In a study of the group, Jønsson et al. (2010) used very young islands with endemics to calibrate a clock: Sangihe

(between Sulawesi and Borneo), dated at 2–3 Ma, and Tanimbar (between Timor and New Guinea), dated at 1 Ma. The authors concluded it is "fairly clear" that much of the species diversity "was generated recently, probably in the Pleistocene" (p. 8), but this result is based entirely on their use of island ages for calibration. They admitted that the calibration is "complicated by the possibility of recently submerged islands in such a dynamic region," but the existence of prior islands around the subduction zones here is not just possible, it is almost certain. Jønsson et al. (2010) considered the problem "impossible to remedy" and in general using island age for calibration around island-generating structures (such as convergent margins) should probably be abandoned. Anderson et al. (2009) suggested that authors use island age as a maximum age constraint for taxa "often through necessity, but perhaps inappropriately." Instead of relying on the stratigraphic age of individual islands, island biogeography is probably better integrated with the tectonic history of the structure that is producing the islands in the region (see below).

The Philippines

In the Philippines, the age estimate of the Palawan Islands clade of the squirrel *Sundasciurus* (6.9 Ma) is older than the geological age estimate of the Palawan Islands themselves (5 Ma) (den Tex et al. 2010).

Southwest Pacific

The genus *Melonycteris*, endemic to the Solomon Islands, forms the basal clade in the fruit bats (Pteropodidae), an abundant and diverse group throughout the Old World tropics (Pulvers and Colgan 2007). The authors wrote that the restriction of *Melonycteris* to these "geographically remote" islands is "puzzling." No formal dating was carried out, but they considered the possibility that the bat has occupied these archipelagos through the course of its evolution, in which case suitable habitat "must have been permanently available in the Melanesian Arc for many millions of years, either as continuously emergent land or as successively emergent, geographically proximal islands" (p. 721). This latter process is typical of subduction zones, such as the Pacific plate margin that the Solomon Islands straddle.

In the Tasman Sea region, the stick insect *Drococelus*, dated at 22 Ma, is endemic to Lord Howe Island (7 Ma) (Buckley et al. 2009). The authors suggested that *Drococelus* may have formerly inhabited what are now submerged seamounts in the vicinity. Likewise, the skink *Cyclodina*, dated at 25 Ma, is endemic to Lord Howe Island and nearby Norfolk Island (3 Ma) (Chapple et al. 2009). These authors gave a similar explanation to that of Buckley et al. (2009) and concluded that island-endemic clades can be older than their islands, even though the calibration they used was based on the assumption that they could not. This means the calculated dates are probably too young and the study warrants some further discussion.

The skink *Oligosoma* is diverse in New Zealand and endemic there, whereas its sister, *Cyclodina*, is on Lord Howe and Norfolk Islands (Chapple et al. 2009). The last two localities are volcanic islands on Lord Howe Rise and Norfolk Ridge, parallel ribbons of Mesozoic continental crust that extend northwest from New Zealand. Within the New Zealand group, species from Northland and its small offshore islands are on basal branches in the phylogeny. The sister of *Oligosoma* and *Cyclodina* is a clade (*Marmorosphax* + *Lioscincus* + *Caledoniscincus* + *Nannoscincus*) endemic to New Caledonia, another emergent part of the Norfolk Ridge north of Norfolk Island. The phylogeny (New Caledonia (Norfolk/Lord Howe Island (Northland (New Zealand)))) comprises a geographic sequence that could reflect either a series of north-to-south founder events (dispersal) or a sequence of north-to-south differentiation events in a widespread ancestor (vicariance).

The basement terranes of New Caledonia are formed from Mesozoic continental crust, but some authors have suggested that the entire island was covered by the sea for 20 myr in the Paleocene and Eocene and emerged only at 37 Ma (Grandcolas et al. 2008). Chapple et al. (2009) accepted this as the age of the island and calibrated a molecular clock for the skinks by assuming that the New Caledonian clade has a maximum age of 37 Ma. Nevertheless, as already noted, they found that the Lord Howe/Norfolk representative of the clade, *Cyclodina*, was much older than the individual islands it is endemic to. The authors suggested that earlier in its history *Cyclodina* had survived on formerly emergent volcanic islands now represented by submarine seamounts along the Lord Howe and Norfolk ridges, and this seems very likely. However, the calibration for the study as a whole was based on the assumption that the New Caledonia members could not have survived on now-sunken islands around New Caledonia. If the Lord Howe/Norfolk species survived on former islands in their vicinity, New Caledonian members may well have done the same, as New Caledonia is a much larger island surrounded by shallow ridges, seamounts, and plateaus. The New Caledonian biota includes many endemic relics, such as the basal angiosperm *Amborella*, that must have survived somewhere (cf. Heads 2008a; Sharma and Giribet 2009). In such a dynamic region, tectonic activity, including uplift and subsidence, is often localized, and without a continuous stratum of a single age, it is difficult for geologists to eliminate the possibility of any former land. Only very small islets are required for the survival of populations of groups such as plants and skinks. Biologists who support the "total submersion" theory have admitted that the presence of numerous relict groups in New Caledonia remains "puzzling" (Murienne 2009, p. 1434) or even "puzzlingly enigmatic" (Grandcolas et al. 2008, p. 3312). Many biologists (e.g., Jolivet 2008; Jolivet and Verma 2008a, 2008b; Lowry 1998) have accepted that refugia must have been present in or around New Caledonia.

From the estimated clade ages, Chapple et al. (2009) concluded that *Cyclodina* and *Oligosoma* reached Norfolk

Island, Lord Howe Island, and New Zealand by long-distance dispersal from New Caledonia, but this was based on using the chronology to rule out earlier vicariance. The chronology in turn was based on the assumption that New Caledonia taxa could not have survived on fragments of emergent land along the Norfolk Ridge and elsewhere. Nevertheless, the analysis of Chapple et al. indicated that the Lord Howe/Norfolk species did just this and so the conclusion supporting long-distance dispersal is not logical.

Elsewhere in the region, the Chatham Islands, east of New Zealand, are the currently emergent parts of the Chatham Rise and stratigraphic evidence suggests they emerged at approximately 2.5 Ma (Campbell 2008, Campbell et al. 2009). An endemic beetle on the Chatham islands, *Geodorcus* sp. (Lucanidae), has been dated at 6 Ma (Trewick 2000). The *Oligosoma* skink endemic on the islands has been dated at 6–7 Ma (Liggins et al. 2008). The calibration this was based on assumed that lizard taxa on the Iranian Plateau could be no older than the uplift of the plateau, but this may not be correct (see below), in which case the ages of the Chatham skink would be underestimates.

The Loyalty Islands of New Caledonia are young (2 myr old), but they are only the currently emergent parts of the Loyalty Ridge that may have a history of volcanism dating back to the Cretaceous and so may have inherited their biota from previous islands. Their rain forest biota is quite distinct from that of the nearby main island of New Caledonia (Grande Terre). For example, the plant *Cyrtandra* (Gesneriaceae) is widespread in the high islands of the Pacific and also on the low flat Loyalty Islands, but this is its geographic limit; it is not on Grande Terre despite much more suitable habitat there, namely steep montane gullies).

Despite this tectonic and biogeographic context, Murienne et al. (2005) assumed that endemic Loyalty Islands taxa could be no older than the islands. They calibrated a molecular clock for the cockroach genus *Angustonicus* by equating the age of species endemic on the islands with the age of the surface rocks (2 Ma). On this basis, they concluded that the diversification of *Angustonicus* in New Caledonia "cannot be dated to earlier than the emergence of the Loyalty Islands," that the palaeogeographic date is "convincing . . . clear and unambiguous," and that *Angustonicus* "first colonised the Loyalty Islands a maximum of 2 Ma from the New Caledonian mainland."

Southeastern Polynesia—Hawaii

In the central Pacific, a clade of trees in *Sideroxylon* (*Nesoluma*) (Sapotaceae) dated at 43–37 Ma is endemic to Hawaii and southeastern Polynesia and only occurs on young islands (Smedmark and Anderberg 2007). The authors calculated that it arose about 30 myr before the formation of any of the islands where the group occurs and suggested "It is possible that the *Nesoluma* lineage has existed on other islands prior to the ones where it is found today." (p. 1501).

A clade in the plant genus *Metrosideros s.str.* (Myrtaceae) is also endemic to Hawaii and southeastern Polynesia and was dated by Percy et al. (2008). They wrote that known volcanic activity in the Austral Islands (southeastern Polynesia) extends back to 58 Ma, but they did not use this date for clock calibrations of *Metrosideros* as it would imply "extremely slow" rates of evolution in the genus and would suggest that it has been in Hawaii since 13 Ma. For these reasons, the age of the youngest hotspot in the region was selected instead.

Neither Smedmark and Anderberg (2007) nor Percy et al. (2008) mentioned the Line Islands, a 4000-km-long swathe of atolls (former high islands) located between Hawaii and southeastern Polynesia. These islands were emplaced in the Cretaceous and Eocene, but they do not show an age progression and are probably not the result of hotspot activity. It is likely that the Hawaii—southeastern Polynesian clades of *Sideroxylon* and *Metrosideros* inhabited these islands before they subsided and the Hawaii—southeastern Polynesia distribution pattern also occurs in many other taxa.

The Hawaiian Islands

The Hawaiian Islands have been studied intensively by geologists and calibrations based on this work have often been used by biologists. For these reasons, the islands are considered here in more detail.

The Hawaiian–Emperor chain is 5800 km long. It extends northwest from Hawaii Island (dated at 0.6 Ma) to the other main Hawaiian Islands, the oldest of which is Kauai (5.1 Ma). Beyond the main islands, the Northwestern or Leeward Islands extend to the oldest emergent Hawaiian island, Kure Atoll (29 Ma). Beyond this point, the Emperor Seamounts extend to the edge of the Aleutian trench, with the oldest being Meiji seamount (85 Ma); others may have been subducted (dates from Koppers 2009).

The Hawaiian–Emperor chain has long been interpreted as a hotspot "conveyor belt" system and so could provide an example of an area where taxa have survived indefinitely as a metapopulation, hopping from older to younger islands. Nevertheless, most biologists have rejected this. For example, Clark et al. (2008) wrote that "although it is highly probable that plant lineages inhabited the Hawaiian Islands throughout their history (>84 Ma), most lineages now present in Hawai'i are thought to have arrived since the formation of the now extant high islands (less than 5 Ma)" (Price and Clague 2002; Price and Wagner 2004). Likewise, following Carson and Clague (1995), Tamura et al. (2004) calibrated a clock for *Drosophila* based on the time of formation of the oldest high island, Kauai. They wrote that "This estimate is considered to be the most reliable estimate and has been used in numerous studies." The large and frequent change in size of gene families across the 12 fully sequenced species of *Drosophila*, with an inferred "revolving door" of gene gain and loss (Hahn et al. 2007) are of great interest, but the rates

that Hahn et al. (2007) inferred are again all based, via Tamura et al. (2004), on the ideas of Carson and Clague (1995).

Thus interpretations of Hawaiian biogeography have been based on two main assumptions.

Assumption 1. The intraplate volcanism on the Hawaiian Islands is well-understood and caused by a fixed mantle plume hotspot.—Mantle material is not normally able to burn its way through the crust or there would be volcanoes everywhere. Volcanoes develop at plate boundaries as the result of plate tectonics, but the cause of intraplate (midplate) volcanism, far from the plate boundaries, is much less obvious. One theory proposes that central Pacific island chains such as the Hawaiian Islands each formed as the Pacific plate moved over a stationary hotspot. This is caused by a mantle plume—a cylindrical vertical jet of abnormally hot material in the mantle—causing melting near the surface. Plate movement would explain the linear age sequence of islands with older ones located progressively further from the hotspot. In this model, successive islands formed individually as separate islands and the standard model of Hawaiian biogeography proposes that new islands have been colonized from older islands downstream of the hotspot (see papers in Wagner and Funk 1995).

But is the hotspot really fixed? Is the mantle below Hawaii in fact hotter than normal? Do mantle plumes even exist? Most biologists have accepted the traditional model, arguing that the geology of Hawaii is "clearly understood" (Cowie and Holland 2006) and fitting biological patterns to the geological scenario. But the whole field of intraplate volcanism and its causes are currently the subject of intense debate among geologists. The American Geological Society has devoted two large volumes to the topic (Foulger et al. 2005; Foulger and Jurdy 2007) and several key papers have discussed alternative interpretations of Hawaii (Anderson 2005; Natland and Winterer 2005; Norton 2007; Sager 2007; Smith 2007; Stuart et al. 2007).

Instead of being caused by narrow vertical mantle plumes, intraplate volcanism could be the result of plate tectonics, with the flexing of plates setting up stress fields that cause narrow horizontal 'hotlines' and propagating fissures. The Hawaiian chain may have originated "by a propagating fracture controlled by the direction of regional stress, the fabric of the seafloor or stresses caused by previously erupted volcanoes" (Neall and Trewick 2008, p. 3304). The distinctive linear age sequence of volcanism could have developed along a propagating fissure instead of at a hotspot.

There is an abrupt 60° change in orientation between the Hawaiian Islands and the Emperor seamounts to the northwest. In the traditional model, this Hawaii–Emperor bend (HEB) has been attributed to a change in the direction of Pacific plate movement, but although similar bends occur in other seamount trails, such as the Tokelau and Gilbert chains, these developed at different times. "The remarkable differences observed in these colinear seamount trails fundamentally question the existence of HEB-type bends in the formation of Pacific plate volcanic lineaments" (Koppers et al. 2007).

Even if the Hawaiian volcanism is caused by a deep-seated hotspot, paleomagnetic data show the islands and seamounts formed at different latitudes, with the hotspot showing rapid southward movement (>4 cm/yr) between 81 and 47 Ma (Tarduno et al. 2003). Tarduno et al. (2009) suggested that the "elegant and captivating geometry of the fixed hotspot idea" (p. 50) prevented the earlier acceptance of hotspot mobility.

Hamilton (2007, p.19), concluded that "Powerful evidence contradicts the notion of fixed hot spots... Geophysics of the Hawaiian region misfits plume predictions... Pacific spreading patterns..., paleomagnetism of Emperor seamounts... and paleomagnetic latitudes of cores from the floor of the Pacific plate... show independently that the Pacific plate did not change direction by 60° above a fixed hot spot at the time of the Emperor elbow, 50 Ma, as required by fixed Hawaiian plume speculation. Other island and seamount chains once conjectured in the absence of data to fit a Hawaiian trajectory in fact misfit it badly in chronology, trends, and geometry . . . Hawaii and other chains are properly explained as responses to within-plate stresses."

Although it is often argued that the islands of Micronesia and Polynesia have all formed at mantle-plume hotspots, a nonplume origin for the volcanism opens up many other possibilities for recurrent volcanism and the survival of terrestrial life in a region. Islands may have formed by recurrent volcanism along orthogonal networks of hot lines and these would have greater potential for preserving biogeographic patterns than the simple parallel lines of hotspot traces. Recurrent volcanism could also bury an island under younger rock.

In any case, there is no need for biologists to accept any one geological theory as the basis for biogeography and to fit a scenario to this. A vast amount of information on biological distributions and phylogenies is now available for comparative analysis and biologists could ask instead what light their own evidence may shed on geological problems. One example of this involves the controversial Trans-Caledonian fault in New Caledonia; some geologists argue that it is a major structure, others deny that it exists. Biogeographic evidence supports the former position (Heads 2008b).

Assumption 2. At one time in the Eocene–Oligocene none of the Hawaiian Islands (or no high islands) were emergent.—Using different assumptions for the Hawaiian Islands (a hotspot origin, estimates of prior island area and slope, rates of erosion and subsidence, etc.) Clague (1996) calculated that there was a period, between 34 and 30 Ma, when no islands were emergent along the chain; "30 Ma marks a time when colonizers from distant continents had to start over completely" (p. 45). Clague emphasized that estimating the longevity of each island "is far more complex and, therefore, far more uncertain

TABLE 1. Actual heights of volcanoes on Maui and Hawaii and maximum heights predicted by Clague (1996)

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

than estimating either the age or size of the volcanoes" (p. 40), but despite this caveat, his estimates and similar ones by Price and Clague (2002) have been accepted uncritically by many biologists. For example, Geiger et al. (2007) wrote that Price and Clague (2002) "provide compelling evidence that the ancestors of extant Hawaiian biota could certainly not have colonized the Hawaiian chain prior to about 23 Ma." In fact, the method that Clague (1996) used to estimate the heights (and therefore the ages) of the former islands underestimated the height of the extant volcanoes on Maui and Hawaii by over 1000 m (Table 1) and so the method could have also underestimated the maximum height of older volcanoes.

Price and Clague (2002) were explicit about the "assumptions and uncertainties" in their model. For example, they accepted a constant rate of erosion and admitted that although this "is probably inaccurate (especially considering the occurrence of massive [submarine] landslides; Moore et al. 1994a), there are too few data to determine how this rate may change over time." (p. 2431). Some of the landslides are more than 200 km long and are among the largest landslides on Earth (Moore et al. 1994b). Price and Clague did not refer to the new interpretations of intraplate volcanism, and these also affect the assumptions that their reconstruction is based on. This sort of modeling is interesting but does not seem reliable enough to serve as the sole basis for analyzing Hawaiian biogeography and, in particular, calibrating evolutionary clocks.

For one seamount in the southern Emperor chain, Koko seamount, Clague et al. (2009) showed that subsidence caused the cessation of growth in shallow-water coral "probably around 33 Ma." This was before the eruption of Kure Atoll (currently the oldest emergent island) at approximately 29 Ma. Based on this evidence Clague et al. wrote in their Abstract: "There was a period between at least 33 and 29 Ma in which no islands existed." But apart from the uncertainty in the dates there are 16 other seamounts between Koko and Kure (Clague 1996) and in the body of their paper Clague et al. (2009) concluded instead: "There was a time period from about 33–30 Ma in which no high islands, and only transient low islands, existed." (p. 10). They also wrote "Koko Seamount was quite distant from these ephemeral islands and was itself a flat, low-lying coral island with limited terrestrial biodiversity" (p.9), but there is no direct evidence for the terrestrial biodiversity. (D. Clague,

personal communication, commented that "The Deep Sea Drilling Project and later Ocean Drilling Program drilled there several times, but always drilled through the carbonate cap and did not start coring until they hit basement rocks, thus passing by any chance of recovering sediments containing pollen or spores"). Some low flat coral islands are biologically depauperate but others are rich, for example, the rain forests on the Loyalty Islands are very diverse. Koko is formed from three large coalesced volcanoes and its flat summit is about 100 km across (Clague et al. 2009, fig. 1c).

Age of individual islands in the Hawaiian chain.—If the Hawaiian Islands 1) formed as the plate moved over a hotspot, and 2) formed separately, then it is possible to date the age of each island simply by dating the exposed rock. But if the chain has formed instead along lines of prior stress, there may be recurrent volcanism and the age of the island might not be the same age as the exposed rock. Apart from the linear age sequence of Hawaiian volcanism, rejuvenated-stage volcanism occurs on Niihau (dated at 2.2–0.4 myr) and Kauai (ongoing since 3 Ma), and the causal mechanisms of this "remain difficult to explain" (Sherrod 2009). If rejuvenated volcanism continued, it could eventually bury an older island under younger rock, leading to an underestimation of the island's age.

In the mantle plume/hotspot theory, it is usually assumed that individual islands in hotspot chains such as the Hawaiian Islands formed separately, but this is also debatable. The modern bathymetry around Hawaii is well known. But it has changed in many ways over time due to regional tectonics, including subsidence and the giant landslides cited above. A hotspot island may grow at one end while subsiding and eroding at the other. This process may continue indefinitely and the eventual result is an island that is very old "as an island", but with stratigraphy composed entirely of young rock. The individual Hawaiian Islands may not all have been joined (the central islands were joined to form "Oahu Nui"), but the channels (between Oahu Nui and Kauai in the north and between Oahu Nui and Hawaii in the south), if they existed, were much narrower in the past and may not have been biologically relevant. Thus, many biogeographic patterns, including endemics on individual islands and other patterns such as eastern Hawaii–eastern Maui endemism, may be older than the individual islands.

In the Hawaiian "progression rule" sequence, the basal clade in a group is on the oldest island (Kauai), and this is often cited in support of the traditional model. On the other hand, there are also many examples of the opposite sequence, in which the basal clade of a group occurs on the youngest island (Hawaii). Holland and Cowie (2007) found this pattern in land snails and described it as "challenging to explain" (p. 2432); it is also recorded in bees (Magnacca and Danforth 2006), moths (Medeiros et al. 2009), damselflies (Jordan et al. 2003), and geese (Paxinos et al. 2002).

Hawaiian taxa dated as older than the islands.—Thomas and Hunt (1991) dated Hawaiian *Drosophila* at 10 Ma, 5 myr older than the main Hawaiian Islands where they are endemic. But their calibration (from Rowan and Hunt 1991) was based on the assumption that a species could no be older than the island it is endemic to and so the dates could, again, be underestimates.

The endemic Hawaiian plant *Hillebrandia* (Begoniaceae) is dated at approximately 50 Ma, predating the oldest emergent island (29 Ma) by about 20 myr (Clement et al. 2004).

Kim et al. (1998) dated the Hawaiian endemic *Hesperomannia* (Asteraceae) at 17–26 Ma, much older than the oldest of the islands it is endemic to (Kauai, 5.1 Ma). They suggested its progenitor arrived on one of the low, Northwestern Islands when these were fully emergent. The time course of the phylogeny was calibrated using a rate from *Dendroseris* (Asteraceae), endemic to Juan Fernandez Islands. This was derived by assuming that *Dendroseris* could be no older than the current Juan Fernandez Islands (4 Ma) (Sang et al. 1994). But other Juan Fernandez endemics include Lactoridaceae, dated to more than 125 Ma (see below). If Lactoridaceae are so much older than the current islands, *Dendroseris* could be too. Thus, the *Dendroseris* dates and the *Hesperomannia* dates based on them could be greatly underestimated.

The passerine *Chasiempis* occurs on Kauai, Oahu, and Hawaii. VanderWerf et al. (2009) found that using the age of Kauai to calibrate the phylogeny was "not appropriate" as it gave a divergence time for the Hawaii species substantially older than the age of the island. An alternative published rate was used instead as this gave an "appropriate" age for the Hawaii species.

Traditional calibrations imply extraordinary rates of evolution in the Hawaiian Islands.—In the Hawaiian cricket genus *Laupala*, Mendelson and Shaw (2005) calibrated a phylogeny by assuming that the clades were no older than the islands they were endemic to. This gave a rate of 4.2 species per million years, a speciation rate that is an order of magnitude greater than the average for arthropods and exceeded in all taxa only by African cichlids. As noted above, the time course of the cichlid phylogeny that is usually cited may be incorrect. It has recently been revised using a calibration based on biogeography and plate tectonics instead of oldest fossils (Genner et al. 2007; Azuma et al. 2008). These indicate that the cichlid clades are older and so the postulated *Laupala* rates may be even more anomalous than was thought.

In the Hawaiian members of the bee *Hylaeus*, Magnacca and Danforth (2006) inferred a center of origin on the island of Hawaii. They assumed that the biota of Hawaii could be no older than the current island and so they proposed that the 60 Hawaiian Islands species of *Hylaeus* have all evolved in the last 700,000 years, "an unusually short time for such a large radiation" (p. 393). They argued that their results "demonstrate

unequivocally that rapid genetic change is taking place" (p. 406), but this depends entirely on the calibration. Later studies showed "low" nuclear DNA variation (Magnacca and Danforth 2007) and confirmed that the bees are "clearly evolving at an elevated rate" (p. 914). Gillespie (2009) wrote that the pattern "awaits explanation." One possibility is that the groups are older than their islands and that what seems to be an anomalously high rate is a methodological artefact.

Survival of Hawaiian taxa on other island groups in the region.—The Hawaiian taxa may have survived on older Hawaiian islands in the northwest of the chain, or on other island groups in the region that have now subsided to form atolls or seamounts. The Cretaceous Line Islands, south of Hawaii, were mentioned above. To the north of Hawaii are the Musicians Seamounts. These formed in the Late Cretaceous and include guyots, flat-topped seamounts that have been eroded to sea level before sinking below sea level (Kopp et al., 2003).

Islands may have also existed to the east of Hawaii. Apart from eroding and subsiding, islands can also be destroyed by processes such as extension or subduction. In the Cretaceous, the second oldest Emperor Seamount (Detroit seamount, 81 Ma; Keller et al. 2000) and also seamounts in the Musicians (Kopp et al. 2003; Li et al. 2008) show signs of interaction with a midocean ridge (a spreading center). These rocks belong to a broad belt of midocean ridge-type volcanism that extends for 7000 km from the Shatsky and Hess Rises to the Mid-Pacific Mountains, the Line Islands, and southeast to the Austral Islands, the Tuamotu Plateau and Easter Island (Watts et al. 2006). This belt of Cretaceous on-ridge volcanism marks the former position of a midocean ridge (the East Pacific Rise) that has produced the Pacific plate to the west, and the Farallon plate and its derivatives to the east. In addition to the eastward movement of the Farallon plate, the ridge itself has moved east to its current position. North of Mexico, the ridge has collided with the west coast of North America (Utsunomiya et al. 2008; Hillier 2006; Smith 2007). Most of the crust it produced to its east has been subducted, and north of Mexico even the younger parts of the Farallon plate have been obliterated.

There are currently no islands between California and the Hawaiian archipelago, and because of this most authors explain the many biogeographic affinities between the two areas as the result of long-distance dispersal. But this overlooks subduction. Since the Cretaceous, when the proto-Hawaii–Emperor chain had already started to form, a vast amount of the seafloor that existed between Hawaii and Califorana (the Farallon plate), along with its seamounts, has been destroyed by subduction. Some surface material of the seafloor (with its seamounts) and also the Caribbean plateau have been accreted rather than subducted, and elements of the biota may also have been accreted. Many Hawaiian taxa show affinities with groups in Alaska, other parts of western America, and the Caribbean.

These suggest former populations on the Musicians seamounts (now subsided), on islands of the Kula plate (north of the Pacific plate; now subducted beneath Alaska), on islands on the Farallon plate (now largely subducted beneath western America), and on islands of the Caribbean plateau (now accreted).

The eastward subduction is recorded in sequences such as the Franciscan Complex of central California, perhaps the world's best-known subduction complex. This comprises rock material that has been scraped off during subduction from 160 Ma to < 20 Ma, including oceanic-island, midoceanic ridge and island arc types of basalts (Saha et al. 2005). The Coastal Belt of the Franciscan Complex was emplaced from 70 to 25 Ma. Within the Coastal Belt, Late Cretaceous basalts may have formed near the Pacific–Farallon ridge and may have been translated northeastwards to reach California in the Paleocene–Middle Eocene (56–40 Ma). In contrast, another unit in the Franciscan Complex, the oceanic Wheatfield Fork terrane, formed in the Eocene. It has been equated with the Siletz (Siletzia) terrane and may have originated on the southeastern Kula plate, accreting by the Miocene (McGlaughlin et al. 2009).

The Siletzia terrane forms the coast of most of Washington and Oregon. It is an oceanic seamount terrane that formed during Paleocene–Eocene time "at some unknown distance offshore" and was accreted early in the Eocene (Dickinson 2004, p. 33). The submarine and subaerial basaltic lavas form a large igneous province possibly >30 km thick. Wells (2007) suggested that the terrane represents an accreted oceanic plateau that has been partially obducted onto the continent and he compared this with the accretion of the Ontong Java plateau onto the Australian plate at the Solomon Islands.

In most cases, seamounts and other seafloor asperities are not accreted but subducted along with the crust and occasionally there is direct evidence for this. For example, tomographic analyses showed that a major earthquake in western Costa Rica in 1990 was caused by a seamount currently subducting at 30 km below the Earth's surface (Husen et al. 2002).

Southeastern Pacific

The Juan Fernandez Islands off central Chile were formed at 4 Ma, but include endemics such as the plant family Lactoridaceae, a group dated to more than 125 Ma using a molecular clock (Wikström et al. 2001).

Eastern Pacific

Jønsson et al. (2010) checked their first rate for the pachycephalids (see Indonesia section above) by comparing it with a rate based on another calibration for passerines (Drovetski et al. 2004, documented more fully in Arbogast et al. 2006). But, as with their first rate, this second rate was also based on the assumption that island taxa could be no older than their islands (*Mimus graysoni* of Socorro Island, west of Mexico, and *Nesomimus parvulus* s.str. of Isabela Island in the Galapagos). Socorro and the Galapagos occur near island-generating structures (active plate margins) and are unlikely to be the first islands generated in their region. Assuming that the endemic taxa are the same age as the island is, again, likely to give dates that are much too young, and so the corroboration of the Indonesian rate by the eastern Pacific rate is not convincing.

Many Galapagos endemics have been dated as older than the islands themselves (4–5 Ma) (see review by Parent et al. 2008). Examples include *Galapaganus* weevils (7.2 Ma), the giant tortoise *Geochelone nigra* (6–12 Ma), differentiation between the endemic marine iguana (*Conolophus*) and its sister the endemic land iguana (*Amblyrhynchus*) (10 Ma), other iguanids (the lava lizards *Microlophus*, formerly *Tropidurus*) and also geckos (*Phyllodactylus*) (both 9 Ma).

The Socorro/Galapagos calibration (Drovetski et al. 2004; Arbogast et al. 2006) has also been used in other studies (e.g., Jordan et al. 2003; Filardi and Moyle 2005; Zink et al. 2006; Joseph and Wilke 2007) and, inevitably, all these found young ages for clades. In monarch flycatchers, for example, Filardi and Moyle (2005) concluded that the results: "strongly support a recent [Pliocene-Pleistocene], rapid sequence of colonization and diversification across all major archipelagos in the Pacific... " (p. 217).

West Indies

Barbados, in the Lesser Antilles, is thought to have emerged about 1 Ma. Creer et al. (2001) concluded that the Barbados endemic lizard *Anolis extremus* is much older than 1 Ma and Thorpe et al. (2005) confirmed that its age (5–6 Ma) is "not in the least compatible with the proposed geological time of emergence of Barbados. Hence, either the molecular clock rate does not apply to the Barbados anole population, or the geological dating of the emergence of Barbados is erroneous. The compatibility of geological times and molecular divergence of this complex on Martinique, together with relative rates tests comparing the rates on Barbados and Martinique, do not suggest atypical clock rates. The question of whether Barbados emerged much earlier than is currently thought, or whether the molecular clock assumptions are inappropriate, remains open" (p. 2087).

Barbados is not a volcanic island; it is composed of sedimentary rocks that form part of an accretionary prism, the wedge of material scraped off and accreted at the subduction zone where the American plate descends below the overriding Caribbean plate. The accretionary prism is up to 50 myr old, but Barbados is thought to have only emerged a million years ago. This is based on the age of the youngest marine sediments on the island. But as Thorpe et al. (2005) emphasized, "one can never be sure that a part of the island was not exposed, when the sedimentation took place in another part" (p. 2094). This is an important point; in dynamic regions around convergent margins, uplift and subsidence are often remarkably local. Thorpe et al. (2005)

wrote that there is no geological evidence for past, now submerged islands in the vicinity. Nevertheless, there is now good biological evidence and the island is right above a subduction zone where different kinds of vertical displacements are more or less expected. Geological evidence indicates that older arcs underlie younger ones in the southern Lesser Antilles (Speed et al. 1993).

In geckos of the Lesser Antilles, a clade dated at 13.4 Ma is endemic to Les Saintes (Guadeloupe), where the oldest exposed rock is dated at 4.7 Ma (Thorpe et al. 2008). Thorpe et al. concluded that the group "occupied the region long before the origin of the younger island arc." Here the authors make the important distinction between the region of endemism, defined by latitude and longitude, and the islands that occur there and currently maintain the endemic population. Thorpe et al. (2008) cited other lizards (anoles) on Les Saintes that also show high levels of differentiation and could have been in the region for as long as the geckos. The authors calibrated the gecko clocks with the age of the oldest exposed rock on the different islands. In particular, the difference between clades of eastern and western Basse Terre was assumed to be no older than the age of the peninsula. However, the pattern on Basse Terre could reflect its colonization from both the east and west by two clades that were already distinct on prior arcs. The calculated dates for the clades would then be underestimates and the clades could have been in the region for even longer than Thorpe et al. (2008) proposed.

Amphisbaenian reptiles, the burrowing worm lizards, are a trans-Atlantic group found in the Americas, Africa, Europe, and the Middle East. Although, reptiles on Caribbean islands may be much older than their island, as just noted, Vidal et al. (2008) calibrated a phylogeny of amphisbaenians using the age of Caribbean islands to date endemic taxa there. They concluded: "Here we show with molecular evidence that oceanic dispersal – on floating islands – played a more prominent role [than vicariance], and that amphisbaenians crossed the Atlantic in the Eocene..." (p. 115). This conclusion is not based on the "molecular evidence" (either the phylogeny or the branch lengths) but simply on the calibration and in particular a type of calibration that can be questioned.

Macaronesia

The moss *Alophosia* is endemic to Madeira (oldest rocks ca. 14 Ma) and the Azores (oldest rocks ca. 8 Ma). The genus is sister to the rest of the class Polytrichopsida and has been dated at 253–207 Ma (Bell and Hyvönen 2010).

Mountains as Islands

As with taxa on oceanic islands, endemics of young volcanoes on continents are often assumed to be no older than the volcano they currently survive on. Nevertheless, counterexamples include insects of the East African rift volcanoes. The volcanic edifice of Mount Kilimanjaro in Tanzania has built up since approximately 2.5 Ma (Nonnotte et al. 2008), but *Monticolaria kilimandjarica* (Orthoptera: Tettigoniidae), endemic to the volcano, was dated as 7–8 myr old (Voje et al. 2009). A population on a single volcanic edifice can survive more or less in situ by constantly colonizing younger lava flows from older ones. As the volcano increases in altitude, so does the population.

Habitats as Islands

Baldwin (1996) used a paleoecological method to date the Madiinae (Asteraceae) of North America, South America, and Hawaii. In the mainland members, 8 of the 14 genera and 73 of the 85 species are endemic to the California Floristic Province. The other 12 species range more widely in western North America, with *Madia sativa* also in Chile and adjacent Argentina, and *Madia chilensis* endemic there. Baldwin and Sanderson (1998) suggested that the "vast majority" of Madiinae are restricted to the California Floristic Province and so the group "must" have originated after the present, summer-dry climate developed there in the Miocene (ca. 15 Ma). This is not necessary though and species of Madiinae such as *Kyhosia* ("*Madia*") *bolanderi* and *Raillardella pringlei* grow in areas with summer-wet climates (Baldwin 1996). Madiinae may have occurred in California before the Miocene despite the different climate then by surviving in refugia, or their ecological preferences may have changed over time, or they may have occurred elsewhere before the Miocene.

There are many endemics in the California Floristic Province, including animals such as the salamander *Batrachoseps* that differentiated "possibly in the late Mesozoic" (Jockusch and Wake 2002, p. 385). It seems unlikely that all the Californian endemics are younger than 15 Ma. Using the postulated 15 Ma age of Madiinae as a calibration gave a very young age (5.2 Ma) for the Hawaiian members, the silversword alliance (Baldwin and Sanderson 1998). Baldwin has argued strongly for the calibration (writing that a "maximum age" of 13–15 Ma for the Madiinae "dictates" that the silversword alliance is ≤ ca 6 Ma; Baldwin 1997; and referring to "The upper limits of conceivable age for the Californian group, 15 Ma"; Baldwin and Sanderson 1998) and it has been widely cited, but the dating is not strongly supported. It has been used to corroborate the Hawaiian calibrations discussed above, but both sets of dates are probably too young.

Metapopulations

The dispersal model of Pacific biogeography argues that because individual volcanic islands were not joined, vicariance is impossible (e.g., van Balgooy et al. 1996). Thus, the model rejects ordinary local dispersal among populations but supports extraordinary long-distance dispersal (founder speciation). An alternative model (Heads 2009) accepts local dispersal among populations (with colonization of new islands) and vicariance

between metapopulations but denies founder speciation. If island taxa exist as metapopulations, the age of the individual islands is irrelevant; island endemics can be much older than their current island and often will be. For more than a century, biogeographers have accepted that the distinction between oceanic and continental islands is fundamental, but if the metapopulation model is correct this distinction is also irrelevant.

The biology of real islands is no more unique than the biology of other ecological "islands," such as mountain peaks, landslides, or puddles. Again, these individual islands may be more or less ephemeral but ancient endemics can survive in situ as dynamic metapopulations. As indicated, conservative molecular clock studies have already indicated that island clades are often older than their islands. Many island endemics are only found on very young islands, but no biologist assumes that species endemic to the puddles or landslides of a region must be younger than each individual puddle or landslide. The faulty conclusion that taxon age must be less than or equal to island age has often been used as evidence for long-distance dispersal; dispersal theorists have argued that because long-distance dispersal must have occurred on Hawaii, Tahiti, and the Galapagos, it can also be an important process elsewhere.

Islands do not form in a spatially random fashion in the middle of an empty ocean. The vast majority do not form far from other islands but around island-producing structures where islands have already been coming and going for millions of years, and maintaining metapopulations.

Corroboration of fossil-calibrated dates with dates calibrated using island age.—*Abrotanella* (Asteraceae) has a disjunct distribution in Australasia and Patagonia. Although Wagstaff et al. (2006) noted that fossil dates only give minimum ages, they transmogrified their fossil-calibrated dates for *Abrotanella* and concluded that the genus "initially diverged during [not 'before'] the Miocene", "about [not 'before'] 3.1 million years ago." Thus, they found that the disjunct distribution "*must* reflect long-distance dispersal" and (in the Abstract) that the species radiations "*undoubtedly* reflect long-distance dispersal...)" (italics added). For three alpine species in New Zealand, Wagstaff et al. wrote that "based on our molecular evidence," that is, the fossil-calibrated rate, "these three species are very closely related and must have diverged during [not 'before'] the past 500 000 years." Again, this is a minimum age only.

Wagstaff et al. corroborated their dates by comparing them with rates of molecular evolution calculated for the Juan Fernandez endemic genera *Dendroseris* and *Robinsonia* (Compositae). They noted that Sang et al. (1994) calculated rates for these genera that were "only slightly slower" than the rates calculated for *Abrotanella*. But, as noted above, the estimated ages for the Juan Fernandez genera used to calibrate the rates are probably

much too young, as the genera were assumed to have differentiated from their respective ancestors only after the formation of the islands. Other endemic taxa there, such as Lactoridaceae, show that this is not necessarily correct.

The Use of Tectonics to Date Clades

Tectonic events that are spatially associated with clade geography provide an alternative to the use of fossil age or island age in dating clades. Many tectonic events have been studied intensively by geologists and are dated with some confidence. Most taxa do not have a good fossil record but do have molecular clades with distinctive structured distributions including boundaries that can be related to regional tectonics. Recent work in ichthyology has calibrated the evolution of molecular clades with tectonic events, avoiding the fossil record and island age altogether. This method has given very interesting results, including bold new hypotheses that contradict the young ages usually accepted for groups such as cichlids (Sparks 2004; Sparks and Smith 2005a, 2005b; Genner et al. 2007; Azuma et al. 2008). The *Oligosoma* skink group cited above, on New Zealand, Lord Howe Island, Norfolk Island and New Caledonia has its sister on Australia (Chapple et al. 2009) and so one option for calibrating the phylogeny would be to utilize the rifting between the Gondwana mainland (Australia) and the Lord Howe Rise/Norfolk Ridge, dated at approximately 85 Ma (Late Cretaceous). This does not seem unreasonable even in the light of the fossil record, as a member of Scincoidea has been described from the Late Cretaceous of Madagascar (Krause et al. 2003). A fossil-calibrated molecular clock study (Hedges and Vidal 2009) placed the origin of Scincidae in the Middle Jurassic. A study utilizing tectonic calibrations has also attributed an Australia–New Zealand disjunction in Onychophora, similar to that seen in the *Oligosoma* clade, to vicariance (Allwood et al. 2010).

The application of the "tectonic" method is not without its own problems. Many tectonic features, such as fault zones and belts of uplift, have been active over a long period or have been reactivated at different times. One tectonic event—the closure of the Panama isthmus at approximately 3.5 Ma—has often been used to calibrate the date of divergence between geminate marine taxa with one member in the east Pacific and the sister group in the Caribbean/Atlantic. But at least some of the taxa concerned diverged long before this (Heads 2005b). Geminate pairs of bivalve molluscs (Arcidae) have been dated at up to 30 Ma (Marko 2002). In the gastropod *Echinolittorina* there are six geminate species pairs. "Despite a preference of the genus for upper intertidal habitats [i.e. populations are likely to have been separated only with final closure], an assumption of a geminate split contemporaneous with the closure of the isthmus would suggest that the genus is only 9 My old, whereas fossil evidence suggests it goes back to

40 My [i.e., a minimum age]" (Lessios 2008, p. 83). To begin with, it is probably best to take a broad, tectonic approach to paleogeographic development rather than a stratigraphic one and Wörner et al. (2009) wrote that "The geological development of Panama's isthmus resulted from intermittent magmatism and oceanic plate interactions over approximately the past 100 m.y.," that is, since the Cretaceous.

In a similar case, the Andes often separate sister taxa and many authors have suggested that the Andes began to rise in the Miocene (Pirie et al. 2006; Linder 2008). In fact, they began to rise as the Atlantic started to open, in the Cretaceous. The first (Peruvian) phase of uplift took place at 90–75 Ma (Late Cretaceous) although evidence is accumulating for an onset of compressional deformation in the Aptian (Early Cretaceous) (Cobbold et al. 2007).

It is now accepted that the plant and animal populations of a mountain range can have been in the region since before uplift of the mountains began and have been passively uplifted with them, rather than colonizing them after they formed (Heads 2006; Ribas et al. 2007; Thomas et al. 2008). This means that montane taxa can be older to much older than the mountain range they occupy and a calibration based on their present altitude will give dates that are underestimates.

Paradisaeidae, the birds of paradise, occur in New Guinea, the Moluccas and northeastern Australia. In their study of the group, Irestedt et al. (2009) used a tectonic event to calibrate the phylogeny and thus avoided relying on oldest-fossil age or island age. Their calibration assumed that the basal differentiation in passerines (New Zealand Acanthisittidae vs. all other passerines) was caused by the split of New Zealand from Antarctica at approximately 76 Ma. This gave an "unexpectedly long history" for the birds of paradise, with most speciation occurring before the Pleistocene (cf. Heads 2001). But if a single tectonic event related to a node that is distant in phylogeny and space can be used to date the overall phylogeny of a group, presumably separate tectonic events can be used to date many individual nodes within the group itself. This approach involves a detailed, systematic engagement of biology with tectonics at many levels, not just in a simplistic preliminary step and has been used in studies of groups such as birds of paradise (Heads 2001) and primates (Heads 2010). Oldest fossils date primates as Paleocene, fossil-calibrated molecular clocks indicate they are Cretaceous, but tectonic calibration suggests they are Jurassic. The two main clades of primates, strepsirrhines (concentrated in East Africa) and haplorhines (concentrated in West Africa) may have diverged with volcanism and buckling on the Lebombo Monocline, a volcanic rifted margin in southeast Africa (Early Jurassic, ca. 180 Ma). Within strepsirrhines, lorises and galagos (Africa and Asia) and lemurs (Madagascar) diverged with the formation of the Mozambique Channel (Middle Jurassic, ca. 160 Ma). Within haplorhines, Old World monkeys and New World monkeys diverged with the opening of the Atlantic (Early Cretaceous, ca. 130 Ma).

CONCLUSIONS

Avise (1992) described a paradox at the heart of biogeography: "concordant phylogeographic patterns… provide evidence of similar vicariant histories… However, heterogeneity of observed genetic distances and inferred separation times are difficult to accommodate under a uniform molecular clock." The usual response to the problem has been to accept a more or less uniform clock, such as the "2% rule" for birds (Weir and Schluter 2008), and infer speciation events at different times, with the implication of separate dispersal events. But this does not account for the geographic concordance in community-wide patterns. Alternatively, different branch lengths may be due not to divergence at different times but to prior differences in genomic architecture and evolutionary potential leading to different clades evolving to different degrees during a given phase of phylogeny. This would allow general, community-wide vicariance and imply "relaxed" clocks in individual clades. Just how relaxed can a clock be? Near and Sanderson (2004) noted that "With respect to rate heterogeneity, once the model of molecular evolution departs from a simple one-rate molecular clock, the divergence time problem enters a realm of model selection in which the number of models is effectively infinite." Fitting tectonic events to nodes suggests that clocks can be very relaxed indeed and this may account for Avise's (1992) paradox.

In any case, calibrating the time course of phylogenies is such a fundamental part of analysis that it deserves much more attention than it has received. Some studies claim that "molecular evidence" shows that a group is, for example, Cenozoic, but the age is determined to a large extent by the calibration. All the dates cited above are calibrated using fossil ages, island ages, or tectonic dates. As indicated, none of the methods is infallible and, as all three methods can give underestimates if not used properly, many of the ages cited will be underestimates.

Calibration of phylogenies with tectonics is still in its infancy, but this approach combines the best of molecular biology (the clades and their distributions) with hard-rock geology (rather than stratigraphy and fossils) and avoids the many problems of fossil calibration. If molecular workers have already dismissed the fossil record of a group as a basis for chronology, as Yoder and Yang (2004, p. 768) did in accepting the "surprisingly ancient" dates for lemurs, tens of millions years older than the oldest fossil, it would be logical to take one more step and not base clock dates on fossils at all. It makes sense to avoid staking the entire chronological analysis of groups such as primates on a "frighteningly incomplete" fossil record (Fleagle 2002), when the distinctive, highly structured biogeography of the molecular clades and accurate radiometric dates can be used instead.

Until recently, biologists have been reluctant to rely on tectonics and geographic distribution in order to calibrate phylogeny, as distribution may seem fluid and transient compared with the fossil record and

morphological and molecular distinctions. Nevertheless, distribution is not just another character and now appears to have a special phylogenetic significance. Many molecular studies have shown that phylogeny correlates better with distribution than with groups based on traditional morphological homologies (e.g., Uit de Weerd et al. 2004; Noonan and Chippindale 2006; Larsen et al. 2007; Stadelmann et al. 2007; Stefanović et al. 2007; Rawlings et al. 2008; Chintauan-Marquier et al. 2010); geographic distribution has turned out to be the "character of characters" for molecular phylogeny in general.

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