Cladistics

Why does the biota of the Madagascar region have such a strong Asiatic flavour?

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Abstract

A corollary of island biogeographical theory is that islands are largely colonized from their nearest mainland source. Despite Madagascar's extreme isolation from India and proximity to Africa, a high proportion of the biota of the Madagascar region has Asian affinities. This pattern has rarely been viewed as surprising, as it is consistent with Gondwanan vicariance. Molecular phylogenetic data provide strong support for such Asian affinities, but often not for their vicariant origin; most divergences between lineages in Asia and the Madagascar region post-date the separation of India and Madagascar considerably (up to 87 Myr), implying a high frequency of dispersal that mirrors colonization of the Hawaiian archipelago in distance. Indian Ocean bathymetry and the magnitude of recent sea-level lowstands support the repeated existence of sizeable islands across the western Indian Ocean, greatly reducing the isolation of Madagascar from Asia. We put forward predictions to test the role of this historical factor in the assembly of the regional biota.

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History and geography play an important role in the build up of ecological communities within regions (Ricklefs, 1987; Ricklefs and Schluter, 1993). It is now widely recognized that the species richness of a community is influenced by both its diversity dynamics (Ricklefs and Bermingham, 2001)—speciation and extinction within taxa—and the immigration of taxa from other biogeographical areas (Pennington and Dick, 2004). Although the role of diversification has been investigated (e.g. McPeek and Brown, 2000), few studies have considered immigration from both historical and geographical perspectives. In particular, the influence of geographical factors over time on local and regional diversity through their effects on immigration is little known.

What determines the proportion of lineages with biogeographical affinities with any particular neighbouring region remains a largely unanswered question in most instances. On the one hand it is clear that the position, size and connectivity of continents is under continual change over geological time (Scotese, 2001). Such fragmentation of continents is expected to result in divergence by vicariance; one may expect the biogeographical affinities of continental and continental island biotas to be skewed towards that of the continent (or continental block) to which they were most recently connected (Murphy and Collier, 1997; Sparks, 2004; Sparks and Smith, 2004, 2005). On the other hand, based on their geological origins, only dispersal can explain the presence of many oceanic island biotas (de Queiroz, 2005); a corollary of island biogeographical theory is the prediction that the largest proportion of lineages immigrating into an island or island region will come from the nearest mainland source (MacArthur and Wilson, 1967). Numerous factors may cause the geographical affinities of communities to differ from both

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continental vicariant and island biogeographical predictions. Such factors may be broadly grouped into regional processes that promote or diminish dispersal in particular directions at a given point in time (e.g. winds, currents, aridity, topography), and historical processes other than continental drift (Ricklefs, 1987, 2004) causing changes both in absolute distances and in ease of dispersal through time.

An insular biota showing strong discrepancies between straight island biogeographical predictions and its geographical affinities is that of the Madagascar region (Madagascar and surrounding archipelagos of the Mascarenes, Seychelles and Comoros). A significant proportion of this biota shows much closer affinities to lineages in Asia (especially India) than to those in Africa (Battistini and Richard-Vindard, 1972; Stoddart, 1984; Cheke and Hume, 2008). Considering the geography of the region (Fig. 1a) from a dispersal perspective, these Asian affinities are surprising given the much greater distance of Madagascar from India (3796 km) than from Africa (413 km), and the present-day expanse of open ocean (2718 km) between the Seychelles and the Indian coastline versus the small distances involved in traversing the Mozambique Channel, either directly from Mozambique to Madagascar by the shortest crossing (413 km) or using the Comoros as stepping-stones (the greatest single crossing being the 302 km between Mayotte and the western Madagascar coast). To put this anomaly in further perspective, the distance between India and Madagascar is approximately the same as the isolation of the Hawaiian archipelago from the nearest continent (3675 km), while the distance between Africa and Madagascar equals that between islands within this archipelago (420 km; Laysan to Gardner). This discrepancy (termed "the strangest of […] anomalies"; Sclater, 1864), along with the long-standing isolation of the Madagascar region, has resulted in the origins of its biota being referred to as "the most difficult enigma in zoological geography" (Cuénot, 1932; our translation) and "one of the greatest unsolved mysteries of natural history" (Krause et al., 1997).

Biogeographers have been aware of this anomaly since at least the mid-19th century (Sclater, 1864; Wallace, 1876; Milne-Edwards and Grandidier, 1879), and evidence for and against such Asian affinities has been used in historical arguments concerning the likelihood of former land bridges and continental drift (Sclater, 1864; Willis, 1932; Millot, 1952; van Steenis, 1962). Sclater (1864) explained peculiar geographical affinities of the Madagascan fauna by proposing that "anterior to the existence of Africa in its present shape, a large continent occupied parts of the Atlantic and Indian Ocean stretching out towards (what is now) America on the west, and to India and its islands on the east". He coined the name "Lemuria" for this vast continent. It was not until the 1960s and 1970s, when a mechanism was found for the theory of continental drift, that there was extensive change in schools of thought. Since this period, Asian affinities of the biota of the Madagascar region have often been viewed as unsurprising (Paulian, 1996), since they can be explained as patterns of vicariance resulting from Gondwanan separation.

The recent accumulation of molecular phylogenetic data for taxa in the Madagascar region permits testing of both Asian affinities and vicariant Gondwanan origins. In reviewing this wealth of new data, both Vences (2004) and Yoder and Nowak (2006) conclude that the great majority of lineages in Madagascar have post-Gondwanan (Cenozoic) origins that are best explained by transmarine dispersal, rather than vicariance. Such conclusions are consistent with a growing body of molecular phylogeographical studies worldwide that support oceanic dispersal rather than vicariance in explaining geographical distributions (de Queiroz, 2005; Riddle et al., 2008). Although a land-bridge between Madagascar and Africa in the mid Eocene to early Miocene has been proposed (McCall, 1997), it is generally believed that this was actually a series of small islands in the Mozambique Channel (de Wit, 2003); such islands would have provided no substitute for transmarine dispersal in reaching Madagascar from Africa, but may have aided in reducing the distance of open ocean to be crossed.

Yoder and Nowak (2006) consider the data across Madagascar's plant, vertebrate and invertebrate groups. Although they conclude that the predominant biogeographical pattern is one of sister-group relationships to African taxa, amalgamation of their Asian subdivisions shows that the Asian component across the sampled faunal and floral groups as a whole (31%) is almost as high as the African one (38%), while in vertebrates the Asian component (32%) exceeds the African one (29%). Furthermore, numerous primary molecular studies (Johnson and Clayton, 1999; Vences et al., 2001; Shapiro et al., 2002; Groombridge et al., 2004; Renner, 2004b) support recent (post-Gondwanan breakup) Asian origins for lineages in the Madagascar region, but do not proffer an explanation as to why the niche(s) in question should have been filled by transoceanic dispersal of a lineage of Asian origin, when the African coast is so much closer.

Two factors may have promoted long-distance dispersal events from Asia towards the Madagascar region, rendering the frequency of arrival of waif dispersers from Asia relative to those from Africa much higher than would be expected on the basis of relative intercontinental distances. First, the Indian winter monsoon winds blow from the Indian subcontinent towards the Madagascar region. Although these winds are reversed in the Indian summer, other winds blow
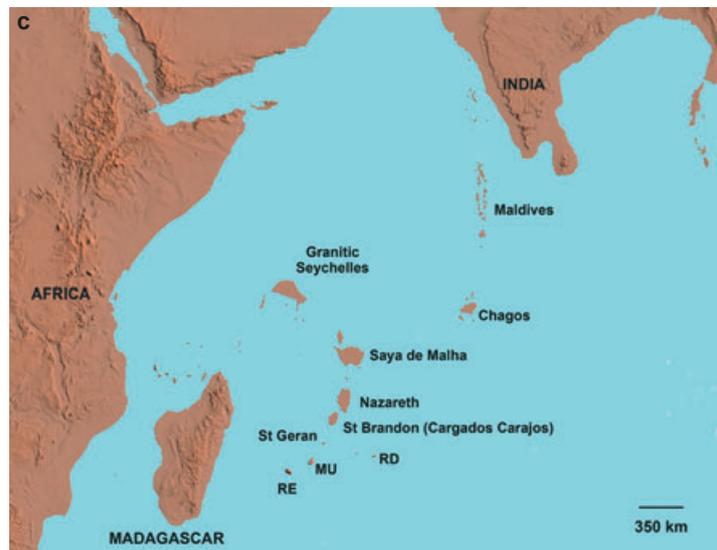
across the Indian Ocean from the direction of Australia and Indonesia towards the Madagascar region in this season, a path also followed by ocean currents (Goswami and Rajagopal, 2003; New et al., 2005; Cheke and Hume, 2008).

Secondly, at repeated times of low sea-level in the recent geological past, a chain of islands may have stretched between the granitic Seychelles, Mascarenes and India, greatly reducing the distance of open ocean to be crossed between India and the Madagascar region. Sea-level fluctuations (Haq et al., 1987; Miller et al., 2005) would have had a profound effect not only on the presence, but also the size, shape and isolation of western Indian Ocean islands.

Here we consider the geological evidence for the existence, position and area of these stepping-stone islands over time. We further review the published molecular phylogenetic data for the timing of divergences between Asia and the Madagascar region, and compare these with the timing of geological events in the western Indian Ocean. Finally, we put forward four predictions that would be expected to hold if the stepping-stone islands were used by lineages dispersing between India and the Madagascar region. These predictions could be tested in the future with further genetic data.

Methods

Geological and bathymetric data

We review the geological evidence for the changing geography of the western Indian Ocean through time. This evidence includes plate tectonics and Gondwanan fragmentation, volcanism, and the emergence of islands through sea-level fluctuations. The position, shape, timing, and duration of stepping-stone islands is estimated for the recent past based on current Indian Ocean bathymetry and the most relevant sea-level change data for each time period. All estimations of past geography were generated using Global Land One-kilometre Baseline Elevation (GLOBE) and ETOPO2 v2 (National Geophysical Data Center, 2006) data. ArcView (ESRI, Redlands, CA, USA) was used to reconstruct maps of the stepping-stone island chain, and to calculate island sizes and the distance of oceanic crossings.

Molecular data

The rapidly accumulating molecular phylogenetic data covering the taxa of the Madagascar region increasingly affords a robust test of an Asian sister relationship with Indian taxa, previously presumed from other sources of information. In addition, examining whether molecular divergence time estimates are consistent with the separation of Madagascar, India, and the Seychelles may be viewed as a test of origins by Gondwanan vicariance. The calibration of molecular clocks (or relaxed clocks) is always based on numerous assumptions that may (Fleischer et al., 1998; Warren et al., 2003; Forest et al., 2007; Rutschmann et al., 2007) or may not have been explicitly stated, and may or may not be valid. Therefore, the divergence time estimates they yield should be viewed with caution. By definition, clocks calibrated using fossils can only be precise as minimum estimates of divergence times (Heads, 2005; Benton and Donoghue, 2007), while those calibrated using volcanic islands (Fleischer et al., 1998; Warren et al., 2003) or lakes (Vences et al., 2001) provide maximum estimates. The conclusion that a divergence event *post-dates* Gondwanan separation is therefore more robust when the clock in question has been established using one of these latter two calibrations.

We surveyed the molecular phylogenetic literature covering taxa in the Madagascar region for dated clear sister-group divergences between clades (or taxa) in the Madagascar region and Asia (including India and south-east Asian islands outside of the Madagascar region, but excluding Australasia). We then compared these dates with tectonic events in the western Indian Ocean, and the timing of existence of stepping-stone islands due to volcanic events and sea-level lowstands. To avoid circularity, we were obliged to ignore several studies that use one or more of these biogeographical events as a calibration point. In other words, we ignored studies in which the calibration point was the separation of the continental blocks under consideration (India, the Seychelles, and Madagascar), or the origin of one of the volcanic islands in the Réunion hotspot chain.

Clearly, a former stepping-stone island chain could have served in transoceanic dispersal of lineages not only travelling from Asia to the Madagascar region, but also those travelling in the opposite direction. For divergence events associated with dispersal rather than continental fragmentation (vicariance), only those associated with a

Fig. 1. The western Indian Ocean region. Topography above and below sea level is shaded in brown and blue, respectively. RE, Réunion; MU, Mauritius; RD, Rodrigues. Geographical coordinate system WGS84. (a) Current geography. (b) Geography at times when sea level was 80 m below present sea level (BPSL), assuming constant ocean floor topography. Based on the most recent sea-level data, this would have occurred at nine different intervals within the last 100 000 years, and around 46 different intervals within the last 1.3 Myr. (c) Geography at times when sea level was 135 m BPSL, assuming constant ocean floor topography. Based on the most recent sea-level data, this would have occurred at around 17 500, 30 000, and 630 000 years ago. Sea-level data for the last 34 000 years come from the Mayotte reef (Comoros archipelago, Madagascar region; Colonna et al., 1996), those from 34 000 to 420 000 years come from the Red Sea (Siddall et al., 2003) and those beyond 420 000 years from the global sea-level estimate (Miller et al., 2005).

colonization of the Madagascar region from Asia (rather than a colonization in the opposite direction) are relevant to the assembly of the biota of the Madagascar region. To infer the ancestral distribution of the node immediately basal to each one of the Asia–Madagascar region divergences under consideration, and in turn the direction of colonization, we used the ancestral areas method of Bremer (1992). This method is cladistic, makes no assumptions about the mechanism of speciation, and relies solely on tree topology. In our application of this method we classed species as occurring in one or a combination of the following geographical regions: the Madagascar region (Madagascar and surrounding archipelagos of the Mascarenes, Seychelles, Aldabra Group, and Comoros), Asia–Australasia (including the Andaman and Nicobar islands, immediately off the Asian coast), Africa, and South America. Tree topologies were taken from the same primary source publications as used for our review of estimated divergence times (see Fig. 3). Phylogenies covering the Mantellinae (Bossuyt and Milinkovitch, 2001) and *Sooglossus* (Biju and Bossuyt, 2003) were excluded, as they do not provide complete species sampling for the key clades of interest, and certain clades represented are likely to contain multiple species with differing distributions. In the case of *Phelsuma*, Harmon et al. (2008) and Rocha et al. (2009) provide improved species sampling over Austin et al. (2004), but do not quote a divergence time estimate for the divergence of the Asian form (*Phelsuma andamanensis*) from the Madagascar region forms. We therefore checked the consistency of results using tree topologies from all three of these publications.

## Results

Geological and bathymetric data

New data on Indian Ocean sea-level changes support lowstands of up to 145 ± 5 m below present sea level (BPSL) at six episodes in the last 0.5 Myr, some of which persisted for up to 50 000 years at a time (Colonna et al., 1996; Rohling et al., 1998; Siddall et al., 2003; Camoin et al., 2004; Fig. 2a). Geological records going back further suggest lowstands of 80–120 m BPSL at 0.64, 0.88, 1.04, 1.26 and 1.54 Ma, and 11 lowstand episodes of 50 m or more BPSL during the last 5 Myr (Miller et al., 2005). Although the topography of the Indian Ocean sea floor has been influenced by tectonic and volcanic activity, evidence suggests that bathymetry has remained largely constant for at least the last 5 Myr. On the basis of current bathymetry, at lowstands of 10 m or more BPSL, a number of additional islands along the line of the Maldives, Chagos, and Mascarene Plateau would have been emergent, forming a stepping-stone chain between India and the Madagascar region (Fig. 1b,c).

Additional islands between the Seychelles and Mascarenes would have further facilitated dispersal within the Madagascar region at these times, the largest being landmasses of 26 405 and 22 099 km^2, currently represented by the Saya de Malha and Nazareth submarine banks, respectively (based on lowstands of 80 m BPSL, and larger still during other lowstands; Fig. 1b,c). Further to the presence of additional islands, a number of islands existing in the present day would have been hugely greater in size. The granitic Seychelles, Maldives, Chagos archipelago, and Saint Brandon (Cargados Carajos), currently 218, 298, 63 and 1 km^2, respectively, would have been sizable regions of 41 615, 18 877, 13 379 and 8973 km^2 (again based on lowstands of 80 m BPSL; Fig. 1b,c). The enlarged size of these islands is likely to have increased the frequency of arrival of waif dispersers, increasing the chances of populations becoming established. Similarly, the enlarged size of these islands would have permitted populations of larger size with an increased potential to serve as the founding population for the colonization of neighbouring islands and continents.

Although the additional islands would have outsized all other islands in the western Indian Ocean (except Madagascar) at lowstands of around 40 m BPSL or more, lowstands of only 10 m BPSL would have been sufficient to expose islands such as Saya de Malha. Consequently, within the last 500 000 years, frequent large reductions in the greatest inter-island oceanic crossing ("hop") between India and the Madagascar

Fig. 2. (a) Sea-level reconstruction for the past 420 000 years. Data for the last 34 000 years come from the Mayotte reef (Comoros archipelago, Madagascar region; Colonna et al., 1996), while those from 34 000 to 420 000 years come from the Red Sea (Siddall et al., 2003). (b) Reconstruction of how the largest inter-island "hop" distance required for an organism colonizing the Madagascar region would change with changing sea level based on current Indian Ocean bathymetry. The most dramatic threshold in this distance at around 10 m below present sea level (BPSL) corresponds to the first appearance of an island in the position of the current Saya de Malha submarine bank, resulting in the largest "hop" being represented by the passage from the Chagos to Saya de Malha rather than the Chagos to Saint Brandon. At 10 m BPSL Saya de Malha would have been a small island in area (14 km^2 based on current bathymetry), supporting viable populations of many immigrating organisms but not others. Therefore, the effective position of this threshold would have been at lowstands of greater depth BPSL for organisms requiring an island of larger size to become established. (c) Reconstruction of how the largest inter-island "hop" distance required for an organism colonizing the Madagascar region would have changed with time in the last 420 000 years based on current Indian Ocean bathymetry. The high ratio of "short hop" versus "long hop" distance applies to organisms capable of establishing a viable population on the small (14 km^2) island of Saya de Malha present at lowstands of 10 m BPSL. For organisms requiring larger islands to be come established, the duration of "long hop" periods would have been increased.
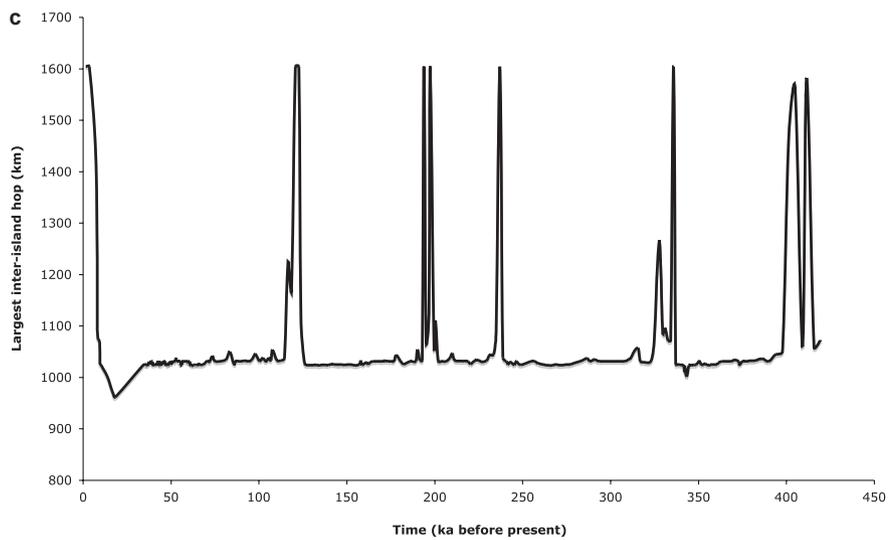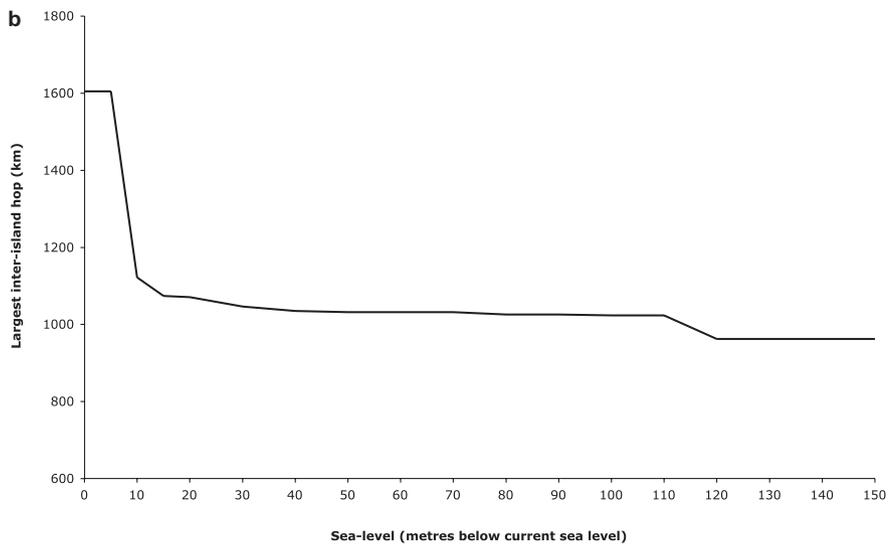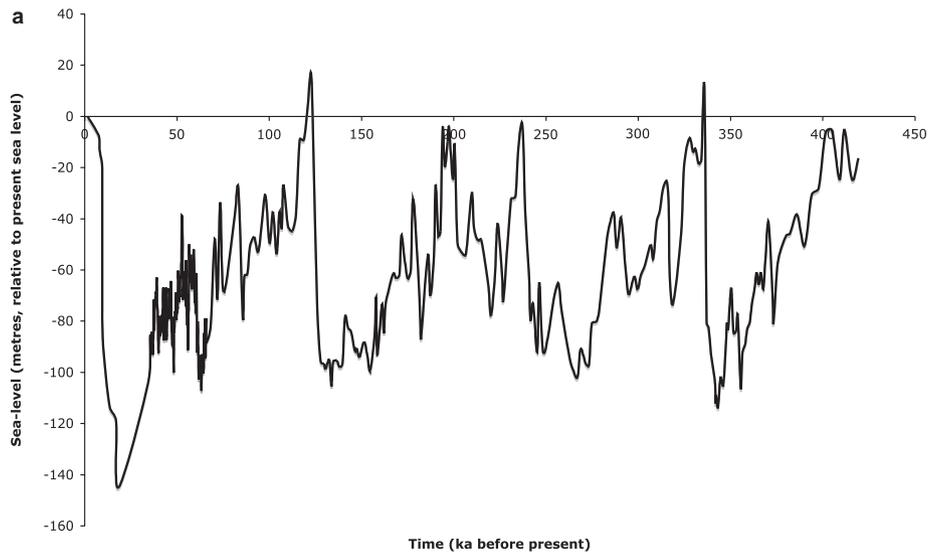
region would have occurred (Figs 2 and 3). The effective duration of these reductions in hop distance for any given organism would have depended on the minimum area required for an island to support a viable population. Periods of effective reduced hop distance would have been of shorter duration the greater the minimum island size required (Fig. 2).

Similar islands are likely to have also existed at earlier periods of low sea level between 5 and 34 Myr ago (Schatz, 1996; Miller et al., 2005). However, as ocean floor bathymetry beyond 5 Myr ago cannot currently be inferred with any accuracy, the precise shapes and areas of these more ancient islands are speculative. Examining the situation further back in time, although the Saya de Malha and Nazareth banks are (like the granitic Seychelles) of continental-relict origin (Pilipenko, 1995; Plummer and Belle, 1995), it is clear from ocean drilling programmes that they also have a major volcanic component, as do the Chagos–Maldives and Saint Brandon (Duncan et al., 1989; Duncan, 1990). The age-progressive chain of volcanic rocks stretching across the Indian Ocean between the Mascarenes and India are generally believed to be the result of Indian and African plate movement over the Réunion hotspot (Bonneville et al., 1988; Duncan et al., 1989; Duncan, 1990; Verzhbitsky, 2003; but see Sheth, 2005). It is likely that many parts would have been subaerial at the time of formation, and would therefore have been available as stepping-stones for lineages dispersing between India and the Madagascar region at periods dating back to the separation of India and the granitic Seychelles at 64 Ma (Plummer and Belle, 1995; Rage, 1996). However, in the absence of any information about the rate of subsidence and erosion of such islands, their duration in the early Cenozoic is uncertain.

Molecular data

We review divergence time estimates for taxa in the Madagascar region with a sister lineage in Asia (Fig. 3). Vicariance resulting from Gondwanan separation seems a likely explanation for the Asian affinities of frogs in the families Mantellinae and Sooglossidae (Bossuyt and Milinkovitch, 2001; Biju and Bossuyt, 2003), although dispersal between recently separated continents (either across narrow ocean passages or late-persisting land connections) cannot be ruled out for the Mantellinae (Roelants et al., 2004; Bossuyt et al., 2006). Vicariance further remains a plausible explanation for the Asian affinities in the frog family Microhylidae (van der Meijden et al., 2007).

The nature of Asian affinities in Malagasy cichlids remains unresolved; Vences et al. (2001) estimated the time of divergence of Malagasy *Paretroplus* from its Indian sister group as post-dating Gondwanan separation, and coinciding with the likely existence of stepping-stone islands. Although such cichlids are currently confined to freshwater, Measey et al. (2007) highlighted the potential role of major discharge pulses of freshwater from the mouth of large rivers in producing paths

Fig. 3. Time line depicting estimates of divergence times between lineages in the Madagascar region and their sister lineages in Asia (black horizontal bars and diamonds) in relation to major geological events in the Indian Ocean (vertical bars: green, tectonic events; red, volcanic events; blue, sea-level lowstands of more than 60 m below current sea level). Sea-level data for the last 34 000 years come from the Mayotte reef (Comoros archipelago, Madagascar region; Colonna et al., 1996), those from 34 000 to 420 000 years come from the Red Sea (Siddall et al., 2003), and those beyond 420 000 years from the global sea-level estimate (Miller et al., 2005). (a) The last 150 Myr (necessarily excluding detail of sea-level lowstands in the last 500 000 years): (i) latest cessation of rifting between Africa and Madagascar–Seychelles–India; (ii) separation of India–Seychelles from Madagascar; (iii) rifting of India from the Seychelles microcontinent, associated with the Deccan volcanic event at the Cretaceous∕Tertiary boundary; (iv) development of the chain of stepping-stone islands between India and the Madagascar region as a result of Réunion hotspot activity, and periodic re-emergence of these islands at times of low sea level. (b) The last 6 Myr with detail of sea-level lowstands. Note that the choice of 60 m below present sea level for the depiction of sea-level lowstands reflects the emergence of islands of large size. Pre-Quaternary lowstands were much smaller in magnitude; based on current bathymetry they would have exposed stepping-stone islands of smaller area. In addition, the detail of particular brief highstand periods (sea level < 60 m below present sea level) had to be omitted because of restrictions of scale. In (a) 45 occur within the last 1.67 Myr while in (b) 20 occur within the last 0.37 Myr. Divergence times for Mantellinae (Bossuyt and Milinkovitch, 2001), *Sooglossus* (Biju and Bossuyt, 2003), *Exacum* (Yuan et al., 2005), *Gaertnera* (Malcomber, 2002; pers. com.), *Monimia* (Renner, 2004c), *Rousseauxia* (Renner and Meyer, 2001), and the older *Paretroplus* estimate (Azuma et al., 2008) are based on fossil calibrations; those of *Hypsipetes* (Warren et al., 2005), *Zosterops* (Warren et al., 2006), and *Phelsuma* (Austin et al., 2004) are based on island calibrations; those of *Papilio* (Zakharov et al., 2004) and the younger *Paretroplus* estimate (Vences et al., 2001) are based on biogeographical calibrations; and those of *Aerodramus* (Johnson and Clayton, 1999), *Alectroenas* (Shapiro et al., 2002), *Psittacula* (Groombridge et al., 2004), and *Raphus-Pezophaps* (Shapiro et al., 2002) are based on external rates taken from other studies. Estimates for *Dyscophus* (van der Meijden et al., 2007), *Otus* (Fuchs et al., 2008), and *Medinilla* (Renner et al., 2001; Renner, 2004a,b) are based on a mixture of different calibrations. [1]An Asian ancestor to the divergence is supported. However, the divergence time estimate supports continental vicariance rather then transmarine dispersal. [2]A lack of species-level sampling and variable distribution of unsampled species precludes ancestral areas analysis. [3]Shapiro et al.'s (2002) fossil calibration yields an unprecedentedly low rate of avian *cytochrome b* evolution of 0.3% per million years. We consider this to be an unrealistic calibration, and apply the commonly used estimate of 2% per million years tick rate of the avian *cytochrome b* clock to the Columbidae divergences (the divergence of *Raphus–Pezophaps* from *Caloenas*, and of *Alectroenas madagascariensis* from *Drepanoptila holosericea*). [4]A Madagascar region ancestor to the divergence is supported. However, as a result of the wide variability in divergence time estimates, whether this divergence reflects continental vicariance or transmarine dispersal is a contentious issue. [5]An African ancestor to the divergence is supported, and therefore the direction of dispersal between Asia and the Madagascar region is unresolved. [6]A South American ancestor to the divergence is supported, and therefore the direction of dispersal between Asia and the Madagascar region is unresolved.
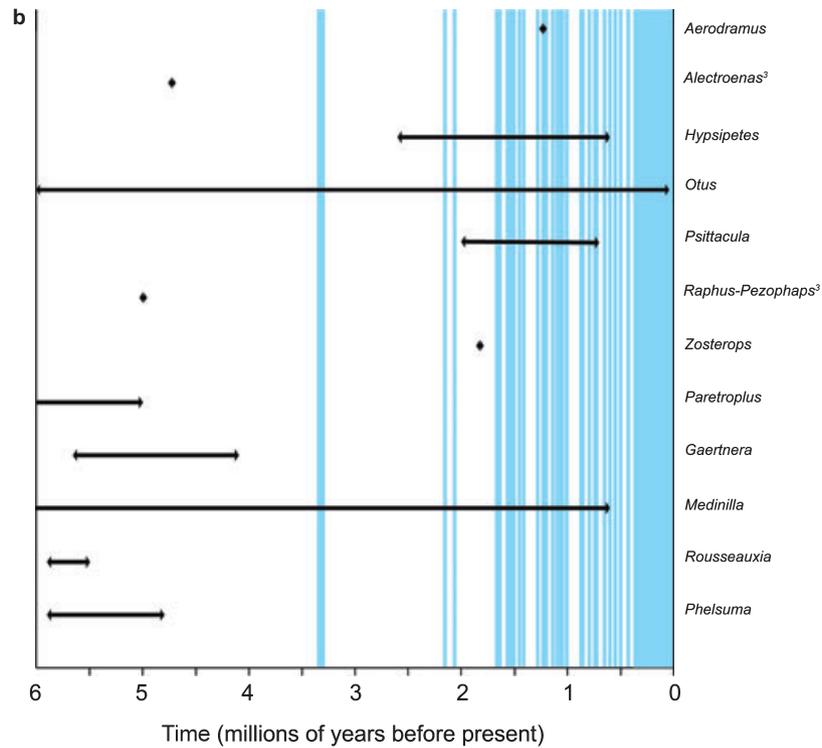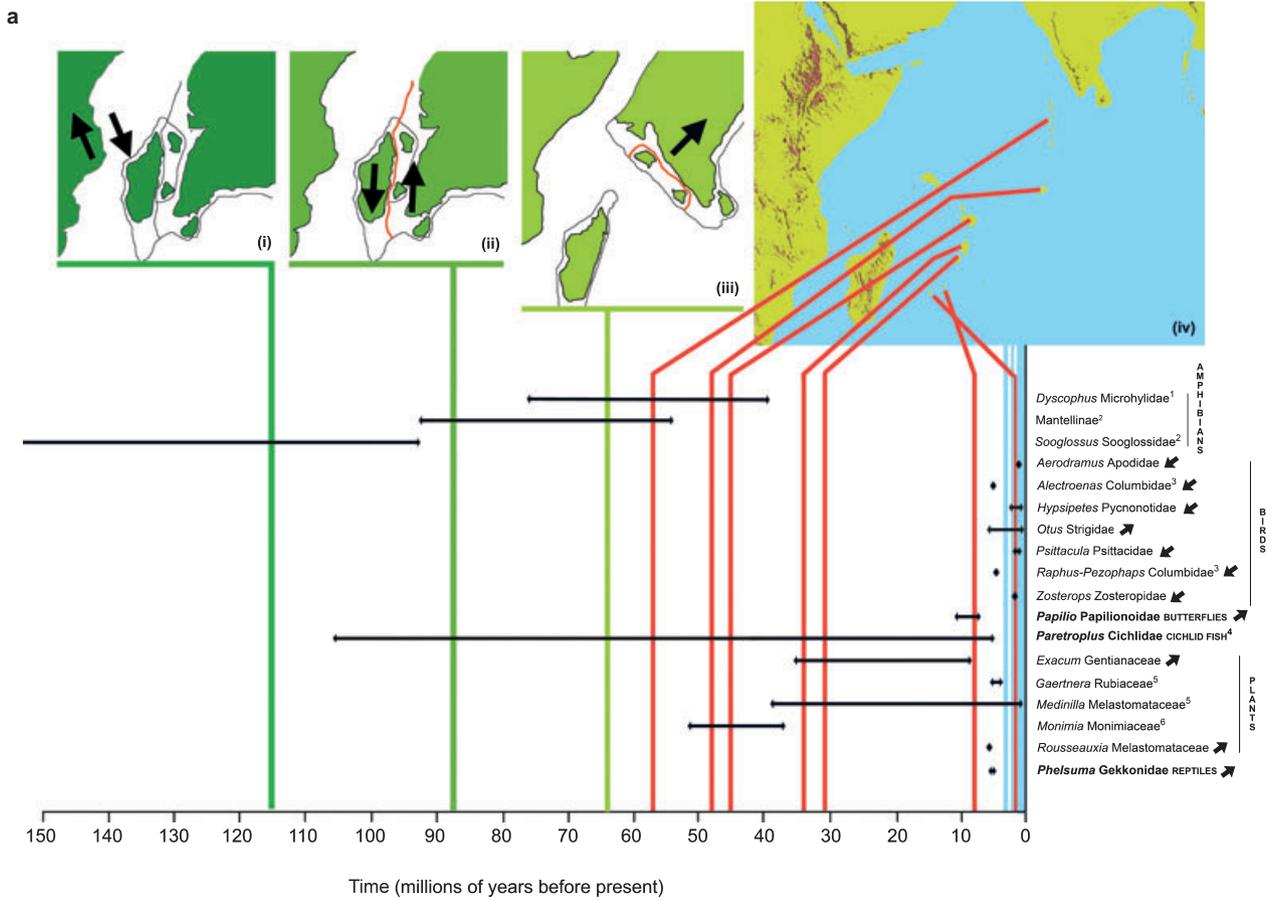
of lowered sea surface salinity, encouraging the waif dispersal of organisms for which salt water is normally an impenetrable barrier. Based on different calibrations, however, the same divergence event was more recently estimated to coincide with continental fragmentation (Azuma et al., 2008). Additionally, concordance between the sequence of continental breakup and the sequence of divergence events between the fish taxa inhabiting such continents strongly supports their vicariant origin (Sparks and Smith, 2005). Nonetheless, Azuma et al.'s (2008) calibration also yields ages for rift valley lake-endemic radiations that pre-date their lakes, and therefore the nature of the Madagascar–India cichlid divergence remains contentious.

Notwithstanding the important contribution of vicariance in shaping the Asian component of the biota of the Madagascar region, the large majority (78%) of dated Asia–Madagascar region divergences (both animal and plant) post-date the separation of India and Madagascar by a considerable margin (up to 87 Myr; Fig. 3). Across the 16 phylogenies analysed, ancestral areas analysis supports an Asian ancestor to the Asia–Madagascar region split in seven cases, and an ancestor in the Madagacar region in six cases (Fig. 3a). Subtracting from these figures the two cases in which divergence estimates pre-date or overlap with continental fragmentation, these results imply six cases of transmarine dispersal from Asia to the Madagascar region (all of which involve birds: *Aerodramus*, *Alectroenas*, *Hypsipetes*, *Psittacula*, *Raphus-Pezophaps*, and *Zosterops*), and five cases of transmarine dispersal in the opposite direction [involving the full spectrum of taxa: *Otus* (encompassing two different Asia–Madagascar region divergences, both of which are inferred to have an ancestor in the Madagascar region), *Papilio*, *Exacum*, *Rousseauxia*, and *Phelsuma*]. In a further three cases, the ancestral area was either unresolved (more than one region being equally parsimonious), or was resolved as a region other than Asia and the Madagascar region, therefore providing no insight into the direction of colonization between Asia and the Madagascar region.

The pattern of dispersal between Asia and the Madagascar region post-dating continental fragmentation has not been biased by our exclusion of certain studies in the interests of avoiding circularity; of the seven such excluded studies, only one (Van Bocxlaer et al., 2006) yields India–Madagascar region divergences old enough (or nearly old enough) to be explained by vicariance. It also seems unlikely that the pattern results from a bias in the type of taxa selected for phylogenetic study. If anything, there is a tendency for researchers to focus on the most distinctive and unique of Madagascar's fauna and flora. Such lineages tend to be the oldest forms and the most highly diverged from their sister taxa on neighbouring continents. Consequently, the dated lineages are more likely to be biased towards being an unrepresentatively old selection of the biota than to being unrepresentatively young. The fact that divergence time estimates post-dating Gondwanan separation are based not only on fossil calibrations, but also island and lake calibrations, further strengthens the conclusion that most such divergences are a result of trans-Indian Ocean dispersal, rather than vicariance.

Discussion

Biogeographical evidence

Whether both the effects of stepping-stones and regional processes (the direction of wind and currents) have worked in unison to facilitate trans-Indian Ocean dispersal, or whether one factor has been much more significant than the other, requires further scrutiny using available biogeographical and genetic data. On the one hand, on the basis of biogeography alone, the apparent Australasian-restricted distribution of the closest relatives of some components of the fauna and flora of the Madagascar region—e.g. the Vangidae radiation (Yamagishi et al., 2001) and *Astelia* (Mabberley, 1987)—highlights the importance that wind direction must have played, as island stepping-stones would have run between the Malagasy region and India, but, on the basis of all geological evidence, never to Australasia. On the other hand, other biogeographical patterns lend weight to the importance of stepping-stone islands. It is striking that both *Euploea* butterflies and *Aerodramus* swiftlets distributed across the Indo-Austro-Pacific are found in the granitic Seychelles and Mascarenes, but are absent from Madagascar as well as Africa. Based on present-day geography, it seems incongruous that winds should have brought these genera to both the granitic Seychelles and Mascarenes, but not to Madagascar. Although the Mascarenes are young islands of volcanic origin that may have presented a vacant niche to waif dispersers, the granitic Seychelles are of the same antiquity as Madagascar (Warren et al., 2003). However, considered in the light of the stepping-stone island locations (Fig. 1b,c), the distribution is less surprising. The crossing between the granitic Seychelles and Mascarenes in former periods would have been shorter than that between either of these archipelagos and Madagascar.

Predictions

Beyond the consideration of biogeographical data alone, the wealth of genetic data being accumulated for the Madagascar region may allow testing of the relative importance of the two factors that we propose to be significant in promoting long-distance dispersal between Asia and the Madagascar region; namely the role of the

stepping-stone island "passage from India" at times of low sea level, versus the role that wind and current direction alone may have played. The bidirectionality of transmarine dispersal inferred from ancestral areas analysis, and the roughly equal number of sampled lineages that are inferred to have dispersed in the two alternative directions, would appear to weigh in favour of a role for the stepping-stone islands. However, the possibility of wind and current reversals as a result of seasonality, freak weather, and changes over geological time can always be used as counterarguments. Avoiding the vagaries of weather, we predict that if the stepping-stone islands were used by lineages dispersing between India and the Madagascar region:

1. Where lineages in the Madagascar region have a sister species with a wide Asian distribution from India eastwards towards Australia, the source population for the lineage colonizing the Madagascar region (or the point of arrival of a lineage travelling in the opposite direction) would have been in India or Sri Lanka, rather than further east.

2. Timings of trans-Indian Ocean dispersal should correspond with timings of sea-level lowstands, illustrated in Fig. 3, when the stepping-stone islands would have been emergent.

Additionally, although the stepping-stone islands would have undoubtedly had high relief following their volcanic origin, the processes of subsidence and erosion would have gradually reduced them to the relatively flat-surfaced features that the submarine banks are today. If the western Indian Ocean's emergent volcanic archipelagos (the Mascarenes and Comoros) can be used as a rough measure, the transformation of a high, mountainous, active volcanic island to a low, relatively flat, inactive volcanic island takes place within 20 Myr following the initiation of volcanism. On the basis of this measure, and Duncan's (1990) dating of the Réunion hotspot chain (and with the exception of the current Mascarene islands: La Réunion, Mauritius, and Rodrigues), it can be postulated that all islands in the stepping-stone chain exposed by sea-level lowstands within the last 10 Myr would have been low-lying and relatively flat. Such islands would likely have presented abundant lowland habitat(s) to colonizing lineages, but an absence of higher-altitude habitat(s). If the stepping-stone "passage from India" was important, two further predictions stem from these inferences:

3. For lineages arriving in the Madagascar region from Asia within the last 10 Myr, the root of the Madagascar region radiation should have been in lowland rather than highland communities.

4. The average time of arrival in the Madagascar region of lineages of Asian origin should be greater for those restricted to high-altitude environments than to those restricted to low-altitude environments.

Prediction 1 could be tested with genetic data in the future. To our knowledge, no suitable dataset is currently available. Predictions 2 and 3 have the potential to be tested with molecular phylogenetic data. However, at present for prediction 2, as a result of uncertainty in molecular dating estimates, we can only expect such timings to fall within a similar time frame as the existence of these islands, rather than showing exact correspondence. A number of the divergence time estimates available (*Zosterops*, *Hypsipetes*, *Psitticula*, *Otus*, and *Aerodramus*) correspond closely to the timing of existence of the stepping-stone islands (Fig. 3), while others of greater antiquity (*Papilio*) and with much wider confidence intervals (*Paretroplus*, *Exacum*, *Medinilla*, and *Monimia*) overlap with the likely more ancient existence of these islands as active or recently active volcanoes. Prediction 4 has the potential to be tested with extensive molecular phylogenetic coverage of communities along any given altitudinal transect in the Madagascar region, and molecular dating of each lineage's arrival. Although we are some way from obtaining the data needed to test these four predictions, it is reasonable to think that it will be forthcoming, given the accelerating pace of molecular phylogenetic coverage of the region's biota.

In conclusion, the biogeographical affinities of the biota of the Madagascar region are difficult to understand on the basis of island biogeographical predictions and current geography alone; other factors have to be invoked. Gondwanan vicariance has undoubtedly had a role to play in the assembly of the modern biota. Nonetheless, the recent (post-Gondwanan) Asian origin of many taxa in the Madagascar region can only be explained by other factors. The most likely of these is a second historical factor: the repeated former existence of a chain of stepping-stone islands between this region and India. However, regional processes—prevailing wind and current directions—are also likely to have contributed to the pattern. Evidence that one of these factors was more important than the other is currently equivocal, and further testing is required. With the ever-growing molecular genetic coverage of the biota of the Madagascar region, the testing of vicariance versus dispersal hypotheses, and the four predictions associated with the past existence of stepping-stone islands, a framework is in place to solve the mystery that the Madagascar region posed to Cuénot (1932) and Krause et al. (1997).

The role of historical processes in shaping modern-day patterns of biodiversity across spatial scales has been the subject of considerable debate over the past two decades (Ricklefs, 1987, 2004, 2008), but it is still often overlooked as a result of the inaccessibility of a historical record with sufficient spatial and temporal resolution for most taxa. Here we proffer an example of how the incorporation of data from the fields of geology, biogeography,

and molecular genetics (phylogenetics and population genetics) might be used in the future to tease apart the influence of historical and regional processes in a biota's assembly.

Acknowledgements

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