


The colonisation of Madagascar by land-bound vertebrates

Jason R. Ali^{1,*}  and S. Blair Hedges²

¹*Department of Earth Sciences, University of Hong Kong, Pokfulam Road, Hong Kong, China*

²*Center for Biodiversity, Temple University, 1925 N 12th Street, Suite 502, Philadelphia, PA 19122, USA*

ABSTRACT

Despite discussions extending back almost 160 years, the means by which Madagascar’s iconic land vertebrates arrived on the island remains the focus of active debate. Three options have been considered: vicariance, range expansion across land bridges, and dispersal over water. The first assumes that a group (clade/lineage) occupied the island when it was connected with the other Gondwana landmasses in the Mesozoic. Causeways to Africa do not exist today, but have been proposed by some researchers for various times in the Cenozoic. Over-water dispersal could be from rafting on floating vegetation (flotsam) or by swimming/drifted. A recent appraisal of the geological data supported the idea of vicariance, but found nothing to justify the notion of past causeways. Here we review the biological evidence for the mechanisms that explain the origins of 28 of Madagascar’s land vertebrate clades [two other lineages (the geckos *Geckolepis* and *Paragehyra*) could not be included in the analysis due to phylogenetic uncertainties]. The podocnemid turtles and typhlopoid snakes are conspicuous for they appear to have arisen through a deep-time vicariance event. The two options for the remaining 26 (16 reptile, five land-bound-mammal, and five amphibian), which arrived between the latest Cretaceous and the present, are dispersal across land bridges or over water. As these would produce very different temporal influx patterns, we assembled and analysed published arrival times for each of the groups. For all, a ‘colonisation interval’ was generated that was bracketed by its ‘stem-old’ and ‘crown-young’ tree-node ages; in two instances, the ranges were refined using palaeontological data. The synthesis of these intervals for all clades, which we term a colonisation profile, has a distinctive shape that can be compared, statistically, to various models, including those that assume the arrivals were focused in time. The analysis leads us to reject the various land bridge models (which would show temporal concentrations) and instead supports the idea of dispersal over water (temporally random). Therefore, the biological evidence is now in agreement with the geological evidence, as well as the filtered taxonomic composition of the fauna, in supporting over-water dispersal as the mechanism that explains all but two of Madagascar’s land-vertebrate groups.

Key words: Davie Ridge, euplerid carnivorans, filtered faunas, land-bridges, lemurs, molecular-clock age-dates, nesomyine rodents, over-water dispersal, tenrecs, vicariance.

CONTENTS

I. Introduction	2
II. How and when did the ancestors of Madagascar’s land-vertebrate clades colonise the island?	2
(1) Development of ideas prior to plate tectonic theory	2
(2) Development of ideas following the introduction of plate tectonics	5
(3) Debate in recent years	8
(4) Assembly of groups reflects the mode of colonisation	8
III. Methods	8
(1) Dating colonisation events using colonisation intervals	8
(2) Assembling the colonisation profile	9
(3) Information sources for each clade’s colonisation interval	9
IV. Results	11

* Author for correspondence (Tel.: +852 5301 3937; E-mail: jrali@hku.hk).

(1) Colonisation intervals for Madagascar's land vertebrates	11
(2) Characteristics of colonisation intervals	13
(3) Comparison of colonisation profiles among groups	13
(4) Generating simulated colonisation profiles	14
(5) Comparing the data with different biogeographic models	15
(a) Comparing the data with a constant rate model	15
(b) Comparing the data with a stochastic rate model	17
(c) Comparing the data with a mid-Cenozoic land-bridge model	17
(d) Comparing the data with a three-period land-bridge model	18
V. Discussion	20
VI. Conclusions	21
VII. Acknowledgements	22
VIII. References	22

I. INTRODUCTION

Madagascar (Fig. 1) has a highly distinctive land-vertebrate assemblage that has been the subject of scientific inquiry for well over 200 years (see Andriamialisoa & Langrand, 2022), with the earliest semi-formal descriptions of the suite dating to the mid-1600s (de Flacourt, 1658). In his *Essais de Zoologie Générale*, Isidore Geoffroy Saint-Hilaire (1841, p. 442) emphasised the island's highly distinctive fauna, noting that it was very different to that on nearby Africa and that it appeared to have closer affinities to the Indian fauna, with some elements linked to taxa in the Moluccas (eastern part of modern-day Indonesia). However, as recently as 2006 there remained a number of critical questions (Krause *et al.*, 2006, p. 43): 'The origin of Madagascar's highly endemic vertebrate fauna remains one of the great unsolved mysteries of natural history. From what landmasses did the basal stocks of this unique and imbalanced fauna come? When and how did the ancestral populations arrive on the island? How rapidly did they diversify, and why?'

Notably, the Malagasy suite comprises relatively few clades, although some of them have speciated dramatically, for instance the *Furcifer–Calumna* chameleons, lemurs, mantellid frogs, microhylid frogs, pseudoxyrhopine snakes, and scincine lizards each comprises several tens or even hundreds of species (Crottini *et al.*, 2012). A widely held view of this pattern is that during the end-Cretaceous mass extinction the land-vertebrate fauna on Madagascar, which was then a fully isolated landmass, was largely eliminated (e.g. Krause *et al.*, 2020). The colonisers that arrived subsequently thus had access to a vast and varied ecospace that enabled them to diversify widely, and generally continuously, at least until the last few million years (e.g. Samonds *et al.*, 2013; Burbrink *et al.*, 2019; Belluardo *et al.*, 2022).

A major impediment to deciphering this faunal suite's colonisation history, as well as its subsequent development, results from a lack of fossil-bearing deposits for the interval between *c.* 70 million years ago (Mya) (latest Late Cretaceous) to *c.* 80 thousand years ago (kya) (Late Pleistocene) (Krause *et al.*, 2006). This was when the ancestors of almost all of the vertebrate assemblage components on Madagascar are believed to have arrived (e.g. Samonds

et al., 2013). As a consequence, for many years opinions were based upon anatomical comparisons of the taxa with their off-island relatives. For instance, Matthew (1915, p. 203) stated that the tenrec ancestor could have been in place prior to the Cenozoic. Simpson (1940) argued for the group dating from the Paleocene, with the lemurs, Eupleridae carnivorans, Nesomyinae rodents and hippopotamuses (now-extinct) arriving in the Eocene, Oligocene, Miocene, and Pleistocene respectively. In recent decades, though, there has been a marked increase in understanding following the application of molecular analyses, and this has allowed quantitative estimates of the ages of the colonisations to be made (e.g. Yoder *et al.*, 1996, 2003; Poux *et al.*, 2005). Interestingly, Simpson's proposals compare reasonably well with the absolute age-date values (see Section IV.3).

II. HOW AND WHEN DID THE ANCESTORS OF MADAGASCAR'S LAND-VERTEBRATE CLADES COLONISE THE ISLAND?

Discussions on Malagasy terrestrial-vertebrate colonisations extend back to the mid-1800s, with explanations centring on land connections, over-water dispersal and relict taxa (Krause, 2010; see also Fig. 2). The issue is complex because, aside from the problematic fossil record outlined above, several geophysical aspects also need to be considered. Notably, although Madagascar is today separated from Africa by deep ocean floor (the shortest distance between the two landmasses is *c.* 430 km; Fig. 1), prior to *c.* 170 Mya (Middle Jurassic) the crustal block sat at the heart of the Gondwana supercontinent, between Africa, Seychelles, India and Antarctica (Ali & Aitchison, 2008; Reeves, 2018).

(1) Development of ideas prior to plate tectonic theory

Philip Sclater (1864) invoked now-sunken land-bridges or continents to explain the similarities of Madagascar's lemurs with the galagos in Africa and the lorises in South Asia and western SE Asia, as well as the island's tenrecs with the sole-nodon insectivores in the Caribbean [note that the molecular

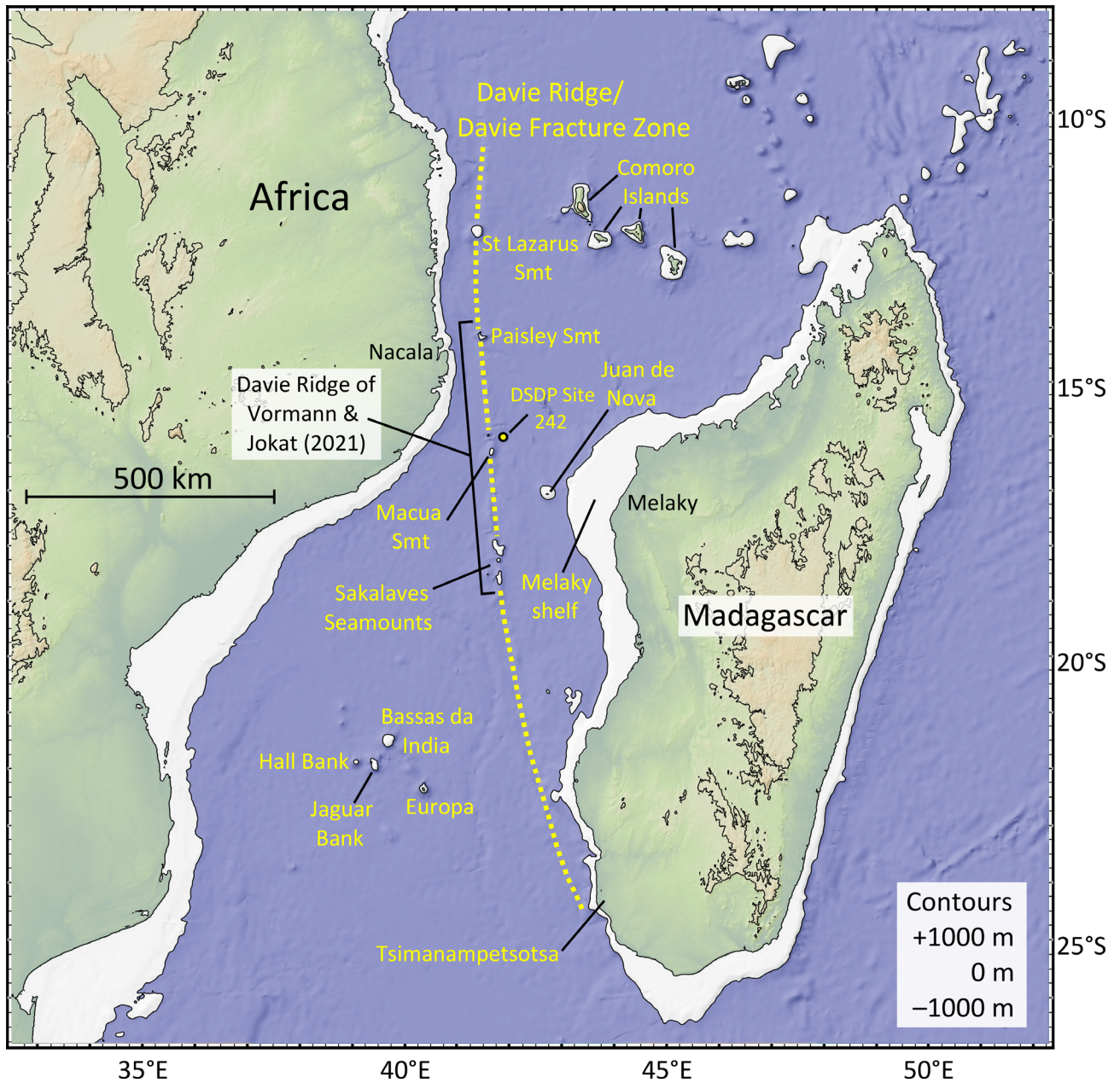


Fig. 1. Map of the Madagascar–SW Indian Ocean region showing key physiographical features. The base image was generated using *GeoMapApp* (Ryan *et al.*, 2009). The shaded contour intervals have 1000-m spacings: dark blue is -1000 m and below, white is -1000 to 0 m, pale green is 0 to $+1000$ m, and khaki is $+1000$ m and above. Note the Davie Ridge continental sliver of Vormann & Jokat (2021; see Figs 3 and 4), while the border between Mozambique and Tanzania meets the coast at *c.* 10.5° S. DSDP, Deep Sea Drilling Project; Smt, Seamount.

study of Stanhope *et al.* (1998) revealed that the latter two groups are actually very distantly related; Brace *et al.* (2016) dates their common ancestor to *c.* 67.5–78.9 Mya]. To explain the primate distribution, Sclater assumed that the Indian Ocean was once occupied by a huge tract of land that he named ‘Lemuria’ (see also, Hartlaub, 1877*a,b*; Sclater & Sclater, 1899; Jacobi, 1900).

The Malagasy fauna was the subject of a dedicated chapter in Alfred Wallace’s *Island Life* (Wallace, 1880). Although

widely regarded as being an over-water dispersalist, he was of the opinion that the lemurs, tenrecs and carnivorans had advanced from Africa along a pre-Eocene land surface (Wallace, 1880, pp. 418–419); at the time, ‘Eocene’ denoted the interval between the ‘Cretaceous’ and the ‘Miocene’ (based on Lyell, 1833); ‘Paleocene’ and ‘Oligocene’ and a concomitantly reduced Eocene, were only formally incorporated into the geological timescale in the late 20th century (Odin, Curry & Hunziker, 1978).

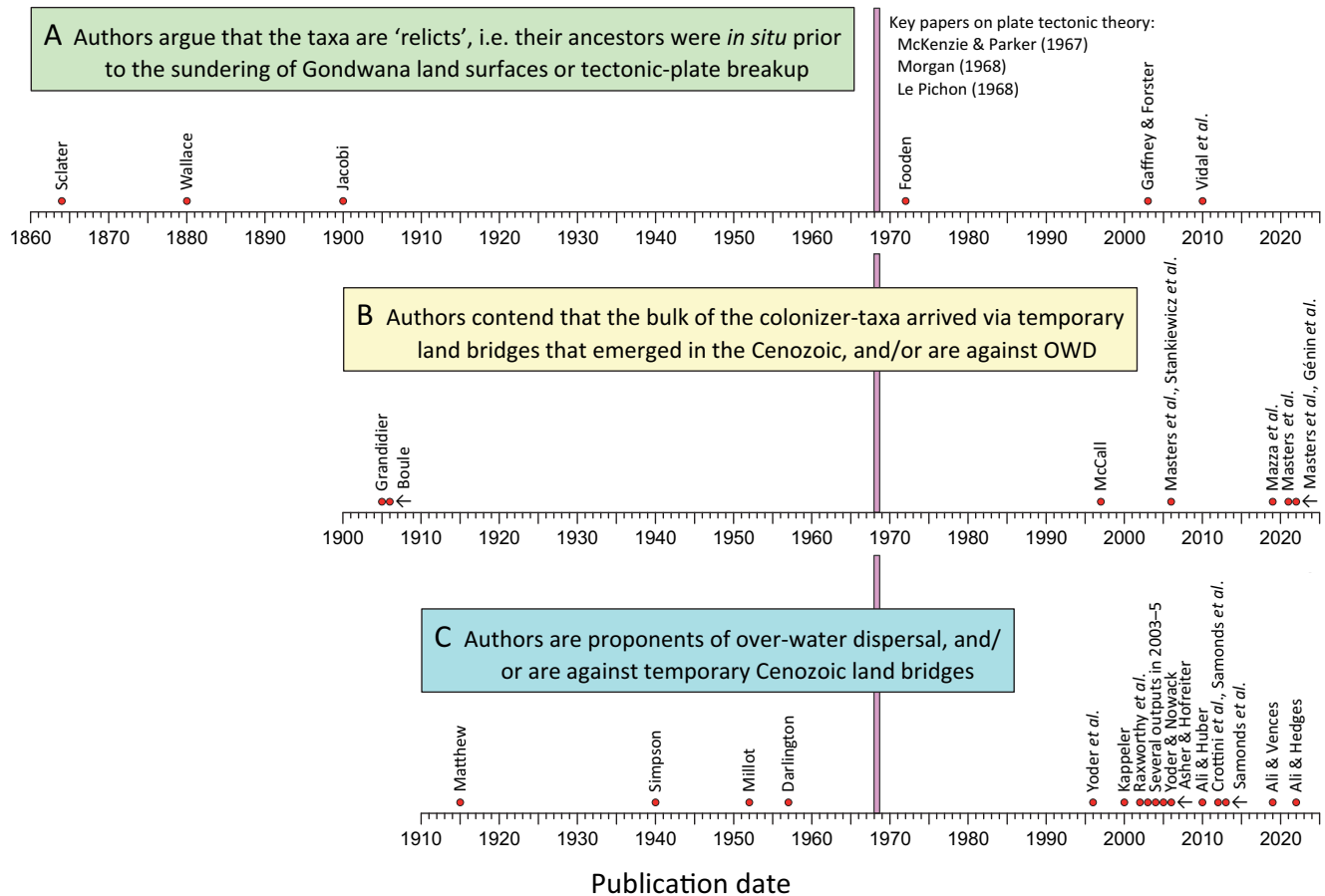


Fig. 2. Chronological summary of the key literature explaining the arrival of the bulk of Madagascar's land-bound vertebrate clades. Effectively, there are three sorts of proposal: the taxa are relicts (A); the taxa walked to the island along causeways/stepping-stone chains that emerged in the Cenozoic and/or they did not over-water disperse (OWD) to the island (B); or the taxa were transported to the island on 'rafts' or floated/swam across, and/or there is no evidence for temporary land bridges (C). With some references, it was not possible to align the labels directly above their red circles thus offsets were made and then 'corrected' with small left-pointing arrows.

In the early 1900s, Guillaume Grandidier (1905, pp. 138–140), son of the famed naturalist Alfred Grandidier, presented a radical hypothesis. He argued that the coloniser taxa had arrived *via* a land bridge (connecting Africa and NW Madagascar) that became emergent in the Cenozoic. His reading of the geological literature was that Madagascar in the Late Cretaceous was an island, and that the ancestors of the extant and recently extinct fauna dated from the Cenozoic based on comparisons with off-island forms. Shortly afterwards, Grandidier's hypothesis was championed by Marcellin Boule (1906) in a five-page summary in the periodical *La Géographié* (Fig. 2).

Over-water dispersal as an explanation for key elements of the Madagascar's land-mammal suite was first proposed by William Matthew (1915, pp. 203–204; Fig. 2): '...the Malagasy mammals point to a number of colonisations of the island by single species of animals at different times and by several methods. Of these colonisations, the Centetidae [tenrecs] are the earliest, perhaps pre-Tertiary; the lemurs,

rodents and viverrines [carnivorans] are derivable from one or more middle Tertiary colonisations: and in both cases the 'raft' hypothesis may reasonably be invoked. The hippopotami may have arrived by swimming and the bush pig and the shrew may have been introduced by man, while the bats may readily have arrived by flight. The extinct ground birds are easily derived from flying birds'.

The idea of over-water dispersal colonisations for Madagascar's non-aquatic land-mammal ancestors was cemented by the publications of Simpson (1940), Millot (1952) and Darlington (1957), the hand-drawn 'sweepstakes' graphic presented by Simpson proving particularly potent. Crucial for Simpson was the idea that if Africa and Madagascar had been linked by a causeway then many more colonisations should have taken place, as has been the situation with the Panama Isthmus where South America's joining with Central and North America *c.* 3 Mya (Late Pliocene) led to a major two-way transfer of land-vertebrate taxa (e.g. Simpson, 1980; O'Dea *et al.*, 2016). Notably,

however, the works of Matthew, Simpson, Millot and Darlington pre-dated plate tectonic theory and their geological model assumed horizontally fixed continents.

(2) Development of ideas following the introduction of plate tectonics

The formulation of plate tectonic theory in the 1960s (McKenzie & Parker, 1967; Morgan, 1968; Le Pichon, 1968) led to associated biogeographical models being proposed for the Malagasy biota. For instance, Fooden (1972; Fig. 2) argued that the 'aboriginal eutherians' (tenrecs, lemurs, rodents, and carnivorans) were relicts that predated a supposed Paleocene–Eocene separation of Africa and Madagascar. However, the plate model Fooden drew upon for the SW Indian Ocean (Dietz & Holden, 1970) was very different from the one that is used today, especially concerning the island's tectonic isolation from the various crustal blocks that once surrounded it at the centre of the Gondwana super-continent, i.e. Africa–South America, Antarctica–Australia, Seychelles and India (Ali & Aitchison, 2008; Reeves, 2018; Tuck-Martin, Adam & Eagles, 2018). In the modern scheme, the separation of Africa–South America (West Gondwana) from Madagascar–Seychelles–India–Antarctica–Australia (East Gondwana) commenced *c.* 170 Mya (Middle Jurassic). The next phase saw Antarctica–Australia break apart from Madagascar–Seychelles–India *c.* 130 Mya (Early Cretaceous). Madagascar finally became isolated with the rifting of Seychelles–India *c.* 85 Mya (mid-Late Cretaceous). Therefore, not only has the block/island been separated from its former neighbours for much longer than Fooden envisaged, but the ultimate event was well after land connections with Africa were severed.

The next significant publication was by McCall (1997; Fig. 2). He proposed that the Davie Ridge, which runs along the centre of the Mozambique Channel (Figs 3 and 4), was instrumental in the mid-Cenozoic mammal colonisations because, in his view, over-water dispersal to Madagascar was problematic (McCall, 1997, p. 663): 'If colonisation of Madagascar was by rafting, there is little reason why other isolated islands would not have been similarly colonised by mammals. Second, the mammalian fauna of Madagascar is dominated by ancient groups and is almost completely lacking in more recent groups present on continental Africa, such as the old-world monkeys, felids and canids (hippopotami are the only representatives of a recent group). It is unlikely that primitive mammals were more suited to rafting than more recent groups'. However, McCall's first sentence indicates that he overlooked the mammal faunas that occupy some truly isolated oceanic islands and archipelagoes, including those on the Canaries, Christmas Island, Galápagos, and the Gulf of Guinea Group (Ali & Vences, 2019). With each, over-water dispersal is the only viable explanation as the sea-bed connecting each of the landmasses to the nearest continent is deep and could never have been exposed. His second point (sentences #2 and #3), disregards the fact that ocean circulation paths are not

fixed, but instead change as the tectonic plates continually re-configure [see below in this section, specifically the reference to Ali & Huber (2010) and the dramatic modification in surface-water flow in the SW Indian Ocean that occurred 15–20 Mya]. In some cases, the oceanographical responses have been profound and geologically rapid, for instance with the formation of the Panama Isthmus (Schneider & Schmittner, 2006), and the openings of both the Tasmanian Gateway (Scher *et al.*, 2015) and the Drake Passage (Toumoulin *et al.*, 2020). McCall then marshalled the geological evidence, concluding that the Davie Ridge was exposed between 45 and 26 Mya. His information base was, however, limited; a small number of drill and dredge sites along the bathymetric high (e.g. Simpson *et al.*, 1974; Leclaire *et al.*, 1989; Bassias, 1992). Material recovered at Deep Sea Drilling Project Site 242 (Fig. 3; 15.84° S, 41.82° E; northeast flank of the Macua Seamount) indicated to him that the locality was sub-aerial until the Late Eocene because the recovered sequence was thought to directly overlie continental basement (such rocks were not cored and the seismic records that were acquired prior to the drilling to establish the pre-expedition stratigraphy proved to be incorrectly interpreted; Simpson *et al.*, 1974). Elsewhere, continental-basement rocks were recovered in dredge hauls on the Davie Ridge [gneisses and meta-arkoses (Leclaire *et al.*, 1989; Bassias, 1992)] and this was taken by McCall as evidence of emergence until the Early Miocene. The key issue here is that submerged continental 'rafts' or 'ribbons' are not uncommon features of ocean basins (Müller *et al.*, 2001; Gaina *et al.*, 2003), with most being generated during the rifting of continental blocks, or subsequent ocean-ridge 'jumps' that reconfigured the plate boundary, in the process calving-off a crustal fragment. Notably, many such 'terraces' are found in the Tasman Sea to the east of Australia (e.g. Collot *et al.*, 2020). The critical factor is that only when the blocks have crusts that are thicker than about 25–30 km will their upper parts rise above sea level due to them floating on the denser mantle below [continental crust is typically 35–40 km thick (Kearey, Klepeis & Vine, 2009; Ali, 2017)]; those that are thinner tend to be submerged.

In the late 1990s to the mid-2000s several molecular-phylogenetic studies were published for land mammals, reptiles, and amphibians in which over-water dispersal was invoked (e.g. Yoder *et al.*, 1996, 2003; Raxworthy, Forstner & Nussbaum, 2002; Vences *et al.*, 2003a,b, 2004; Poux *et al.*, 2005; Asher & Hofreiter, 2006; Fig. 2). The key factor here was that that extant taxa were derived from a small number of colonisation events that post-dated Madagascar's isolation (*c.* 85 Mya; Storey *et al.*, 1995; Torsvik *et al.*, 1998), plus they were not clustered in time. Thus, it affirmed Simpson's view that the suite had been stochastically assembled. Notably, Rabinowitz & Woods (2006) assessed the available geological and geophysical evidence and drew similar conclusions. Interestingly, at about the same time Noonan & Chippindale (2006) argued that at *c.* 80 Mya Madagascar was linked to Antarctica *via* India and the Kerguelen Plateau and/or the Gunnerus Ridge as a means of explaining the island's boid snakes, iguanid lizards

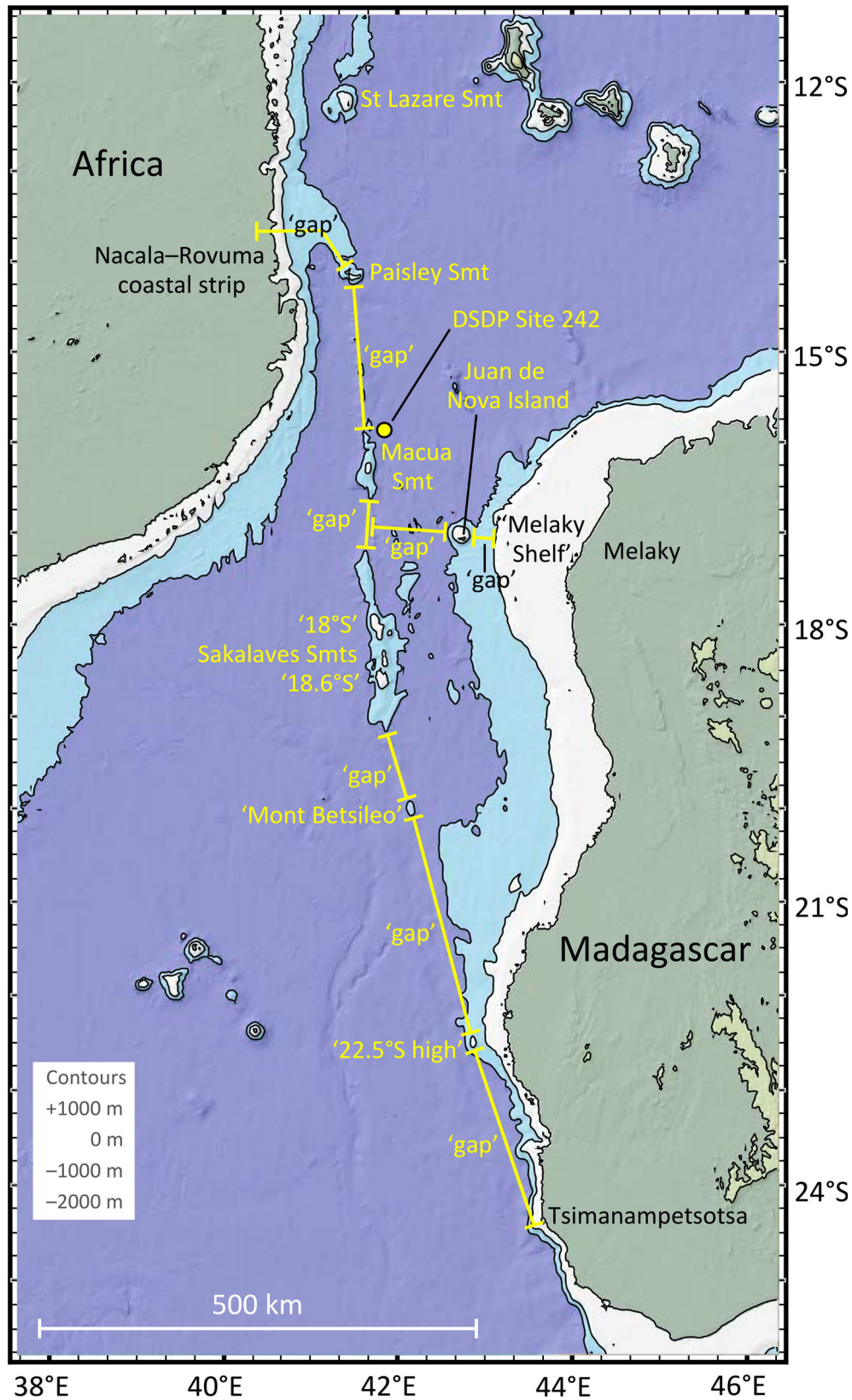


Fig. 3. Map showing the various elements in the set of land bridge models of Masters *et al.* (2021, 2022), which aid with interpreting the connectivity arrays shown in Fig. 5 (see Ali & Hedges, 2022). The base image was generated using *GeoMapApp* (Ryan *et al.*, 2009). (Figure 3 legend continues on next page.)

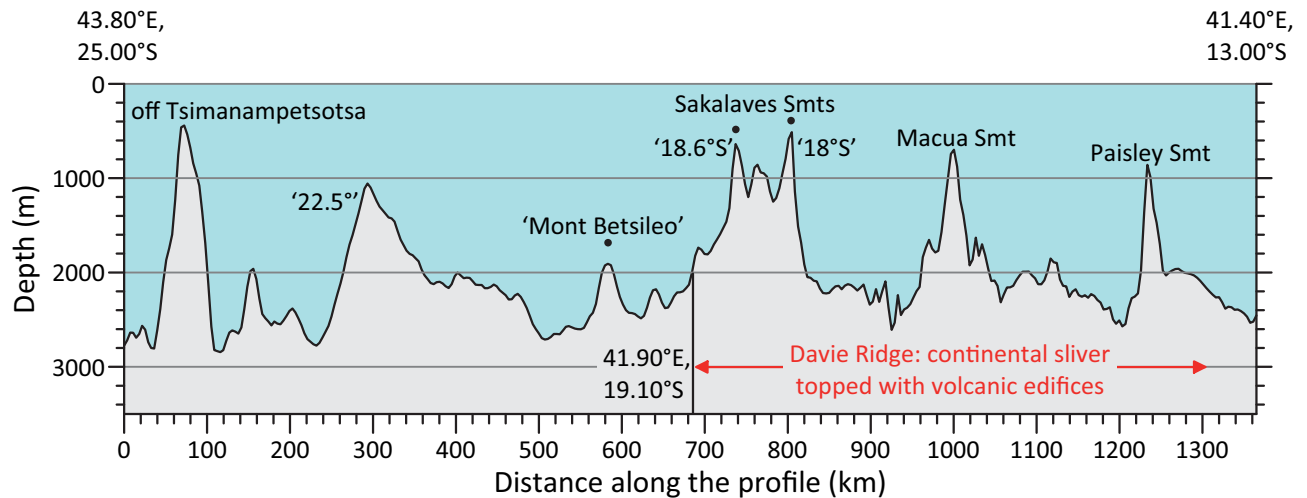


Fig. 4. Bathymetric profile of the Davie Ridge/Fracture Zone. Based on depth data from *GeoMapApp* (Ryan *et al.*, 2009), the viewing direction is towards the west. To accommodate a small change in the orientation of the feature, the path is re-aligned at 41.90° E, 19.10° S. Note the approximate extent of the Davie Ridge continental sliver of Vormann & Jokat (2021). Some physiographic features have names that are listed in the *GEBCO Atlas* (<https://www.gebco.net>; e.g. Sakalaves Seamounts, Macua Seamount, Paisley Seamount), whereas others carry informal labels, e.g. 'Mont Betsileo' and the '18.6° S' and '18° S' pinnacles on the Sakalaves (see Ali & Hedges, 2022). The small dots above the two highs on the Sakalaves Seamounts are sea-level depths of 375 and 475 m that were reported in Courgeon *et al.* (2018), while the one above 'Mont Betsileo' is from *GeoMapApp* (c. 1680 m).

and podocnemid turtles (based on molecular data). However, Ali & Aitchison (2009) and Ali & Krause (2011) reviewed the geological and geophysical evidence and argued that there was no support for either routeway proposal.

In a major review of the geology of Madagascar, de Wit (2003) mentioned the lemur colonisation problem in light of the known geological data, i.e. that the event post-dated by quite some time Madagascar's isolation. Later, de Wit formed part of a team (Stankiewicz *et al.*, 2006; Fig. 2) that focused on evaluating various aspects of Simpson's sweepstake hypothesis. First, they examined Simpson's (1952) ideas on over-water dispersal probabilities. Then, they reviewed the region's modern-day ocean currents and atmospheric patterns, before considering the potential for through-air transportation of animals by tornadoes and cyclones. They concluded that the colonisations involving water passages and/or wind-carry were effectively impossible. At the same time, Masters, de Wit & Asher (2006, p. 443) discussed the then newly published work of Poux *et al.* (2005) on land-mammal colonisations noting that: 'Simpson's (1940) prediction that sweepstakes dispersal events should occur at random intervals is not borne out by the mammal data. According to the molecular divergence dates estimated by Poux *et al.* (2005), sweepstakes events seem to have occurred very early in the history of a clade, and never again'. This phase of the debate prompted important reviews by Yoder &

Nowack (2006; Fig. 2) and Tattersall (2006a,b). The former favoured over-water dispersal, while the latter opined (Tattersall, 2006b, p. 35): 'Clarification of the mechanisms of origin of Madagascar's terrestrial mammal fauna is thus as likely to come from studies of the surrounding seafloor geology as it is to emerge from examinations of the fossil record and systematics of the island's fauna itself'.

Ali & Huber (2010; Fig. 2) brought new insights through computer simulations of the former climatic and oceanographic conditions in the SW Indian Ocean region. Contrary to Stankiewicz *et al.* (2006), they showed that over-water dispersal from Africa to Madagascar was in fact feasible in the early and middle Cenozoic, but at about 15–20 Mya the system flipped to the modern-day arrangement where such transfers have a much lower probability (see also Lutjeharms, Wedepohl & Meeuwis, 2000; de Ruijter, Ridderinkof & Schouten, 2005). The critical factor was that between the Paleocene and Early Miocene, Africa and Madagascar were some distance south of their present locations (at 66 Mya, c. 14° of latitude or 1550 km). Consequently, the air flows and surface-water currents in the SW Indian Ocean region then interacted very differently with the various landmasses. Ali & Huber (2010) suggested that on timescales of approximately 100 years, the Austral-summer conditions were such that rafts washing off the northern Mozambique–southern Tanzania (Fig. 1) could have been carried to northern

(Figure legend continued from previous page.)

The shaded contour intervals have 1000-m spacings: dark blue is –2000 m and below, pale blue is –2000 to –1000 m, white is –1000 to 0 m, green is 0 to +1000 m, and pale green is +1000 m and above. Some of the features carry informal names and are thus placed in quotation marks (see Fig. 4). The Davie Ridge continental crustal sliver of Vormann & Jokat (2021) extends from just south of the Sakalaves Seamounts to north of Paisley Seamount (also see Fig. 1). DSDP, Deep Sea Drilling Project; Smt, Seamount.

Madagascar in around 30 to 35 days. A one-million-year interval would therefore present around 10,000 conducive transfer ‘seasons’. Building upon this work, over-water dispersal explanations featured prominently in the land-vertebrate colonisation syntheses of Crottini *et al.* (2012) and Samonds *et al.* (2012, 2013).

(3) Debate in recent years

In recent years, the rafters/floaters *versus* causeway-walkers debate has been reinvigorated. Mazza, Buccianti & Savorelli (2019; Fig. 2) questioned the over-water dispersal mechanism, and expressed their concerns for it accounting for Madagascar’s land-bound vertebrate clades. One issue related to the perceived physiological inadequacies of land mammals; death through starvation and/or dehydration would, they argued, make it impossible for adrift waifs to survive all but the shortest of sea passages. They also asserted that the founder populations would have highly restricted gene pools due to the small number of individuals being carried over (potentially, just gravid individuals), which would consequently render them vulnerable to selection pressures, and thus prone to extinction. To provide an alternative mode of colonisation, Mazza *et al.* (2019) also explored the idea of the Davie Ridge having once been emergent. Ali & Vences (2019) countered, demonstrating that, globally, all of the sister land-mammal clades that have geographical distributions that are separated by open ocean (in some cases, the gaps are appreciably greater than the width of the Mozambique Channel) are from specific branches on the mammal phylogenetic tree (i.e. Afrosoricida–Eulipotyphla, Carnivora, Primates and Rodentia). Crucially, the various taxa possess a number of physiological and/or life-history traits (low energy requirements related to small body size, ability to enter into torpor, a hibernation phase) that increase their chances of surviving protracted over-water journeys [see also Kappeler (2000) and Nowack & Dausmann (2015)]. Ali & Vences (2019) also challenged the assumptions related to a lack of food and fresh water during the journeys. Moreover, the idea of genetic ‘bottlenecking’ does not preclude the long-term success of a migrant group. One example of this is provided by a translocated community of mouflon sheep on Haute Island (6.5 km²) in the Kerguelen Archipelago. Following the introduction of a pair of animals in 1957, the population since the 1970s has on a 4- to 5-year cycle oscillated between about 200 and 650 individuals. Notably, there has been unexpected growth of genetic diversity, which is thought to have arisen through selection (Kaeuffer *et al.*, 2006). Concerning the Davie Ridge’s palaeogeography, Ali & Vences (2019) acknowledged that although small sections of it were probably emergent at various times in the Cretaceous and Cenozoic (based on Bassias, 2016), there was no evidence for it ever having formed a continuous causeway. Instead, they suggested it comprised a smattering of dispersed islands, mostly low-elevation carbonate platforms. Masters *et al.* (2021, 2022), as well as the associated paper of Génin *et al.* (2022), revisited the debate and (i) restated the main ideas in Mazza *et al.* (2019), (ii) questioned the palaeoclimatological and palaeo-oceanographical modelling in

Ali & Huber (2010), and (iii) argued for Madagascar being connected by land bridges or stepping-stone chains three times in the Cenozoic: 66–60 Mya, 36–30 Mya and 12–5 Mya. The ‘Early Paleocene’ route was thought to account for the lemurs and tenrecs, the Hyperoliidae, Mantellidae and Microhylidae frogs, plus reptiles of the families Boidae, Chamaeleonidae, Gekkonidae, Gerrhosauridae, Scincidae, Typhlopidae, and Xenotyphlopidae. The Eocene–Oligocene causeway was claimed to have facilitated the arrivals of the carnivorans, rodents, and lamprophiid snakes. The ‘Late Miocene’ path was purportedly used by hippopotamuses, crocodiles, *Hemidactylus* geckos and Ptychadenid frogs (notably, mainly semi-aquatic taxa which Masters *et al.* (2021) thought could cross a number of open-water gaps along the trail). Some taxa were not linked to a particular pathway; Opluridae and Podocnemididae were thought to be Gondwanan relicts, while Testudinidae was not accounted for. In response, Ali & Hedges (2022) evaluated the land-bridges part of the proposal using a topological framework that incorporated all of the elements in the three routeways (e.g. Fig. 5). It was shown that just one high-elevation volcanic island existed (in the northern Sakalaves Seamount group with an area of *c.* 220–250 km²; Fig. 5B) and that was in the Early Oligocene (also see Courgeon *et al.*, 2018); by the time of the youngest supposed path it formed an at-sea level carbonate platform (see Fig. 17 in Ali & Hedges, 2022). Notably, the only other offshore area that appears to have been exposed was the Juan de Nova atoll (*c.* 14-km-diameter), and this may have persisted throughout the Cenozoic (also see Delaunay, 2018). In summarising their review, Ali & Hedges (2022, p. 12) stated: ‘As is the case today, the extent of dry land in the Mozambique Channel in the early, middle and late Cenozoic was negligible’.

(4) Assembly of groups reflects the mode of colonisation

Range expansion across land-bridges and over-water dispersal colonisations are predicted to imprint the development of an assemblage differently (see Simpson, 1940). With the use of land bridges, there should be (i) many clades, comprising (ii) a broad sample of the fauna that is present in the source area, and (iii) their arrival times should be ostensibly synchronous (note that there should also be island-to-continent transfers). By contrast, a suite that has been stocked through over-water dispersal events will have (iv) few clades, that together comprise (v) a strongly screened subset of the source assemblage, with (vi) the landings being temporally scattered. Below, these ideas are explored for Madagascar.

III. METHODS

(1) Dating colonisation events using colonisation intervals

Most studies that have examined Madagascar’s colonisation history, whether of single or multiple clades, utilize either the timing of the split with the genetically nearest mainland

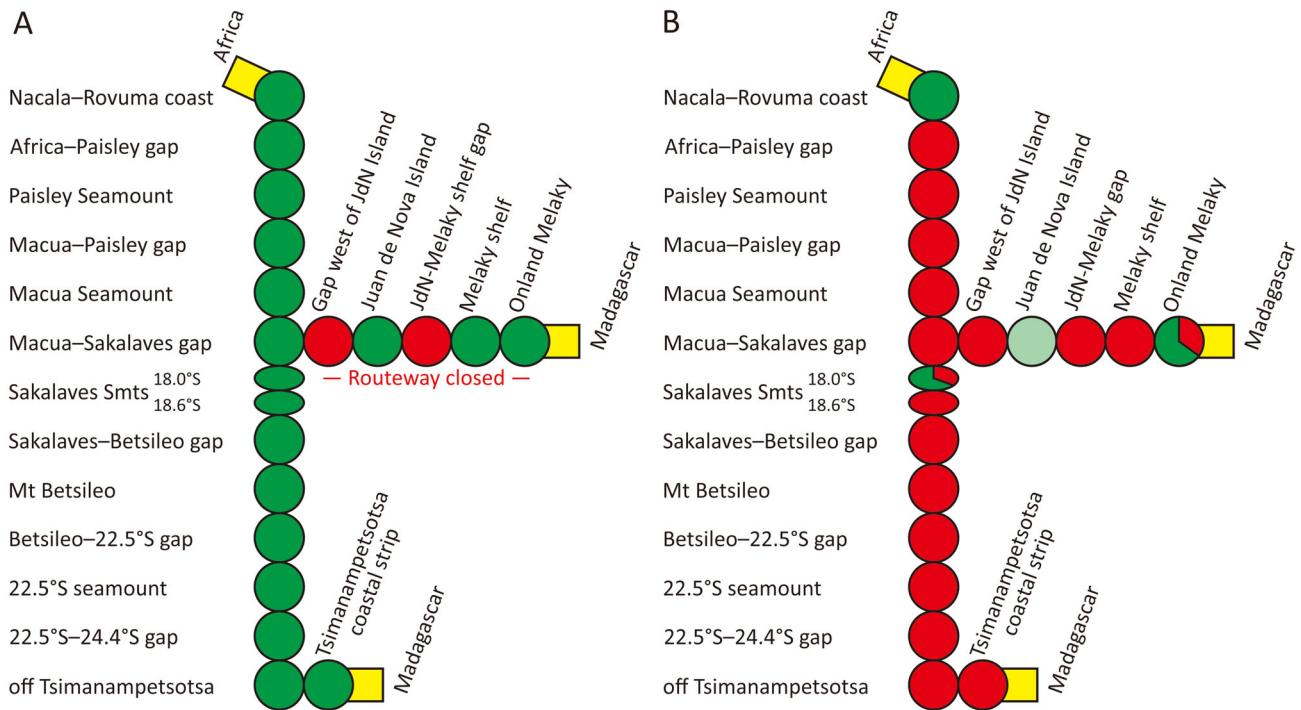


Fig. 5. Evaluation of the land-bridge connectivity schema proposed by Masters *et al.* (2021, 2022) for the Eocene–Oligocene boundary time, 36–30 Mya, based on Ali & Hedges (2022). The hypothesised configuration of Masters *et al.* (2021, 2022) is shown in A, while the likely arrangement, based on Ali & Hedges (2022), is presented in B. In A, green and red circles respectively indicate supposed land and no path. In B, the green, light green and red circles/ellipses correspond to true dry land, low-elevation atoll, and no path. Where sectors formed land for part of the 6-million-year interval, the circles/ellipses are used as clock dials in which 36 and 30 Mya are set at 12 o'clock and the 'pie-slices' reflect the intervals of submergence and exposure.

relative ('stem-age'), or the oldest on-island divergence ('crown-age'). Examples of the former include Nagy *et al.* (2003), Vences *et al.* (2003b), and Crottini *et al.* (2012), whilst the latter was employed by Yoder *et al.* (1996, 2003) and Roos, Schmitz & Zischler (2004). Poux *et al.* (2005) instead defined the colonisation events as falling between the stem-old age and the crown-young age, consistent with biogeographical studies in other regions [e.g. Hedges, 1996; Ali & Hedges, 2021; also see the recent compilation by Antonelli *et al.* (2022) for a large suite of Malagasy animal and plant taxa]. Notably, this provides a maximum and minimum constraint for an arrival that is more robust than the stem or crown ages alone (Fig. 6A–C). Also, it brings to the fore the idea that extinctions on Africa and/or Madagascar will almost certainly have removed the true sister lineages, thereby increasing the stem ages and decreasing the crown ages. Furthermore, for two Malagasy clades it was possible to reduce the 'colonisation interval' using fossil/sub-fossil data (Fig. 6D–F). Actually, in studies involving island faunas, colonisation intervals can also be refined using age dates associated with the formation of the landmass, particularly with volcanic edifices (Fig. 6G), or continental breakup (Fig. 6H). Additionally, regional or global mass extinctions should be considered when a colonisation interval straddles such an event (Fig. 6I), especially the end-Cretaceous mass extinction (e.g. Longrich, Bhullar & Gauthier, 2012; Longrich, Scriberas & Wills, 2016).

(2) Assembling the colonisation profile

The mode of colonisation for an island land-vertebrate assemblage will leave a strong temporal imprint on the extant suite. One way of exploring the effect involves the 'stacking' of the individual colonisation intervals for each of the clades to generate for the assemblage a 'colonisation profile'. Any bumps, troughs, plateaus, rises and falls, etc., that emerge on the generated plot will reflect how the fauna was seeded, in particular if there were conspicuous concentrations and/or reduced influxes of arrivals.

(3) Information sources for each clade's colonisation interval

The clade list below is built around that presented by Crottini *et al.* (2012). However, the main lemurs and the aye-ayes (*Daubentonia*) are separated following Gunnell *et al.* (2018). In the older scheme, the ancestor to the single clade was thought to have arrived in Madagascar between the Late Cretaceous and Middle Eocene (e.g. Poux *et al.*, 2005); with the new phylogeny, the two colonisations took place within the middle to late Cenozoic. The proposal of Gunnell *et al.* (2018) appears to carry weight because it has not been refuted with data-based evidence. Moreover, the scenario shortens the 15- to 20-million-year delay between the main

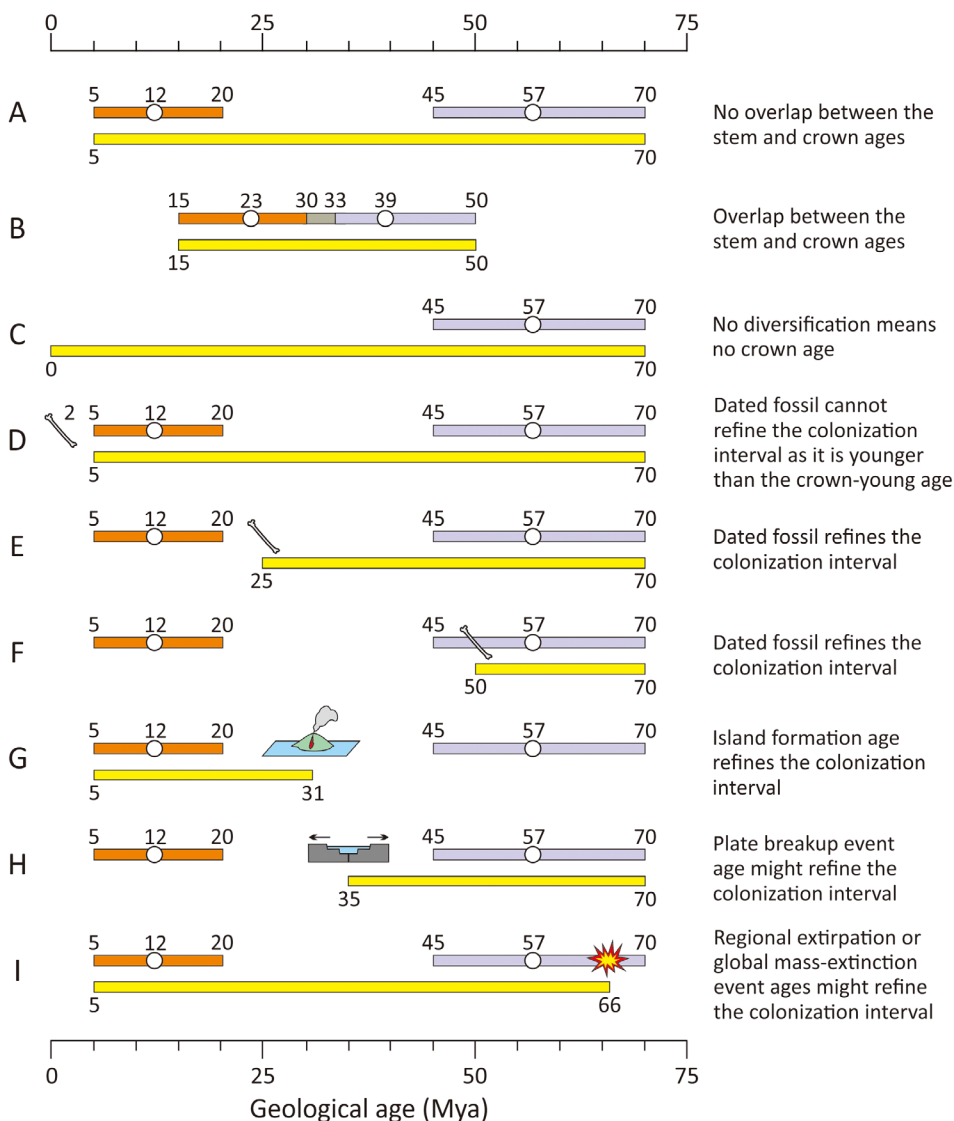


Fig. 6. Schematic diagram showing how ‘colonisation intervals’ are determined for a clade’s arrival on an insular landmass. White circles mark the ages of the stem and crown tree-branch nodes, with the lilac-grey and orange bars respectively indicating the associated uncertainties. The yellow bars denote the colonisation intervals and span the stem-old end to the crown-young end (the temporal limits of a clade’s arrival). For a majority of lineages, there are age data for both the stem and crown (A, B). However, without any evidence for on-island divergence, or at least relevant data, the young end of the colonisation interval is set at 0 Mya (C). In certain cases, colonisation intervals can be refined using ages associated with fossils (D, E, F), landmass-emergences (G), tectonic-plate rifting events (H), and regional extirpations/global mass-extinction events (I).

lemur clade’s colonisation and the start of the explosive radiation that took place in the mid-Cenozoic (Kistler *et al.*, 2015; Herrera & Dávalos, 2016). Crucially, Madagascar in the early Cenozoic must have been prime for biotic diversification; it was a huge island in the temperate-climate belt with, presumably, a multitude of empty or near-empty niches.

Regarding the blindsnakes, the typhlopoids originated on Indigascar (India + Madagascar) and split into an Indian clade (Gerrhopilidae) and a Madagascar clade

(Xenotyphlopidae + Typhlopidae) in the mid-Cretaceous (Vidal *et al.*, 2010). Around the Mesozoic/Cenozoic boundary (66 Mya) the typhlopids diversified globally into four major groups with representatives on Madagascar (*Madatyphlops*), Africa, Eurasia–Australia, and South America–West Indies (Vidal *et al.*, 2010; Hedges *et al.*, 2014). As the relationships of the four were uncertain in that study, the simplest hypothesis is to assume that *Madatyphlops* represents a surviving Malagasy clade of the typhlopoid stock that originated in Madagascar. That *Madatyphlops* is more closely

related to non-Malagasy typhlopids than to *Xenotyphlops* (Xenotyphlopidae) is well established (Vidal *et al.*, 2010; Hedges *et al.*, 2014; Miralles *et al.*, 2018), but this does not contradict the hypothesis because it is expected that a dispersal will leave behind lineages that are their closest relatives.

A subsequent study that focused on deeper relationships in snake evolution (Miralles *et al.*, 2018) included nine additional genes but a much smaller sampling of typhlopoid species (19 versus the 76 in Vidal *et al.*, 2010). It found that *Madatyphlops* was not nested within any of the four geographic clades of typhlopids, but was the closest relative of the African clade, which in turn was the closest relative of the Eurasia–Australian clade. That tree suggested an initial dispersal out of Madagascar and then a reverse colonisation back to Madagascar for typhlopids. However, the first of those two nodes (*Madatyphlops* + Africa clade) has a non-significant bootstrap support value of 55%, leaving *Madatyphlops* essentially in an unresolved polytomy with the African and Eurasian–Australian clades. This single node still creates a ‘nesting’ for *Madatyphlops*, and could be interpreted as a reverse dispersal of typhlopids back to Madagascar, but renders uncertainty as to the source continent. As the study with better taxonomic sampling (Vidal *et al.*, 2010) supports the simpler hypothesis (no dispersals for *Madatyphlops* versus one in Miralles *et al.*, 2018), we consider that *Madatyphlops* and *Xenotyphlops* both represent ancient resident clades of Malagasy typhlopoids until future data show otherwise.

Due to a lack of phylogenetic data, three gecko genera, *Ebenavia*, *Geckolepis* and *Paragehyra*, were left out of the analysis of Crottini *et al.* (2012). Concerning *Ebenavia*, more recent work by Hawlitschek *et al.* (2017, 2018) confirmed the suspicion of Crottini *et al.* (2012) that this genus was derived from *Paroedura*, indicating a single colonisation from Africa. Those investigations also revealed a complicated biogeographical history with *Ebenavia* colonisations of the nearby Comoros Islands (Fig. 1), plus Pemba off mainland Tanzania with, potentially, back-transfers to Madagascar. However, as the present synthesis is focused on land-vertebrate colonisations from the main continents to Madagascar, not back-and-forth events to and from nearby landmasses, we omit them from our investigation but still include the origin of the clade from Africa as an event, labelling it ‘*Paroedura–Ebenavia*’. Concerning the *Geckolepis* and *Paragehyra* geckos, molecular data have been published for both groups (Lemme *et al.*, 2013; Scherz *et al.*, 2017; Crottini *et al.*, 2015). However, none of the studies included timetrees, nor did they propose colonisation times, thus we cannot incorporate them into the present analysis.

Information sources of the node-age determinations for the various clades are presented below (see also Table 1), with ‘stem’ and ‘crown’ abbreviated to *st.* and *cr.*, while the frequently occurring reference for *TimeTree* is Kumar *et al.* (2017). The assemblage is separated into reptiles, land mammals and amphibians, and the number codes, respectively 1–18, 19–23 and 24–28, are applied based on the stem-old ages, from high to low: 1, *Erymnochelys*

madagascariensis side-necked turtle: *st.* Vargas-Ramírez, Castaño-Mora & Fritz (2008) and a fossil age based on Gaffney & Forster (2003), see also Pérez-García, de Lapparent de Broin & Murelaga (2017); 2, typhlopoid snakes: *st.* and *cr.* Vidal *et al.* (2010); 3, boid snakes: *st.* and *cr.* *TimeTree*; 4, *Uroplatus* geckos: *st.* and *cr.* *TimeTree*; 5, *Lygodactylus* geckos: *st.* and *cr.* Gippner *et al.* (2021); 6, *Phelsuma* geckos: *st.* and *cr.* *TimeTree*; 7, *Paroedura–Ebenavia* geckos: *st.* and *cr.* *TimeTree*; 8, *Brookesia–Palleon* chamaeleons: *st.* and *cr.* Tolley, Townsend & Vences (2013), see also Glaw, Hawlitschek & Ruthensteiner (2013); 9, Malagasy iguanas (Opluridae): *st.* and *cr.* Welt & Raxworthy (2022); 10, zonosaurine lizards: *st.* and *cr.* *TimeTree*; 11, scincid skinks: *st.* and *cr.* *TimeTree*; 12, *Blaesodactylus* geckos: *st.* and *cr.* *TimeTree*; 13, *Furcifer–Calumma* chamaeleons: *st.* and *cr.* Tolley *et al.* (2013); 14, *Trachylepis* skinks: *st.* and *cr.* Lima *et al.* (2013); 15, pseudoxyrhophine snakes: *st.* and *cr.* *TimeTree*; 16, *Astrochelys–Pyxis* tortoises: *st.* and *cr.* Kehlmaier *et al.* (2019); 17, psammophine snakes: *st.* *TimeTree*, no crown; 18, *Hemidactylus mercatorius* gecko: *st.* Crottini *et al.* (2012), no crown; 19, tenrecs: *st.* and *cr.* Everson *et al.* (2016); 20, main lemurs: *st.* and *cr.* Gunnell *et al.* (2018); 21, aye-ayes: *st.* and *cr.* Gunnell *et al.* (2018) and a sub-fossil age based on Simons (1994) and Godfrey, Jungers & Schwartz (2006); 22, nesomyid rodents: *st.* and *cr.* Poux *et al.* (2005); 23, euplerid carnivorans: *st.* and *cr.* Nyakatura & Bininda-Emonds (2012); 24, mantellid frogs: *st.* and *cr.* *TimeTree*; 25, cophyline–scaphiophrynine frogs: *st.* and *cr.* *TimeTree*; 26, dyscophine frogs: *st.* and *cr.* *TimeTree*; 27, hyperoliid frogs: *st.* and *cr.* *TimeTree*; 28, Ptychadenid frogs: *st.* and *cr.* Vences *et al.* (2004) and Crottini *et al.* (2012). Unfortunately, Madagascar's Cenozoic fossil record is no older than about 80 kya (Late Pleistocene; Samonds, 2007), so it is not feasible to greatly refine practically all of the colonisation intervals using this type of information (although see Clades #1 and #21 in Table 1).

IV. RESULTS

(1) Colonisation intervals for Madagascar's land vertebrates

The colonisation intervals for Madagascar's 28 land-vertebrate clades are shown in Fig. 7A–C. The accompanying line plot (Fig. 7D) highlights the sizable range in the differences between some of the stem and crown ages. In some cases, the split with a mainland relative was followed by an almost immediate diversification event on Madagascar (e.g. *Furcifer–Calumma* chamaeleons, #13; cophyline–scaphiophrynine frogs, #25) whereas with others there was major delay (boid snakes, #3; Malagasy iguanas, #9; dyscophine frogs, #26). Importantly, this emphasises the limitations of determining a clade's arrival based solely on its stem age or crown age (Fig. 7D). Another noteworthy issue is that just five of the clades (podocnemid turtles, #1; typhlopoid snakes, #2; boid snakes, #3; *Uroplatus* geckos, #4; *Lygodactylus* geckos, #5) have colonisation intervals that extend beyond 75 Mya; the bulk of the assemblage comprises groups whose ancestors appear

Table 1. Colonisation-interval data for Madagascar's land-locked vertebrate clades. All of the ages are in million years ago (Mya). CIMP, colonisation interval mid-point.

Clade #	Reptiles	Information sources	Crown			Stem			CIMP	Comment
			Age	Low age	High age	Age	Low age	High age		
1	<i>Eymnocheilus madagascariensis</i>	Gaffney & Forster (2003); Vargas-Ramirez <i>et al.</i> (2008)	*69.1	66.0	72.1	78.5	25.9	131.1	98.6	*Young age bound is based on fossil material
2	Typhlopoid snakes	Vidal <i>et al.</i> (2010)	96.0	80.9	112.0	107.0	90.9	122.0	101.5	
3	Boid snakes	TimeTree (Kumar <i>et al.</i> , 2017)	23.0	16.5	29.5	79.7	69.8	89.7	53.1	
4	<i>Uroplatus geckos</i>	TimeTree (Kumar <i>et al.</i> , 2017)	51.0	42.7	59.4	85.0	80.5	89.6	66.2	
5	<i>Lygodactylus</i> geckos	Gippner <i>et al.</i> (2021)	46.7	34.4	60.5	61.5	48.1	77.3	55.9	
6	<i>Phelsuma</i> geckos	TimeTree (Kumar <i>et al.</i> , 2017)	39.5	34.6	44.4	66.5	58.5	74.5	54.6	
7	<i>Paroedura-Ebenavia</i> geckos	TimeTree (Kumar <i>et al.</i> , 2017)	42.4	33.7	51.1	67.5	60.6	74.4	54.1	
8	<i>Brookesia-Palleon</i> chamaeleons	Tolley <i>et al.</i> (2013); Glaw <i>et al.</i> (2013)	59.0	52.0	66.0	65.0	57.0	73.0	62.5	
9	Malagasy iguanas (Opluridae)	Welt & Raxworthy (2022)	19.0	7.5	33.0	59.2	48.6	72.9	40.2	
10	Zonosaurine lizards	TimeTree (Kumar <i>et al.</i> , 2017)	39.8	27.6	52.0	57.2	42.3	72.2	49.9	
11	Scincid skinks	TimeTree (Kumar <i>et al.</i> , 2017)	52.5	46.8	58.2	60.7	51.4	70.0	58.4	
12	<i>Blaesodactylus</i> geckos	TimeTree (Kumar <i>et al.</i> , 2017)	32.9	23.1	42.7	47.8	41.6	54.1	38.6	
13	<i>Fureifer-Calumma</i> chamaeleons	Tolley <i>et al.</i> (2013)	46.0	40.0	52.0	47.0	40.0	54.0	47.0	
14	<i>Trachylepis</i> skinks	Lima <i>et al.</i> (2013)	36.0	30.0	42.0	43.0	37.0	50.0	40.0	
15	Pseudoxyrhophine snakes	TimeTree (Kumar <i>et al.</i> , 2017)	35.5	26.2	44.8	41.6	35.4	47.8	37.0	
16	<i>Astrocheilus-Pyxis</i> tortoises	Kehlmaier <i>et al.</i> (2019)	26.4	21.5	32.0	28.7	23.2	34.2	27.9	
17	Psammophine snakes	TimeTree (Kumar <i>et al.</i> , 2017)	0.0	0.0	0.0	23.1	18.2	28.0	14.0	No crown time available
18	<i>Hemidactylus mercatorius</i>	Crottini <i>et al.</i> (2012)	0.0	0.0	0.0	4.0	1.0	10.0	5.0	

Clade #	Land-locked mammals	Information sources	Crown			Stem			CIMP	Comment
			Age	Low age	High age	Age	Low age	High age		
19	Tenrecs	Everson <i>et al.</i> (2016)	34.9	29.6	41.8	47.5	40.7	55.6	42.6	
20	Lemurs	Gunnell <i>et al.</i> (2018)	20.0	14.7	25.8	41.0	36.2	46.0	30.4	
21	Aye-ayes	Godfrey <i>et al.</i> (2006); Gunnell <i>et al.</i> (2018)	*0.001	0.001	0.001	28.0	21.0	35.8	17.9	*Young age bound is based on sub-fossil material
22	Nesomyidae	Poux <i>et al.</i> (2005)	20.1	15.4	25.7	23.5	18.2	29.6	22.5	
23	Eupleridae	Nyakatura & Bininda-Emonds (2012)	18.0	16.8	19.3	21.3	19.3	23.4	20.1	

(Continues on next page)

Table 1. (Cont.)

Clade #	Amphibians	Information sources	Crown			Stem			CIMP	Comment
			Age	Low age	High age	Age	Low age	High age		
24	Mantellid frogs	Time Tree (Kumar <i>et al.</i> , 2017)	52.5	47.6	57.5	69.8	65.2	74.3	61.0	
25	Cophylinae–scaphiophryninae frogs	Time Tree (Kumar <i>et al.</i> , 2017)	62.8	55.6	70.1	66.3	59.8	72.7	64.2	
26	Dyscophinae frogs	Time Tree (Kumar <i>et al.</i> , 2017)	21.4	18.6	24.1	60.7	54.9	66.6	42.6	
27	Hyperoliid frogs	Time Tree (Kumar <i>et al.</i> , 2017)	19.4	14.4	24.5	37.5	30.4	44.6	29.5	
28	Ptychoadenid frogs	Vences <i>et al.</i> (2004); Croft <i>et al.</i> (2012)	3.4	3.4	3.4	8.0	2.0	20.0	11.7	

to have arrived after the end-Cretaceous mass extinction (Fig. 7A–C). Of all groups, the podocnemid turtles (#1) and typhlopoid snakes (#2), are the only ones that exhibit deep-time divergences that could be related to key Gondwana break-up events. Concerning the latter, the initial time of separation (182–90.9 Mya), isolating Typhlopoidea and Leptotyphlopoidea, straddles the period of rifting between East and West Gondwana (Vidal *et al.*, 2010). A second divergence (122–80.9), which split Typhlopidae and Gerrhopilidae, corresponds to the break-up of the palaeolandmass of Indigascar into Madagascar and Seychelles–India (Vidal *et al.*, 2010), respectively. As our study's focus is the origin of clades in Madagascar, not earlier events, we consider only the second vicariance episode.

(2) Characteristics of colonisation intervals

In Fig. 8A, each of the colonisation intervals depicted in Fig. 7A–C is plotted as colonisation interval mid-point (CIMP) against interval age range. The accompanying graph (Fig. 8B), presents best-fit lines for all of the stem-old and the crown-young age dates, with best-fit lines calculated: $cr\text{-young} = (0.818 \times \text{CIMP}) - 7.823$, $R^2 = 0.784$; $st\text{-old} = (1.182 \times \text{CIMP}) + 7.823$, $R^2 = 0.883$ (in both cases $N = 26$, not 28). The two equations are used in Sections IV.3–5 to generate simulated colonisation profiles. In both plots, the two oldest clades, the podocnemid turtles and typhlopoid snakes, stand out substantially from the others in age, although both sit close to the relevant best-fit lines for the other taxa. As the colonisation intervals for the two groups correspond with an 'origin by vicariance' (Gaffney & Forster, 2003; Vidal *et al.*, 2010), both clades are not considered further in the analyses.

(3) Comparison of colonisation profiles among groups

Four colonisation profiles are shown in Fig. 9A–D: reptiles, land mammals, amphibians and the three groups combined. The reptile data are of most interest, as the silhouettes for the other two groups are comparatively subdued; each has relatively few clades. Notably, the combined plot (and the reptile plot) shows a distinctive broad peak between 73 and 16 Mya, the significance of which will be explored in Section IV.5.

The first part of our evaluation investigates the degree of smoothing that occurs during the derivation of the stem-old and crown-young equations in Fig. 8B. Figure 10A plots the 'actual' data (grey-shaded region, red line) together with a 'back-modelled' profile that uses the calculated CIMP values (blue line; these are shown in Fig. 7). Using a simple measure of fit [based on $(C_{\text{tot}} - C_{\text{nm}})/C_{\text{tot}}$, where C_{tot} is the total number of cells associated with the 'actual' data, and C_{nm} is the number of non-matching cells], the match is 0.835; clearly, some of the system's inherent complexity is being lost. To acknowledge this, for most simulation assessments we present both lines and report the two fit values.

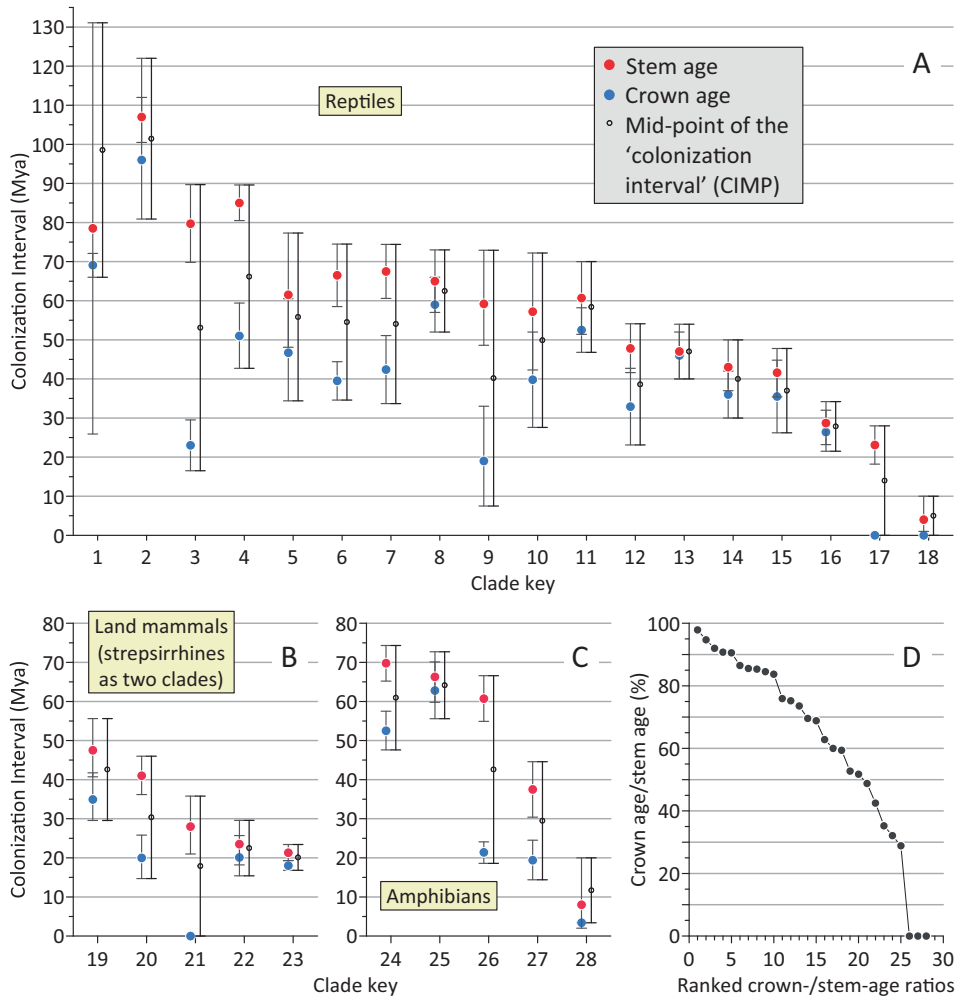


Fig. 7. Colonisation interval data for Madagascar's land-bound vertebrate clades: reptiles (A), mammals (B) and amphibians (C). (D) Line plot showing the clade crown age/stem age ratio as a percentage. Clade key: 1, *Erymnochelys madagascariensis* side-necked turtle; 2, typhlopoid snakes; 3, boid snakes; 4, *Uroplatus* geckos; 5, *Lygodactylus* geckos; 6, *Phelsuma* geckos; 7, *Paroedura–Ebenavia* geckos; 8, *Brookesia–Palleon* chamaeleons; 9, Malagasy iguanas (Opluridae); 10, zonosaurine lizards; 11, scincid skinks; 12, *Blaesodactylus* geckos; 13, *Furcifer–Calumma* chamaeleons; 14, *Trachylepis* skinks; 15, pseudoxyrrophine snakes; 16, *Astrochelys–Pyxis* tortoises; 17 psammophine snakes; 18, *Hemidactylus mercatorius* gecko; 19, tenrecs; 20, main lemurs; 21, aye-ayes; 22, nesomyid rodents; 23, euplerid carnivorans; 24, mantellid frogs; 25, cophyline-scapthiophrynine frogs; 26, dyscophine frogs; 27, hyperoliid frogs; 28, Ptychadenid frogs. Note that some clades do not have crown ages and these are set at 0 Ma [psammophine snakes, *Hemidactylus mercatorius* (gecko)]; the aye-aye clade has a very young crown age of *c.* 1 kya based on subfossil material from *Daubentonia robusta* (see Section III.3). The uncertainties regarding the crown age for the Ptychadenid frogs are zero and error bars are not plotted.

However, note that the differences between the latter are typically just a few per cent. A chi-squared test was used to evaluate a variety of simulated colonisation profiles against either the 'actual' or 'back-modelled' profiles (Table 2) for data binned at 1-million-year (Myr) intervals.

(4) Generating simulated colonisation profiles

To compare the observed data with biogeographic models, we generated simulated colonisation profiles using the equations presented in the previous section. Hence, it is possible to

construct plots using the CIMP values that, to a first approximation, mimic constant-rate- (Fig. 10B), random- (Fig. 10C–E) and concentrated-arrival (Fig. 10F) scenarios. We used 26 clades from our Madagascar assemblage compilation (the typhlopoid snakes and podocnemid turtles were excluded) in these simulations. One potential issue is related to the back-modelling of the 'actual' profile. If the scatter associated with *cr.*-young and *st.*-old ages is not too great, and the data set is sufficiently large, the 'actual' and the 'back-modelled' profiles should be similar (Fig. 10A).

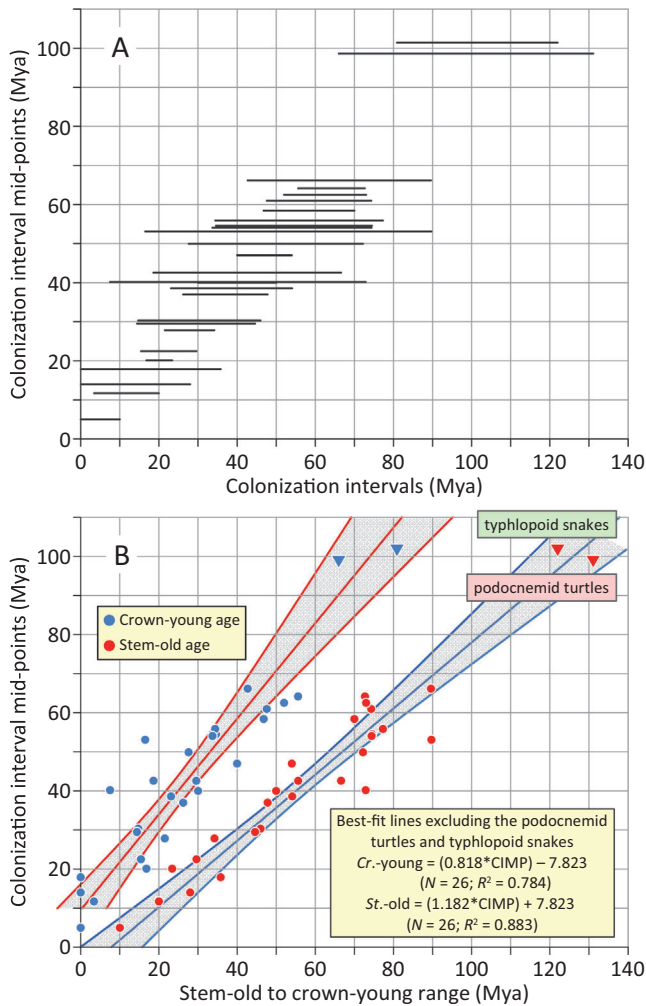


Fig. 8. (A) Individual colonisation intervals plotted against their midpoint value. (B) Best-fit lines through the stem-old ages and the crown-young ages are used to generate simulated colonisation profiles (see Section IV.3–5). CIMP, colonisation interval mid-point; *Cr.*, crown; *St.* stem.

(5) Comparing the data with different biogeographic models

In Sections IV.5a–d, we compare the Madagascar colonisation profile with different biogeographic models, including those based upon the ideas of McCall (1997) and Masters *et al.* (2021, 2022). Unfortunately, it is not possible to carry out a statistical comparison of the colonisation model developed here with those of McCall (1997) and Masters *et al.* (2021, 2022) because those studies considered only a fraction of the land-vertebrate clades incorporated in our review. Specifically, McCall (1997) focused exclusively on the land-mammal assemblage, and thus overlooked reptiles and amphibians. Masters *et al.* (2021, 2022) used only four clades of the possible five each for amphibians and land-mammals, and their reptile catalogue was limited to nine clades out of a possible 18.

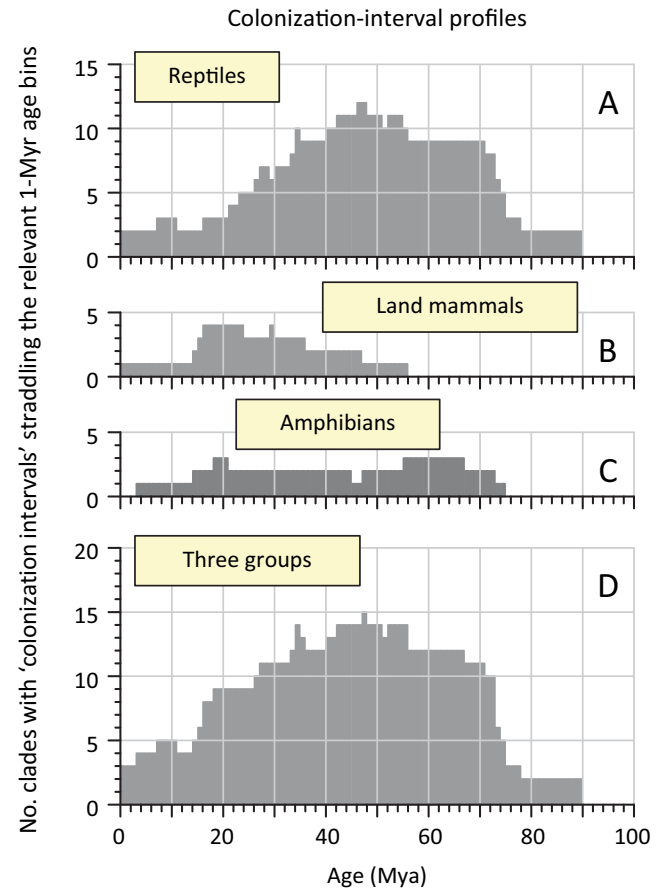


Fig. 9. Colonisation profiles for the various land-vertebrate groups on Madagascar: reptiles (A), mammals (B), amphibians (C), and the three groups combined (D). In all cases, each clade is counted in all of the 'bins' it can occupy, each bin being 1 Myr.

However, we are able to assess whether our data fit the general features of the biogeographic models proposed in these studies, across all clades, by using simulated colonisation profiles.

(a) Comparing the data with a constant rate model

First, we generated a 'constant-rate' model (Fig. 10B) in which the 26 clades were modelled with CIMPs every 2.7 Myr, starting at 68.85 Mya and ending at 1.35 Mya. Here, the maximum stem-old age is 89.2 Mya, which is close to the maximum value in the 'actual' data set, 89.7 Mya (Clade #3). The resulting profile is remarkably similar to the 'actual' data (fit = 0.810) and 'back-modelled' data (fit = 0.784); the chi-squared test *P*-values of 0.99 and 0.95 respectively, indicating a very close match (see Table 2). This suggests that the observed colonisation record (Figs 10A, 9D) is unlikely to be the result of one or more focused influxes; its humped shape is better explained by a steady build-up of clades combined with the more recent colonisation intervals shortening (see Fig. 8B). Also note the difference in the

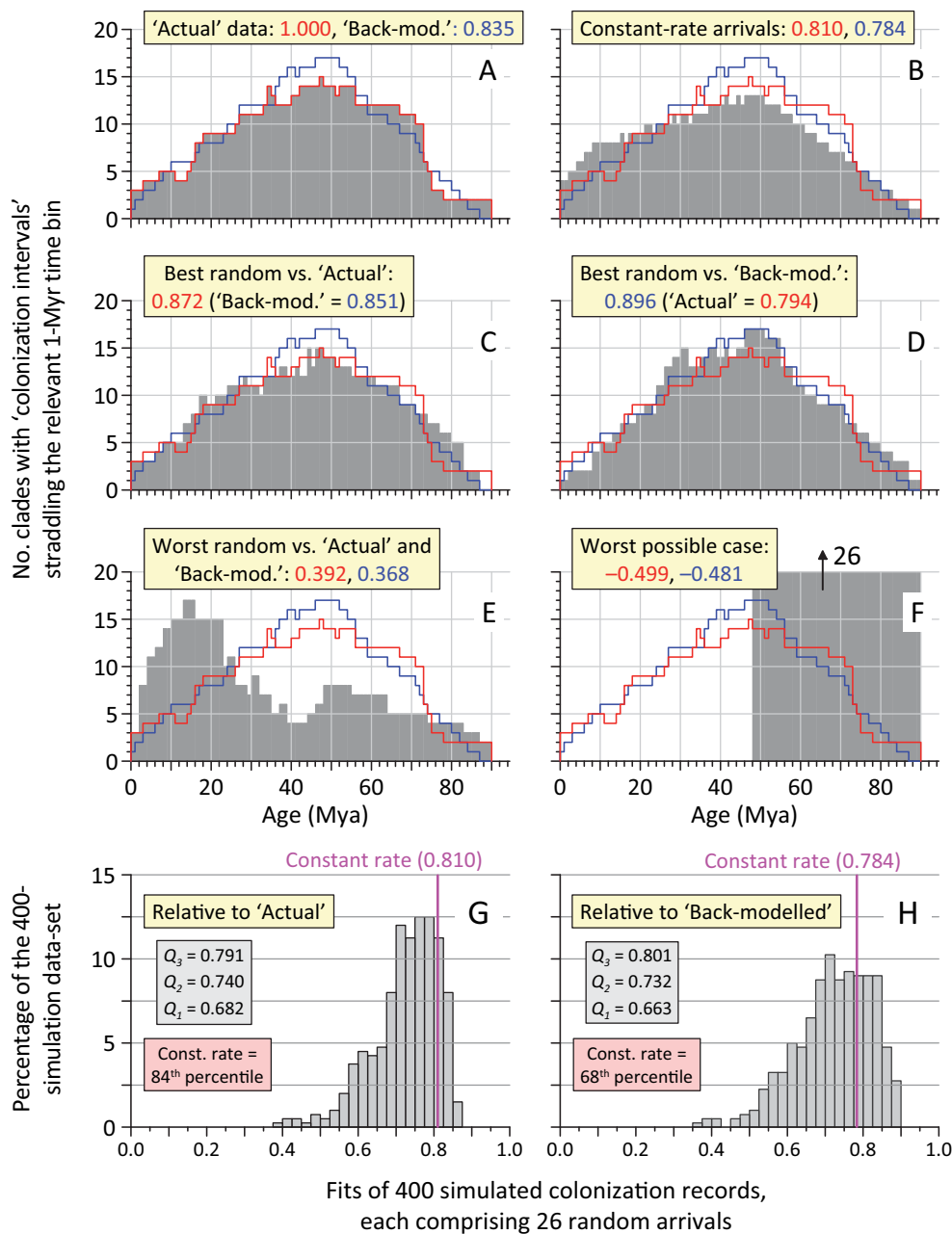


Fig. 10. Initial evaluation of the Madagascar land-vertebrate colonisation data. (A) The colonisation profile associated with the 'actual' data (grey shaded region and red line) and with the 'back-modelled' data (blue line) (see Section IV.3). The fit values, in red and dark blue above the plots, provide a simple measure of the match (see Section VI.3). (B–F) Comparisons of the profiles shown in A with results from various simulations (grey regions). In B, a colonisation occurs every 2.7 Myr starting at 68.85 Mya and ending at 1.35 Mya (26 clades), a scenario that is termed 'constant rate'. In C–E, the plots show random simulations (from a total of 400), with 26 arrivals in any one of the 26 available instants between 68.85 and 1.35 Mya. Of these, C and D are the best-fit simulations relative to the 'actual' and 'back-modelled' colonisation profiles, while E is the worst fit for both the 'actual' and 'back-modelled' profiles. The worse-case scenario, F, would be if all 26 arrivals took place at 68.85 Mya, and here both of the fits would be negative. The overall distributions of fits relative to the 'actual' and 'back-modelled' values are shown in G and H respectively.

modelled plot silhouette from the 'actual' and 'back-modelled' lines for the interval 16–0 Mya. The lower values for the 'actual' and 'back-modelled' data may reflect the switch

in regional ocean circulation that Ali & Huber (2010) suggested took place 20–15 Mya that would have made it more difficult for vegetation rafts to reach Madagascar from Africa.

Table 2. Statistical data from comparisons of the simulations with the ‘actual’ and ‘back-modelled’ data. n is the number of 1-million-year (Myr) age bins associated with each simulation test. The associated fit values are listed towards the right-hand side of the table. The right-hand column lists the relevant figure; a few are not depicted (ND). Model types: ‘back-modelled’, simulations with data modelled using the equations in Fig. 8B applied to the ‘actual’ CIMP values (listed in Table 1); constant rate, a clade arrives every 2.7 Myr from 68.85 to 1.35 Mya; mid-Cenozoic land bridge ‘perfect’, all 26 arrivals take place between 45 and 26 Mya at equally spaced intervals of 760 kyr; notation $x:y:z$ indicates number of species arriving in a three-panel land-bridge model, e.g. 8:9:9 denotes eight colonisations in the Late Miocene, nine in the Eocene–Oligocene, and nine in the Early Paleocene (see Section-IV.5.d), ‘perfect’ indicates one arrival taking place at each available, and equally spaced, colonisation instant.

Model to be tested	Comparison	χ^2	P -value	n	Fit	Fig.
‘back-modelled’	‘actual’	38.2	1.000	90	0.835	10A
constant rate	‘actual’	59.5	0.993	90	0.810	10B
constant rate	‘back-modelled’	66.1	0.945	87	0.784	10B
mid-Cenozoic perfect	‘actual’	580.5	<0.001	90	0.236	11A
mid-Cenozoic perfect	‘back-modelled’	505.2	<0.001	87	0.301	11A
mid-Cenozoic best fit ‘actual’	‘actual’	495.2	<0.001	90	0.328	11C
mid-Cenozoic best fit ‘back-modelled’	‘back-modelled’	410.5	<0.001	87	0.433	11D
8:9:9 perfect	‘actual’	207.0	<0.001	90	0.685	12A
9:8:9 perfect	‘actual’	248.2	<0.001	90	0.641	12D
9:9:8 perfect	‘actual’	215.9	<0.001	90	0.647	12G
8:9:9 perfect	‘back-modelled’	200.5	<0.001	87	0.673	12A
9:8:9 perfect	‘back-modelled’	258.6	<0.001	87	0.626	12D
9:9:8 perfect	‘back-modelled’	238.1	<0.001	87	0.636	12G
5:12:9 perfect	‘back-modelled’	115.0	0.020	87	0.752	13H
5:11:10 perfect	‘back-modelled’	127.2	0.003	87	0.747	13I
4:12:10 perfect	‘back-modelled’	119.5	0.010	87	0.756	13O
5:10:11 perfect	‘actual’	224.7	<0.001	90	0.771	13J
4:11:11 perfect	‘actual’	224.2	<0.001	90	0.778	13P
4:10:12 perfect	‘actual’	278.8	<0.001	90	0.770	13Q
4:10:12 best fit	‘actual’	249.5	<0.001	90	0.786	14Q
4:11:11 best fit	‘actual’	199.8	<0.001	90	0.790	14N
5:10:11 best fit	‘actual’	186.8	<0.001	90	0.790	14K
5:12:9 best fit	‘back-modelled’	105.4	0.076	87	0.759	14C
5:12:9 best χ^2	‘back-modelled’	99.7	0.149	87	0.753	ND
Note ¹ : 10 from 100 simulations with P -values ≥ 0.05 , but all <0.15					≥ 0.747	
5:11:10 best fit	‘back-modelled’	116.0	0.017	87	0.768	14F
5:11:10 best χ^2	‘back-modelled’	101.0	0.129	87	0.763	ND
Note ² : 2 from 100 simulations with P -values ≥ 0.05 , but each <0.13					≥ 0.763	
4:12:10 best fit	‘back-modelled’	104.3	0.087	87	0.780	14I
4:12:10 best χ^2	‘back-modelled’	99.9	0.145	87	0.767	ND
Note ³ : 14 from 100 simulations with P -values ≥ 0.05 , but all <0.15					≥ 0.749	

(b) Comparing the data with a stochastic rate model

To investigate in more detail the effects of different random arrival rates, 400 simulations were generated with fits for each calculated relative to the ‘actual’ and ‘back-modelled’ profiles. The absolute best fits were slightly better than the ‘constant rate’ model, with values of 0.872 (Fig. 10C) and 0.896 (Fig. 10D) respectively; the worst fits were <0.4 (Fig. 10E). Note that the worst possible case would be if all 26 arrivals took place at 68.85 Mya, and would result in negative fit values (Fig. 10F; incidentally, equating to a 1 in $>10^{36}$ chance). Figure 10G,H provides an overview of the distributions of fits relative to the ‘actual’ (Fig. 10G) and ‘back-modelled’ profiles (Fig. 10H). These plots show that between one-sixth and one-third of all random arrival scenarios would generate fits that are better than or equal to the ‘constant rate’ scenario, depending on whether the comparison is with the ‘actual’ or ‘back-modelled’ data.

(c) Comparing the data with a mid-Cenozoic land-bridge model

To test the mid-Cenozoic land-bridge scenario proposed by McCall (1997), we modelled the 26 arrivals as taking place between 45 and 26 Mya (Fig. 11). Here, a ‘perfect’ arrivals sequence, comprises one colonisation every 760 kyr. The results show a prominent, slightly asymmetrical, flat-topped peak that is centred on 28–38 Mya (Fig. 11A); the fits relative to the ‘actual’ and ‘back-modelled’ profiles were only 0.236 and 0.301 respectively (Table 2). From a suite of 400 random-arrival simulations that span 45–26 Mya, Fig. 11B–D presents the most extreme examples. The plots of fits in Fig. 11E, F show that the means of the fit values relative to the ‘actual’ profile is 0.222 ($\sigma = 0.0407$) and to ‘back-modelled’ 0.294 ($\sigma = 0.0484$). In all cases, the chi-squared tests gave $P < 0.001$ (Table 2). Thus, we reject the speculative McCall (1997)-based proposal that the Malagasy land-bound vertebrate assemblage results from a Middle Eocene through Late Oligocene ‘invasion’.

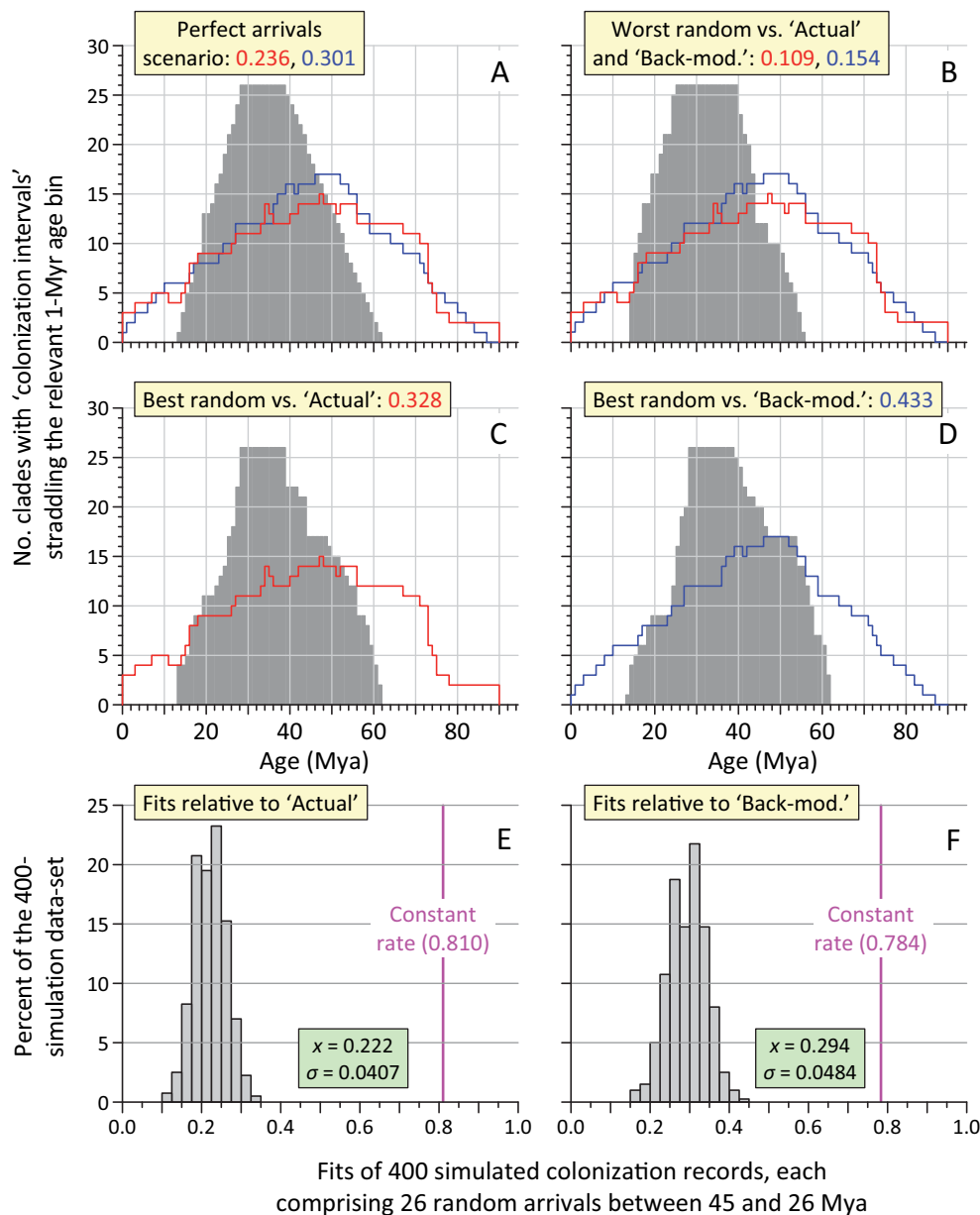


Fig. 11. Evaluation of a mid-Cenozoic land-bridge model in which all arrivals take place between 45 and 26 Mya. (A) ‘Perfect’ arrivals scenario where a colonisation takes place every 760 kyr. (B–D) Worst and best fits results from 400 random simulations. (E, F) Overview of the distributions of fits. Other details are as described in Fig. 10.

(d) Comparing the data with a three-period land-bridge model

Masters *et al.* (2021, 2022) argued that concentrations of colonisations took place at 66–60, 36–30 and 12–5 Mya as a result of Madagascar and Africa potentially being linked at those times by causeways or arrays of closely spaced islands. To investigate this suggestion, a suite of simulations was generated to explore the outcomes of approximately equal numbers of arrivals occurring in each of the three time-windows. Here we use the notation style 10:8:6 to indicate 10 colonisations in the Late Miocene, eight in the Eocene–Oligocene and six in the Early Paleocene. Thus, we ran simulations for 8:9:9, 9:8:9 and 9:9:8 colonisations. In the ‘perfect’ arrival scenarios, one

arrival took place at each available, and equally spaced, colonisation instant within each of the three windows. Conspicuous features of the ‘perfect’ arrival simulation graphs (Fig. 12A,D, G) are the three plateaus, with spikes at *c.* 45 Mya (caused by the colonisation intervals of the Early Paleocene and Eocene–Oligocene windows having a small amount of overlap), and the small troughs at *c.* 16 Mya. We then ran 100 simulations of different arrival patterns during these colonisation windows, and the fits for these are plotted in Fig. 12B,C,E,F,H,I. These fit values are again rather low (typically 0.60–0.66); chi-squared tests comparing the ‘actual’ and ‘back-modelled’ data yielded $P < 0.001$ in all cases (Table 2), indicating that

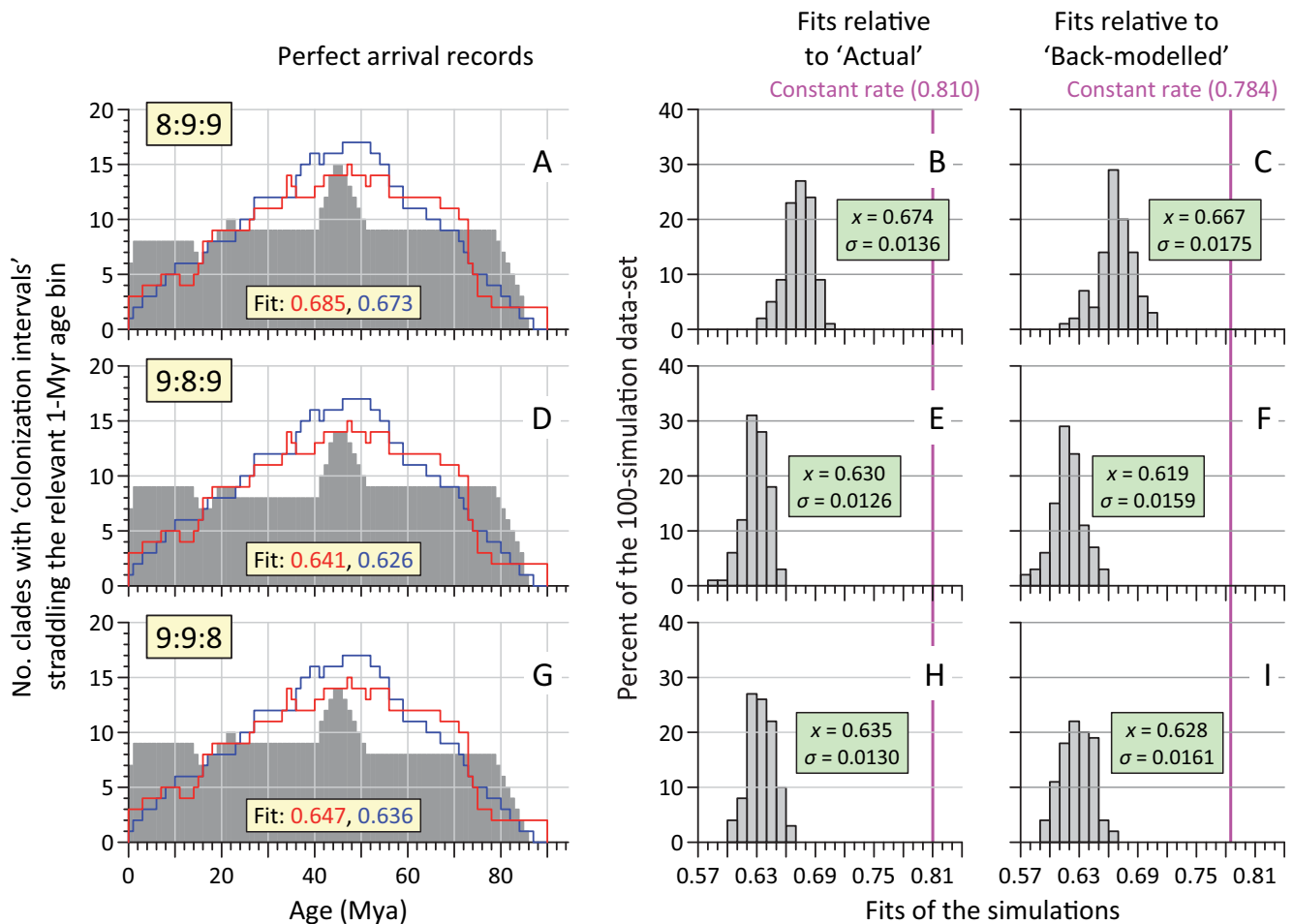


Fig. 12. Evaluation of the multiple land-bridge model, with arrivals in the intervals 66–60, 36–30 and 12–5 Mya, with similar numbers of incoming clades during each of the time windows. The notation 8:9:9: indicates eight arrivals in the youngest interval and nine each in the middle and oldest intervals. The plots in the left-hand column represent ‘perfect’ arrival scenarios (one arrival at each of the available, and equally spaced, colonisation instants within the three windows). The middle column shows the general distribution of the fits for each scenario, each based on 100 simulations, relative to the ‘actual’ data. The right-hand column shows these fits relative to the ‘back-modelled’ data. For reference, the two lines denoting the fit values for the ‘constant-rate’ model are also included. Other details are as described in Fig. 10.

this suite of scenarios can be rejected as explanations for the data.

From Fig. 12, it is clear that better fits would result from higher levels of colonisation in the Early Paleocene and Eocene–Oligocene windows and lower ones in the Late Miocene. We thus generated a suite of simulations in which the Late Miocene interval contained between six and three colonisations and the other two windows had incrementally varied proportions of the remaining events (Fig. 13; all are ‘perfect arrival’ simulations). Here, the associated plateaus are more obvious than in the previous modelling (Fig. 12), often sitting at three different levels, with the best fits (0.770–0.778 relative to ‘actual’ and 0.747–0.756 against the ‘back-modelled’ profile) occurring for four or five arrivals in the Late Miocene window and approximately equal arrivals for the two earlier periods (Fig. 13H–J,O–Q; Table 2). Figure 14 illustrates the variability associated with

the simulated scenarios. Importantly, for all simulations within the best three ensembles as compared with the ‘actual’ profiles, 5:10:11 (Fig. 14J), 4:11:11 (Fig. 14M) and 4:10:12 (Fig. 14P), $P < 0.001$ (Table 2), thus indicating that this suite of scenarios can be rejected as explanations for the data. However, for a small number of simulations within the best three ensembles as compared with the ‘back-modelled’ profiles, [5:12:9 (10 simulations), 5:11:10 (two simulations) and 4:12:10 (14 simulations)], P -values ranged from ≥ 0.05 to < 0.15 (χ^2 range 100–110; Table 2), indicating that this subset of scenarios cannot be rejected as explanations for the data. However, a comparison of ‘constant rate’ with ‘back-modelled’ data yielded a P -value of 0.95 (Table 2). Therefore, the proposal that the Malagasy land-bound vertebrate suite could have resulted from focused influxes of taxa in the early, middle and late Cenozoic appears less likely than a ‘constant rate’ arrivals model.

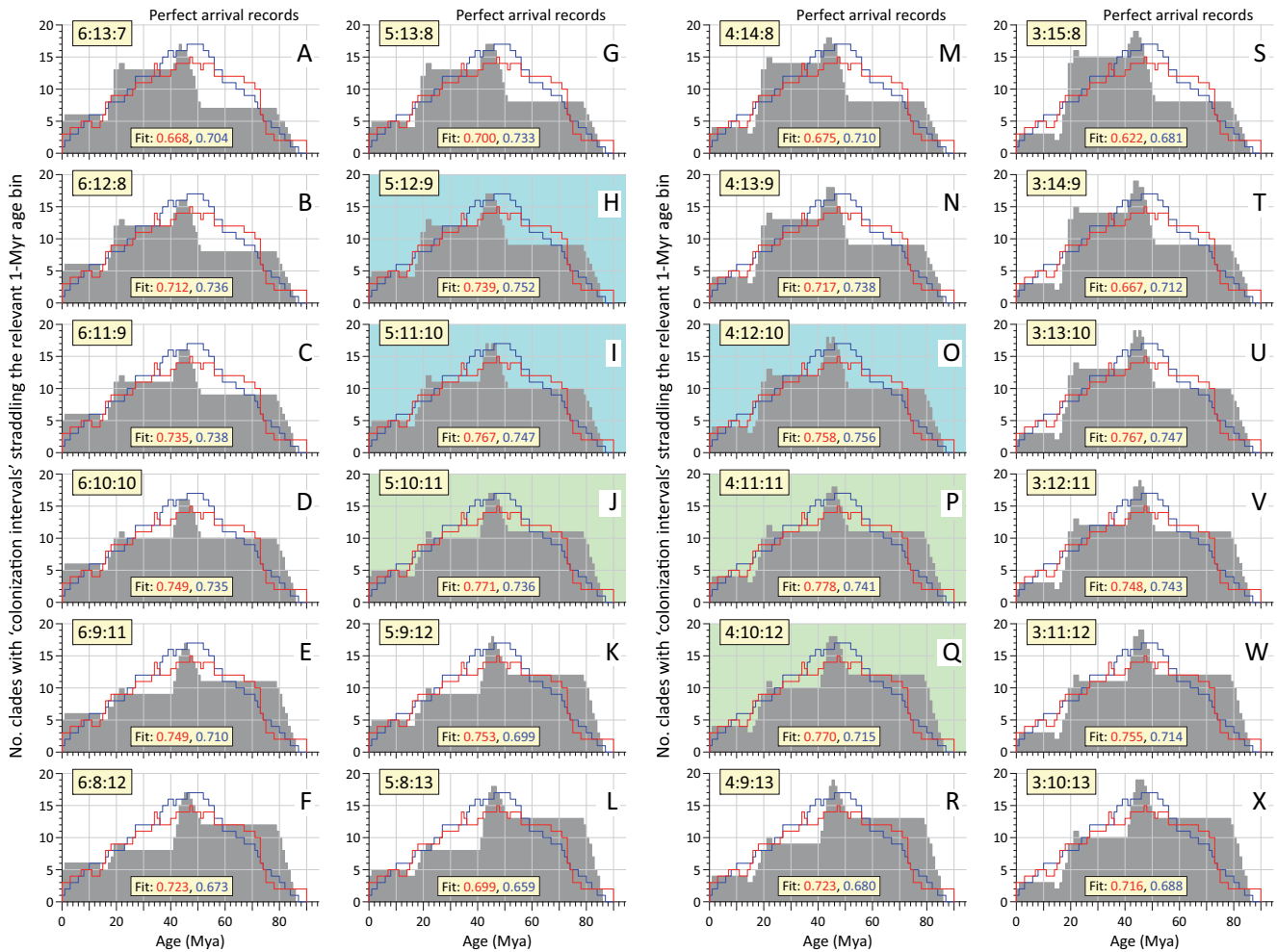


Fig. 13. Evaluation of the multiple land-bridge model, with fewer recent colonisation events. All arrivals take place during the intervals 66–60, 36–30 and 12–5 Mya, but with the younger window allocated fewer events; the Late Miocene has six (A–F), five (G–L), four (M–R) or three (S–X) arrivals, while the number of arrivals in the two older periods are adjusted incrementally to accommodate the remaining available events. The plots with green or blue backgrounds indicate the best fits relative to the ‘actual’ or ‘back-modelled’ data respectively (also see Fig. 14). Other details are as described in Fig. 10.

V. DISCUSSION

The analysis reveals that the ancestors of all but two of Madagascar’s 28 land-vertebrate groups are likely to have colonised the island in a series of temporally stochastic events, primarily in the Cenozoic, but with a small number possibly in the Late Cretaceous (after 75 Mya). It implies that the assemblage was created by a slow and random arrival of over-water dispersed waifs. The podocnemid-turtle and typhlopoid-snake clades are, however, different and their colonisations likely pre-dated the breakup of the Madagascar and India–Seychelles crustal blocks *c.* 85 Mya. Critically, there is no evidence for any of the arrivals being clustered through time, which is a key element of models invoking short-term land bridges (e.g. McCall, 1997, Masters *et al.*, 2021, 2022). Still, a model implying an equal probability of colonisation through time overlooks two important factors.

First, the end-Cretaceous mass extinction (e.g. Longrich *et al.*, 2012, 2016) must have shaped the early record of arrivals, and many groups are likely to have been eliminated during this event. Second, the ocean circulation patterns in the SW Indian Ocean–Mozambique Channel are thought to have changed in the Early Miocene. At present, vegetation rafts from Africa are unlikely to be transported to Madagascar, and this appears to have been the case back to about 15 or 20 Mya (Ali & Huber, 2010), prior to when circulation patterns are thought to have been more conducive to successful colonisation. It should be emphasised that the suite of land vertebrates appears ‘highly screened’, which is another characteristic of over-water transfer. Notably, in other island systems where non-volant vertebrates are present and land bridges could not have facilitated the ancestors’ passages, assemblages are dominated by reptile clades, with mammal and amphibian groups being fewer or even absent, e.g. Christmas Island

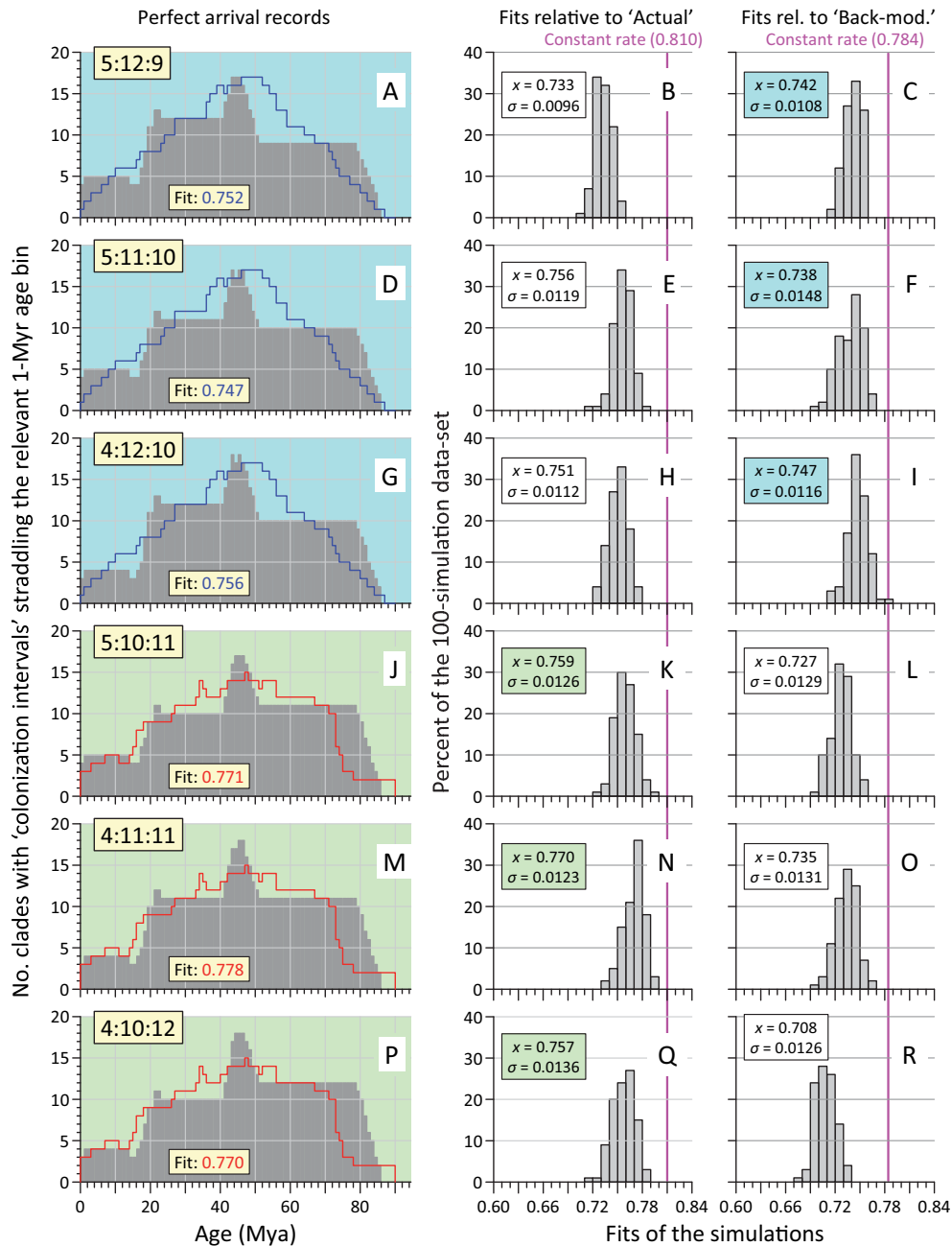


Fig. 14. Selection of the best 'perfect' arrival simulations for the analysis in Fig. 13. The plots on the left with blue and green backgrounds indicate the better/best fits relative to the 'back-modelled' and 'actual' data respectively. The middle column shows the overall distributions of the fits for each scenario, each based on 100 simulations, relative to the 'actual' data and the column on the right shows these fits relative to the 'back-modelled' data. For reference, two lines denoting the fit values for the 'constant-rate' model are also shown. Other details are as described in Fig. 10.

(Ali, Aitchison & Meiri, 2020), Galápagos Archipelago (Ali & Fritz, 2021), Greater Antilles (Ali & Hedges, 2021), and Gulf of Guinea (Ceriaco *et al.*, 2022). The Malagasy land-vertebrate suite follows this pattern. Furthermore, the island's five land-mammal clades comprise a small subset of the taxa that occupied Africa in the early and middle Cenozoic (Seiffert, 2010; Werdelin, 2010; Werdelin & Sanders, 2010).

VI. CONCLUSIONS

(1) On Madagascar, there are 28 native and independent land-vertebrate clades (18 reptile, five land-mammal, and five amphibian; freshwater fish were not considered) that have published times of divergence based on molecular clock analyses and fossil data that are relevant for understanding

their biogeographic origins. Two other groups exist, both geckos (*Gekolepis* and *Paragehyra*), but key uncertainties associated with their timetrees means that they could not be included in the present analysis.

(2) The ancestors of the podocnemid turtles and typhlopoid snakes were almost certainly on Madagascar before the land-mass became tectonically and geographically isolated c. 85 Mya (middle Late Cretaceous), thus these clades are considered vicariant relicts.

(3) For the remaining 26 clades, colonisation intervals (representing the earliest and latest times of origin for each clade) were used to create a single ‘colonisation profile’ for the assemblage. This enabled us quantitatively to evaluate predictions associated with various biogeographic models. Using simulations and statistical tests, we showed that stochastic over-water dispersal through time best explains the observed profile, rather than passage along temporary causeways. This finding is congruent with the geological evidence that rejects the suggestion that Africa and Madagascar were connected by land bridges/stepping-stone chains in the Cenozoic.

(4) A characteristic of the Malagasy fauna is the preponderance of reptile clades over land-mammal and amphibian groups, both of which are less resistant to desiccation. This pattern is common on islands and archipelagoes that are known never to have been connected to a continent and where over-water dispersal colonisation is the only possible colonisation mode. Furthermore, the Malagasy mammal-clade suite is itself strongly filtered.

(5) The novel colonisation-interval profile approach presented herein could be applied to the land-vertebrate assemblages on other marine islands and archipelagoes.

VII. ACKNOWLEDGEMENTS

Terence Lam and Stephen Lee helped and advised with the simulations. Steve Goodman and Dave Krause shared information. S. B. H. was supported by grant 1932765 from the U.S. National Science Foundation. Formal reviews by Angelica Crottini and Shai Meiri were very useful in helping us improve the manuscript.

VIII. REFERENCES

ALI, J. R. (2017). Islands as biological substrates: classification of the biological assemblage components and the physical Island types. *Journal of Biogeography* **44**, 984–994.

ALI, J. R. & AITCHISON, J. C. (2008). Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through end Eocene (166–35 Ma). *Earth-Science Reviews* **88**, 145–166.

ALI, J. R. & AITCHISON, J. C. (2009). Kerguelen Plateau and the Late Cretaceous southern-continent bioconnection hypothesis: tales from a topographical ocean. *Journal of Biogeography* **36**, 1778–1784.

ALI, J. R., AITCHISON, J. C. & MEIRI, S. (2020). Redrawing Wallace’s line based on the fauna of Christmas Island, eastern Indian Ocean. *Biological Journal of the Linnean Society* **130**, 225–237.

ALI, J. R. & FRITZ, U. (2021). Origins of the Galápagos’ land-bound vertebrates: what, whence, when, how? *Biological Journal of the Linnean Society* **134**, 261–284.

ALI, J. R. & HEDGES, S. B. (2021). Colonizing the Caribbean: new geological data and an updated land-vertebrate colonization record challenge the GAARlandia land-bridge hypothesis. *Journal of Biogeography* **48**, 2699–2707.

ALI, J. R. & HEDGES, S. B. (2022). A review of geological evidence bearing on proposed Cenozoic land connections between Madagascar and Africa and its relevance to biogeography. *Earth-Science Reviews* **232**, 104103.

ALI, J. R. & HUBER, M. (2010). Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* **463**, 653–656.

ALI, J. R. & KRAUSE, D. W. (2011). Late Cretaceous bio-connections between Indo-Madagascar and Antarctica: refutation of the Gunnerus ridge causeway hypothesis. *Journal of Biogeography* **38**, 1855–1872.

ALI, J. R. & VENCES, M. (2019). Mammals and long-distance over-water colonization: the case for rafting dispersal; the case against phantom causeways. *Journal of Biogeography* **46**, 2632–2636.

ANDRIAMALISOA, F. & LANGRAND, O. (2022). The history of zoological exploration of Madagascar. In *The New Natural History of Madagascar* (ed. S. M. GOODMAN), pp. 1–38. Princeton University Press, Princeton.

ANTONELLI, A., SMITH, R. J., PERRIGO, A. L., CROTTINI, A., HACKEL, J., TESTO, W., FAROOQ, H., TORRES JIMÉNEZ, M. F., ANDELA, N., ANDERMANN, T., ANDRIAMANOHERA, A. M., ANDRIAMBOLOLONERA, S., BACHMAN, S. P., BACON, C. D., BAKER, W. J., ET AL. (2022). Madagascar’s extraordinary biodiversity: evolution, distribution, and use. *Science* **378**, eabf0869.

ASHER, R. J. & HOFREITER, M. (2006). Tenrec phylogeny and the noninvasive extraction of nuclear DNA. *Systematic Biology* **55**, 181–194.

BASSIAS, Y. (1992). Petrological and geochemical investigations of rocks from the Davie Fracture zone (Mozambique Channel) and some tectonic implications. *Journal of African Earth Sciences* **15**, 321–339.

BASSIAS, Y. (2016). Was the Mozambique Channel once scattered with islands? *GeoExPro* **13**(3), 58–63.

BELLUARDO, F., SCHERZ, M. D., SANTOS, B., ANDREONE, F., ANTONELLI, A., GLAW, F., MUÑOZ-PAJARES, A. J., RANDRIANIRINA, J. E., RASELIMANANA, A. P., VENCES, M. & CROTTINI, A. (2022). Molecular taxonomic identification and species-level phylogeny of the narrow-mouthed frogs of the genus *Rhombophryne* (Anura: Microhylidae: Cophylinae) from Madagascar. *Systematics and Biodiversity* **20**(1), 1–13.

BOULE, M. (1906). Lémuriens et Lémurie. *La Géographie*, *Séries 4* **8**(1), 19–23.

BRACE, S., THOMAS, J. A., DALÉN, L., BURGER, J., MACPHEE, R. D. E., BARNES, I. & TURVEY, S. T. (2016). Evolutionary history of the Nesophontidae, the last unplaced recent mammal family. *Molecular Biology and Evolution* **33**, 3095–3103.

BURBRINK, F. T., RUANE, S., KUHN, A., RABIBISOA, N., RANDRIAMAHANTSOA, B., RASELIMANANA, A. P., ANDRIANARIMALALA, M. S. M., CADLE, J. E., LEMMON, A. R., MORIARTY LEMMON, E., NUSSBAUM, R. A., JONES, L. N., PEARSON, R. & RAXWORTHY, C. J. (2019). The origins and diversification of the exceptionally rich gemsnakes (Colubroidea: Lamprophiidae: Pseudoxrhophiinae) in Madagascar. *Systematic Biology* **68**(2019), 918–936.

CERÍACO, L. M. P., DE LIMA, R. F., MELO, M. & BELL, R. C. (2022). *Biodiversity of the Gulf of Guinea Oceanic Islands*. Springer, Cham.

COLLOT, J., PATRIAT, M., SUTHERLAND, R., WILLIAMS, S., CLUZEL, D., SETON, M., PELLETIER, B., ROEST, W. R., ETIENNE, S., BORDENAVE, A. & MAURIZOT, P. (2020). Geodynamics of the SW Pacific: a brief review and relations with New Caledonian geology. In *New Caledonia: Geology, Geodynamic Evolution and Mineral Resources* (Volume 51, eds P. MAURIZOT and N. MORTIMER), pp. 13–26. Geological Society of London Memoir, London.

COURGEON, S., BACHELERY, P., JOUET, G., JORRY, S. J., BOU, E., BOUDAGHER-FADEL, M. K., RÉVILLON, S., CAMOIN, G. & POLI, E. (2018). The offshore East African rift system: new insights from the Sakalaves seamounts (Davie Ridge, SW Indian Ocean). *Terra Nova* **30**, 380–388.

CROTTINI, A., HARRIS, D. J., MIRALLES, A., GLAW, F., JENKINS, R. K. B., RANDRIANANTOANDRO, J. K., BAUER, A. M. & VENCES, M. (2015). Morphology and molecules reveal two new species of the poorly studied gecko genus *Paragehyra* (Squamata: Gekkonidae) from Madagascar. *Organisms Diversity & Evolution* **15**, 175–198.

CROTTINI, A., MADSEN, O., POUX, C., STRAUß, A., VIEITES, D. R. & VENCES, M. (2012). Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K-T boundary in Madagascar. *Proceedings of the National Academy of Sciences, USA* **109**, 5358–5363.

DARLINGTON, P. J. (1957). *Zoogeography: the Geographical Distribution of Animals*. John Wiley & Sons, New York.

DE FLACOURT, E. (1658). *Histoire de la grande Isle Madagascar*. Recdition facsimile. A.R.5. Terres Creoles, La Réunion.

DE RUIJTER, W. P. M., RIDDERINKHOF, H. & SCHOUTEN, M. W. (2005). Variability of the Southwest Indian Ocean. *Philosophical Transactions of the Royal Society of London A* **363**, 63–76.

DE WIT, M. J. (2003). Madagascar: heads it’s a continent, tails it’s an Island. *Annual Review of Earth and Planetary Sciences* **31**, 213–248.

- DELAUNAY, A. (2018). Les mouvements verticaux de Madagascar (90–0 Ma): Une analyse couplée des formes du relief et de l'enregistrement sédimentaire des marges ouest Malgaches. PhD Thesis: Université de Rennes 1, Rennes.
- DIETZ, R. S. & HOLDEN, J. C. (1970). Reconstruction of Pangaea: breakup and dispersion of continents, Permian to Present. *Journal of Geophysical Research* **75**, 4939–4956.
- EVERSON, K. M., SOARIMALALA, V., GOODMAN, S. M. & OLSON, L. E. (2016). Multiple loci and complete taxonomic sampling resolve the phylogeny and biogeographic history of tenrecs (Mammalia: Tenrecidae) and reveal higher speciation rates in Madagascar's humid forests. *Systematic Biology* **65**, 890–909.
- FOODEN, J. (1972). Breakup of Pangaea and isolation of relict mammals in Australia, South America, and Madagascar. *Science* **175**, 894–898.
- GAFFNEY, E. S. & FORSTER, C. A. (2003). Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar. *American Museum Novitates* **3397**, 1–13.
- GAINA, C., MÜLLER, R. D., BROWN, B. J. & ISHIHARA, T. (2003). Microcontinent formation around Australia. In *Evolution and Dynamics of the Australian Plate* (Volume 22, eds R. R. Hillis and R. D. Müller), pp. 399–410. Geological Society of Australia Special Publication, Sydney.
- GÉNIN, F., MAZZA, P. P., PELLEN, R., RABINEAU, M., ASLANIAN, D. & MASTERS, J. C. (2022). Co-evolution assists geographic dispersal: the case of Madagascar. *Biological Journal of the Linnean Society* **137**, 163–182.
- GEOFFROY SAINT-HILAIRE, I. (1841). *Essais de Zoologie Générale*. Roret, Paris.
- GIPPNER, S., TRAVERS, S. L., SCHERZ, M. D., COLSTON, T. J., LYRA, M. L., MOHAN, A. V., MULTZSCH, M., NIELSEN, S. V., RANCILHAC, L., GLAW, F., BAUER, A. M. & VENCES, M. (2021). A comprehensive phylogeny of dwarf geckos of the genus *Lygodactylus*, with insights into their systematics and morphological variation. *Molecular Phylogenetics and Evolution* **165**, 107311.
- GLAW, F., HAWLITSCHKE, O. & RUTHENSTEINER, B. (2013). A new genus name for an ancient Malagasy chameleon clade and a PDF-embedded 3D model of its skeleton. *Salamandra* **49**, 237–238.
- GODFREY, L. R., JUNGERS, W. L. & SCHWARTZ, G. T. (2006). Ecology and extinction of Madagascar's subfossil lemurs. In *Lemurs: Ecology and Adaption* (eds L. Gould and M. L. Sauter), pp. 41–64. Developments in Primatology: Progress and Prospect, Springer, Boston.
- GRANDIDIER, G. (1905). *Recherches sur les Lémuriens disparus et en particulier sur ceux qui vivaient à Madagascar*, Edition (Volume 4), pp. 1–144. Nouvelles Archives du Muséum, Paris.
- GUNNELL, G. F., BOYER, D. M., FRISCHIA, A. R., HERITAGE, S., MANTHI, F. K., MILLER, E. R., SALLAM, H. M., SIMMONS, N. B., STEVENS, N. J. & SEIFFERT, E. R. (2018). Fossil lemurs from Egypt and Kenya suggest an African origin for Madagascar's aye-aye. *Nature Communications* **9**, 3193.
- HARTLAUB, G. (1877a). *Die Vögel Madagascars und der Benachbarten Inselgruppen. Ein Beitrag zur Zoologie der Äthiopischen Region*. Druck und Verlag von H. W. Schmidt, Halle.
- HARTLAUB, G. (1877b). General remarks on the avifauna of Madagascar and the Mascarene Islands. *Ibis* **1**, 334–336.
- HAWLITSCHKE, O., SCHERZ, M. D., RUTHENSTEINER, B., CROTTINI, A. & GLAW, F. (2018). Computational molecular species delimitation and taxonomic revision of the gecko genus *Ebenavia* Boettger, 1878. *The Science of Nature* **105**, 49.
- HAWLITSCHKE, O., TOUSSAINT, E. F. A. T., GEHRING, P. S., RATSOAVINA, F. M., COLE, N., CROTTINI, A., NOPPER, J., LAM, A. W., VENCES, M. & GLAW, F. (2017). Gecko phylogeography in the western Indian Ocean region: the oldest clade of *Ebenavia inunguis* lives on the youngest Island. *Journal of Biogeography* **44**, 409–420.
- HEDGES, S. B. (1996). The origin of West Indian amphibians and reptiles. In *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz* (eds R. Powell and R. W. Henderson), pp. 95–128. Society for the Study of Amphibians and Reptiles, Ithaca.
- HEDGES, S. B., MARION, A. B., LIPP, K. M., MARIN, J. & VIDAL, N. (2014). A taxonomic framework for typhlopod snakes from the Caribbean and other regions (Reptilia, Squamata). *Caribbean Herpetology* **49**, 1–61.
- HERRERA, J. P. & DÁVALOS, L. M. (2016). Phylogeny and divergence times of lemurs inferred with recent and ancient fossils in the tree. *Systematic Biology* **65**, 772–791.
- JACOBI, A. (1900). Lage und form biogeographischer gebiete. *Zeitschrift der Gesellschaft für Erdkunde zu Berlin* **35**(3), 147–238.
- KAEUFFER, R., COLTMAN, D. W., CHAPUIS, J. L., PONTIER, D. & RÉALE, D. (2006). Unexpected heterozygosity in an Island mouflon population founded by a single pair of individuals. *Proceedings of the Royal Society of London B* **274**, 527–533.
- KAPPELER, P. M. (2000). Lemur origins: rafting by groups of hibernators? *Folia Primatologica* **71**, 422–425.
- KEAREY, P., KLEPEIS, K. A. & VINE, F. J. (2009). *Global Tectonics*, Third Edition. Wiley-Blackwell, Chichester.
- KEHLMAIER, C., GRACIÁ, E., CAMPBELL, P. D., HOFMEYER, M. D., SCHWEIGER, S., MARTÍNEZ-SILVESTRE, A., JOYCE, W. & FRITZ, U. (2019). Ancient mitogenomics clarifies radiation of extinct Mascarene giant tortoises (*Cylindraspis* spp.). *Scientific Reports* **9**, 17487.
- KISTLER, L., RATAN, A., GODFREY, L. R., CROWLEY, B. E., HUGHES, C. E., LEI, R., CUI, Y., WOOD, M. L., MULDOON, K. M., ANDRIAMALISON, H., MCGRAW, J. J., TOMSHO, L. P., SCHUSTER, S. C., MILLER, W., LOUIS, E. E., YODER, A. D., MALHI, R. S. & PERRY, G. H. (2015). Comparative and population mitogenomic analyses of Madagascar's extinct, giant 'subfossil' lemurs. *Journal of Human Evolution* **79**, 45–54.
- KRAUSE, D. (2010). Washed up in Madagascar. *Nature* **463**, 613–614.
- KRAUSE, D. W., HOFFMANN, S., HU, Y., WIBLE, J. R., ROUGIER, G. W., KIRK, E. C., GROENKE, J. R., ROGERS, R. R., ROSSIE, J. B., SCHULTZ, J. A., EVANS, A. R., VON KOENIGSWALD, W. & RAHANTARISOA, L. J. (2020). Skeleton of a Cretaceous mammal from Madagascar reflects long-term insularity. *Nature* **581**, 421–427.
- KRAUSE, D. W., O'CONNOR, P. M., RASOAMIARAMANANA, A. H., BUCKLEY, G. A., BURNEY, D., CARRANO, M. T., CHATRATH, P. S., FLYNN, J. J., FORSTER, C. A., GODFREY, L. R., JUNGERS, W. L., ROGERS, R. R., SAMONDS, K. E., SIMONS, E. L. & WYSS, A. R. (2006). Preserving Madagascar's natural heritage: the importance of keeping the island's vertebrate fossils in the public domain. *Madagascar Conservation & Development* **1**, 43–47.
- KUMAR, S., STECHER, G., SULESKI, M. & HEDGES, S. B. (2017). TimeTree: a resource for timelines, timetrees, and divergence times. *Molecular Biology and Evolution* **34**, 1812–1819.
- LE PICHON, X. (1968). Sea-floor spreading and continental drift. *Journal of Geophysical Research* **73**, 3661–3697.
- LECLAIRE, L., BASSIAS, Y., CLOCCHIATTI, M. & SEGOUFIN, J. (1989). La Ride de Davie dans le Canal de Mozambique: approche stratigraphique et géodynamique. *Comptes Rendus de l'Académie des Sciences, Paris Serie II* **308**, 1077–1082.
- LEMME, I., ERBACHER, M., KAFFENBERGER, N., VENCES, M. & KÖHLER, J. (2013). Molecules and morphology suggest cryptic species diversity and an overall complex taxonomy of fish scale geckos, genus *Gekko*. *Organisms, Diversity & Evolution* **13**, 87–95.
- LIMA, A., HARRIS, D. J., ROCHA, S., MIRALLES, A., GLAW, F. & VENCES, M. (2013). Phylogenetic relationships of *Trachylepis* skink species from Madagascar and the Seychelles (Squamata: Scincidae). *Molecular Phylogenetics and Evolution* **67**, 615–620.
- LONGRICH, N. R., BHULLAR, B. A. S. & GAUTHIER, J. A. (2012). Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. *Proceedings of the National Academy of Sciences, USA* **109**, 21396–21401.
- LONGRICH, N. R., SCRIBERAS, J. & WILLS, M. A. (2016). Severe extinction and rapid recovery of mammals across the Cretaceous–Palaeogene boundary, and the effects of rarity on patterns of extinction and recovery. *Journal of Evolutionary Biology* **29**, 1495–1512.
- LUTJEHARMS, J. R. E., WEDEPOHL, P. M. & MEEUWIS, J. M. (2000). On the surface drift of the East Madagascar and the Mozambique currents. *South African Journal of Science* **96**, 141–147.
- LYELL, C. (1833). *Principles of Geology*, Edition (Volume 3). John Murray, London.
- MASTERS, J. C., DE WIT, M. J. & ASHER, R. J. (2006). Reconciling the origins of Africa, India and Madagascar with vertebrate dispersal scenarios. *Folia Primatologica* **77**, 399–418.
- MASTERS, J. C., GÉNIN, F., PELLEN, R., MAZZA, P., ZHANG, Y. R., HUCK, T., RABINEAU, M. & ASLANIAN, D. (2022). Geodispersal as a biogeographic mechanism for Cenozoic exchanges between Madagascar and Africa. In *The New Natural History of Madagascar* (ed. S. M. Goodman), pp. 78–81. Princeton University Press, Princeton.
- MASTERS, J. C., GÉNIN, F., ZHANG, Y., PELLEN, R., HUCK, T., MAZZA, P. P. A., RABINEAU, M., DOUCOURÉ, M. & ASLANIAN, D. (2021). Biogeographic mechanisms involved in the colonization of Madagascar by African vertebrates: rifting, rafting and runways. *Journal of Biogeography* **48**, 492–510.
- MATTHEW, W. D. (1915). Climate and evolution. *Annals of the New York Academy of Sciences* **24**, 171–318.
- MAZZA, P. P. A., BUCCIANTI, A. & SAVORELLI, A. (2019). Grasping at straws: a re-evaluation of sweepstakes colonisation of islands by mammals. *Biological Reviews* **94**, 1364–1380.
- MCCALL, R. A. (1997). Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **264**, 663–665.
- McKENZIE, D. P. & PARKER, R. L. (1967). The North Pacific: an example of tectonics on a sphere. *Nature* **216**, 1276–1280.
- MILLOT, J. (1952). La faune Malgache et le mythe Gondwanien. *Mémoires de l'Institut Scientifique de Madagascar, Series A* **7**, 1–36.
- MIRALLES, A., MARIN, J., MARKUS, D., HERREL, A., HEDGES, S. B. & VIDAL, N. (2018). Molecular evidence for the paraphyly of *Scolecophidia* and its evolutionary implications. *Journal of Evolutionary Biology* **31**, 1782–1793.
- MORGAN, W. J. (1968). Rises, trenches, great faults, and crustal blocks. *Journal of Geophysical Research* **73**, 1959–1982.
- MÜLLER, R. D., GAINA, C., ROEST, W. R. & HANSEN, D. L. (2001). A recipe for microcontinent formation. *Geology* **29**, 203–206.
- NAGY, Z. T., JOGER, U., WINK, M., GLAW, F. & VENCES, M. (2003). Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from

- nuclear and mitochondrial gene phylogenies. *Proceedings of the Royal Society of London B* **270**, 2613–2621.
- NOONAN, B. P. & CHIPPINDALE, P. T. (2006). Vicariant origin of Malagasy reptiles supports late Cretaceous Antarctic land bridge. *American Naturalist* **168**, 730–741.
- NOWACK, J. & DAUSMANN, K. H. (2015). Can heterothermy facilitate colonization events? *Mammal Review* **45**, 117–127.
- NYAKATURA, K. & BININDA-EMONDS, O. R. (2012). Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* **10**, 12.
- O'DEA, A., LESSIOS, H. A., COATES, A. G., EYTAN, R. I., RESTREPO-MORENO, S. A., CIONE, A. L., COLLINS, L. S., DE QUEIROZ, A., FARRIS, D. W., NORRIS, R. D., STALLARD, R. F., WOODBURN, M. O., AGUILERA, O., AUBRY, M. P., BERGGREN, W. A., *ET AL.* (2016). Formation of the Isthmus of Panama. *Science Advances* **2**, e1600883.
- ODIN, G. S., CURRY, D. & HUNZIKER, J. Z. (1978). Radiometric dates from NW European glauconites and the Palaeogene time-scale. *Journal of the Geological Society of London* **135**, 481–497.
- PÉREZ-GARCÍA, A., DE LAPPARENT DE BROIN, F. & MURELAGA, X. (2017). The *Erymnochelys* group of turtles (Pleurodira, Podocnemididae) in the Eocene of Europe: new taxa and paleobiogeographical implications. *Palaeontologia Electronica* **20**(1), 14A.
- POUX, C., MADSEN, O., MARQUARD, E., VIEITES, D. R., DE JONG, W. W. & VENCES, M. (2005). Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Systematic Biology* **54**, 719–730.
- RABINOWITZ, P. D. & WOODS, S. (2006). The Africa–Madagascar connection and mammalian migrations. *Journal of African Earth Sciences* **44**, 270–276.
- RAXWORTHY, C. J., FORSTNER, M. R. J. & NUSSBAUM, R. A. (2002). Chameleon radiation by oceanic dispersal. *Nature* **415**, 784–787.
- REEVES, C. V. (2018). The development of the East Africa margin during Jurassic and Lower Cretaceous times: a perspective from global tectonics. *Petroleum Geoscience* **24**, 41–56.
- ROOS, C., SCHMITZ, J. & ZISCHLER, H. (2004). Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences, USA* **101**, 10650–10654.
- RYAN, W. B. F., CARBOTTE, S. M., COPLAN, J. O., O'HARA, S., MELKONIAN, A., ARKO, R., WEISSEL, R. A., FERRINI, V., GOODWILLIE, A., NITSCH, F., BONGCZKOWSKI, J. & ZEMSKY, R. (2009). Global multi-resolution topography synthesis. *Geochemistry, Geophysics, Geosystems* **10**, Q03014.
- SAMONDS, K. E. (2007). Late Pleistocene bat fossils from Anjohibe Cave, northwestern Madagascar. *Acta Chiropterologica* **9**, 39–65.
- SAMONDS, K. E., GODFREY, L. R., ALI, J. R., GOODMAN, S. M., VENCES, M., SUTHERLAND, M. R., IRWIN, M. T. & KRAUSE, D. W. (2012). Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type. *Proceedings of the National Academy of Sciences, USA* **109**, 5352–5357.
- SAMONDS, K. E., GODFREY, L. R., ALI, J. R., GOODMAN, S. M., VENCES, M., SUTHERLAND, M. R., IRWIN, M. T. & KRAUSE, D. W. (2013). Imperfect isolation: factors and filters shaping Madagascar's extant vertebrate fauna. *PLoS One* **8**, e62086.
- SCHER, H., WHITTAKER, J., WILLIAMS, S., LATIMER, J. C., KORDESCH, W. E. C. & DELANEY, M. L. (2015). Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies. *Nature* **523**, 580–583.
- SCHERZ, M. D., DAZA, J. D., KÖHLER, J., VENCES, M. & GLAW, F. (2017). Off the scale: a new species of fish-scale gecko (Squamata: Gekkonidae: *Gekko*) with exceptionally large scales. *Pearl* **5**, e2955.
- SCHNEIDER, B. & SCHMITTNER, A. (2006). Simulating the impact of the Panamanian seaway closure on ocean circulation, marine productivity and nutrient cycling. *Earth and Planetary Science Letters* **246**, 367–380.
- SCLATER, P. L. (1864). The mammals of Madagascar. *Quarterly Journal of Science* **1**, 213–219.
- SCLATER, W. L. & SCLATER, P. L. (1899). *The Geography of Mammals*. Kegan Paul, Trench, Trübner & Co. Ltd, London.
- SEIFFERT, E. R. (2010). Chronology of Paleogene mammal localities. In *Cenozoic Mammals of Africa* (eds L. WERDELIN and W. J. SANDERS), pp. 19–26. University of California Press, Berkeley.
- SIMONS, E. L. (1994). The giant aye-aye *Daubentonia robusta*. *Folia Primatologica* **62**, 14–21.
- SIMPSON, E. S. W., SCHLICH, R., GIESKES, J. M., GIRDLEY, W. A., LECLAIRE, L., MARSHALL, B. V., MOORE, C., MULLER, C., SIGAL, J., VALLIER, T. L., WHITE, S. M. & ZOBEL, B. (1974). *Leg 25 of the cruises of the Drilling Vessel Glomar Challenger, Port Louis, Mauritius to Durban, South Africa June–August 1972*. Initial Reports of the Deep Sea Drilling Project. U.S. Government Printing Office, Washington DC.
- SIMPSON, G. G. (1940). Mammals and land bridges. *Journal of the Washington Academy of Sciences* **30**, 137–163.
- SIMPSON, G. G. (1952). Probabilities of dispersal in geologic time. *Bulletin of the American Museum of Natural History* **99**, 163–176.
- SIMPSON, G. G. (1980). *Splendid Isolation: the Curious History of South American Mammals*. Yale University Press, New Haven.
- STANHOPE, M. J., WADDELL, V. G., MADSEN, O., DE JONG, W., HEDGES, S. B., CLEVEN, G. C., KAO, D. & SPRINGER, M. S. (1998). Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *Proceedings of the National Academy of Sciences, USA* **95**, 9967–9972.
- STANKIEWICZ, J., THIART, C., MASTERS, J. C. & DE WIT, M. J. (2006). Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals. *Journal of Biogeography* **33**, 221–235.
- STOREY, M., MAHONEY, J. J., SAUNDERS, A. D., DUNCAN, R. A., KELLEY, S. P. & COFFIN, M. F. (1995). Timing of hotspot-related volcanism and the breakup of Madagascar and India. *Science* **267**, 852–855.
- TATTERSALL, I. (2006a). Historical biogeography of the Strepsirrhine primates of Madagascar. *Folia Primatologica* **77**, 477–487.
- TATTERSALL, I. (2006b). Mechanisms of faunal origin and diversity in Island environments: the case of Madagascar's mammals. *Hellenic Journal of Geoscience* **41**, 35–46.
- TOLLEY, K. A., TOWNSEND, T. M. & VENCES, M. (2013). Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. *Proceedings of the Royal Society of London B* **280**, 20130184.
- TORSVIK, T. H., TUCKER, R. D., ASHWAL, L. D., EIDE, E. A., RAKOTOSOLOFO, N. A. & DE WIT, M. J. (1998). Late Cretaceous magmatism in Madagascar: paleomagnetic evidence for a stationary Marion hotspot. *Earth and Planetary Science Letters* **164**, 221–232.
- TOUMOULIN, A., DONNADIEU, Y., LADANT, J. B., BATENBURG, S. J., POBLETE, F. & DUPONT-NIVET, G. (2020). Quantifying the effect of the Drake Passage opening on the Eocene Ocean. *Paleoceanography and Paleoclimatology* **35**, e2020PA003889.
- TUCK-MARTIN, A., ADAM, J. & EAGLES, G. (2018). New plate kinematic model and tectono-stratigraphic history of the East African and West Madagascan Margins. *Basin Research* **30**, 1118–1140.
- VARGAS-RAMÍREZ, M., CASTAÑO-MORA, O. V. & FRITZ, U. (2008). Molecular phylogeny and divergence times of ancient South American and Malagasy river turtles (Testudines: Pleurodira: Podocnemididae). *Organisms Diversity & Evolution* **8**, 388–398.
- VENCES, M., KOSUCH, J., GLAW, F., BÖHME, W. & VEITH, M. (2003a). Molecular phylogeny of hyperoliid treefrogs: biogeographic origin of Malagasy and Seychellian taxa and reanalysis of familial paraphyly. *Journal of Zoological Systematics and Evolutionary Research* **41**, 205–215.
- VENCES, M., KOSUCH, J., RÖDEL, M. O., LÖTTERS, S., CHANNING, A., GLAW, F. & BÖHME, W. (2004). Phylogeography of *Phrynobatrachus mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. *Journal of Biogeography* **31**, 593–601.
- VENCES, M., VIEITES, D. R., GLAW, F., BRINKMANN, H., KOSUCH, J., VEITH, M. & MEYER, A. (2003b). Multiple overseas dispersal in amphibians. *Proceedings of the Royal Society of London B* **270**, 2435–2442.
- VIDAL, N., MARIN, J., MORINI, M., DONNELLAN, S., BRANCH, W. R., THOMAS, R., VENCES, M., WYNN, A., CRUAUD, C. & HEDGES, S. B. (2010). Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters* **6**, 558–561.
- VORMANN, M. & JOKAT, W. (2021). Crustal variability along the rifted/sheared East African margin: a review. *Geomarine Marine Letters* **41**, 19.
- WALLACE, A. R. (1880). *Island Life*. Macmillan & Co, London.
- WELT, R. S. & RAXWORTHY, C. J. (2022). Dispersal, not vicariance, explains the biogeographic origin of iguanas on Madagascar. *Molecular Phylogenetics and Evolution* **167**, 107345.
- WERDELIN, L. (2010). Chronology of Neogene mammal localities. In *Cenozoic Mammals of Africa* (eds L. WERDELIN and W. J. SANDERS), pp. 27–43. University of California Press, Berkeley.
- WERDELIN, L. & SANDERS, W. J. (2010). *Cenozoic Mammals of Africa*. University of California Press, Berkeley.
- YODER, A. D., BURNS, M., ZEHR, S., DELEFOSSE, T., VERON, G., GOODMAN, S. M. & FLYNN, J. J. (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature* **421**, 734–737.
- YODER, A. D., CARTMILL, M., RUVOLO, M., SMITH, K. & VILGALYS, R. (1996). Ancient single origin of Malagasy primates. *Proceedings of the National Academy of Sciences, USA* **93**, 5122–5126.
- YODER, A. D. & NOWAK, M. D. (2006). Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology, Evolution, and Systematics* **37**, 405–431.

(Received 8 August 2022; revised 14 April 2023; accepted 17 April 2023)