The colonisation of Madagascar by land-bound vertebrates

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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/drifting. 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.

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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, 1650). 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–Calumma chameleons, lemurs, mantellid frogs, microhyd frogs, pseudoxyrine 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; Burbrik 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 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 carnivores, 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 solenodon insectivores in the Caribbean [note that the molecular
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, 1877a,b; Sclater & Schletter, 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 carnivores 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).
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 Géographie* (Fig. 2).

**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.

Over-water dispersal as an explanation for key elements of 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, Foooden (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 Foooden 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 Foooden 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 Madagas- cary 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 (Tounoulin 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; Gaima 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 ‘terranes’ 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; Pou 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., 1993; 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).

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and podocnemid turtles (based on molecular data). However, Ali & Atchison (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 sweepstakes 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 sweepstake 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), sweepstake 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 mechanics 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, Riddlerinkof & 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.

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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. Afrotheria–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 & Daumann (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 an 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 palaeo-climatological 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 Hyperoliiidae, Mantellidae and Microhyliidae frogs, plus reptiles of the families Boophidae, Chamaeleonidae, Gekkonidae, Gerrhosauridae, Scincidae, Typhlopidae, and Xenotyphlopidae. The Eocene–Oligocene causeway was claimed to have facilitated the arrivals of the carnivorans, rodents, and lampropholid snakes. The ‘Late Miocene’ path was purportedly used by hippopotamuses, crocodylidae, Hemidactylus geckos and pygchyadnil 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. 3). It was shown that just one high-elevation volcanic island existed (in the northern Sakalava Seaamount 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

Bibliography

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(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, plateaux, 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 lemur 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
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

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**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).
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–Australasian 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–Australasian 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 gekco 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 *Paragehyra*, indicating a single colonisation from Africa. Those investigations also revealed a complicated biogeographical history with *Ebenavia* colonisations of the nearby Comores 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; 2, Vargas-Ramirez, Castro-Mora & Fritz (2008) and a fossil age based on Gaffney & Forster (2003), see also Pérez-Garcia, de Lapparent de Broin & Murlaga (2017); 2, typhlopoid snakes: *st.* and *cr.* Vidal et al. (2010); 3, boid snakes: *st.* and *cr.* TimeTree; 4, *Uropeltis* 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–Palme* chamaeleons: *st.* and *cr.* Tolley, Townsend & Vences (2013), see also Glaw, Hawlitschek & Rutheinsteiner (2013); 9, Malagasy iguanas (*Ophidura*): *st.* and *cr.* Welt & Raxworthy (2022); 10, zonosaurus lizards: *st.* and *cr.* TimeTree; 11, scincid skinks: *st.* and *cr.* TimeTree; 12, *Blasodactylus* 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, psmampholine snakes: *st.* TimeTree, no crown; 18, *Himadrides mercuratus* 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 carnivores: *st.* and *cr.* Nyakatura & Bininda-Emonds (2012); 24, mantellid frogs: *st.* and *cr.* TimeTree; 25, cophylines–scaphiophrynine frogs: *st.* and *cr.* TimeTree; 26, dyscophine frogs: *st.* and *cr.* TimeTree; 27, hyperolids 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; cophylines–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; *Uropeltis* 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.

### Colonisation-interval mid-point data for Madagascar’s land-locked vertebrate clades.

<table>
<thead>
<tr>
<th>Clade #</th>
<th>Reptiles/Clade</th>
<th>Information sources</th>
<th>Crown</th>
<th>Stem</th>
<th>CIMP</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low age</td>
<td>High age</td>
<td>Low age</td>
<td>High age</td>
</tr>
<tr>
<td>1</td>
<td>Erymnochelys madagascariensis</td>
<td>Gaffney &amp; Forster (2003); Vargas-Ramirez et al. (2008)</td>
<td>66.0</td>
<td>72.1</td>
<td>78.5</td>
<td>131.1</td>
</tr>
<tr>
<td>2</td>
<td>Typhlopoid snakes</td>
<td>Vidal et al. (2010)</td>
<td>96.0</td>
<td>112.0</td>
<td>107.0</td>
<td>122.0</td>
</tr>
<tr>
<td>3</td>
<td>Boit snakes</td>
<td>TimeTree (Kumar et al. 2017)</td>
<td>23.0</td>
<td>29.5</td>
<td>79.7</td>
<td>89.7</td>
</tr>
<tr>
<td>4</td>
<td>Uropodatus geckos</td>
<td>TimeTree (Kumar et al. 2017)</td>
<td>51.0</td>
<td>59.4</td>
<td>85.0</td>
<td>89.6</td>
</tr>
<tr>
<td>5</td>
<td>Lygodactylus geckos</td>
<td>Gippner et al. (2021)</td>
<td>46.7</td>
<td>60.5</td>
<td>61.5</td>
<td>77.3</td>
</tr>
<tr>
<td>6</td>
<td>Pteleopus geckos</td>
<td>TimeTree (Kumar et al. 2017)</td>
<td>39.5</td>
<td>44.4</td>
<td>66.5</td>
<td>74.5</td>
</tr>
<tr>
<td>7</td>
<td>Paroedura–Ebenavia geckos</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>42.4</td>
<td>51.1</td>
<td>67.5</td>
<td>74.4</td>
</tr>
<tr>
<td>8</td>
<td>Brookesia–Palleon chameleons</td>
<td>Tolley et al. (2013); Glaw et al. (2013)</td>
<td>59.0</td>
<td>66.0</td>
<td>65.0</td>
<td>73.0</td>
</tr>
<tr>
<td>9</td>
<td>Malagasy iguanas (Ophuridae)</td>
<td>Welt &amp; Raxworthy (2022)</td>
<td>19.0</td>
<td>33.0</td>
<td>59.2</td>
<td>72.9</td>
</tr>
<tr>
<td>10</td>
<td>Zonosaurine lizards</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>39.8</td>
<td>52.0</td>
<td>57.2</td>
<td>72.2</td>
</tr>
<tr>
<td>11</td>
<td>Scincid skinks</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>52.5</td>
<td>58.2</td>
<td>60.7</td>
<td>70.0</td>
</tr>
<tr>
<td>12</td>
<td>Blenosaurus geckos</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>32.9</td>
<td>42.7</td>
<td>47.8</td>
<td>54.1</td>
</tr>
<tr>
<td>13</td>
<td>Furax–Calumma chameleons</td>
<td>Tolley et al. (2013)</td>
<td>46.0</td>
<td>52.0</td>
<td>47.0</td>
<td>54.0</td>
</tr>
<tr>
<td>14</td>
<td>Tachiepini skinks</td>
<td>Lima et al. (2013)</td>
<td>36.0</td>
<td>42.0</td>
<td>43.0</td>
<td>50.0</td>
</tr>
<tr>
<td>15</td>
<td>Pseudoscorpionine snakes</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>35.5</td>
<td>44.8</td>
<td>41.6</td>
<td>47.8</td>
</tr>
<tr>
<td>16</td>
<td>Astrochelys–Pyxis tortoises</td>
<td>Kehlmaier et al. (2019)</td>
<td>26.4</td>
<td>32.0</td>
<td>28.7</td>
<td>34.2</td>
</tr>
<tr>
<td>17</td>
<td>Pseudomorphine snakes</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>18</td>
<td>Hemidactylus mercatorius</td>
<td>Crottini et al. (2012)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

### Land-locked mammals

<table>
<thead>
<tr>
<th>Clade #</th>
<th>Land-locked mammals</th>
<th>Information sources</th>
<th>Crown</th>
<th>Stem</th>
<th>CIMP</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low age</td>
<td>High age</td>
<td>Low age</td>
<td>High age</td>
</tr>
<tr>
<td>19</td>
<td>Tenrecs</td>
<td>Everson et al. (2016)</td>
<td>29.6</td>
<td>41.8</td>
<td>47.5</td>
<td>55.6</td>
</tr>
<tr>
<td>20</td>
<td>Lemurs</td>
<td>Gunnell et al. (2018)</td>
<td>14.7</td>
<td>25.8</td>
<td>41.0</td>
<td>46.0</td>
</tr>
<tr>
<td>21</td>
<td>Aye-ayes</td>
<td>Godfrey et al. (2006); Gunnell et al. (2018)</td>
<td>0.001</td>
<td>0.001</td>
<td>28.0</td>
<td>35.8</td>
</tr>
<tr>
<td>22</td>
<td>Nesomyidae</td>
<td>Poux et al. (2005)</td>
<td>15.4</td>
<td>25.7</td>
<td>23.5</td>
<td>29.6</td>
</tr>
<tr>
<td>23</td>
<td>Eupleridae</td>
<td>Nyakatura &amp; Bininda-Emonds (2012)</td>
<td>16.8</td>
<td>19.3</td>
<td>21.3</td>
<td>23.4</td>
</tr>
</tbody>
</table>

(Continues on next page)
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: 

\[
\text{cr.-young} = (0.818 \times \text{CIMP}) - 7.823, \quad R^2 = 0.784; \\
\text{st.-old} = (1.182 \times \text{CIMP}) + 7.823, \quad R^2 = 0.883 \quad \text{[in both cases N = 26, not 28].}
\]

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 \((C_{\text{tot}} - C_{\text{nn}})/C_{\text{tot}}\) where \(C_{\text{tot}}\) is the total number of cells associated with the ‘actual’ data, and \(C_{\text{nn}}\) 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.

Table 1. (Cont.)

<table>
<thead>
<tr>
<th>Clade #</th>
<th>Amphibians</th>
<th>Information sources</th>
<th>CIMP</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td>Mantellid frogs</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>52.5</td>
<td>Low age 65.2, High age 74.3</td>
</tr>
<tr>
<td>25</td>
<td>Cophyline–scaphiophrynine frogs</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>57.5</td>
<td>Low age 69.8, High age 77.7</td>
</tr>
<tr>
<td>26</td>
<td>Dyscophine frogs</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>62.8</td>
<td>Low age 66.3, High age 77.7</td>
</tr>
<tr>
<td>27</td>
<td>Hyperoliid frogs</td>
<td>TimeTree (Kumar et al., 2017)</td>
<td>21.4</td>
<td>Low age 24.1, High age 33.6</td>
</tr>
<tr>
<td>28</td>
<td>Ptychadenid frogs</td>
<td>Vences et al. (2004); Crottini et al. (2012)</td>
<td>3.4</td>
<td>Low age 3.4, High age 3.4</td>
</tr>
</tbody>
</table>
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 typhlopid 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. 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, typhlopid snakes; 3, boid snakes; 4, *Uroplatus* geckos; 5, *Lygodactylus* geckos; 6, *Phelsuma* geckos; 7, *Pareodura–Ebenavia* geckos; 8, *Brookesia–Pteleon* chameleons; 9, Malagasy iguanas (Opluridae); 10, zonosaurus lizards; 11, scincid skinks; 12, *Blacodactylus* geckos; 13, *Furcifer–Calumma* chameleons; 14, *Trachylepsis* skinks; 15, pseudoxyrhophine snakes; 16, *Astrochelys–Pyxis* tortoises; 17 psammophine snakes; 18, *Hemidactylus mercurialis* gecko; 19, tenrecs; 20, main lemurs; 21, aye-ayes; 22, nesomyid rodents; 23, euplerid carnivorans; 24, mantellid frogs; 25, cophyline-scaphiophrynine 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 mercurialis* (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.
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.

(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
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. 3B 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 $\chi^2$ 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.

<table>
<thead>
<tr>
<th>Model to be tested</th>
<th>Comparison</th>
<th>$\chi^2$</th>
<th>P-value</th>
<th>n</th>
<th>Fit</th>
<th>Fig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘back-modelled’</td>
<td>‘actual’</td>
<td>38.2</td>
<td>1.000</td>
<td>90</td>
<td>0.835</td>
<td>10A</td>
</tr>
<tr>
<td>constant rate</td>
<td>‘actual’</td>
<td>59.5</td>
<td>0.993</td>
<td>90</td>
<td>0.810</td>
<td>10B</td>
</tr>
<tr>
<td>constant rate</td>
<td>‘back-modelled’</td>
<td>66.1</td>
<td>0.945</td>
<td>87</td>
<td>0.784</td>
<td>10B</td>
</tr>
<tr>
<td>mid-Cenozoic perfect</td>
<td>‘actual’</td>
<td>580.5</td>
<td>&lt;0.001</td>
<td>90</td>
<td>0.236</td>
<td>11A</td>
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<td>‘back-modelled’</td>
<td>505.2</td>
<td>&lt;0.001</td>
<td>87</td>
<td>0.301</td>
<td>11A</td>
</tr>
<tr>
<td>mid-Cenozoic best fit ‘actual’</td>
<td>‘actual’</td>
<td>495.2</td>
<td>&lt;0.001</td>
<td>90</td>
<td>0.328</td>
<td>11C</td>
</tr>
<tr>
<td>mid-Cenozoic best fit ‘back-modelled’</td>
<td>410.5</td>
<td>&lt;0.001</td>
<td>87</td>
<td>0.433</td>
<td>11D</td>
<td></td>
</tr>
<tr>
<td>8:9:9 perfect</td>
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<td>207.0</td>
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<td>0.685</td>
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<td>9:8:9 perfect</td>
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<td>8:9:8 perfect</td>
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<td>215.9</td>
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<td>0.647</td>
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<td>0.636</td>
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<td>87</td>
<td>0.752</td>
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<td>0.003</td>
<td>87</td>
<td>0.747</td>
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<td>‘back-modelled’</td>
<td>119.5</td>
<td>0.010</td>
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<td>0.756</td>
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<td>‘actual’</td>
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<td>0.771</td>
<td>13J</td>
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<td>‘actual’</td>
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<td>&lt;0.001</td>
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<td>0.778</td>
<td>13P</td>
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<td>‘actual’</td>
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<td>87</td>
<td>0.753</td>
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Note1: 10 from 100 simulations with P-values $\geq$0.05, but all <0.15

(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 $>10^{10^{26}}$ 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 28–30 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 ($p = 0.0407$) and to ‘back-modelled’ 0.294 ($p = 0.0484$). 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’.
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

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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. (G, H) Overview of the distributions of fits. 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–1L, 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’ 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 fit for 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 bar 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 thought to have been more conducive to successful colonisation.
(Ali, Aitchison & Meiri, 2020), Galápagos Archipelago (Ali & Fritz, 2021), Greater Antilles (Ali & Hedges, 2021), and Gulf of Guinea (Ceríaco 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

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**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.
their biogeographic origins. Two other groups exist, both geckos (Geckolopsis and Parasphaera), 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 tychoploid snakes were almost certainly on Madagascar before the landmass became tectonically and geographically isolated. c. 85 Mya (middle Late Cretaceous), thus these clades are considered vicariant relics.

(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 suggests 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

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VIII. REFERENCES


