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# Land Bridges and Rafting Theories to Explain Terrestrial-Vertebrate Biodiversity on Madagascar

Jason R. Ali<sup>1</sup> and S. Blair Hedges<sup>2</sup>

<sup>1</sup>Museum of Zoology, Senckenberg Dresden, Dresden, Germany;  
email: jason.ali@senckenberg.de

<sup>2</sup>Center for Biodiversity, Temple University, Philadelphia, Pennsylvania, USA

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## Keywords

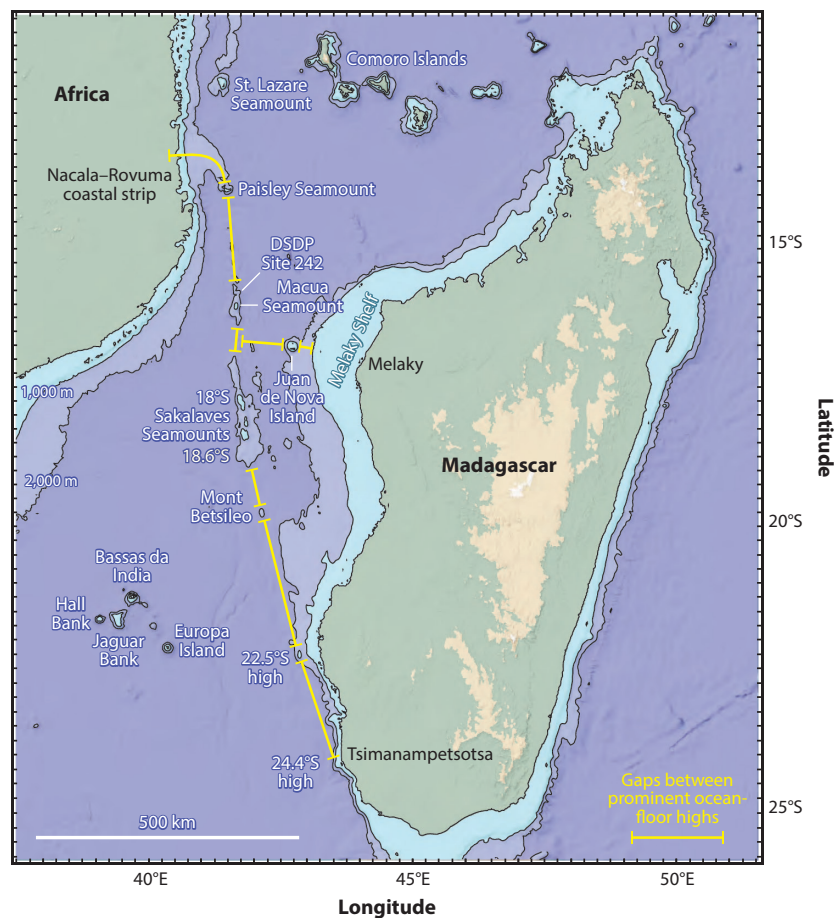
Davie Ridge, lemurs, molecular-clock age dates, Mozambique Channel, overwater dispersal, vicariance

## Abstract

Madagascar's celebrated land-vertebrate assemblage has long been studied and discussed. How the ancestors of the 30 different lineages arrived on the island, which has existed since 85 Mya and is separated from neighboring Africa by 430 km of water, is a deeply important question. Did the colonizations take place when the landmass formed part of Gondwana, or did they occur later and involve either now-drowned causeways or overwater dispersal (on vegetation rafts or by floating/swimming)? Following a historical review, we appraise the geological–geophysical evidence and the faunal-suite colonization record. Twenty-six of the clades are explained by temporally stochastic overwater dispersals, spanning 69–0 Mya, while two others are considered Gondwanan vicariant relicts. Due to a lack of information, the remaining two groups cannot be evaluated. The findings thus appear to resolve a debate that has rumbled along, with sporadic eruptions, since the mid-1800s.

## 1. INTRODUCTION

The iconic land-vertebrate assemblage on the southwest Indian Ocean island of Madagascar (**Figure 1**) is unlike that on any of the other continental landmasses, including nearby Africa's (e.g., Smith et al. 2023). A defining feature is that it comprises relatively few clades (groups of organisms whose member species have all descended from a common ancestor), with 5 amphibian, 5 land-mammal, and 20 reptile clades presently recognized. One of the consequences of this restricted high-order taxonomic diversity is that a number of lineages have radiated into many tens or even hundreds of species to fill an extensive array of ecological niches, including the *Furcifer–Calumma* chameleons, lemurs, mantellid frogs, microhylid frogs, pseudoxyrhophine



**Figure 1**

Map of the Madagascar–southwest Indian Ocean region showing the key physiographical features. The base chart was generated using GeoMapApp (Ryan et al. 2009). Also shown are various bathymetric highs (some of which are formally recognized, e.g., Macua Seamount and Sakalaves Seamounts, and some of which are not, e.g., Mont Betsileo and the 22.5°S high) and a number of intervening gaps. Together, the features are used in evaluations of land-bridge models (McCall 1997, Masters et al. 2021), particularly those associated with topological connectivity arrays, an example of which is shown in **Figure 3** (see Ali & Hedges 2022). The Davie Ridge continental crustal sliver of Vormann & Jokat (2021b) extends from the southern end of the Sakalaves Seamounts to just north of the Paisley Seamount. Abbreviation: DSDP, Deep Sea Drilling Project. Figure adapted from Ali & Hedges (2023).

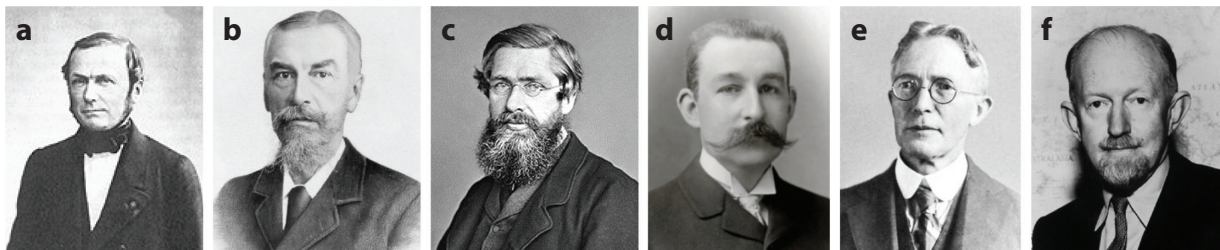


**Figure 2**

Examples of Madagascar's spectacular land-vertebrate biodiversity. The leaf-tailed gecko, *Uroplatus phantasticus* (panel *a*), has camouflaging that makes it look like leaves. The chameleon *Brookesia nana* (panel *b*), is approximately the size of a fingertip, whereas *Calumma parsonii* (panel *c*), one of its cousins from a different clade, is  $\sim 29,000$  times larger. The aye-aye primate, *Daubentonia madagascariensis* (panel *d*), uses its extended middle finger to probe tree cavities for grubs. Panel *a* provided by Piotr Łukasik; panels *b* and *c* provided by Frank Glaw; panel *d* drawn by Joseph Wolf and reproduced from Owen (1863).

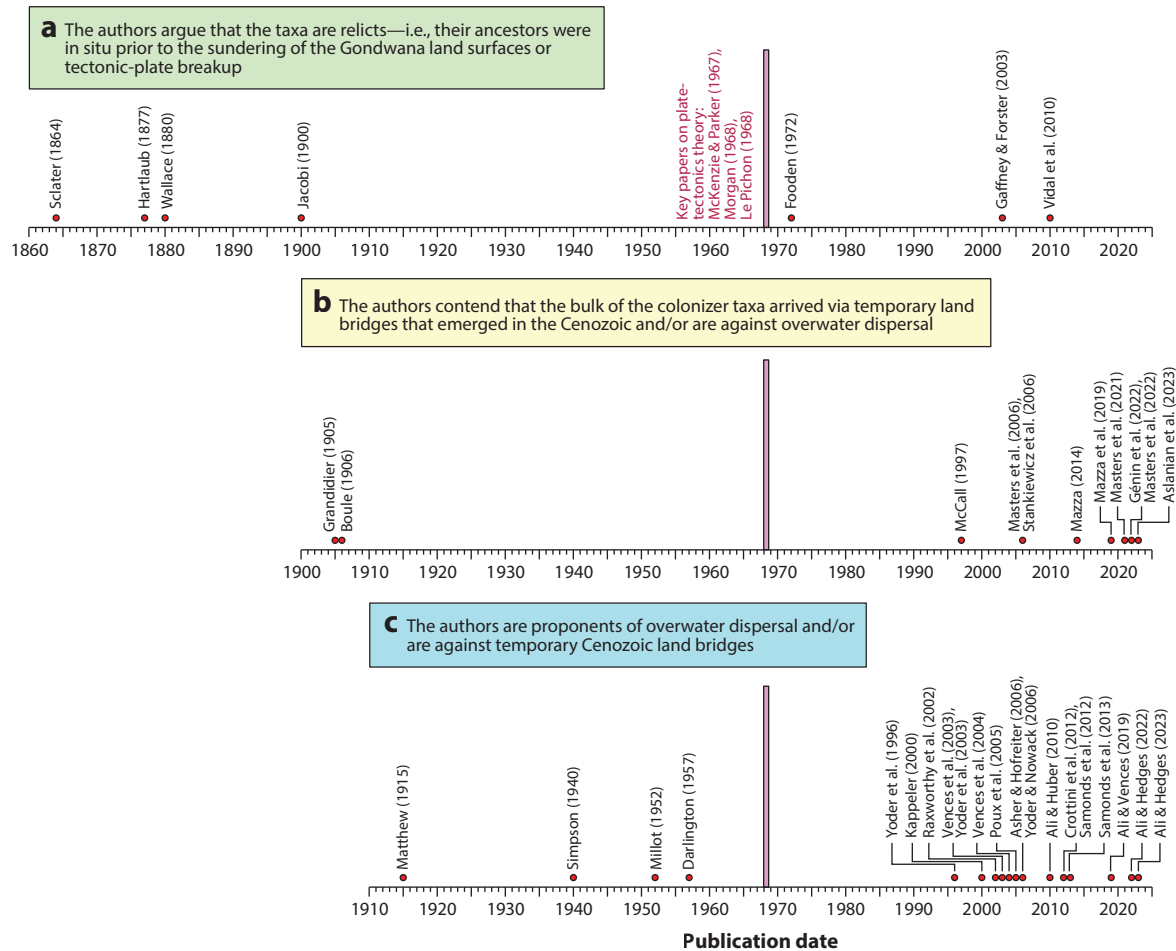
snakes, and scincine lizards (Crottini et al. 2012). Additionally, some taxa have evolved into noteworthy or even bizarre physical forms. For instance, the leaf-tailed geckos (*Uroplatus*) have camouflaging that makes them look like bark, leaves, or lichen (Ratsoavina et al. 2013) (**Figure 2a**). There are chameleons that range from the fingertip-scale *Brookesia nana* (**Figure 2b**) to the  $\sim 29,000$ -times-larger *Calumma parsonii* (**Figure 2c**); these two species are, however, the result of separate colonization events (Tolley et al. 2013) and thus are somewhat distantly related. The aye-aye primate, *Daubentonia madagascariensis* (**Figure 2d**), has an extended middle finger that it uses as a grub fisher for probing tree cavities (Sterling & McCreless 2007).

Initial documentation of the Malagasy fauna was carried out by de Flacourt (1658) a century and a half after Europeans first sighted and landed on the island (1500 CE) as trade routes with Asia were being established (Thomaz 2009). By the mid-1800s, people were comparing the faunal components with taxa elsewhere. Notably, Isidore Geoffroy Saint-Hilaire (1841, p. 442) (**Figure 3a**) observed that a number were very different from those in Africa, with some having closer affinities to ones in India and Southeast Asia. Thus, the origins debate (whence, when, and how) had commenced. It should also be said that establishing the colonization history



**Figure 3**

Some of the important historical figures associated with explanations for the colonization of Madagascar by land-locked vertebrates: (*a*) Isidore Geoffroy Saint-Hilaire, (*b*) Philip L. Sclater, (*c*) Alfred R. Wallace, (*d*) Guillaume Grandidier, (*e*) William D. Matthew, and (*f*) George G. Simpson (see also **Figure 4**). Panel *c* image provided by George W. Beccaloni; all other images are public domain.



**Figure 4**

Chronological summary of the key proposals for the mode of arrival of the bulk of Madagascar’s land-bound vertebrate clades. Essentially, there are three types of proposal: (a) that the taxa are vicariant relicts that pre-date Madagascar’s beginning as an island, which is now thought to be ~85 Mya; (b) that the taxa walked to the island in the Cenozoic along temporary causeways or stepping-stone chains and/or did not overwater disperse to the island; and (c) that the taxa were carried to the island on rafts or floated/swam across, and/or there is no evidence for temporary land bridges. Also shown are the publications of McKenzie & Parker (1967), Le Pichon (1968), and Morgan (1968) that together formulated plate-tectonics theory. References in the figure that are not cited elsewhere in the article: Hartlaub (1877), Jacobi (1900), Boule (1906), Millot (1952), Darlington (1957), Fooden (1972), Kappeler (2000), Raxworthy et al. (2002), Gaffney & Forster (2003), Yoder et al. (2003), Vences et al. (2004), Asher & Hofreiter (2006), Yoder & Nowak (2006), Vidal et al. (2010), Samonds et al. (2012, 2013), and Génin et al. (2022). Figure adapted from Ali & Hedges (2023).

of the Malagasy land-vertebrate suite has been greatly impeded by the effective absence of a Cenozoic terrestrial-fossil record (Krause et al. 2006), as the only such material dates from the last 80,000 years (Late Pleistocene and Holocene).

## 2. BY LAND OR BY SEA: THE DEVELOPMENT OF IDEAS ON MADAGASCAR’S BIOGEOGRAPHY

The development of ideas related to the Malagasy land-vertebrate components’ ancestral colonizers was recently outlined by Ali & Hedges (2023). **Figure 4** summarizes the history and

### ISLANDS WHERE THE LAND-VERTEBRATE ASSEMBLAGES COLONIZED VIA TEMPORARY LAND BRIDGES

There are numerous islands and archipelagoes where the land-vertebrate fauna results from temporary land bridges, including Bioko, Great Britain, Hainan, Taiwan, and Tasmania (Ali 2018). In all cases, the islands sit within the continental shelf of the adjacent continent. During sea-level lows associated with the recent glacial periods, the intervening ocean floor was exposed, typically down to 90–120 m below the present datum (e.g., Bintanja et al. 2005). Thus, it was relatively easy for taxa that were present on the various mainland areas to expand their ranges and colonize the landmasses. Notably, the insular assemblages are very similar to those in the source areas, plus there are a wide variety of morpho- and physiotypes. Also, endemic species are rare and tend to be restricted to particular niches, notably the high ground, where the habitat may be somewhat different from that of the coastal areas of the mainland (the biota on Taiwan provides an excellent example).

includes the key publications plus important consolidation outputs. Here, we focus on the former, i.e., works that drove the discussion—often forward, but occasionally sideways and sometimes backward (at least in our opinion).

For the period up until 1915, explanations for the terrestrial-vertebrate colonizations were based around now-sunken landmasses (see the sidebar titled *Islands Where the Land-Vertebrate Assemblages Colonized via Temporary Land Bridges*). It should be recognized, however, that plate-tectonics theory was then many decades away (McKenzie & Parker 1967, Le Pichon 1968, Morgan 1968), and the overwater-dispersal mechanism (e.g., Darwin 1859) was then only partially developed. To account for Madagascar's lemurs, Africa's galagos, and South and Southeast Asia's lorises, Philip Sclater (1864) (**Figure 3b**) argued for a drowned continent, which he called Lemuria, occupying the northern half of the Indian Ocean basin. Alfred Wallace (1880) (**Figure 3c**) proposed what was, in effect, a Cretaceous-age land surface between Madagascar and Africa to explain the lemurs, tenrecs, and carnivorans, which he viewed as old (see Ali & Hedges 2023). The slightly different idea of younger temporary causeways, which some researchers espouse today (**Figure 4**), was first mooted by Guillaume Grandidier (1905) (**Figure 3d**) (not to be confused with his father, the famed natural historian Alfred Grandidier). There were two elements to his argument. First, based on the geological literature, he considered Madagascar to have already been an island in the Late Cretaceous. Second, his comparisons of the island's extant and subfossil taxa with off-island forms led him to believe that their ancestors were not as ancient as Wallace had assumed, with their arrivals likely dating from the Cenozoic.

Figuratively and literally speaking, William Matthew (1915) (**Figure 3e**) fleshed out the overwater-dispersal mechanism by considering how it might apply to land mammals and by exploring it more deeply (see the sidebar titled *Direct Evidence for Overwater Dispersal*). Thus, he reconfigured the entire debate (**Figure 4**). In his memoir, he explained how it might apply to Madagascar:

The Malagasy mammals point to a number of colonizations of the island by single species of animals at different times and by several methods. Of these colonizations, the Centetidae [tenrecs] are the earliest, perhaps pre-Tertiary; the lemurs, rodents and viverrines [carnivorans] are derivable from one or more middle Tertiary colonizations: 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. (Matthew 1915, pp. 203–4)



## DIRECT EVIDENCE FOR OVERWATER DISPERSAL

An oft-cited work documenting overwater dispersal was published by Censky et al. (1998). In October 1995, at least 15 individuals of the lizard species *Iguana iguana* washed up on the island of Anguilla in the eastern Caribbean, along with large volumes of flotsam; the species is not native to the landmass. Notably, in the month prior, the region had been affected by two hurricanes, which could have generated both rafts and reptile passengers. Based on an analysis of the storm tracks, the island of Guadalupe, ~240 km to the south-southeast, was identified as the likely source. A second classic example concerns a giant tortoise from the western Indian Ocean island of Aldabra (referred to as *Dipsosaurus dussumieri* in the original work, now called *Aldabrachelys gigantea*) that washed up on coast of Tanzania in December 2004 (Gerlach et al. 2006). In making the crossing, the emaciated female traveled at least ~770 km, in the process acquiring skirt of barnacles, indicating that it must have been at sea for a protracted period.

A quarter of a century later, George Simpson (1940) (**Figure 3f**) followed up. A key issue for him was the idea that if Africa and Madagascar had once been linked by a causeway, then appreciably more colonizations should have taken place, as has been the case following the formation of the Isthmus of Panama ~3 Mya (Late Pliocene) (see also Simpson 1980, O’Dea et al. 2016). Instead, the Malagasy fauna was heavily filtered, with the various groups representing just a fraction of those that would have been present on Africa when the colonizations were made. This led Simpson to coin the term sweepstakes dispersal: A small number of taxa could potentially make such crossings (today viewed as those with small body masses as well as conducive physiologies and/or life traits), that is, participate in the lottery, but with the number of winning tickets being minuscule (see the sidebar titled Further Insights into the Overwater Dispersal Mechanism).

Toward the end of the twentieth century, the application of the then recently developed molecular phylogenetics and associated age-calibrated time trees provided quantitative information to constrain the arrival times of the different clades (the earlier, anatomically based ages were, in comparison, informed guesses). Numerous studies demonstrated that the bulk of the Madagascar colonizations occurred well after the island had become geotectonically isolated, a process that started ~160 Mya (Middle Jurassic) and culminated ~85 Mya (Late Cretaceous) (see Ali & Aitchison 2008), thus requiring overwater dispersal or passage across a land bridge. The first associated publication (Yoder et al. 1996) was for the lemurs and showed that the group was the result of a single colonization between 62 and 54 Mya (Early Paleocene–Early Eocene) (**Figure 4**); more recently, Gunnell et al. (2018) used paleontological data from Africa to argue that the aye-aye formed a separate clade and that the two primate lineages arrived in the middle of the Cenozoic.

## FURTHER INSIGHTS INTO THE OVERWATER DISPERSAL MECHANISM

Additional insights in support of raft-related colonizations are provided by a number of key works. Houle (1998 and references therein) and Matthew (1915) showed that sizable rafts have been documented numerous times in open-ocean settings. Van Duzer (2004) reviewed the enormous literature on floating islands and their encounters by people. The supplementary materials associated with the study by O’Dea et al. (2016) link to a video of an ~150-m-long vegetation mat, resplendent with several upright trees, racing down the in-flood Chagres River of Panama. Ali et al. (2021) documented a tree-dotted raft floating down Colombia’s Magdalena River carrying a troop of red howler monkeys (*Alouatta seniculus*).

At about the same time, but without apparent prompting by Yoder et al. (1996), McCall (1997) dismissed the idea of rafting/floating colonizations, although, curiously, he failed to acknowledge either Matthew (1915) or Simpson (1940). Instead, he proposed that between 45 and 26 Mya Madagascar and Africa had been connected because the Davie Ridge was purportedly exposed (**Figure 4**). However, the supporting geological data (Simpson et al. 1974, Leclaire et al. 1989, Bassias 1992) were rather scant (this was explored in detail by Ali & Hedges 2022). McCall's digression aside, though, overwater dispersal was called upon in numerous molecular studies (**Figure 4**), notably by Vences et al. (2003) in a work dealing with a frog clade [*Heterixalus* genus; almost all amphibian species find it difficult to overwater disperse due to their vulnerability to saltwater desiccation (Hopkins & Brodie 2015)] and Poux et al. (2005) in a study of the then four land-mammal groups.

Almost inevitably, the growing body of literature arguing for water transport triggered a reaction from those who were skeptical of its role, such as Masters et al. (2006) and Stankiewicz et al. (2006). The latter questioned the probability scenarios that Simpson (1952) had explored [incidentally, Matthew (1915) and Darlington (1938) had presented similar sorts of theoretical musings]. Then, they considered the modern-day ocean currents and atmospheric patterns in and over the southwest Indian Ocean–Mozambique Channel region, as well as the possibility that tornadoes and cyclones carried animals through the air. They concluded that colonizations of Madagascar by rafting/floating or by wind transport were impossible. In response, Ali & Huber (2010) presented paleoceanographic models based on numerical-simulation data that Huber had then recently generated. For ~40 Mya (late Middle Eocene), they showed that the regional surface-water circulation paths were very different from those of today, with Africa-to-Madagascar flows occurring during the austral summers. Furthermore, on roughly 100-year timescales, the streams were markedly faster and would have been capable of transporting rafts across the northern Mozambique Channel in 30–35 days. However, by 20–15 Mya, the system had evolved into the modern-day one, where west–east flows between the two landmasses are rare; the root cause of this change was almost certainly Africa–Madagascar's northward drift relative to the northwest corner of the Indian Ocean Gyre, in the process reconfiguring the subregional currents (see also Garrison 2010).

The notion of rafting, however, continued to trouble some researchers (e.g., Mazza 2014). Subsequently, Mazza et al. (2019) put together a major review where they argued against the mechanism. They argued that food and freshwater were absent during the journeys, which, when combined with the stresses imposed by a salty environment, precluded mammals from making all but the shortest of overwater passages. Another concern for them was the restricted size of the colonizer groups' gene pools (conceivably, a fertilized female and the brood or egg clutch she might later deliver). Deleterious inbreeding issues would, they thought, make it impossible for founding populations to survive beyond the first few generations.

Ali & Vences (2019) countered each argument and pointed out that the various land-mammal taxa from around the globe that were explained by the mechanism were somewhat unusual in that they had life histories and/or physiological traits (e.g., a hibernation phase, the ability to enter into torpor, and/or low energy requirements related to their small size) that greatly enhanced the chances that they would survive a lengthy overwater crossing (see the sidebar titled Truly Isolated Islands and Archipelagoes Where Overwater Dispersal Must Have Taken Place). However, this failed to assuage the antirafters, and Masters et al. (2021) responded with an even stronger dismissal of the process as well as a rejection of the paleoceanographic modeling that had been carried out by Ali & Huber (2010). Furthermore, to advance their case, they postulated a scenario whereby Africa and Madagascar had been connected by land bridges or stepping-stone chains at three separate times in the Cenozoic: 66–60, 36–30, and 12–5 Mya. Related arguments were also presented by Aslanian et al. (2023). However, because these arguments were responding to

## TRULY ISOLATED ISLANDS AND ARCHIPELAGOES WHERE OVERWATER DISPERSAL MUST HAVE TAKEN PLACE

Christmas Island in the eastern Indian Ocean, the São Tomé and Príncipe islands in the Gulf of Guinea, and the Galápagos Archipelago in the eastern Pacific Ocean are three locations where overwater dispersal must have taken place. All form the tops of volcanic edifices that rise from a deep ocean floor, and there is no possibility that any were ever connected to a continent by a causeway. Notably, each one hosts multiple reptile and land-mammal clades, with the Gulf of Guinea group also having amphibians (Ali et al. 2020, Ali & Fritz 2021, Bell et al. 2022). Moreover, since Christmas Island and the Galápagos have only existed since 4–5 Mya, this indicates that colonization events are reasonably frequent, at least on geological timescales.

ideas in two recent publications of ours—the first on the southwest Indian Ocean region’s palaeogeographical development (Ali & Hedges 2022) and the second on Madagascar’s land-vertebrate colonization record (Ali & Hedges 2023)—which we summarize in Sections 3.1 and 3.2, they are addressed afterward, in Section 3.3.

### 3. A TWO-PRONGED EXAMINATION OF THE ISSUE

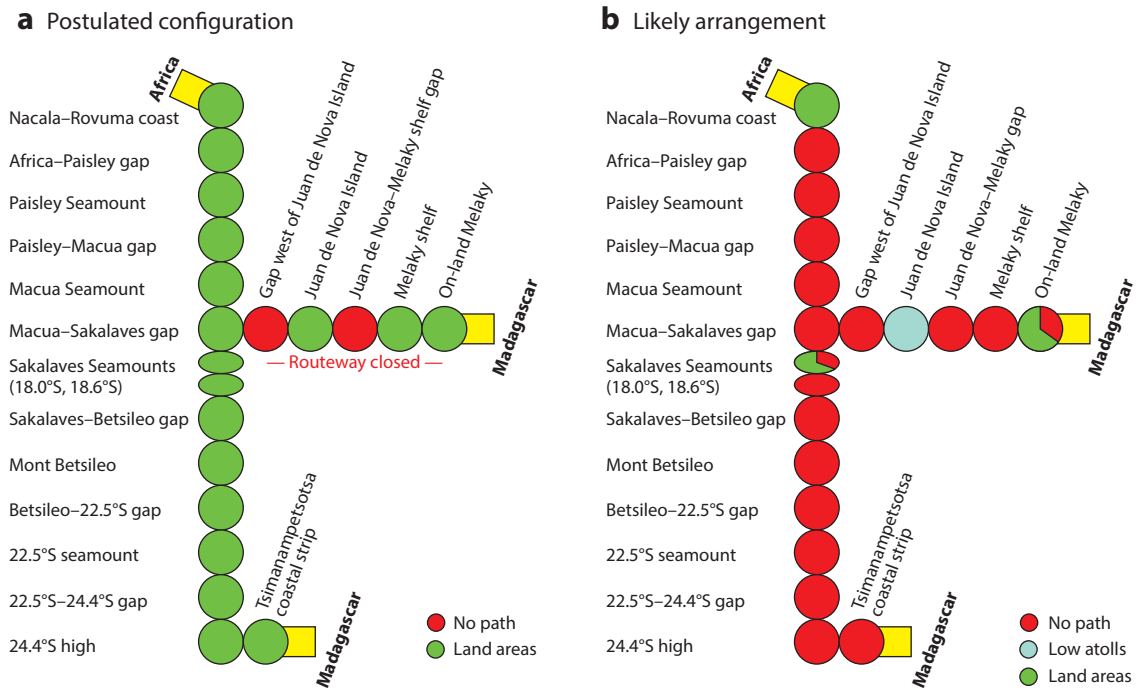
With the discussions on the Madagascar land-vertebrate colonizations seemingly more polarized than at any time in the past, we sought to throw new light on the issue in the form of a two-pronged evaluation. The first comprised an exhaustive review of the geological and geophysical data that were relevant to each of the elements in the land-bridge proposals (Ali & Hedges 2022). The second focused on the arrival records of the different land-vertebrate clades (Ali & Hedges 2023) for which a sizable body of data was then available; temporal clustering would be strongly supportive of short-lived, dry-land paths, whereas establishment events that had occurred randomly through time would be a key expectation of overwater dispersal.

#### 3.1. Geological and Geophysical Evidence for Land Bridges Between Africa and Madagascar

Prior to 2010, the literature base for assessing land bridges between Africa and Madagascar was relatively small and comprised studies of a somewhat reconnaissance nature. Deep Sea Drilling Project Leg 25 (June–August 1972) cored 676 m into the seabed a short distance to the north-northeast of the Macua Seamount (Site 242) (**Figure 1**), with the principal findings published by Leclaire (1974) and Simpson et al. (1974). Seismic data (reflection and/or refraction) were presented by Lort et al. (1979), Mougénot et al. (1986), Masclé et al. (1987), and Malod et al. (1991), and results from dredge-haul sampling and shallow-penetration piston coring at many spots along the Davie Ridge (between the Paisley Seamount and the Sakalaves Seamounts) (**Figure 1**) were reported by Leclaire et al. (1989), Bassias & Leclaire (1990), and Bassias (1992). Useful information on the paleogeography of Africa’s Nacala–Rovuma coastal strip was provided by Salman & Abdula (1995) and Key et al. (2008).

In contrast, the last decade has seen the publication of vast amounts of high-quality information, including focused studies of several bathymetric highs within the Mozambique Channel (Courgeon et al. 2016, 2017, 2018; Jorry et al. 2016; Leroux et al. 2020) and numerous regional-scale seismic surveys (Leinweber et al. 2013; Mahanjane 2014; Franke et al. 2015; Castelino et al. 2016; Klimke et al. 2016; Mueller & Jokat 2017; Tuck-Martin et al. 2018; Müller & Jokat 2019; Vormann et al. 2020; Dofal et al. 2021; Vormann & Jokat 2021a,b). Additionally, the



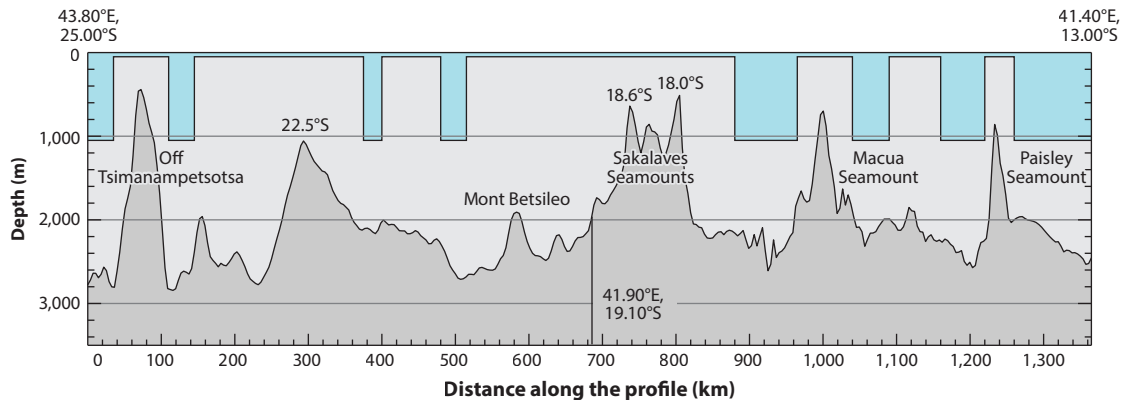


**Figure 5**

Evaluation of the land-bridge connectivity schema proposed by Masters et al. (2021) for 36–30 Mya (Eocene–Oligocene boundary time), based on the analysis of Ali & Hedges (2022). The hypothesized configuration is shown in panel *a*, while the likely arrangement is presented in panel *b*. In panel *a*, the green and red circles indicate supposed land and areas with no path, respectively, whereas in panel *b*, the green, aqua, and red circles/ellipses correspond to true dry land, low-elevation atolls, and areas with no path, respectively. Where sectors formed land for part of the 6-million-year interval, the circles/ellipses are used like clock dials, where 36 and 30 Mya are set at 12 o’clock and the pie slices reflect the intervals of submergence and exposure. Figure adapted from Ali & Hedges (2023).

industry-supported PhD thesis of Delaunay (2018) provided critical insights into the geology and paleogeography of the eastern side of the Mozambique Channel and the western half of Madagascar. Using this information, it was possible for us to scrutinize the land-bridge proposals of McCall (1997) and Masters et al. (2021). However, one of the problems with their models concerned the vagaries of the geographical descriptions and definitions. Therefore, to keep both the evaluations and the discussions focused, we developed a topological schema using the bathymetric highs as well as the intervening gaps that are portrayed in **Figure 1**. It was thus possible to reconstruct the various hypothesized pathways before interrogating the literature cited above to deduce the actual configuration. An example is shown in **Figure 5**, which is the 36–30-Mya arrangement of Masters et al. (2021). Here, as well as with the others of Masters et al. (2021) (66–60 and 12–5 Mya) plus the one by McCall (1997) (45–26 Mya), the idea that causeways or closely spaced sets of stepping stones ever linked Africa and Madagascar in the Cenozoic can be dismissed. Since the start of that era, and well before, the amount of exposed ground in the Mozambique Channel has always been negligible.

A critical final point on this topic is demonstrated in **Figure 6**, which shows a bathymetric profile of the Davie Ridge/Fracture Zone with the 12–5-Mya routeway proposal of Masters et al. (2021) overlaid. Assuming the latter had dimensions of 1,200 km × 20 km × 2.5 km, and allowing for several small breaks, its volume would have been ~50,000 km<sup>3</sup>. As the modern-day



**Figure 6**

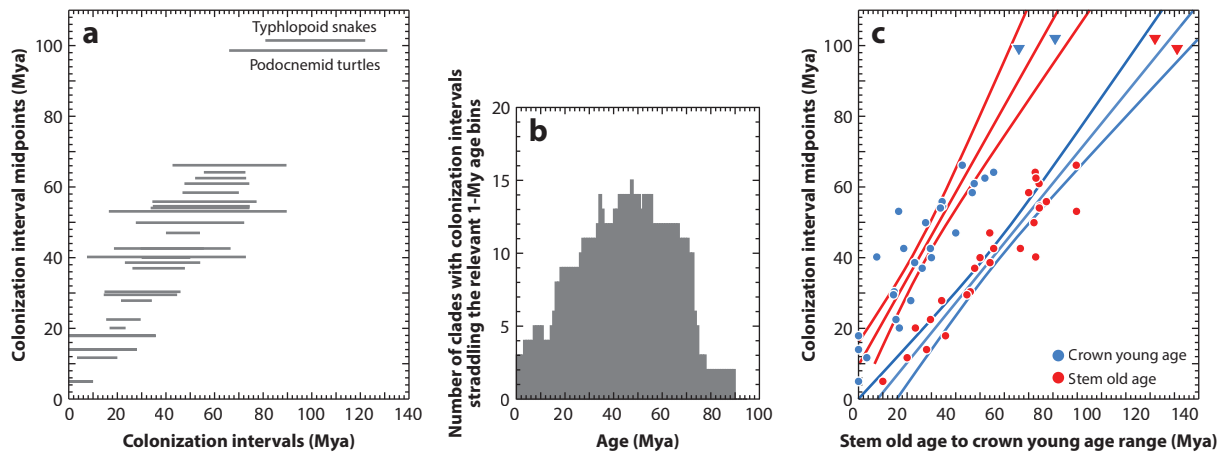
Modern-day profile of the Davie Ridge/Fracture Zone (*dark gray*) using data extracted from GeoMapApp (Ryan et al. 2009), with the 12–5-Mya land bridge of Masters et al. (2021) (*light gray*) overlaid. The second minus the first is the ocean floor that has supposedly been removed since 5 Mya and equates to  $\sim 40,000 \text{ km}^3$  of rock, assuming the bathymetric high had an average width of 20 km. Figure adapted from Ali & Hedges (2022).

high accounts for  $\sim 20\%$  of this,  $\sim 40,000 \text{ km}^3$  of rock must have been removed since the Early Pliocene. Arguably, this number could be reduced to  $\sim 32,500 \text{ km}^3$  if the 375 m of subsidence that has taken place since  $\sim 5$  Mya at the  $18^\circ\text{S}$  high on the Sakalaves Seamounts (Courgeon et al. 2018) was applied to the whole of the Davie Ridge. However, the core of the edifice is the product of localized magmatism along the lineament; therefore, the downward motion, which is almost certainly related to lithospheric cooling and contraction, likely has a relatively small geographical extent. There are two obvious questions. First, what was the mechanism that stripped off all of the rock? And second, where is that material now? Significantly, none of the geophysical surveys of the Davie Ridge area (e.g., Mougenot et al. 1986, Mascle et al. 1987, Malod et al. 1991, Vormann & Jokat 2021a) have identified detritus piles that could be related to the feature.

### 3.2. New Method for Probing the Madagascar Assemblage's Colonization Record

To quantitatively evaluate the Madagascar land-vertebrate colonization record, we devised a probabilistic clade-arrival method (Ali & Hedges 2023). The first step in the process required us to establish the time window for each clade's arrival. The second involved summing those data to generate an assemblage colonization profile.

**3.2.1. Colonization intervals determined for each clade.** In developing our assemblage-assembly approach (Ali & Hedges 2023), we generated a colonization record marking the earliest and latest possible times of arrival for each of the Malagasy clades (figure 7 in Ali & Hedges 2023; a lack of key information for the *Geckolepis* and *Paragehyra* geckos meant that they had to be omitted from the analysis). The values for the first were based on the older-age uncertainty of each lineage's molecular-clock stem age (i.e., the time of splitting with the genetically nearest off-island relative), while the values for the latter were based on the younger-age uncertainty of the crown age (i.e., when divergence within the insular clade first took place). In some cases, the latter could be refined using fossil-related age dates (i.e., proof of earlier presence). Where there was no record of divergence, the limit had to be set at 0 Mya (see also figure 6 in Ali & Hedges 2023).

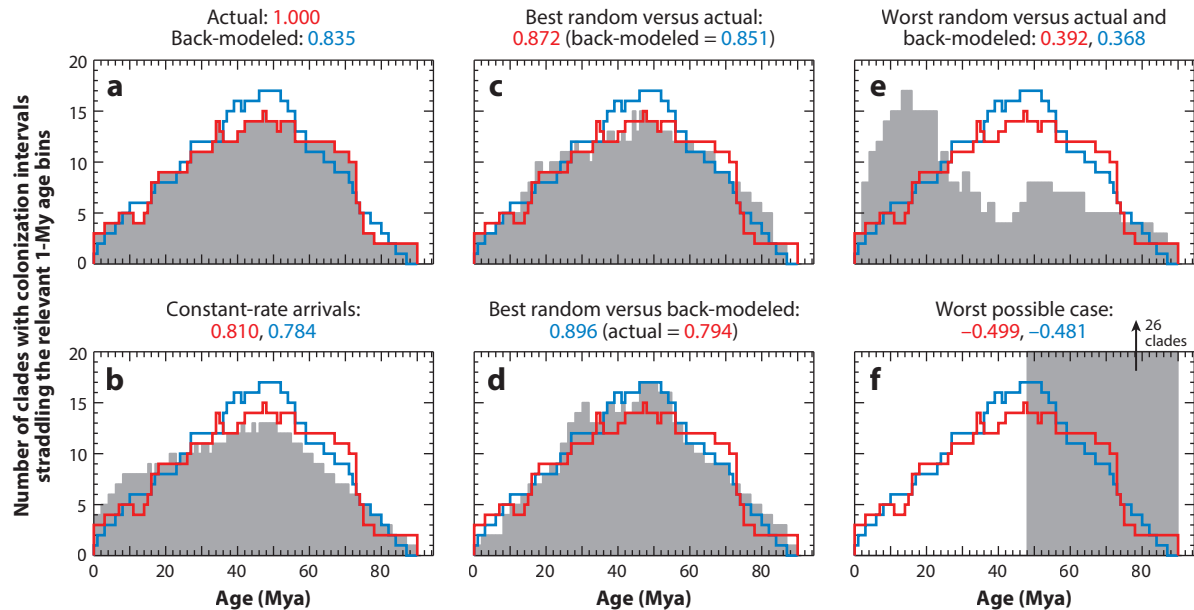


**Figure 7**

(a) Individual colonization intervals for 28 clades plotted against their midpoint values. (b) Colonization profile for 26 of the land-mammal, amphibian, and reptile clades (excluding the podocnemid turtles and typhlopoid snakes). In all cases, each clade is counted in all of the bins it can occupy, with each bin being 1 My. (c) Simulated colonization profiles based on best-fit lines through the stem old ages and crown young ages, calculated as stem old age =  $(1.182 \times \text{CIMP}) + 7.823$  ( $N = 26$ ,  $R^2 = 0.883$ ) and crown young age =  $(0.818 \times \text{CIMP}) - 7.823$  ( $N = 26$ ,  $R^2 = 0.784$ ), where CIMP is the colonization interval midpoint. Figure adapted from Ali & Hedges (2023).

**3.2.2. Colonization intervals combined to create an assemblage colonization profile.** The next stage in the process was to stack the colonization intervals to create a colonization profile [as the podocnemid-turtle and typhlopoid-snake clades had conspicuously old arrival windows, indicating they were probably present on Madagascar prior to its tectonic isolation  $\sim 85$  Mya (middle Late Cretaceous, related to the India–Seychelles block’s rifting from the island), they were excluded from the analysis]. This is perhaps best visualized as lowering each of the colonization intervals shown in **Figure 7a** onto the plot’s  $x$  axis, thus creating **Figure 7b**. Additionally, using the old and the young ages of the colonization intervals combined with the colonization interval midpoints (**Figure 7c**) made it possible to generate synthetic colonization intervals, of specific instants in time, for use in simulation modeling; the related equations are included in the caption for **Figure 7**. An important related check involved back-modeling the colonization profile using the actual colonization interval midpoints for each of the clades and the equations given in the figure caption to generate a synthetic profile to see how well it matched the actual data (**Figure 8a**). To quantify this comparison as well as the comparisons with other simulations, two metrics were used. The first was a simple measure of fit based on  $(C_{\text{tot}} - C_{\text{nm}})/C_{\text{tot}}$ , where  $C_{\text{tot}}$  is the total number of cells associated with the actual data and  $C_{\text{nm}}$  is the number of nonmatching cells. The second made use of the chi-squared test; for each 1-My age bin, there is an observed value related to the simulation as well as an expected value based on the actual data. With the first, the fit of the back-modeled data profile is 0.835, while  $p = 1$ . With most subsequent simulations, the values for comparisons with both the actual and back-modeled profiles are reported, and in graphical presentations the two histogram-enveloping lines are shown (key data are presented in table 2 of Ali & Hedges 2023).

A suite of allied simulations are shown in **Figure 8b–e**. The constant-rate simulation (**Figure 8b**), which involves one arrival every 2.7 My starting at 68.85 Mya and ending at 1.35 Mya, provides excellent matches. Here, the fits against the actual and back-modeled data profiles are 0.810 and 0.784, respectively, with  $p$  values of 0.993 and 0.945, respectively (table 2



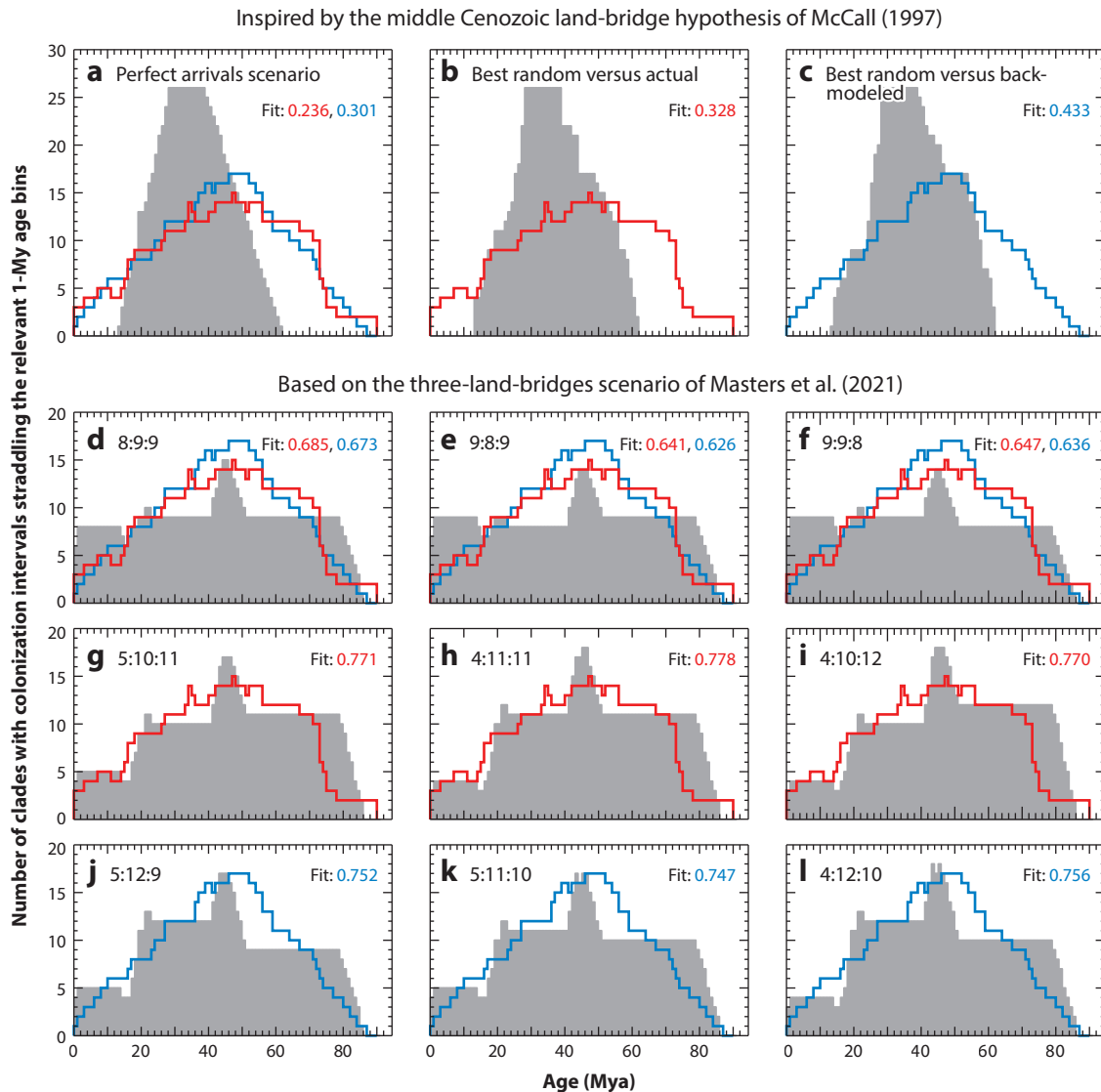
**Figure 8**

Initial evaluation of the Madagascar land-vertebrate colonization data. Panel *a* shows the colonization profile associated with the actual data (gray shaded region and red line) and with the back-modeled data (blue line). The fit values (shown in red and blue above each plot) provide a simple measure of the match. Various simulations are shown in panels *b–f*, with the profiles from panel *a* overlaid. In panel *b*, a colonization occurs every 2.7 My starting at 68.85 Mya and ending at 1.35 Mya (26 clades), a scenario that is termed constant-rate arrivals. Panels *c–f* show 4 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. Panels *c* and *d* show the best-fit simulations relative to the actual and back-modeled colonization profiles, panel *e* shows the worst-fit simulation, and panel *f* shows the worst possible case. Figure adapted from Ali & Hedges (2023).

of Ali & Hedges 2023). However, these are values bettered by approximately one-sixth (against the actual data profile) to one-third (against the back-modeled profile) of the 400 random-arrival simulations (e.g., **Figure 8c,d**).

Concerning the land-bridge proposals of McCall (1997) and Masters et al. (2021), it was not possible to directly test any of their scenarios, as they were based on smaller subsets of the clades that were included in our analysis. However, we were able to generate simulations that were rooted in their ideas. The notion that the clades arrived by way of a middle Cenozoic (45–26 Mya) causeway, in line with the proposal of McCall (1997), can be rejected because the fits with the actual and back-modeled profiles are poor (e.g., **Figure 9a–c**) (in all cases,  $p \leq 0.001$ ). Concerning the proposal of three temporally distinct land bridges (Masters et al. 2021), all simulations where there are close to equal numbers of arrivals at 12–5, 36–30, and 66–60 Mya (8:9:9, 9:8:9, and 9:9:8) can be also be rejected (**Figure 9d–f**). In fact, the best matches were for the simulations associated with the ensembles 5:12:9 and 4:12:10 (table 2 in Ali & Hedges 2023) (**Figure 9j,l**), but they are still not as good as the random-arrival ensemble that **Figure 8** is based on.

In summary, the idea that Madagascar’s amphibians, land mammals, and reptiles colonized the island via temporary dry-land conduits can be rejected on the grounds that there is no pronounced temporal clustering in their arrivals. Instead, the landings occurred close to randomly through time, which is an expectation of the overwater-dispersal mechanism. Moreover, the heavy screening of the African faunal-group types that established themselves on the landmass offers further support for this process.



**Figure 9**

Colonization profiles for example model-test simulations, each with 26 arrivals. Apart from panels *b* and *c*, all of the scenarios are perfect in that one clade arrives at each available colonization instant. The simulations shown in the top row (panels *a–c*) are inspired by the mid-Cenozoic (45–26 Mya) land-bridge proposal of McCall (1997). The other rows are scenarios that draw on the proposal of Masters et al. (2021, 2022), i.e., three short-lived land bridges/stepping-stone chains at 12–5, 36–30, and 66–60 Mya. Here, the three-number ratios (e.g., 8:9:9 or 5:12:9) indicate the respective numbers of establishment events during those time windows. The simulations associated with the third and fourth rows (panels *g–l*) show the better fit and chi-squared values when each of the windows has stochastic arrivals, but these are still lower than those with 26 completely random arrivals (associated with **Figure 8**). Figure adapted from Ali & Hedges (2023).

### 3.3. Criticism and Response

As mentioned above, Aslanian et al. (2023) challenged our recent works, claiming that the paleogeographical review, which showed no land bridges (Ali & Hedges 2022), and the interpretation of

the clade-colonization record, which demonstrated a lack of temporal clustering as well as strong physiotype filtering (Ali & Hedges 2023), were flawed and that the three-causeway hypothesis of Masters et al. (2021) remained valid. However, no explanation was offered as to why our appraisal of the geological evidence, showing an absence of subaerial paths in the past, was incorrect. Instead, they repeated their primary reasoning (from Masters et al. 2021) that land bridges were needed for the physiological well-being of the dispersing animals, a hypothesis that we had falsified with geological data. Moreover, the colonization record they compiled (summarized as figure 3 in Aslanian et al. 2023) was based on on-island divergence instants, but instead of just using clade crown ages, they mixed in clade stem ages and sometimes the dates of subfossil material. Notably, in all cases there were no data-error bounds. This contrasts with the colonization interval approach we adopted (Ali & Hedges 2023), which fully accommodated the temporal uncertainties associated with each clade's arrival. Also, there were further issues with the way that Aslanian et al. (2023) compiled and handled the biological data. For instance, the main group of lemurs was treated as four assemblage-building records (for *Cheirogaleus*, *Indri*, lemurs, and sportive lemurs), which is flawed because they are the result of a single establishment event (e.g., Gunnell et al. 2018). Additionally, the now-separate aye-aye primate clade was overlooked, while only 11 reptile groups were included when there are 18 (from 20 in total) that can be used for the testing of colonization models (Ali & Hedges 2023). Aslanian et al. (2023) also included in their analysis 17 land-bird and bat lineages. However, the volant vertebrates are usually omitted in analyses focused on the testing of land-bridge colonization models because they readily disperse (e.g., MacCracken et al. 1997, Russell et al. 2015, Valente et al. 2020) and hence confound the results.

#### 4. CONCLUSIONS AND OUTLOOK

The means by which Madagascar's land-vertebrate groups arrived on the mini-continent has puzzled scientists for well over 150 years. Early explanations argued that these groups were Mesozoic relict lineages that ambled over to the landmass before becoming trapped when Madagascar became an island (e.g., Sclater 1864, Wallace 1880). Subsequently, researchers invoked first temporary land bridges (e.g., Grandidier 1905) and then overwater dispersal (e.g., Matthew 1915, Simpson 1940) to explain the colonizations. A recent review of the geological and geophysical evidence (Ali & Hedges 2022) ruled out the emergent-causeways option, notably the proposals of McCall (1997) and Masters et al. (2021). At no time during the Cenozoic has there been a continuous dry-land connection between Madagascar and Africa, nor has there been a collection of islands that formed a stepping-stone chain. Furthermore, a detailed examination of the biological record (Ali & Hedges 2023) indicated that the bulk of the clades (26 out of 30) are best explained by temporally stochastic arrivals, which is consistent with chance overwater-dispersal events. Most of these took place during the Cenozoic (66–0 Mya), with perhaps one or two dating to the latest Cretaceous. Additionally, two appreciably older colonizations, associated with the podocnemid turtles and typhlopoid snakes, likely pre-dated Madagascar's tectonic isolation ~85 Mya (middle Late Cretaceous). Unfortunately, due to phylogenetic uncertainties, two gecko clades, *Geckolepis* and *Paragehyra*, could not be included in the assessment.

Concerning future studies, we anticipate that both the paleogeographical evaluation scheme developed by Ali & Hedges (2022) and the colonization-profile analysis method of Ali & Hedges (2023) will find application in other marine-island biogeographical studies. Systems that date from the Miocene or earlier, especially those where the mode of colonization is contested—such as the Galápagos Islands, the Greater Antilles, New Caledonia, New Zealand, Seychelles, Socotra, Sri Lanka, and Sulawesi—are obvious targets.



## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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