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A review of geological evidence bearing on proposed Cenozoic land connections between Madagascar and Africa and its relevance to biogeography

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ABSTRACT

For a variety of reasons, Madagascar's rich and highly distinctive faunal assemblage has long attracted attention. Recurring questions with the associated studies have concerned when and how the ancestors of the various clades reached the island. For the land-bound animals, the common view is that they arrived after the Cretaceous on 'rafts' that washed in from Africa. However, this centuries-old discussion has been periodically spiked with proposals for land-bridges, with a recent one arguing for three separate causeways or stepping-stone chains connecting Africa and Madagascar in the early, middle, and late Cenozoic (66–60 Ma, 36–30 Ma, and 12–5 Ma). Here, the general idea of former causeways spanning the Mozambique Channel is evaluated based on an extensive survey of the related geological and geophysical literature, a large portion of which dates from the last half-decade. The analysis, which makes use of a newly-developed topological schema, indicates that only a small number of the supposed dry-land sub-paths were actually subaerial during each of the postulated colonization windows. Notably, during the Early Oligocene, a 220–250 km^2 pinnacle in the Sakalaves Seamount group formed a volcanic 'high-island'. The other offshore sectors that were exposed would have been atoll crowns: Juan de Nova Island throughout the Cenozoic and the northern Sakalaves in the Late Miocene. However, it would have been challenging for most land animals to exist on those low-elevation carbonate platforms for any length of time. Therefore, the notion of Africa and Madagascar being linked in the Cenozoic by terrestrial walkways can be regarded as falsified. Over-water dispersal best explains how 26 of Madagascar's 27 land-vertebrate clades colonized the landmass. The exception, a group of small, soil-dwelling snakes, is likely a relict lineage whose ancestors were present on the island prior to Madagascar's geographical isolation that resulted from the tectonic block's breakup with India-Seychelles *c.* 85 Ma.

1. Introduction

Although Madagascar's iconic land-bound vertebrate assemblage comprises >900 species, this diversity has developed from no more than about thirty reptile, land-mammal, and amphibian clades (Crottini et al., 2012). For instance, the four extant land-mammal groups, (carnivorans, lemurs, rodents, and tenrecs), are today represented by between 10 and 100 species (Mittermeier et al., 2021). The marked difference between Madagascar's mammal suite and the one on Africa combined with its highly unbalanced/filtered nature led William D. Matthew (1915) to propose that the colonizations had resulted from over-water dispersal events (as opposed to range expansion via a former land-route) at various times in the early and middle Cenozoic, and possibly the Cretaceous. The issue was further considered by George G. Simpson (incidentally, Matthew's protégé), who developed the associated 'Sweepstakes' colonization concept (1940). The land-mammal taxa that crossed from Africa were 'drawn' from a pool of small-bodied animals and transported passively to the island aboard vegetation rafts (see also O'Dea et al., 2016; Ali et al., 2021). Key to Simpson's argument was the idea that if a land-bridge had connected the two landmasses, then appreciably more colonizations should have taken place, as has been the case with the Panama Isthmus. In that example, the joining of South America with Central America (and North America) *c.* 3 Ma led to a large bi-directional transfer of land-vertebrate genera (e.g. Simpson, 1980;

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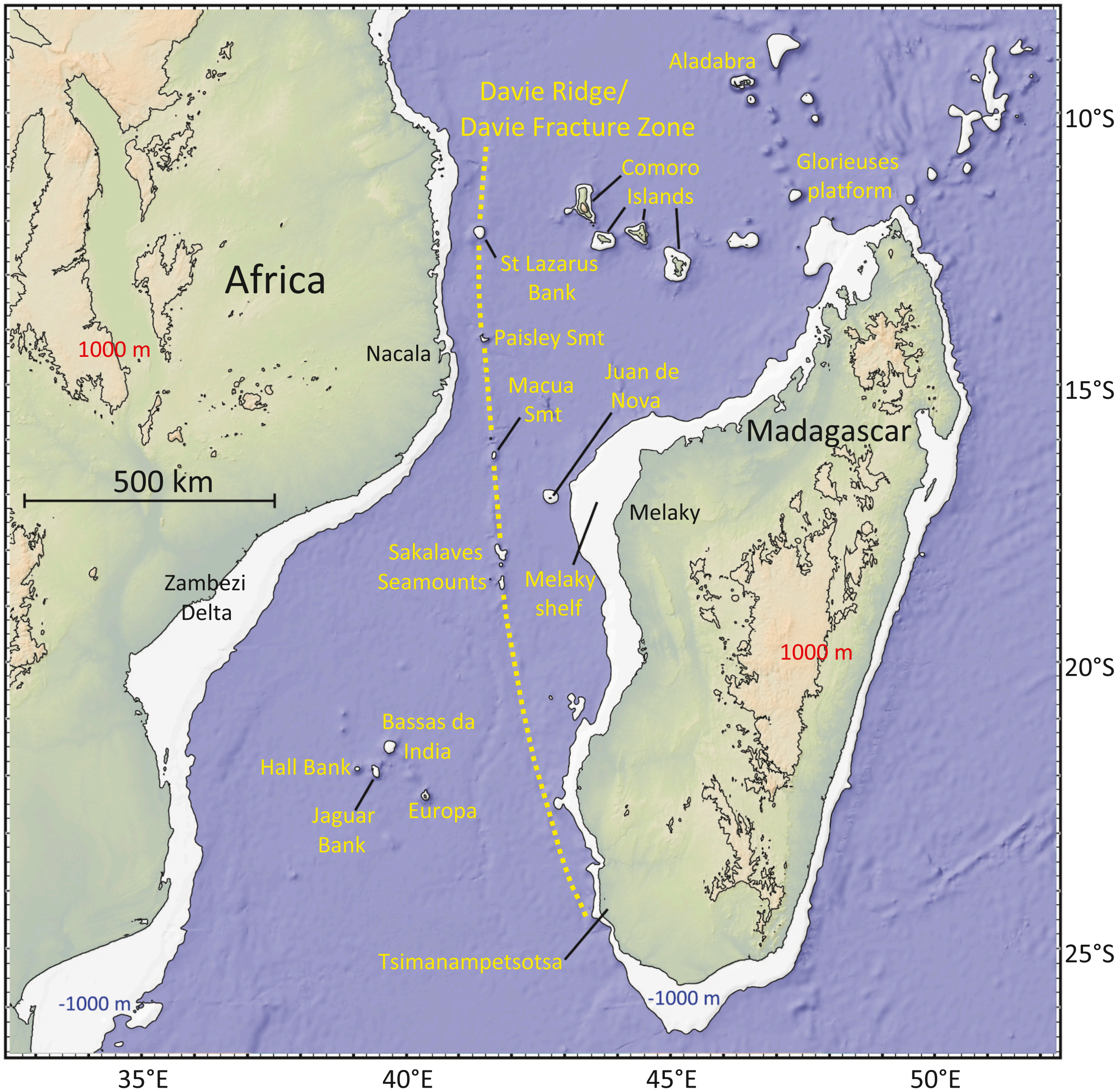

Fig. 1. Map of the south-west Indian Ocean region showing the physiographical features mentioned in the text. The base image was generated using *GeoMapApp* (Ryan et al., 2009).

O'Dea et al., 2016). However, despite the Matthew-Simpson view having garnered wide acceptance (e.g. Krause, 2003; de Queiroz, 2005, 2014; Vences, 2004; Rabinowitz and Woods, 2006; Yoder and Nowak, 2006; Van der Geer et al., 2010; Samonds et al., 2012), it has at various times been challenged (McCall, 1997; Stankiewicz et al., 2006; Masters et al., 2006; Mazza, 2014; Mazza et al., 2019). Resistance to the view is rooted in the belief that land vertebrates, especially the land-locked mammals, cannot survive such journeys, which would take a few to several weeks (Ali and Huber, 2010), due to a lack of food and an absence of freshwater. Furthermore, those waifs that endured the passages, as well as their near descendants, would have been susceptible to extirpation through selection pressures due to their restricted genetic diversity. Ali and Vences (2019) countered all three of these arguments and emphasized the fact that the sorts of land mammals that had established themselves on the remote islands and archipelagoes, for instance on the Canaries, Christmas Island, Galápagos Islands, and Madagascar, had one or more characteristics that facilitated the process: small body mass, low energy requirement, ability to go into torpor, and propensity to hibernate. When Mammalia are viewed as a whole, very few taxa emerge as victors in a 'Simpson lottery.'

Unencumbered by these considerations, however, Masters et al. (2021, 2022) have recently proposed that Madagascar's land-vertebrates colonized the island via three temporally-separate cause-ways at 66–60 Ma, 36–30 Ma, and 12–5 Ma. It should be noted, though, that the notion of former terrestrial connections is not new. McCall (1997) surmised that a land-bridge existed 45–26 Ma based on a combination of biological and geological data. Much earlier, and well before the theories of continental drift and plate tectonics had been formulated, Wallace (1880) argued for a Cretaceous-age routeway. This was preceded by Sclater's (1864) proposal for Madagascar having once being connected to Africa, the Indian subcontinent and Southeast Asia via a now-sunken landmass that he labelled 'Lemuria'.

As Madagascar's biota is the focus of an enormous amount of research activity, and where the interpretation of a clade's history is dependent upon knowing the time since it ancestral colonization event, that in turn reflects the mode of arrival, this review evaluates the geological evidence for former land-bridges. The proposals of Masters et al. (2021, 2022) are the primary focus, but it is straightforward to extend the analysis to the model of McCall (1997). Also, it is possible to consider other issues and to touch upon the palaeogeographical scenarios of Sclater (1864) and Wallace (1880).

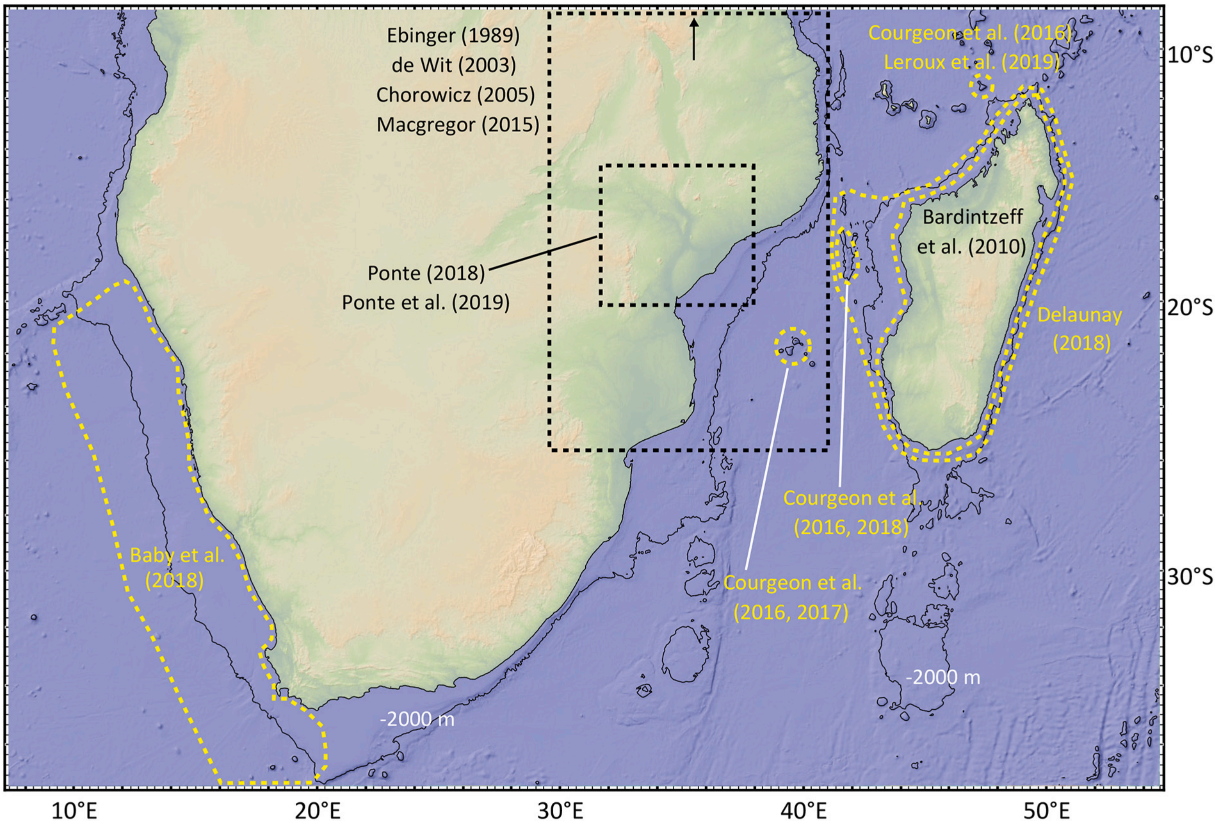

Fig. 2. Map showing the study locations/areas that form the basis of the Masters et al. (2021) causeway proposals. The base image was generated using *GeoMapApp* (Ryan et al., 2009).

2. Publications underpinning the Masters et al. 'three-causeways' model

The palaeogeographical aspect of Masters et al. (2021, 2022) was constructed around three physiographical maps of the Mozambique Channel at the aforementioned time windows. To facilitate discussions, we label the scenarios/land-bridges 'Early Paleocene' for 66–60 Ma, 'Eo-Oligocene' for 36–30 Ma and 'Late Miocene' for 12–5 Ma. However, with the first and the third there are slight discrepancies with regards to the formally defined geological intervals (e.g. Walker et al., 2018); the Early Paleocene spanned 66.0–61.7 Ma while the Late Miocene was 11.6–5.3 Ma. In their caption for Fig. 4, Masters et al. (2021) stated that the reconstructions were developed from Baby et al. (2018), Courgeon et al. (2017), Delaunay (2018), Leroux et al. (2020), Ponte (2018), and Ponte et al. (2019); the names of the study locations/areas and the researchers who reported on them are shown in Fig. 1 and Fig. 2, respectively. The Courgeon et al. (2017) citation was, though, an apparent under-sight as it focused on the developments of three neighbouring seamounts in the southern Mozambique Channel: Bassas da India, Hall Bank, and Jaguar Bank (Fig. 1, Fig. 2). Instead, Courgeon et al. (2016) had a broader coverage and included not only those edifices, but the Sakalaves range on the Davie Ridge, and the Glorieuses atolls to the north of Madagascar (Fig. 1, Fig. 2; see also Leroux et al., 2020). Courgeon et al. (2018) presented a detailed examination of the physiographical evolution of the Sakalaves Seamounts based on seismic and dredge-sample data (Fig. 1, Fig. 2). Additionally, the Early Paleocene scenario drew upon Bardintzeff et al. (2010), which was an investigation of the Late Cretaceous and Cenozoic volcanic activity on Madagascar (Fig. 2). For the Eo-Oligocene causeway, Ebinger (1989), de Wit (2003), Chorowicz (2005), and Macgregor (2015) were cited (Fig. 2), all with regards to the initiation of tectonic activity in the East African Rift system. However, as will be shown below, the body of geological evidence does not support the idea of Africa and Madagascar having been connected in the Cenozoic by terrestrial pathways.

3. Basis for McCall's 45–26 Ma land-bridge

McCall (1997) proposed that the Davie Ridge (Fig. 1) played a key role in the lemur, tenrec, carnivoran, and rodent colonizations. First, he presented biological arguments suggesting it was impossible for land-mammals to over-water disperse from Africa to Madagascar. He then made the case for a land-bridge, summarizing key geological data from areas along and adjacent to the Davie Ridge. Notably, the sedimentary sequence recovered at DSDP Site 242 (676-m-long) on the Macua Seamount's northeast flank (15.84°S, 41.82°E; Fig. 2) indicated to him that the locality was emergent until the Late Eocene, but this was simply because the succession was considered to rest upon a continental basement. Actually, such rocks were not sampled; the seismic records that were acquired prior to the coring to establish a working-model stratigraphy were mistakenly interpreted (Simpson et al., 1974). Elsewhere, gneisses and meta-arkoses that had been recovered alongside Lower Miocene carbonates during dredging on the Davie Ridge (Leclaire et al., 1989; Bassias, 1992) were taken as evidence of subaerial exposure until as recently as the Early Neogene. Guided by biological data (molecular-clock and palaeontological considerations), McCall (1997) reasoned that the Davie Ridge was subaerial between about 45 and 26 Ma. However, he was unaware of the many small continental blocks that litter the deep ocean basins (Müller et al., 2001; Gaina et al., 2003; Collot et al., 2020), with most being related to plate rifting and ridge-jumping. The critical issue is that such fragments need their crusts to be thicker than about 25 to 30 km before their upper parts rise above sea level due to them being buoyed isostatically by the underlying mantle; those that are thinner are often submerged.

4. Other relevant issues

4.1. Davie Ridge

The Davie Ridge (Fig. 1) underpins all the land-bridge/stepping-stone routes between Africa and Madagascar. Although no parts of the high are presently exposed, the feature is now reasonably well known due to it having been studied for over half a century through geophysical surveys, dredging and drilling (e.g. Heirtzler and Burroughs, 1971; Simpson et al., 1974; Mougenot et al., 1986; Mascle et al., 1987; Coffin and Rabinowitz, 1987; Leclaire et al., 1989; Hall et al., 2017). In the last decade, a group led by Wilfried Jokat (Alfred Wegener Institute, Germany) has reported the results of several geophysical surveys of the coastal plain and offshore areas of central and northern Mozambique (Leinweber et al., 2013; Mueller and Jokat, 2017; Vormann et al., 2020; Vormann and Jokat, 2021a).

Recently, Vormann and Jokat (2021b) synthesized the data for the area in and around the Davie Ridge. Based on its geophysical properties and bathymetric expression the Davie Ridge, from just north of the Paisley Seamount to a short distance south of the Sakalaves Seamounts, was interpreted to comprise a sliver of continental crust that had moved to its present position during the rift-drift of East Gondwana from West Gondwana. Although this is a somewhat radical proposal, its origins extend back to the mid-1980s (Mougenot et al., 1986; Mascle et al., 1987). However, although those author teams also suggested that feature was 'continental', they did not define its geographical extent, nor did they develop an associated geotectonic model. Notably, Vormann & Jokat's 'continental-sliver' proposal is compatible with some of the distinctive lithologies that have been recovered in dredge-hauls of the feature, including the aforementioned gneisses and meta-arkoses (Leclaire et al., 1989; Bassias and Leclaire, 1990; Bassias, 1992). Using the 2000-m-isobath as a guide (Fig. 3), the terrane extends *c*. 620 km, from about *c*. 13.5°S, 41.3°E to *c*. 19.2°S, 41.9°E (see Fig. 4). To explain how it arrived at its present position, Vormann and Jokat's (2021b) included a tectonic model that drew heavily upon Müller and Jokat (2019); it is worth noting that Phethean et al. (2016) presented an ostensibly identical scenario, indicating a general consensus. Between 182 and 162 Ma, West Gondwana (Africa and South America) and East Gondwana (Madagascar, Seychelles, India, Antarctica and Australia) rifted and began to drift apart. Here, the movement was orthogonal to the edges of the main blocks (Fig. 5), with the Davie Ridge forming part of western southern Madagascar. However, at about 157 Ma the plate boundary switched to being a right-lateral transform, with East Gondwana having a southerly motion (Fig. 5). Around 139 Ma, the system reconfigured with the fault jumping a short distance to the east, in the process calving the Davie Ridge off from Madagascar and transferring it to the African plate. Spreading in the Somali Basin continued until *c*. 126 Ma; since then Africa, the Davie Ridge and Madagascar have all been locked in

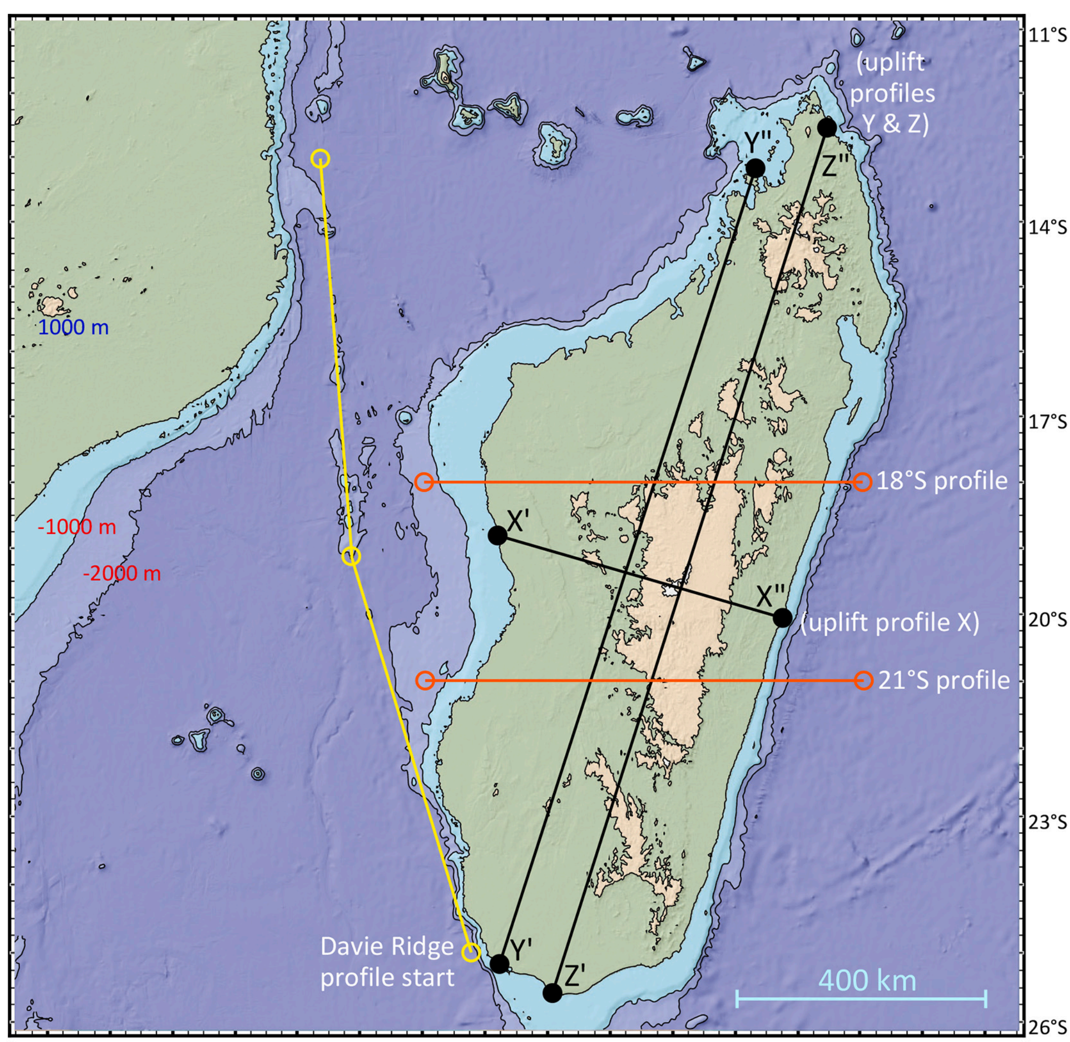

Fig. 3. Relief map for the SW Indian Ocean region showing the traces of the various bathymetric (Fig. 4), topographic (Fig. 6) and uplift-history (Fig. 7) profiles. The base image was generated using *GeoMapApp* (Ryan et al., 2009).

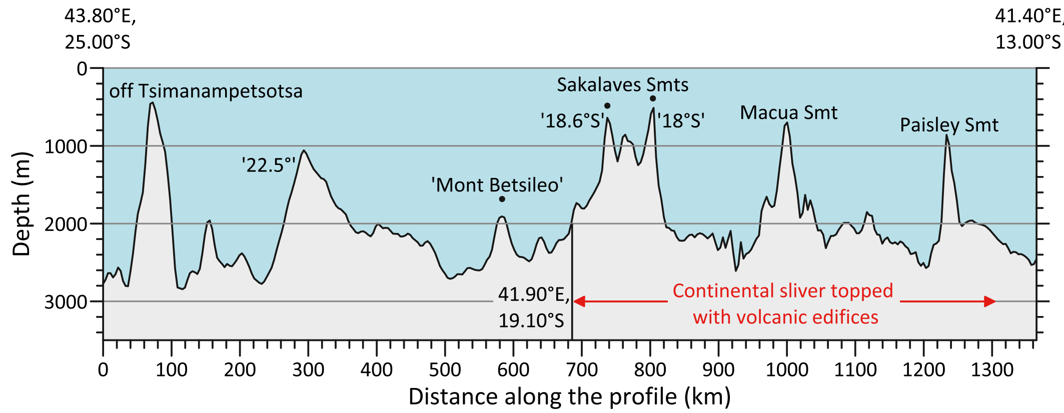

Fig. 4. Bathymetric profile of the Davie Ridge/Fracture Zone (the viewing direction is towards the west) based on depth data from *GeoMapApp* (Ryan et al., 2009). To accommodate a small change in the orientation of the feature, the path is re-aligned at 41.90°E, 19.10°S. Note the approximate extent of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

their current relative positions (Fig. 5). Crucially, with this model there is a *c*. 360-km-wide expanse between the southern end of the Davie Ridge and the point where the Davie Fracture zone runs close to Madagascar, at about 22.3°S, 42.7°E (see Fig. 1).

4.2. Neogene to recent uplift of Madagascar

Madagascar has distinctive asymmetrical geomorphology with a wide planation surface that is tilted gently towards the west, an elevated NNE-SSW aligned 'spine' that runs along the island's axis, and a prominent ESE-facing escarpment (Fig. 6, see also Fig. 3). The formation of this uplifted landscape, as well as its relationship to the one that has developed on mainland Africa, has long-attracted attention: Dixey (1960), Burke (1996), de Wit (2003), Burke and Gunnell (2008), O'Malley et al. (2021), Wang et al. (2021). Today, the widely accepted view is that in the latter third/quarter of the Cenozoic the island has risen substantially due to convective upwelling of 'warm' asthenospheric mantle beneath the region (see Winterbourne et al., 2014; Castelino et al., 2016; Stephenson et al., 2021). Importantly, the idea is supported by Madagascar's volcanism record (Bardintzeff et al., 2010); from global-scale gravity investigations (Tapley et al., 2005) and studies of earthquake shear-waves that have passed through the mantle that underlies the SW Indian Ocean region (Ritsema et al., 2011; Pratt et al., 2017); and the presence of Upper Cretaceous through Neogene sedimentary units that accumulated in shore-line or shallow-shelf settings that today are well above sea level (see the compilation in Stephenson et al., 2019).

A decade ago, Roberts et al. (2012) presented a detailed model of Madagascar's ascent based on an analysis of knick-points on 98 river profiles from across the island. Although strongly theoretical, the authors used various sorts of geological information to corroborate their findings (Roberts et al., 2012, pp. 14–16). The study indicates that since 15 Ma parts of Madagascar close to its 'back-bone' (Fig. 1) have risen by 1–2 km. To demonstrate the system's evolution, the paper made use of three uplift-history profiles, one across the 'belly' of the island and two parallel to its long-axis (Fig. 3). The lines are re-presented in Fig. 7. Concerning the proposals of Masters et al. (2021, 2022), the crucial issue is that Madagascar has never been more elevated than it is today. Importantly, if uplift increases land-connectivity, as Masters et al. argued on many occasions, it is difficult to see how Madagascar in the Late Miocene, which would then have sat lower, would have had higher rates of colonization than is the case with the modern-day configuration.

4.3. Shifts in global sea level during the three land-bridge periods

In carrying out evaluations of former geographical configurations that include the land-sea boundary, it is important to consider the eustatic sea-level record. To this end, the smoothed Cenozoic plot of Miller et al. (2020) is presented in Fig. 8. For the Early Paleocene causeway interval, the surface was well above the present level, but there was a major relative fall from +65 m at 63.9 Ma to +26 m at 60 Ma. The second hypothesized land-bridge straddled the Eo-Oligocene boundary. Then, the sea level dropped almost 70 m within *c*. 1 m.y., from +47 m to −21 m, although it rebounded to close to the present-day datum by 30 Ma. During the final window, there was a notable reduction from +6 m at 10.8 Ma to −25 m at 8.3 Ma. These pieces of information are important as each of the Masters et al. land-bridge proposals contain a tectonic-uplift component. However, none is accompanied by a quantitative statement. Furthermore, there is little consideration for the effects induced by the downward shifts in sea level; these might easily be conflated with local or regional tectonic uplifts.

4.4. Low-elevation atolls as colonization stepping-stones: Problematic issues

Implicit in the three scenarios presented by Masters et al. is that all of the passages to Madagascar involved island-hopping between atolls or walking substantial distances along reef platforms. This is a consequence of many of the lengths of the purported paths sitting at or near sea level (shallower than 100 m), allowing lowstands to expose terrestrial corridors. Notably, for animals whose recent ancestors had evolved in continental settings on Africa, the habitats on these types of land surface would be extremely demanding (see Fosberg, 1949). Actually, useful insights can be gleaned from the region's Europa Island (Fig. 9), Glorieuses Islands, and Juan de Nova Island (Fig. 10) (see Jorry et al., 2016). On each, the native land-vertebrate fauna is represented by two endemic reptile species, mainly skinks, but with one gecko (Sanchez et al., 2019); a small number of other non-endemic lizard species are present, some possibly introduced. Notably, though, there are no native amphibians or mammals. Even more challenging conditions exist at Bassas da India; during tidal peaks the exposed reef tops (up to 3-m-high) are often submerged. A final matter concerning island-hopping between atoll-crowned seamounts relates to the scrubby flora that dominates their shorelines (e.g. Gibson and Phillipson, 1983; Boullet et al., 2018). The chances are small that such plants could be dislodged, moved to the edge of the reef, boarded by land-vertebrates, that would then carry their

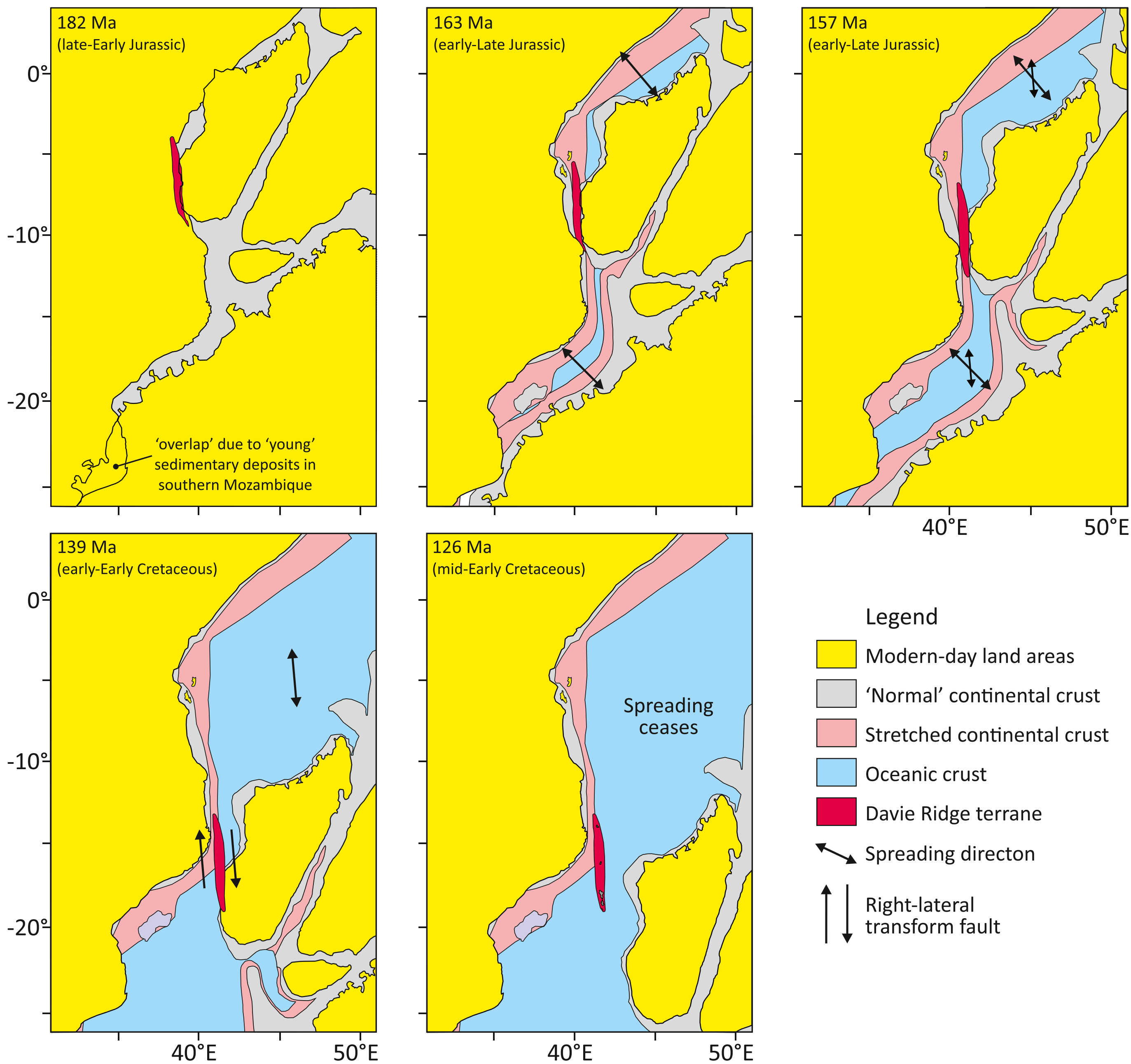

Fig. 5. Redraft of the Vormann and Jokat (2021b) tectonic model explaining how the Davie Ridge arrived at its present location. The ridge was portrayed slightly differently in Figures 1 and Figures 3, so here the terrane's southern limit is based on the 2000 m isobath in *GeoMapApp* (Ryan et al., 2009).

'passengers' to another low-elevation landmass or Madagascar. This is in contrast to island-hopping between larger, higher and well-vegetated islands (Censky et al., 1998) that are more likely to generate flotsam, and to also provide a range of environments that could host a diverse fauna.

5. Masters et al. land-bridge models

To support discussions of the proposals of Masters et al., renditions are presented of their three palaeogeographical maps (Figs. 11–13). Each shows land, seabed 0–100 m deep, seabed >100 m deep, and the inferred locations of volcanic centres. Notably, although they are less complex than the originals, they retain all of the information for making an assessment. Alongside each plot is a related figure from the PhD thesis of Antoine Delaunay (2018). Although Masters et al. constructed their scenarios drawing upon a dozen or so works (see above), Delaunay (2018) is especially important due to its geographical focus and influence on their thinking. Significantly, Figures 4a, 4b and 4c in Masters et al. (2021), as well as Figures 1A, 1B 1C in Masters et al. (2022), match closely three of his maps (Figures 2.7b, 2.8c and 2.9e respectively). In Delaunay's work, the portrayed elements were land, delta, shelf (*c.* ≤ 200 m water-depth), shelf-slope, deep basin and seabed highs (labelled "palaeo-highs"). Crucially, though, the last were re-presented by Masters et al. as sea-floor that was 0–100 m deep, despite the fact that there is nothing in Delaunay indicating they could be interpreted as such. These bathymetrically raised areas were important to Delaunay for at least two reasons. First, they guided the accumulation of sediment in the deeper areas, sometimes acting as barriers or traps, and in others instances as funnels (see also Lort et al., 1979). Second, because they sit above the levels of the adjacent basins, they likely received mainly pelagic sediments, which have very low deposition rates. Importantly, material associated with the faster-accumulating turbidity currents (e.g.

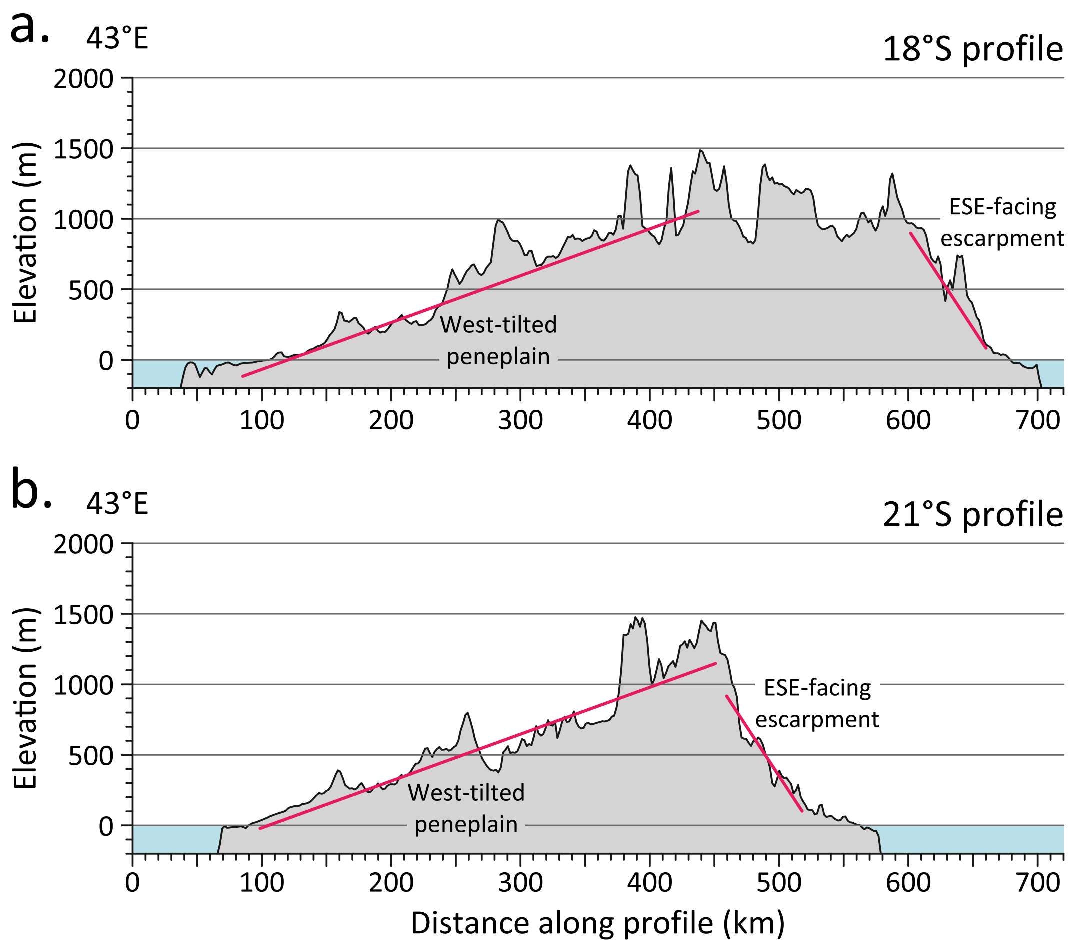

Fig. 6. Two latitude-parallel topographic sections across Madagascar at 18°S (a) and 21°S (b) showing the west-tilted peneplain and the ESE-facing scarp, the start point for both being the 43°E meridian (the viewing direction is towards the north). The elevation data were taken from *GeoMapApp* (Ryan et al., 2009).

Mutti et al., 2009) would have been minimal as much of it would have ponded in the lows, with little carrying up on to the highs (see Delaunay, 2018, Fig. 2.10). One possibility for the mis-portrayal by Masters et al. is that they misunderstood Delaunay's maps. Notably, for each of his time windows an isopach map and a depositional environments map were shown next to one another. Perhaps revealingly, for 66.0–33.9 Ma (Fig. 2.8b) and 33.9–23.0 Ma (Fig. 2.8c) many parts of the Davie Ridge and the Juan de Nova area appeared with packages that were 0–100 m thick and comprised hemipelagic sediments. However, with the 12.0–5.3 Ma interval (Fig. 2.8d) most locations on the features were 100–400 m thick. Thus, the isopach values appear to have critically influenced the way that Masters et al. constructed their palaeogeographical models, and this is especially significant for those patches of seabed they thought were exposed during lows in sea level.

6. Evaluating the land-bridge models of Masters et al. and McCall

Due to the large amount of information that is contained within the various land-bridge scenarios, particularly those of Masters et al., it is a challenge to comprehend the various elements. It was thus decided to simplify matters by converting the four proposed pathways into topological models, and to then compare each with data-validated ones (see below). Here, the obvious physiographic elements have their own 'sectors' for instance 'Macua Seamount', 'Juan de Nova Island', but so do the intervening gaps, for example 'Paisley-Macua' and 'Juan de Nova-Melaky Shelf' (Fig. 14). Furthermore, there are several sea-bottom features in the Mozambique Channel that are unnamed in the GEBCO Atlas (https://www.gebco.net) for which it is possible to apply informal labels and to incorporate them into the framework also. These include two distinctive pinnacles within the Sakalaves Seamounts at *c.* 18°S and *c.* 18.6°S, a knoll at *c.* 20°S ('Mont Betsileo'), and conspicuous highs at *c.* 22.5°S and *c.* 24.4°S (Fig. 14). Notably, in working through the literature associated with the various elements, it became apparent that a number of relevant publications, sometimes contradictory, had not been cited by Masters et al., for instance Simpson et al. (1974), Mascle et al. (1987), Malod et al. (1991), Salman and Abdula (1995), Key et al. (2008), Mahanjane (2014), Franke et al. (2015) and Hall et al. (2017). Here, these, as well as a number of others, inform the analysis.

Below, each of the sectors within the land-bridge proposals are evaluated (Figs. 15–18). They are documented first in the sequence they appear advancing south along the Davie lineament, and then east along the Juan de Nova 'arm'. The appraisal makes regular use of the abbreviation 'mbsl', which stands for 'metres below sea level'.

6.1. *Nacala-Rovumba coastal strip*

The syntheses of Salman and Abdula (1995) and Key et al. (2008) provide important data on the geographical configuration of the Nacala-Rovuma coastal strip in northern Mozambique at various times back to the Triassic, shortly before Gondwana began to break apart. For each of the land-bridge intervals, the former shore-line approximates roughly to the modern-day one thus in the four topological maps the area is coded as land.

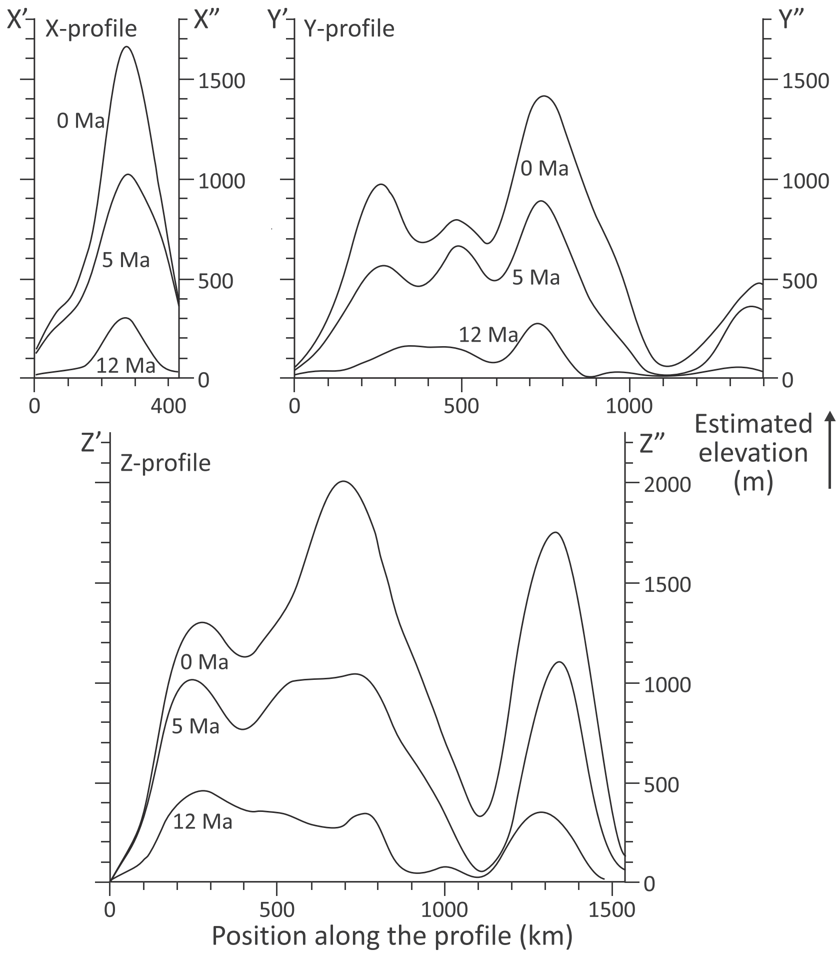

Fig. 7. Estimated uplift histories at various locations on Madagascar based on Roberts et al. (2012, Figure 15). Those for 12 Ma and 0 Ma are direct traces from the original figures, while the one for 5 Ma is an interpolation of the 4 Ma and 6 Ma lines (note that for Profile X the viewing direction is towards the NNE while for Profiles Y and Z it is towards WNW). The first and second are important as they bracket the period for the Late Miocene land-bridge of Masters et al. The lines have smoothed appearances due to the data processing. Also, there are discrepancies with reality, especially towards the ends of the X and Y profiles – see Roberts et al. (2012, p. 15).

6.2. Nacala-Paisley gap

Using Salman and Abdula (1995) and Key et al. (2008), it is reasonable to infer that the gap between mainland Africa and the Paisley Seamount (70–80 km) was covered by sea during each of the Masters et al. land-bridge periods, as well as the one of McCall. Additionally, neither of the associated seismic traces in Mougenot et al. (1986, Figure 2; Lines M84–21 and M84–22), nor the one in Franke et al. (2015, Figure 7; Line C) suggest that the low-relief seabed was ever subaerial.

6.3. Paisley Seamount

The Paisley Seamount is about 70 km from the Mozambique coast at *c.* 14.17°S, 41.46°E. Its highest point is at about 300 mbsl (*GeoMapApp*). The edifice was imaged on seismic line M84–23 in Mougenot et al. (1986, Figure 2), as well as on WG506-WG504 in Mahanjane (2014, Figure 3B), and in both cases it appears not to have been eroded. Based on various geophysical properties, it was thought to be a basaltic construction (see also Vormann and Jokat, 2021a, 2021b). Considering the patterns of regional volcanism (e.g. Mahanjane, 2014), it is likely that the seamount did not exist until the late Cenozoic. In the various topological maps, it is assumed to have been submerged during all of the proposed causeway intervals.

6.4. Paisley-Macua gap

Key data on past conditions at the Paisley-Macua gap (*c.* 185 km) resulted from studies of sedimentary sequences at Deep Sea Drilling Project (DSDP) Site 242 (15.84°S, 41.82°E), which was located on the northeast flank of the Macau Seamount where the seabed is 2275 mbsl (Simpson et al., 1974). Nannofossils in the lowermost part of the 676-m-long succession were assigned to the NP19 zone, which equates to a mid-Late Eocene age. Leclaire (1974, p. 484) noted:

> "…..the lithologic record obtained at Site 242 is characterized by remarkably similar sediments throughout the cored interval. These deposits contain from 45 to 70 percent of calcareous biogenic deposits mixed with an important clay fraction (30%–50%). Typically, this kind of deposit is considered to be hemipelagic with the pelagic part dominant."

The recovered sequence indicates a lack of emergence since *c.* 35 Ma. Furthermore, the site can be used as a proxy for conditions nearby, especially the Macua Seamount. If material had been eroding off a proximate, subaerial part the Davie Ridge, it is likely that some of it would have been deposited at Site 242, and/or would be conspicuous on neighbouring seismic lines (M84–31 of Mougenot et al., 1986, and other traces obtained during the DSDP expedition).

More recently, International Ocean Discovery Program Expedition 351 cored a series of holes at Site U1476, which was close to Site 242 (15.82°S, 41.77°E; Hall et al., 2017). The deepest one, U1476E, extended to 234.8 metres below the sea-floor and the lowermost sediments were assigned to the NN11 nannofossil zone and given an absolute age of 6.91 Ma (see also, Agnini et al., 2017). The fine-grained detritus comprises mainly the remains of pelagic micro-organisms, affirming the idea that the area was submerged during the final part of the Late Miocene land-bridge period of Masters et al.

Additional information on the Paisley-Macua gap is provided by a seismic trace in Franke et al. (2015, Figure 8; Line D). The line runs

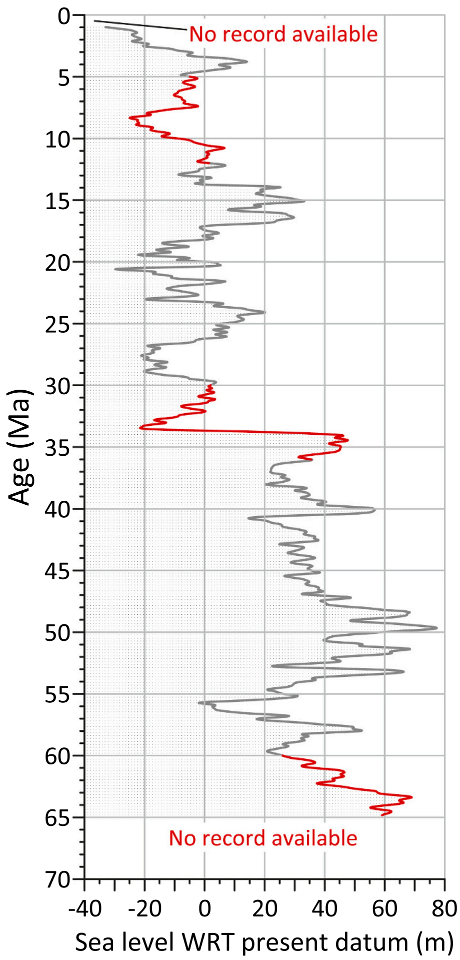

Fig. 8. The smoothed (20-k.y.-averaged) record of global sea level during the Cenozoic. The data are from Miller et al. (2020). The traces for 64.82–60 Ma, 36–60 Ma and 12–5 Ma are emphasized. Note that their processing resulted in a lack of information for >64.82 Ma and <0.98 Ma.

across the Davie Ridge to the west of Site 242, and again shows no evidence of subaerial erosion.

6.5. *Macua Seamount*

The Macua Seamount (*c.* 16.31°S, 41.65°E) rises to within 600 m of the ocean surface. Seismic line M84–33 in Mougenot et al. (1986, Figure 2) captured the feature; there is no indication that the ridge crest was ever eroded, nor is it capped with a drowned atoll.

6.6. *Macua-Sakalaves gap*

The Macua-Sakalaves gap is about 160 km. Seismic traces were presented by Mascle et al. (1987, Figure 13; M84–34) and Courgeon et al. (2018, Figure 4b; PTO-SR099, relief varies from *c.* 1850 mbsl to *c.* 2500 mbsl). There is nothing on either line to indicate that the seabed

Fig. 10. Oblique aerial photograph of Juan de Nova Island (image from Wikipedia). The viewing direction is towards the NW. For scale, the landing strip is about 1.3 km long and the WNW-ESE long-axis of the island is about 5.6 km. Note the large expanse of reef that rims the vegetated part of the platform.

Fig. 9. Oblique aerial photograph of Europa Island (image from Wikipedia; credit Roger Kerjouan). The viewing direction is towards the SW. For scale, the landing strip is just under 1.4 km long and the straight section of coast towards the left is about 3.05 km.

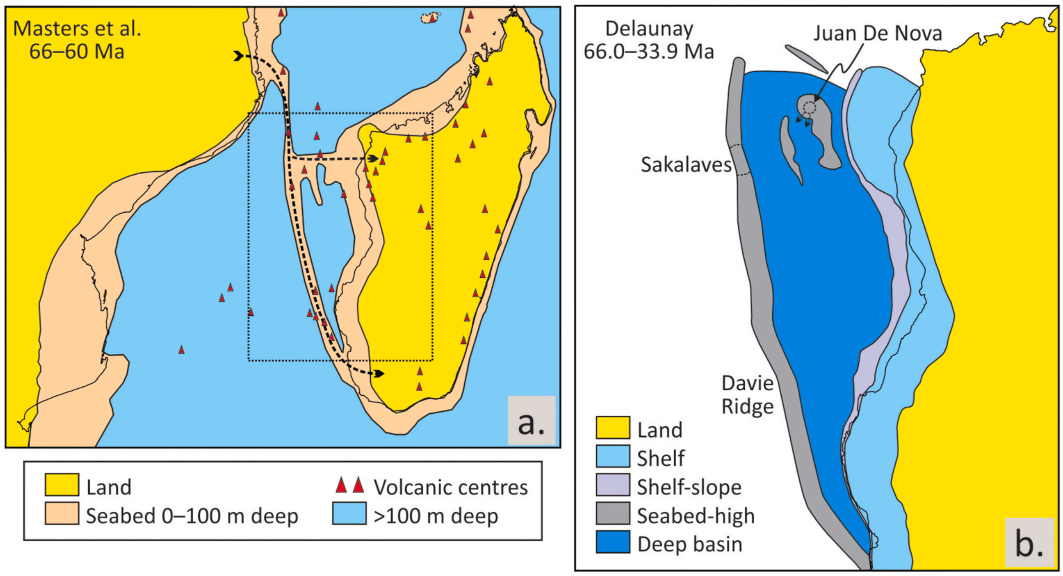

Fig. 11. Simplified version of the Masters et al. geographical configuration during the supposed Paleocene land-bridge (66–60 Ma). To the right, is a rendition of Figure 2.7b from Delaunay (2018). Note that Delaunay uses the term 'palaeo-high' for a number of features, including the Davie Ridge and Juan de Nova Seamount. Such features sat above the surrounding ocean floor, but there is no evidence they were ever exposed – see text. Here, they are labelled 'seabed-highs'.

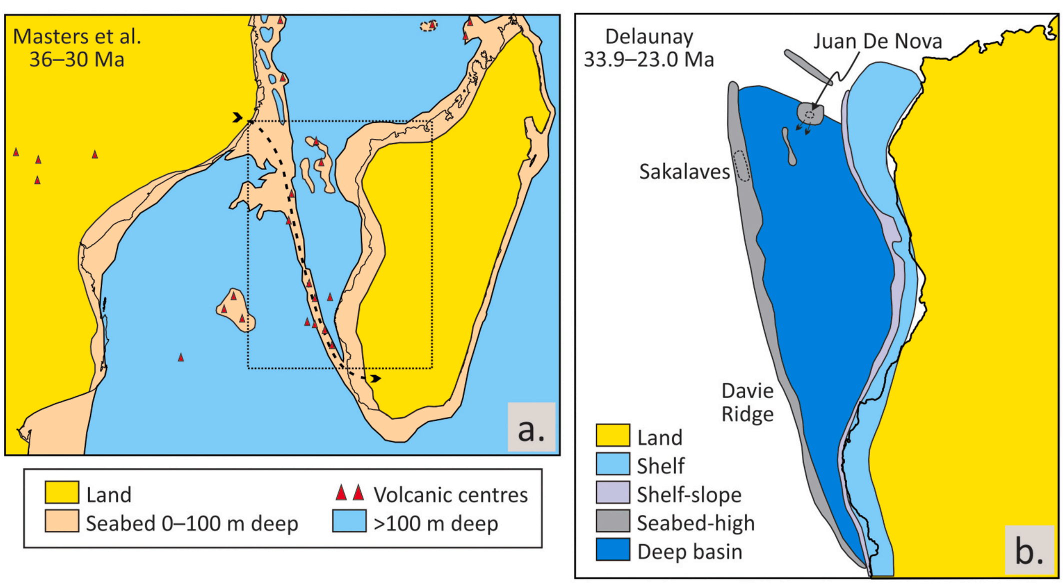

Fig. 12. Simplified version of the Masters et al. geographical configuration during the supposed Eo-Oligocene land-bridge (36–30 Ma). To the right, is a rendition of Figure 2.8c from Delaunay (2018). Note the comment in the Fig. 11 captionregarding Delaunay's use of the term 'palaeo-high'.

there was ever subaerial. Notably, the more recent survey identified two volcanic edifices, one *c.* 50-m-high and another 200 m, that each had sharp flanks thus indicating a lack of erosion.

6.7. Sakalaves Seamounts

The Sakalaves Seamounts are centred on *c.* 18.28°S, 41.84°E, and the group includes three separate pinnacles, two of which rise to within 500 mbsl (*GeoMapApp*; Ryan et al., 2009). Courgeon et al. (2018) presented key data for the two highs. The northern one, *c.* 18.03°S, 41.78°E, is notable for having a flat-topped area, estimated to be *c.* 235 km^2, whose highest point is *c.* 375 mbsl (Courgeon et al., 2018, Figs. 2 and 5). Using seismic records and dredge-sample data, Courgeon et al. (2018, Figure 3) argued that the seamount formed a volcanic high-island in the Early Oligocene, although by the Oligocene it had been reduced to sea-level. It persisted as an atoll from then until the end of the Miocene before drowning in the Pliocene. Actually, assuming that during the construction phase the island had slopes of *c.* 7°, with the island being *c.* 10.5 km wide its peak would have been approximately 650 m above sea level. Moreover, shortly after the cessation of volcanism, the landmass may have looked like Moheli Island in the Comoros (centred on *c.* 12.32°S, 43.71°E); the pair have similar aerial footprints, although the modern island is a little taller at 790 m. Concerning the southernmost high (*c.* 18.62°S, 41.81°E), it sits slightly deeper (peak at 475 mbsl) and was probably never exposed as its top shows no sign of planation (Fig. 4b in Courgeon et al., 2018). Furthermore, two small volcanic cones (100–150 m relief) that grew from it look pristine (line PTO-SR112) thereby supporting this assertion.

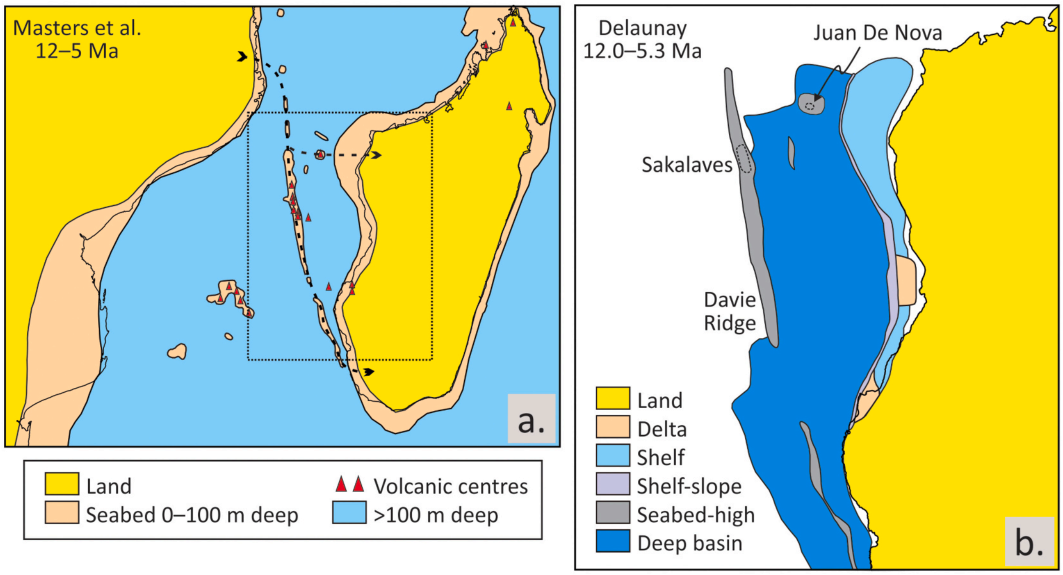

Fig. 13. Simplified version of the Masters et al. geographical configuration during the supposed Late Miocene land-bridge (12–5 Ma). To the right, is a rendition of Figure 2.9e from Delaunay (2018). Note the comment in the Fig. 11 caption regarding Delaunay's use of the term 'palaeo-high'.

6.8. Sakalaves-Betsileo gap

The Sakalaves- Betsileo gap is about 95 km. Using Delaunay (2018), we can infer that this area was covered by deep water throughout the Cenozoic.

6.9. Mont Betsileo

Bathymetric charts for the region show a knoll at *c*. 20.00°S, 42.14°E (peak at *c*. 1680 mbsl; *GeoMapApp*). Malod et al. (1991) labelled the feature 'Mont Betsileo'. Two seismic lines have imaged the feature, M84–02 in Mascle et al. (1987, Figure 12), and M89–21 in Malod et al. (1991, Figure 1). The Davie Ridge here is faulted and folded, akin to a transpressive flower-structure in a strike-slip shear zone. Crucially, it is not eroded, suggesting it was never emergent.

6.10. Betsileo-22.5°S gap

The Betsileo-22.5°S gap is about 245 km. Using Delaunay (2018), it can be inferred that during the various causeway windows this stretch of the Davie lineament was covered by deep ocean.

6.11. 22.5°S high

The '22.5°S high' is centred on *c*. 22.49°S, 42.86°E and has a peak at *c*. 800 mbsl. Seismic line M89–12 in Malod et al. (1991, Figure 1) ran close to the feature. Delaunay (2018) shows the area occupying a deep-basin setting during each of the four time-windows.

6.12. 22.5°S-24.4°S gap

The 22.5°S-24.4°S gap is about 220 km. Using Delaunay (2018), we surmise that the area was under deep water during each of the purported land-bridge periods.

6.13. 24.4°S high off Tsimanampetsotsa

This locality (24.38°S, 43.62°E) forms part of the continental shelf close to Tsimanampetsotsa. Delaunay (2018) shows this area as being covered by deep water during all four time-windows.

6.14. Tsimanampetsotsa coastal strip

Tsimanampetsotsa on the coast of western southern Madagascar is where the southernmost Davie Ridge 'offramp' is located. Delaunay (2018) depicts the area as being submerged throughout the Paleocene and Eocene and emergent from the Miocene to the present.

6.15. Davie Ridge-Juan De Nova Island gap

The gaps between the Macua Seamount and Juan De Nova Island and the Sakalaves Seamounts and Juan De Nova Island are about 125 km and 130 km respectively. Delaunay (2018) portrays deep-water conditions throughout the Cenozoic.

6.16. Juan De Nova Island

Today, Juan de Nova Island is a low-elevation island (17.06°S, 42.73°E) that sits on the southern side of a *c*. 14-km-diameter sub-circular atoll (see Jorry et al., 2016). The structure rises about 2200 m from the nearby ocean floor. Dofal et al. (2021) recently suggested that the construction has a volcanic base, *c*. 2.5-km-thick, that is topped with a 4-km-thick sedimentary cap (the underlying crust will be depressed due to the weight of the seamount locally loading it). For the first two causeway periods, Delaunay (2018) showed the feature shedding material into the basin to the south, suggesting it was emergent. Notably, he also included it on a 90–66 Ma palaeogeographical map, where it was volcanically active and again supplying sediment (Delaunay, 2018, Fig. 2.8a). Moreover, in a cross-section that was presented in Fig. 2.10 (d) a volcanic massif to the south ('Vaucluse') was shown forming in the early-Late Cretaceous, 100–90 Ma. Importantly, this is about the time when Madagascar experienced widespread magmatism as the India-Seychelles tectonic block broke away from the island (Storey et al., 1995; Torsvik et al., 1998; Bardintzeff et al., 2010). On the basis that Juan de Nova had likely eroded down to sea-level by the Cretaceous-Paleogene boundary, here it is assumed that during the four land-bridge periods it formed an atoll.

6.17. Juan De Nova Island- Melaky Shelf gap

The gap between Juan de Nova Island and the shelf to the west of Melaky is *c*. 40 km. Throughout the Cenozoic, Delaunay (2018) portrays

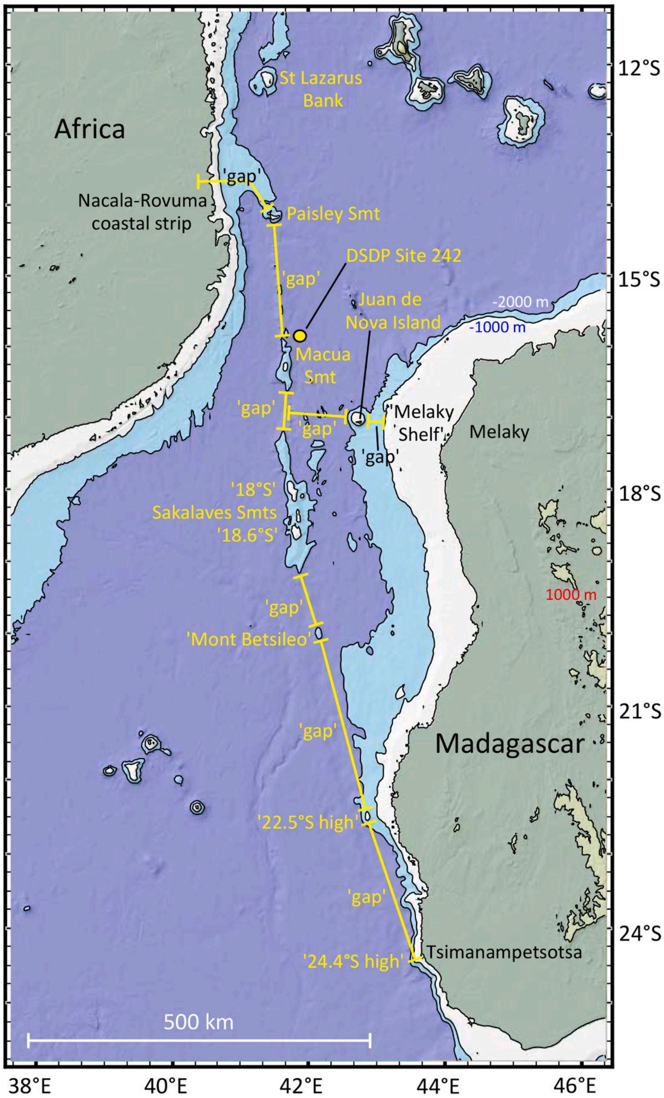

Fig. 14. Map showing the various elements in the three land-bridge connectivity 'arrays' (Figs 15–18). The base image was generated using *GeoMapApp* (Ryan et al., 2009).

deep-water conditions.

6.18. Melaky Shelf

The modern-day continental shelf between Madagascar's Melaky province and Juan de Nova Island is *c*. 95-km-wide. Delaunay (2018) depicts the area as being covered in shallow sea for all of the land-bridge intervals.

6.19. Onland Melaky

Delaunay (2018) shows the coastal area of Madagascar's Melaky Province as being covered by shallow sea during the Paleocene and Eocene, and subaerial since the start of the Oligocene. For the appraisal of the mid-Cenozoic land-bridges, the area is shown as submerged for 36 to 33.9 Ma and as hosting land thereafter.

7. Testing times

7.1. Early Paleocene land-bridge proposal of Masters et al

The Masters et al. model for 66–60 Ma and the data-evaluated configuration are shown in Fig. 15. With the former, all sectors are assumed to been exposed. However, the analysis carried out here indicates that only the coast strip at Nacala was truly dry, whilst Juan de Nova Island was an atoll. All other elements were covered by water.

7.2. Eo-Oligocene land-bridge proposal of Masters et al

The Masters et al. model for 36–30 Ma and the data-evaluated configuration are shown in Fig. 16. With the former, the Juan de Nova-Melaky Province route was deemed to be closed, so the postulated colonization route was from the Nacala 'onramp' all the way along the Davie lineament to the Tsimanampetsotsa 'offramp'. The northern end was exposed throughout, whereas the southern one was submerged (it became subaerial after the start of the Miocene). The only other properly dry sector would have been the 18°S seamount (area *c*. 235 km^2) in the northern Sakalaves during the Early Oligocene, which is currently *c*. 260 km to Africa and *c*. 170 km to Madagascar. Incidentally, the Juan de Nova Island area likely formed a low-elevation carbonate platform.

7.3. Late Miocene land-bridge proposal of Masters et al

The Masters et al. model for 12–5 Ma and the data-evaluated configuration are shown in Fig. 17. The proposed scenario incorporated a number of pathway gaps – the animals that supposedly passed along them had aquatic/semi-aquatic lifestyles that facilitated their crossings. In reality, the onramp and the two offramps were the only pathway elements that were properly dry; the seamount at 18°S and Juan de Nova formed atolls, while all of the other sectors were submerged.

7.4. Mid-Cenozoic land-bridge proposal of McCall

The 45–26 Ma land-bridge model of McCall (1997) and the data-evaluated configuration are shown in Fig. 18. The postulated path and land-availability scenario is broadly similar to that in the Eo-Oligocene model of Masters et al. There is no evidence to support the causeway McCall hypothesized.

8. Discussion

None of three land-bridge proposals of Masters et al. (2021, 2022), nor the one of McCall (1997), stands up to scrutiny. Africa and Madagascar were not connected by continuous causeways or stepping-stone chains at any time in the last 66 million years. As is the case today, the extent of dry land in the Mozambique Channel in the early, middle and late Cenozoic was negligible. A better explanation for Madagascar's land-fauna colonizations is centred around many over-water dispersal events that occurred randomly through time, as suggested originally by Matthew (1915) and elaborated upon by Simpson (1940). The one exception, out of a total of 27 land-vertebrate clades, concerns the burrowing snakes of the family Typhlopidae. The molecular-dating study of Vidal et al. (2010) indicated that its ancestor was likely present on 'Indigascar' (the landmass of Madagascar and India-Seychelles) prior to its tectonic breakup *c*. 85 Ma (Torsvik et al., 1998). Its modern-day descendants are thus regarded as deep-time vicariant relicts.

Concerning Wallace's (1880) suggestion of a Cretaceous land-surface linking Africa and Madagascar, this was constructed solely on taxonomic-based colonization-age estimations of the arrivals of the ancestors to the lemurs, tenrecs, Eupleridae carnivorans, and Nesomyinae rodents. However, more recent molecular studies have shown indicate

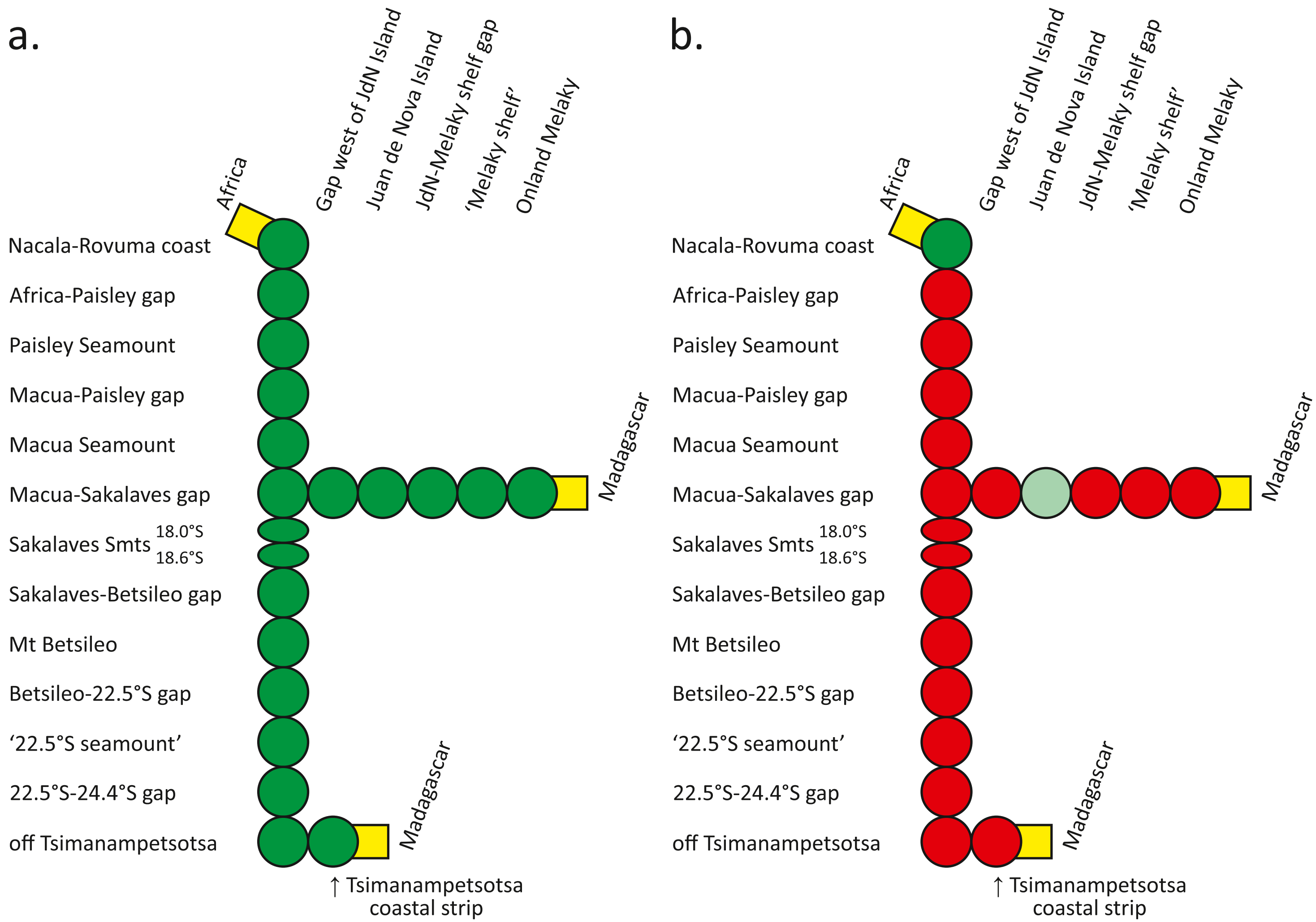

Fig. 15. Land-bridge connectivity schema for the Early Paleocene, 66–60 Ma. The hypothesized configuration of Masters et al. (2021, 2022) is shown in a, while the likely one appears as b. With the former, green and red circles respectively indicate supposed land and no path. With the latter, the green, light green and red circles correspond to true dry land, low-elevation atoll and no path. For an explanation of the various sectors, see Fig. 14.

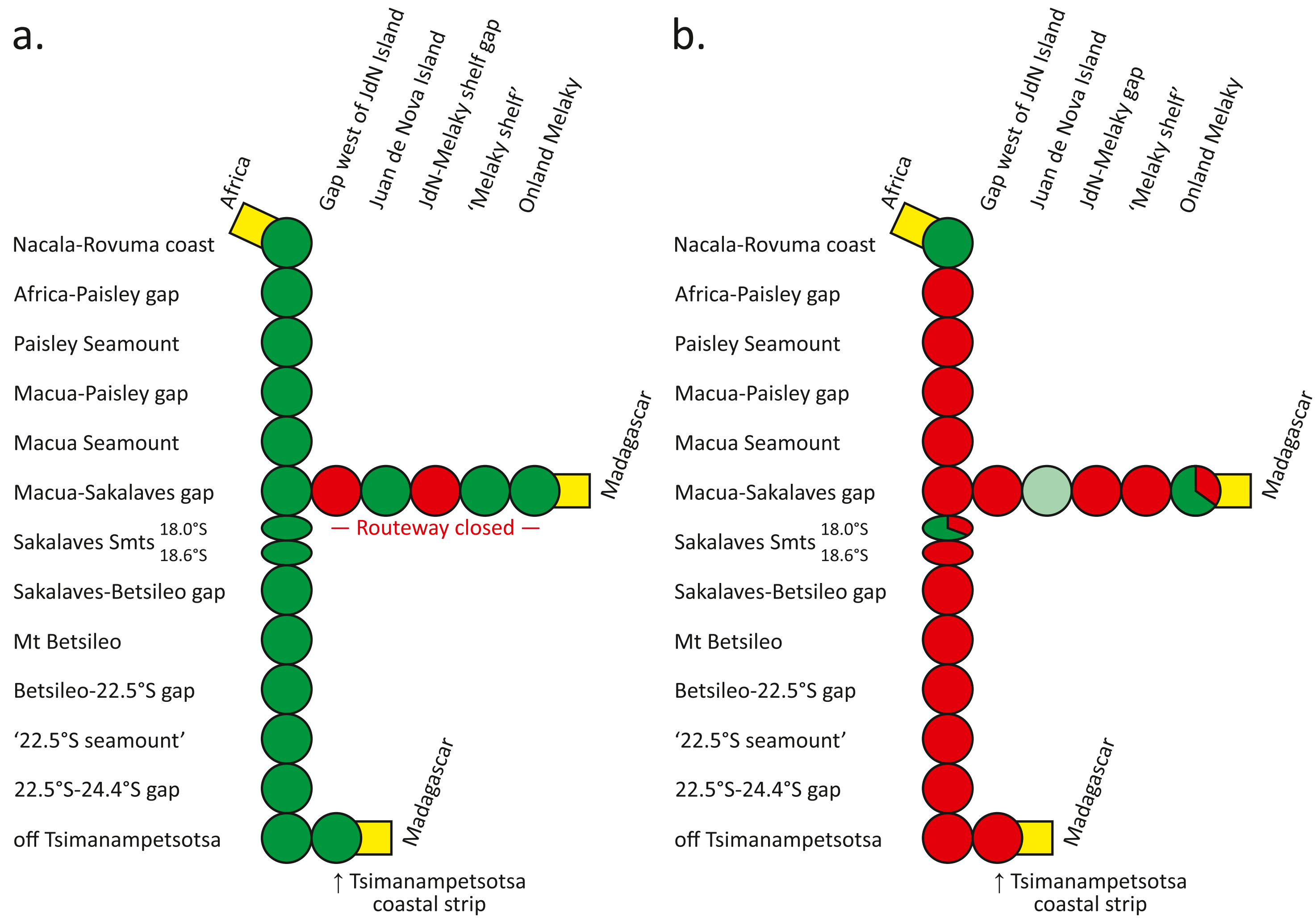

Fig. 16. Land-bridge connectivity schema for the Eo-Oligocene, 36–30 Ma. The hypothesized configuration of Masters et al. (2021, 2022) is shown in a, while the likely one appears as b. With the latter, some sectors formed land for part of the 6-m.y.-interval, and here we use the circles/ellipses like clock dials where 36 and 30 Ma are set at 12 o'clock and the 'pie-slices' reflect the periods of submergence and exposure. For an explanation of the various sectors, see Fig. 14; colour coding as in Fig. 15.

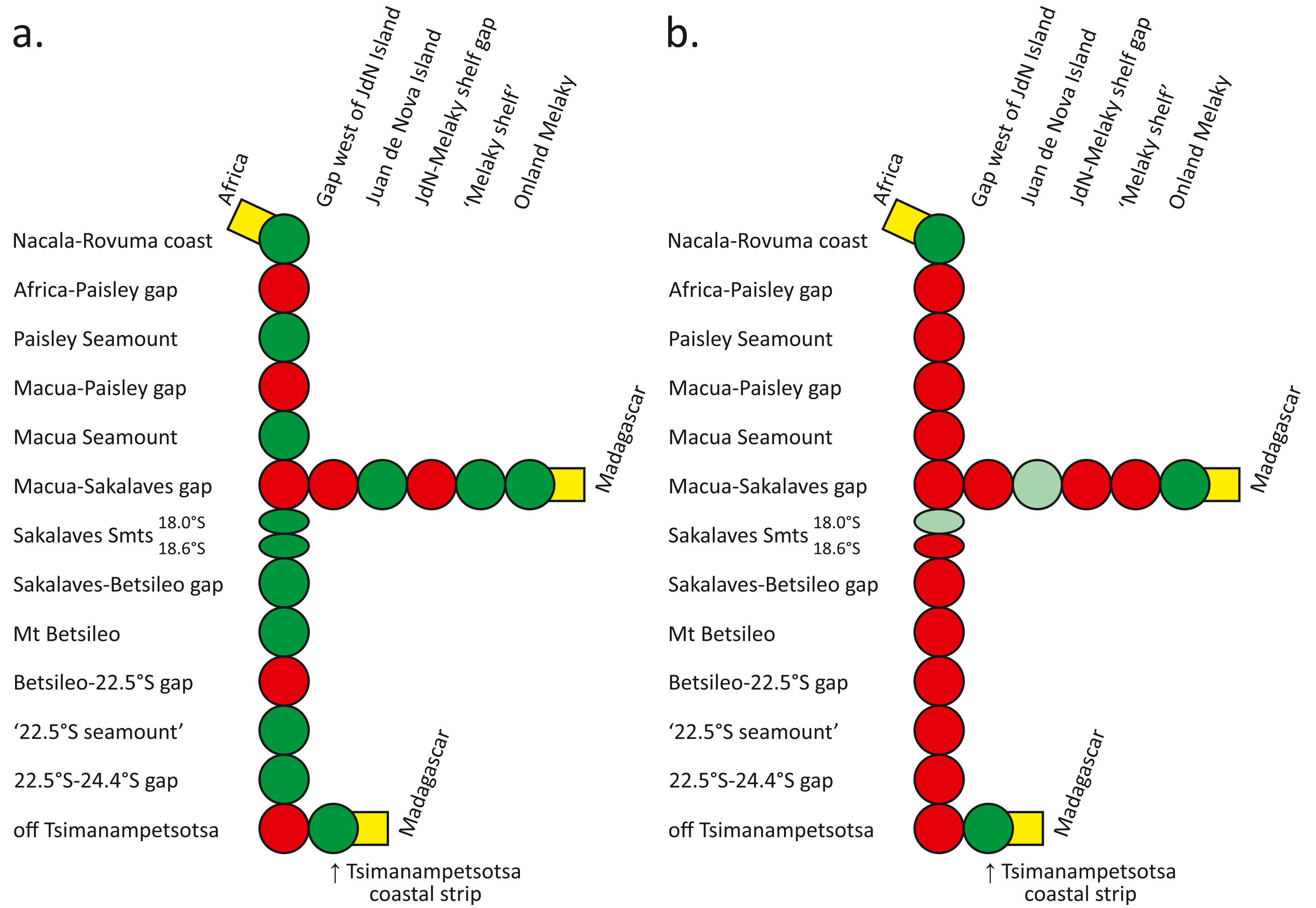

Fig. 17. Land-bridge connectivity schema for the Late Miocene, 12–5 Ma. The hypothesized configuration of Masters et al. (2021, 2022) is shown in a, while the likely one appears as b. For an explanation of the various sectors, see Fig. 14; colour coding as in Fig. 15.

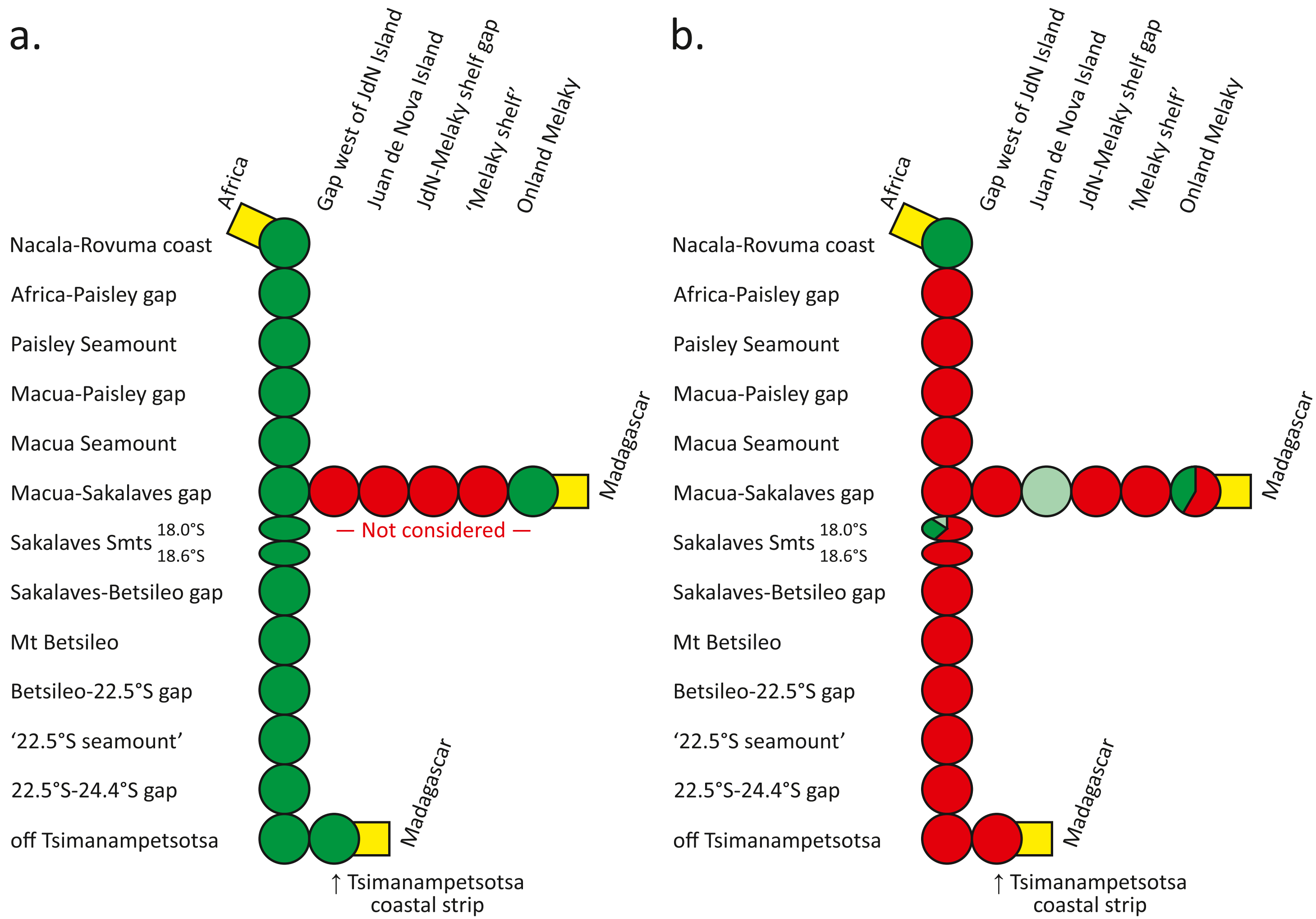

Fig. 18. Land-bridge connectivity schema for the period 45–26 Ma (Middle Eocene through Late Oligocene). The hypothesized configuration of McCall (1997) is shown in a, while the likely one appears as b. With the latter, some sectors formed formed land for part of the 19-m.y.-interval, and here we use the circles/ellipses like clock dials where 45 and 26 Ma are set at 12 o'clock and the 'pie-slices' reflect the periods of submergence and exposure. For an explanation of the various sectors, see Fig. 14; colour coding as in Fig. 15.

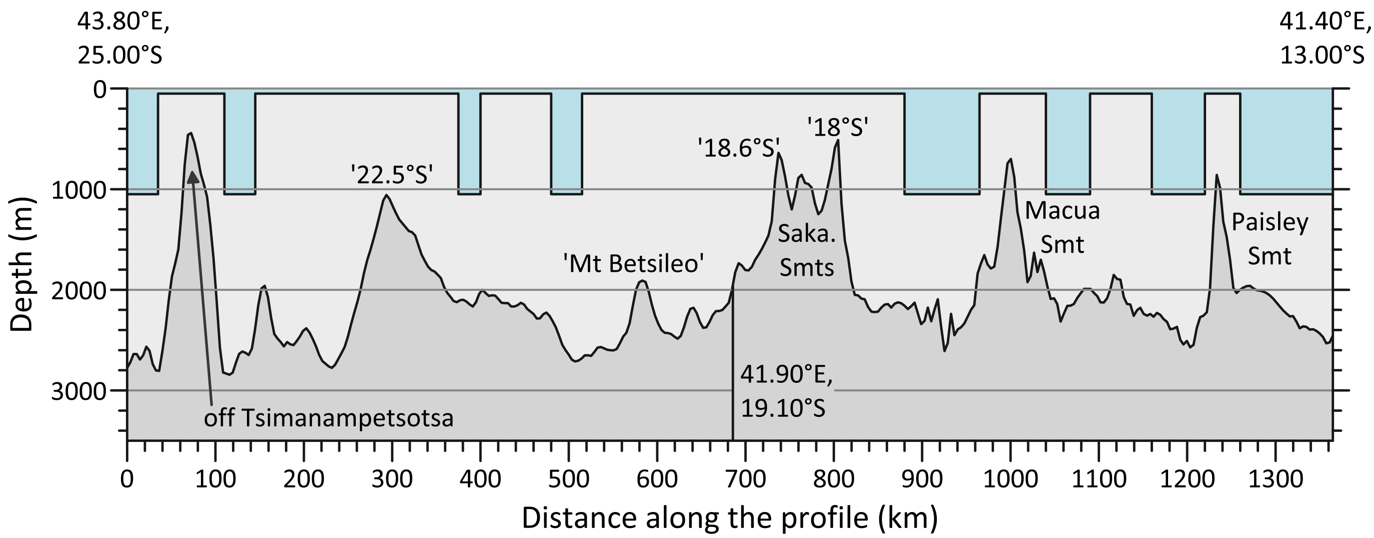

Fig. 19. Bathymetric profile of the 'Late Miocene' land-bridge (12–5 Ma) of Masters et al. superimposed on the modern-day profile for the Davie Ridge/Fracture Zone (Fig. 4). The first minus the second is the seabed that was supposedly lost since 5 Ma (see text).

that all four events date from the early and middle Cenozoic (e.g. Poux et al., 2005), thereby nullifying the original proposition. Regarding Sclater's (1864) 'Lemuria' continent that he imagined once joining the landmasses rimming the northern Indian Ocean, decades of surveying (marine geophysics and satellite) and drilling indicates that there is no basis for the idea (e.g. Bouysse et al., 2004). Moreover, plate models (e.g. Ali and Aitchison, 2008; Tuck-Martin et al., 2018) do not require such an entity.

Beyond Madagascar, the basic topological system we developed to evaluate the various pathway proposals could easily be adapted to other marine-island biotic systems where the mode of colonization is also disputed. Importantly, it reduces ambiguity with the analyses and the discussions. Finally, one matter that cannot be ignored regarding the Masters et al. and McCall models concerns the fate of the material that formed the hypothesized causeways. For instance, if the Late Miocene Nacala-Tsimanampetsotsa route is assumed to have been 1200-km-long by 20-km-wide by 2.5-km-high, then, and allowing for some small gaps, its volume would have been *c.* 50,000 km^3. If 20% of it remains today (Fig. 19), then *c.* 40,000 km^3 of rock needs to be accounted for. Obvious questions include how was it removed, and where did it go? Tellingly, however, none of the geophysical studies of the Davie Ridge area has reported seabed detritus piles that could be related (e.g. Mougenot et al., 1986; Mascle et al., 1987; Malod et al., 1991; Vormann and Jokat, 2021a).

9. Conclusions

Since the mid-19th century, biologists have proposed ancient land-bridges and stepping-stone paths linking Africa and Madagascar to explain Madagascar's unique biota. The hypothesized routeways are significant because they were thought to have enabled the mini-continent to be colonized by the ancestors of its extant and recently-extinct land-bound vertebrate clades (*c.* 30). As the Malagasy assemblage is scientifically important at a global level, the age and origin of its constituent lineages is of great interest. We therefore reviewed the geological evidence bearing on the purported land-bridges. Based around a topological framework, we examined systematically the literature and physical settings of each of the routeway sectors. For all of the supposed connection periods, few of elements were ever subaerial. The only high-island (*c.* 235 km^2) was a volcanic edifice in the Sakalaves Seamounts during the Eo-Oligocene window; by the Late Oligocene-Early Miocene it formed an atoll that persisted until it drowned in the Pliocene. Elsewhere, the carbonate platform that Juan de Nova Island presently sits upon was likely at or just above sea level for all three periods. Crucially, none of the other offshore sectors ever appear to have formed land. In summary, we find no geologic support for the presence of ancient land-bridges that would have provided a dry walkway, or even a stepping stone path, for land-dwelling vertebrates. Thus, aside from the clade of burrowing snakes that were present before Madagascar separated from Africa (e.g., Vidal et al., 2010), the island's biota must have arisen by over-water dispersal. Interestingly, some years ago Ian Tattersall (2006, p. 35) wrote:

"Clarification of the mechanisms of origin of Madagascar's terrestrial mammal fauna is thus as likely to come from studies of the surrounding seafloor geology as it is to emerge from examinations of the fossil record and systematics of the island's fauna itself."

Hopefully, the analysis presented above brings closure to this matter.

Data availability

No primary data were generated for this contribution. At the time of writing, e-versions of the PhD theses of Delaunay (2018) and Ponte (2018) were available on-line, respectively at https://tel.archives-ouvertes.fr/tel-01865476 and https://tel.archives-ouvertes.fr/tel-01865479. If required, pdfs can be obtained from JRA.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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