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Biogeographic mechanisms involved in the colonization of Madagascar by African vertebrates: Rifting, rafting and runways

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Abstract

Aim: For 80 years, popular opinion has held that most of Madagascar's terrestrial vertebrates arrived from Africa by transoceanic dispersal (i.e. rafting or swimming). We reviewed this proposition, focussing on three ad hoc hypotheses proposed to render this unlikely scenario more feasible: (a) Could hibernation have helped mammals to reach Madagascar? (b) Could the aquatic abilities of hippopotamuses have enabled them to swim the Mozambique Channel? (c) How valid is the Ali-Huber model predicting that eastward Palaeogene surface currents allowed rafts to reach Madagascar in 3–4 weeks? Finally, we explored the alternative hypothesis of geodispersal via short-lived land bridges between Africa and Madagascar.

Location: East Africa, Madagascar, Mozambique Channel.

Taxa: Fish, amphibians, reptiles, birds, mammals.

Methods: We established colonization timeframes using molecular divergence dates estimated for Malagasy vertebrate lineages. We reviewed the likelihood of the “torpid waif” and “swimming hippopotamus” hypotheses, and re-investigated Ali and Huber's model of Eocene jet-like currents by tracking particle trajectories in currents simulated using the Institut Pierre-Simon Laplace Earth System Model. Finally, we summarized recent geological findings from the Mozambique Channel, and used them to compile palaeosedimentological maps using PLACA4D.

Results: Madagascar's vertebrate fauna has complex origins. Hibernation is probably an adaptation to Madagascar's hypervariable climate, rather than a facilitator of mammal dispersal. Hippopotamus physiology precludes the ability to cross an oceanic channel deeper than 4 m and hundreds of km wide. The Ali-Huber model of Palaeogene currents considerably underestimated the time required to cross the Mozambique Channel under simulated palaeogeographic conditions. New geological data indicate the existence of three short-lived land bridges between Africa and Madagascar at 66–60 Ma, 36–30 Ma and 12–05 Ma.

Main conclusion: The three Cenozoic land bridges afford a more grounded hypothesis for the dispersal of Madagascar's extant biota than transoceanic rafting or swimming, although vicariance, island hopping and limited rafting also played a role.

KEYWORDS

dispersal, hibernation, Indian Ocean, land bridges, mammals, surface currents, transoceanic

1 | INTRODUCTION: RIFTING VERSUS RAFTING

Biogeography was a crucial argument in Darwin's (1859) case against special creation, and islands were key witnesses. Darwin noted that insular animals and plants generally have their closest relatives on the nearest mainland. Terrestrial mammals and amphibians are often missing from islands that are isolated by wide tracts of ocean; e.g. the only indigenous mammals in New Zealand are bats. In the years following the publication of *Origin of Species*, several scientists focussed their attention on the island of Madagascar and the processes that underlay its faunal population. More than one author hypothesized a sunken continent in the Indian Ocean, which Sclater (1864) named Lemuria in his article, *The Mammals of Madagascar*. Haeckel (1876) proposed this lost continent as the cradle of primate evolution, including humankind. Wallace (1880) toyed with the possibility of sunken continents, before renouncing them in *Island Life*.

Late nineteenth and early twentieth century scientists, of course, laboured under the assumption that Earth's major landmasses had always occupied their current positions, making fragmented distributions, particularly on islands and archipelagos, difficult to explain. Dispersal by land bridges, sunken continents and ocean-going rafts of vegetation seemed the only solutions to such biogeographic patterns. The fauna of Madagascar presented a particularly knotty problem: the island presently lies at a minimal distance of 415 km east of the African coast, and the Agulhas current that follows the coast southwards is one of the fastest in the world, reaching instantaneous speeds >2 m/s and time-averaged speeds of 0.45 m/s (Ridderinkhof et al., 2010). Nevertheless, Madagascar has a diverse vertebrate fauna, including freshwater fish, frogs, reptiles and mammals. In the past, it was also home to dinosaurs, mammaliaform gondwanatheres, giant flightless birds and dwarf hippopotamuses (Goodman & Benstead, 2003).

Two 20th century scientific revolutions had the potential to resolve this conundrum. First, geologists developed the theory of plate tectonics to explain continental drift: the landmasses have not always been in their present positions, and continental fragmentation might resolve previously intractable problems. Several phylogenetic trees reflected the break-up sequence of Gondwana: Malagasy freshwater fish have closer affinity to taxa in India than Africa, while the African clades have closer relationships to South American populations (Farias et al., 1999; Murphy & Collier, 1997; Orti & Meyer, 1997; Sparks & Smith, 2005; Vences et al., 2001). Many of Madagascar's ancient taxa (abelisauroid dinosaurs, cheilonyans, gondwanatheres, iguanas, insects, myriapods) show kinship to South American faunas (Crottini et al., 2012; Krause et al., 2014; Paulian, 1961; Rage, 1996; Sampson et al., 1998,

2001), while others (amphibians, chameleons) have Asian affinities (Crottini et al., 2012; Rage, 1996; Raxworthy et al., 2002; Warren et al., 2009).

The second revolution, in molecular phylogenetics, meant not only that relationships between lineages could be investigated more "objectively" using DNA sequence data but also the timing of divergences could be estimated using sophisticated models of nucleotide substitution. Ironically, molecular clock estimates were often way out of step with the geological dates of continental ruptures (Poux et al., 2005; Vences et al., 2001, 2004; Warren et al., 2009; Yoder et al., 1996). Some early models of the Gondwana break-up positioned Madagascar opposite Mozambique and assumed the island had moved eastwards, giving rise to a belief that Madagascar was much closer to Africa (~80 km distant) during the early Eocene (e.g. Walker, 1972), which seemed to fit with molecular estimates. This idea was not sustained by later research, which confirms that Madagascar began its separation from the Tanzanian coast in the Kimmeridgian (157 Ma), and has remained at the same distance from Africa since the Aptian (120 Ma; Davis et al., 2016; Reeves et al., 2016; Thompson et al., 2019).

The greatest ages attributed to the world's living orders of mammals, using molecular clock estimates or fossils, respectively, range from the latest Cretaceous (90–70 Ma; Bininda-Emonds et al., 2007; Springer et al., 2012) to the Cretaceous–Palaeocene boundary (66 Ma; Alroy, 1999; Wible et al., 2007). Given the disjunction between the reconstructed divergence dates of living mammal clades and the continental drift histories of Africa and Madagascar, biogeographers have had little choice but to revert to the old "fixed-continent" models of inter-continental dispersal (Darlington, 1957; Simpson, 1940). Transoceanic journeys on rafts of vegetation have become, once again, the only imaginable means of Madagascar's colonization by Cenozoic clades of terrestrial animals (Ali & Huber, 2010; Ali & Vences, 2019; Kappeler, 2000; Krause, 2010; Krause et al., 2020; Mahé, 1972; Martin, 1972; Nagy et al., 2003; Quammen, 1996; Samonds et al., 2012, 2013; Stuenes, 1989; Vences et al., 2004; Yoder, 1996; Yoder et al., 2003; Yoder & Nowak, 2006). In the absence of contradictory information, the scenario has assumed the following elements:

1. Cenozoic colonization events originated in enigmatic Africa.
2. The colonizers rafted across the Mozambique Channel in defiance of prevailing ocean currents; early Cenozoic currents were more conducive to a west-east crossing.
3. Successful colonists were drawn from riverine or estuarine habitats; when the rivers came down in flood, the riparian inhabitants were swept downstream together with uprooted vegetation.
4. Natural rafts can remain intact for long periods on the open ocean, and may carry trees, food and fresh water.

- In the case of mammals, with high metabolic demands, the waifs coped with thirst and starvation by entering a state of hibernation during the voyage.
- The founding waifs were either pregnant females or small groups that reproduced upon landing on the western coast of Madagascar.
- Hippopotamuses probably swam across the channel.
- A highly unlikely event becomes very likely over millions of years of geological time.

This is an appealing, widely accepted narrative, although aspects of it continue to raise questions among earth and life scientists. Here, we review the more problematic aspects of the rafting scenario, and present an alternative hypothesis based on recent findings by a French-led project, PAMELA (Passive Margins Exploration Laboratories), based in the Mozambique Channel. We integrate the new palaeotopographic, sedimentological and tectonic data with recent understanding in ecophysiology, oceanography, palaeontology and phylogenetics.

2 | ESTIMATING THE AGES OF MADAGASCAR'S VERTEBRATE FAUNA

Deciphering the origins of Madagascar's biota is greatly impeded by the absence of Cenozoic fossils older than 80 ka (Samonds, 2007). The island hosts lush forests with highly acidic and leaching soils (Sommer et al., 2013), which form some of the worst environments

for bone preservation (Noto, 2011). Much of Madagascar's fossil record was probably erased by unfavourable taphonomic conditions, and molecular divergence dates provide the only guide to origination times for most of its vertebrate lineages. Molecular clock estimates are notoriously difficult to compare across studies because of variable substitution rates in different genomic sequences and lineages. Crottini et al. (2012) ameliorated this problem by reconstructing a single phylogeny of 188 living Malagasy vertebrate taxa, each represented by 1,747 base pairs comprising two nuclear genes, and calculating the stem ages of these taxa. Their analysis revealed a complex biogeographic pattern, including the presence of Cretaceous (possibly vicariant) taxa; lineages that colonized Madagascar from Africa and/or Asia between 80 and 30 Ma; and a few late comers that arrived in the Neogene (Figure 1).

While sweepstakes dispersal, based on irregular, stochastic opportunities, predicts a random model of colonization, Figure 1 indicates a more constrained pattern. The iguanas (Opluridae) and river turtles (Podocnemididae) are likely to have been present on the Gondwanan supercontinent, alongside the extinct Cretaceous fauna (gondwanatheres, dinosaurs, early birds; Krause et al., 1997, 2020). The South American affinities of these ancient taxa imply the existence of a late Cretaceous land connection between Madagascar and the South America–Antarctica–Australia landmass (Krause et al., 1997; Masters et al., 2006; Noonan & Chippendale, 2006; Sampson et al., 1998; Yoder & Nowak, 2006). The extinct elephant birds were once considered part of this ancient fauna, but molecular studies suggest they arrived much later, potentially by flying, and were the sister-taxon to kiwis (Mitchell et al., 2014). By 84 Ma,

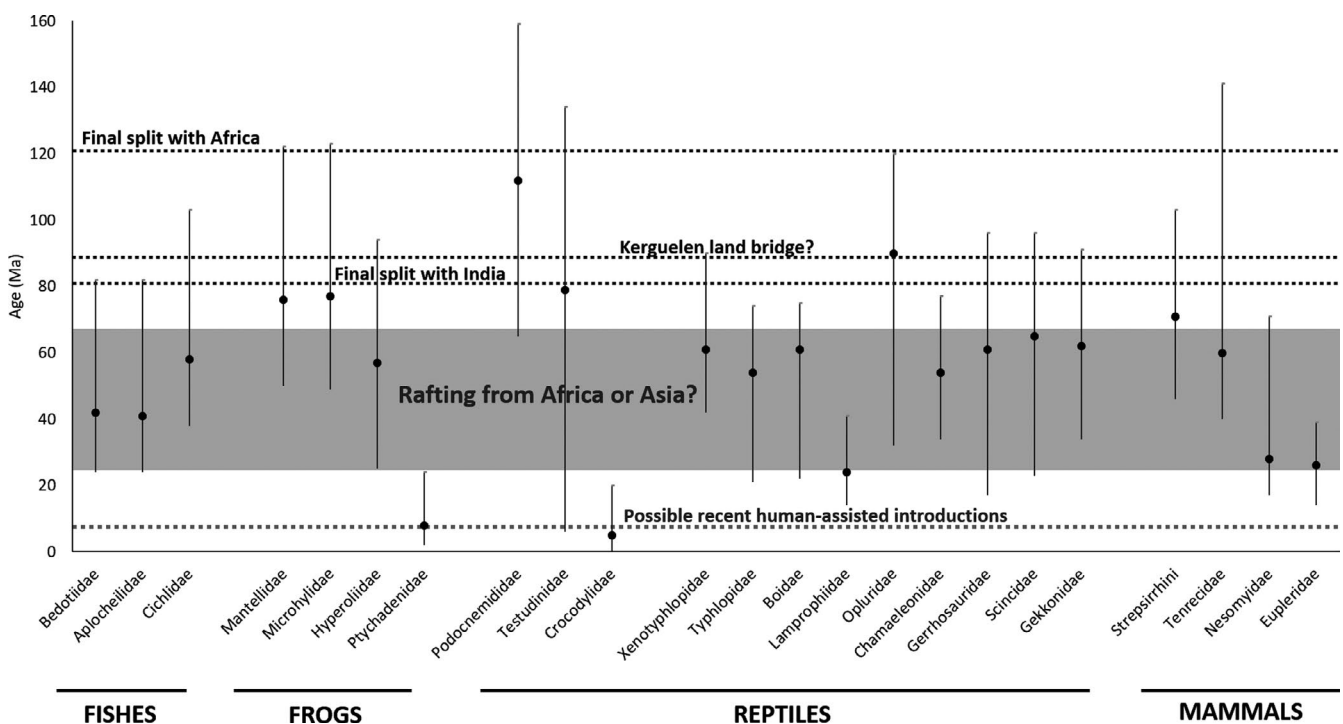


FIGURE 1 Divergence dates (black dots) of extant, non-volant Malagasy vertebrate families estimated by Crottini et al. (2012). Associated bars show maximum and minimum ages. Horizontal dotted lines indicate possible biogeographic influences. The grey area encompasses most of the divergences

Madagascar was unambiguously isolated from all surrounding landmasses.

3 | WHAT MAKES MADAGASCAR UNIQUE, AND WHY IS ITS COLONIZATION SO DISPUTED?

Islands, like unhappy families, are all insular in their own way, and Whittaker and Fernández-Palacios (2007) advised that generalizations about them have a high probability of being wrong. Madagascar is Earth's fourth largest island, after Greenland, New Guinea and Borneo. It is narrow longitudinally (43–51°E) and extensive latitudinally (12–25°S), with three mountain massifs roughly aligned along its major axis. Its present geographic location and physiography determine a rain-shadow effect, creating steep longitudinal environmental gradients with rain forests on the east coast and a dry western versant (Goodman & Benstead, 2003). The topography generates a wide variety of habitats, many of which form distinct islands within the main island. The timing of the uplifts that generated this heterogeneity, however, has been difficult to assess. Some researchers (e.g. Ohba et al., 2016) have assumed that Madagascar's current topography was present in the Cretaceous, while others (de Wit, 2003; Delaunay, 2018) considered it more recent, and formed in discrete phases: in the Palaeocene, Late Eocene and Late Miocene.

In biogeography, most islands are categorized as either oceanic (i.e. formed over oceanic plates and never connected to a continent) or continental (i.e. located on continental shelves and connected to the mainland during sea level low stands; Ali, 2017; Whittaker & Fernández-Palacios, 2007). Madagascar is as isolated as an oceanic island, but differs in its geotectonic origins: it is a fragment of India's Dharwar craton, stranded in the southern Indian Ocean when Greater India began its rapid migration north (Agrawal et al., 1992). Like a continental island, Madagascar had an indigenous flora and fauna prior to colonization, although much of this biota was lost during the global mass extinction 66 Ma ago (Crottini et al., 2012; Krause et al., 2020). Despite its isolation, Madagascar has endemic mammals and amphibians. Although it is generally viewed as too large to experience "island effects" like Foster's Rule, both dwarfing and gigantism have occurred among its endemic vertebrate fauna (Jungers et al., 2008; Masters et al., 2014; Weston & Lister, 2009). In accordance with the island syndrome, mainland herbaceous plants became woody bushes and trees on Madagascar (Carlquist, 1974).

Madagascar is idiosyncratic. In some aspects, it conforms to expectations arising from insularity; in others, it does not. This goes some way towards explaining its unique biota, but the pattern of colonization indicated by vertebrate divergence dates (Figure 1) demands closer inspection. McCall (1997) proposed that the Davie Ridge, the elevated topographic structure that marks the shear zone between Africa and Madagascar, was at least partially emergent between 45 and 26 Ma, and could have assisted Cenozoic dispersals. His hypothesis was essentially dismissed, both because of the discontinuous nature of the subaerial exposures, and a lack of

congruence between the emergence dates and the estimated arrival times of Madagascar's terrestrial mammals (Poux et al., 2005). Furthermore, the divergence dates of lemurs and tenrecs differ by tens of millions of years from those estimated for carnivores and rodents (Poux et al., 2005; Yoder et al., 1996, 2003), and this asynchrony was also adduced as evidence against the land bridge hypothesis (Yoder & Nowak, 2006). Sweepstakes dispersal seemed the only plausible explanation.

4 | PROBLEMS WITH TRANSOCEANIC DISPERSAL

Several aspects of the popular scenario for Madagascar's colonization have little or no evidence to support them, and few avenues available to test them. The physiological and oceanographic challenges involved in waif dispersal are severe (Tattersall, 2006; Masters et al., 2006; Stankiewicz et al., 2006; Masters et al., 2007; Mazza et al., 2019), leading to the generation of ad hoc hypotheses to render the unlikely scenario more feasible. One such hypothesis, originally proposed by Simpson (1940), is based on probability theory: if an event is very unlikely (e.g. has a 1 in 1,000,000 chance of occurring), over many millions of years it becomes much more likely. We have discussed in some detail why this popular view is problematic (Mazza et al., 2019; Stankiewicz et al., 2006). In this review, we focus on three ad hoc hypotheses that we believe fail in their intent to render sweepstakes dispersal between Africa and Madagascar more plausible.

4.1 Was the mammal colonization of Madagascar made more likely by their capacity for hypothermy (torpor)?

4.2 Could the aquatic abilities of hippopotamuses have rendered them capable of long-distance transoceanic dispersal?

4.3 A widely cited model (Ali & Huber, 2010) proposing that strong surface currents flowed east from Africa during the Palaeogene is viewed as having facilitated sweepstakes dispersal from Africa to Madagascar. How valid is this proposal?

Finally, we develop an alternative hypothesis to the rafting scenario based on recent geological research in the Mozambique Channel.

4.1 | Did hibernation facilitate mammal migrations to Madagascar?

The unusual occurrence of heterothermy in small-bodied Malagasy primates inspired a refinement of the transoceanic rafting scenario that seemed to render it more plausible. Birds and mammals are endothermic, actively maintaining a constant body temperature despite ambient fluctuations, whereas ambient temperatures determine body temperature in ectothermic animals. Hypothermy is a term only applicable to endotherms, and describes an ectothermy-like cessation of endothermy. Heterothermy is the ability to switch



from endothermy to hypothermy. Torpor is adaptive (i.e. controlled) hypothermy, as opposed to pathological hypothermy (as carried off most victims of the Titanic). Daily torpor is hypothermy limited to the resting phase of the daily cycle (<24 hr). Hibernation occurs when torpor bouts last longer than 24 hr (McNab, 2002).

Hibernation was long considered an adaptation to cold regions, but has since been shown to occur in the tropics (Dausmann et al., 2004; Lovegrove, 2012; Nowack et al., 2020). Endothermy is energetically costly, and most endotherms cannot survive long periods of starvation. A months-long journey rafting passively across ~500 km of surging ocean would require special physiological adaptations to withstand food and water shortages, and exposure to the elements. Mammal waifs are, hence, proposed to have survived in floating hollow trees or on mats of vegetation in a state of hibernation (Martin, 1972; Yoder, 1996). Some animals hibernate in family groups (McNab, 2002), which would facilitate the establishment of viable populations after making landfall (Kappeler, 2000). Seasonal hibernation (May–September) has been observed in lemurs (Blanco et al., 2018; Dausmann et al., 2004; Génin & Perret, 2003) and tenrecs (Lovegrove & Génin, 2008; Treat et al., 2018), and is known to occur in rodents and carnivores in other parts of the world (McNab, 2002). Thus, the use of torpor is invoked as having increased the probability of surviving a transoceanic crossing for four of the orders of terrestrial mammals that arrived on Madagascar during the Cenozoic (Ali & Vences, 2019; Kappeler, 2000; Martin, 1972; Yoder, 1996; Yoder et al., 2003), but not for hippopotamuses.

This narrative, however, relies on the assumption that the ability to enter hibernation was already present in the African ancestors of Malagasy mammals prior to colonization. This supposition is contentious. Although various forms of hypothermy may have evolved as early as the Late Cretaceous (Lovegrove, 2012), hibernation additionally requires the capacity to store fat seasonally, the evolution of which depends on environmental seasonality. Génin and Masters (2016) investigated the evolution of hypothermy in the Malagasy mouse and dwarf lemurs (Cheirogaleidae), the only living primates known to use hibernation (facultative in *Microcebus* spp. and obligate in *Cheirogaleus* spp.). Given the Miocene origins of these genera (Herrera & Dávalos, 2016), hypothermy is likely to have evolved relatively recently in response to gradually deteriorating environmental conditions prior to the Pliocene (Fedorov et al., 2010; Zachos et al., 2001), and probably in association with several episodes of phyletic dwarfing (Génin & Masters, 2016; Masters et al., 2014).

Unusual physiologies are common in Malagasy mammals, supporting the idea that they are adaptations to the island's hyper-variable environment (Dewar & Richard, 2007) and evolved in situ. Comparisons between Malagasy mammals and their close relatives in Africa endorse this interpretation. For example, despite the common ancestry of African lorisiform and Malagasy lemuriform primates, and striking convergences in lifestyles, daily torpor is absent in the African taxa (Mzilikazi et al., 2006; Nowack et al., 2010), some of which experience cold, dry winters with minimum temperatures often falling below 0°C. This is anomalous, as daily torpor is relatively common among Africa's small-bodied mammals (Hallam &

Mzilikazi, 2011; Mzilikazi & Lovegrove, 2004). Hibernation, in contrast, is rare in Africa, and has only been observed in cold regions among animals of Palaearctic origin: bats and dormice (Geiser & Stawski, 2011; Mzilikazi et al., 2012; Nowack et al., 2020).

The most persuasive physiological argument against floating hibernacula, however, is a practical one. As an anti-predator measure, animals rapidly come out of torpor when they are disturbed. A natural raft of vegetation would hardly provide the quiet, dry conditions required for sustained hibernation. Because arousal from torpor is generally active (e.g. in cheirogaleids; Génin et al., 2003), frequent warm-ups would suppress the energetic benefit of hypothermy. Finally, authors have rarely considered how a raft would actually form. If a landslide or a flood takes a dead tree down, animals present on or in the tree would immediately flee, rather than going back to sleep. Semi-aquatic animals like marine iguanas and polar bears sometimes climb on floating wood or ice rafts, and a swimming tenrec or lemur might also find refuge on a floating object, but they would not decide to hibernate there together with their families.

4.2 | How well do the aquatic abilities of hippopotamuses fit them for transoceanic dispersal?

The timing of the arrival of *Hippopotamus* in Madagascar is unknown, as is the number of colonization events involved, although it is commonly assumed to be Late Pleistocene (Ali & Huber, 2010; Simpson, 1940). Six Malagasy sites have yielded radiocarbon-dated remains of three extinct species (Burney et al., 2004; Faure et al., 2010; Goodman & Benstead, 2003; Stuenes, 1989): *H. laloumena*, *H. lemerlei* and *H. madagascariensis*. The imperfectly known *H. laloumena* was intermediate in size between extant *H. amphibius* and extinct *H. lemerlei* and *H. madagascariensis*, both of which were dwarf forms, and is the oldest subfossil taxon: remains dated at approximately 20 ka have been recovered from Mahajanga province in western Madagascar (Faure et al., 2010). Other Malagasy hippopotamus subfossils range in age from ~6 ka (*H. lemerlei* from Anjohibé) to 660–1,400 BP (*Hippopotamus* sp. from Itampolo; Burney et al., 2004). The most parsimonious scenario is that the three descendant taxa evolved from a common ancestral population. *Hippopotamus laloumena* appears to be a less modified form, perhaps closer to the colonists than *H. lemerlei* and *H. madagascariensis*. Despite the fact that *Hippopotamus* is represented by a single species today, hippopotamids were far more diverse in the past (Late Miocene–Early Pliocene), when each basin of the Arabo-African continent hosted its own exclusive suite of species (Boisserie et al., 2011).

It is highly unlikely that three speciation events occurred on Madagascar within 20 ka, implying that hippopotamuses colonized Madagascar much earlier, and evidence was not captured by the limited fossil record. Hippopotamidae are the extant representatives of Africa's oldest terrestrial cetartiodactyl lineage (Lihoreau et al., 2015) and estimated to be ~16 Ma old (Orliac et al., 2010). Their greatest diversity (30–40 species; Lihoreau et al., 2015), according to their extensive fossil record, occurred around 7.5 Ma, in the Late

Miocene, and the oldest *Hippopotamus* fossil is at least 5 Ma old. If hippopotamids arrived in Madagascar at the peak of their diversity, then *H. laloumena*, *H. lemerlei* and *H. madagascariensis* are the end members of a long, largely undocumented history, as is the case for living lemurs.

Hippopotamids are assumed to have reached Madagascar by swimming (Ali & Vences, 2019; Stuenkel, 1989; van der Geer et al., 2014) because of their aquatic adaptations. This assessment is rather extravagant because, irrespective of their swimming capacity, crossing a distance of 400–500 km (perhaps 300 km at an extreme sea level low-stand), swimming against the current and strong eddies, loops and back-loops of the Mozambique Channel without a specific landing area in sight, is logistically not credible (Mazza et al., 2019). Additional difficulties include the physiological facts that living hippopotamuses need 43–72 L of freshwater per day (Calder, 1984), and are highly sensitive to prolonged exposure to salt water and sunlight. The clincher, however, is that hippopotamuses are notoriously bad swimmers (Mazza, 2014, 2015), despite the claim that they are “known to swim significant ocean distances” (Ali & Huber, 2010, p. 653). They have poorly streamlined, barrel-like bodies (Coughlin & Fish, 2009; Fish, 2001) and their feet make bad paddles (Coughlin & Fish, 2009; Eltringham, 1999; Howell, 1930). When moving in water, they keep their feet firmly in contact with the river- or lakebed, galloping short distances during brief unsupported intervals (Coughlin & Fish, 2009; Eltringham, 1999; Fisher et al., 2007; Inuzuka, 2000; Klingel, 1991). They walk on the bottom “as astronauts on the moon” (Estes, 1992), but have never been observed floating or propelling themselves through water. The depth of water bodies in which hippopotamuses can live is further constrained by the need for adults to resurface to breathe every 3–6 min, and juveniles, every 2–3 min (Eltringham, 1999). They avoid deep water (Jackson & Gartlan, 1965) where hydrostatic pressure can hinder resurfacing. To counter buoyancy, which may lead to their rolling over and capsizing, the distal ends of the medullary cavities of hippopotamus limb bones are tightly packed with cancellous bone, shifting the centre of gravity beneath the centre of buoyancy (Coughlin & Fish, 2009; Fish, 2002; Mazza, 2014; Thewissen et al., 2009; Wall, 1983). Salt water increases buoyancy; for hippopotamuses to survive in sea water, they need the stabilizing effect of regular contact with the substrate. Excursions into pounding surf can be fatal: photographic evidence of a hippopotamus fighting for its life to return to the beach is not the behaviour one expects of a transoceanic migrant (see Appendix S1).

Because adult hippopotamuses have difficulty swimming, some researchers have posited that the hippopotamid colonization of Madagascar was accomplished by calves (Ali & Vences, 2019; van der Geer et al., 2014): juveniles are lighter, more buoyant, and good swimmers and may have been swept across to Madagascar by raging currents, where they grew up to found viable populations. This postulate overlooks the fact that juvenile hippopotamuses require an extended period of maternal care to survive. During the 10- to 12-month nursing period, calves grow from a body weight of 5–6 kg to 400–500 kg (Eltringham, 1999) – around a quarter of their adult body weight. A yearling would be more independent, but would

experience many of the hydrostatic restrictions facing a mature adult. We consider it unlikely that juvenile hippos, torn from their mothers and dragged across the Mozambique Channel by hurricanes or tsunamis, survived to found viable populations on Madagascar's foreign shore.

Could hippopotamuses have rafted to Madagascar? Adults weigh between 1.5 and 3 metric tons. A tangled mat of vegetation capable of carrying one or more animals this heavy is difficult to countenance. It seems inescapable that Madagascar's founding hippopotamuses arrived by way of subaerial or shallow marine connections between Africa and Madagascar.

4.3 | Testing Ali and Huber's (2010) model of enhanced transoceanic dispersal

Ali and Huber (2010) proposed that sweepstakes dispersal from Africa to Madagascar was expedited during the Palaeogene, when both landmasses were approximately 10–15° (1,100–1,650 km) south of their present-day position. Even though mean current direction was south-westward, “[t]rajectories starting in the northeast region of Mozambique and Tanzania sporadically experience enhanced eastward velocities of >20 cm/s and could therefore have crossed the necessary distance in 25–30 days” (Ali & Huber, 2010, p. 654). Their estimates were based on simplified calculations based on maximum velocity and the straight-line distance across the Mozambique Channel, although the frequency of such events, and whether they would last sufficiently long to allow the crossing, are unclear. Their reference to a potential contribution by eddy-related jet-like currents to eastward transport remains vague.

Lagrangian analysis provides a more accurate method for investigating both the feasibility and travel time of such a west-east journey. It computes the trajectories of thousands of virtual particles released in Madagascar's vicinity within a time-evolving velocity field, and tracked back to their sources using the tool Ariane (Blanke & Raynaud, 1997). We used the backward mode in our experiments because it allowed us to prioritize those particles that reached Madagascar; a forward release of particles from Africa or India would include many particles that missed the focal area. In our model, each particle's back trajectory was integrated in time until it reached one of three specified sources: Madagascar itself, the East African coast or Palaeo-India.

Surface ocean currents were simulated using a comprehensive ocean–sea ice–atmosphere coupled palaeoclimatic model, and an early Eocene (55 Ma) simulation performed with the Institut Pierre-Simon Laplace (IPSL) Earth System Model (Zhang et al., 2020). Boundary conditions followed the protocol of DeepMIP (Deep-Time Model Inter-comparison Project; Lunt et al., 2017), and were similar to those employed by Ali and Huber (2010). For the Lagrangian analysis, we added eddy-induced velocities resulting from the parameterization of the unresolved mesoscale turbulence (Gent & McWilliams, 1990) to the surface velocity. The eddy contribution was small overall, and orientated south-westward on the west

side of the Mozambique Channel and south-eastward in the east. Owing to the southerly position of Madagascar in the Eocene, the Mozambique Channel carried the strong southward western boundary current of the anticlockwise subtropical gyre extending from Africa to South America. Annual mean currents were dominated by southward currents (Figure 2a), although there were some seasonal effects.

We conducted two Lagrangian simulations to determine the proportion of particles that arrived in Madagascar from the African coast and the time required to finish their journey. For the first simulation (SIM 1), we released 18,757 virtual particles each month over a single climatological year. The year was synthesized from the monthly means of the last 100 years of the 4000-year-long IPSL model simulation, once equilibrium had been reached, and, hence, represented “average” monthly currents. In the second simulation (SIM 2), we released particles continuously each month over a period of 120 years to catch inter-annual current variations, and assess whether sporadic events could significantly shorten travel times.

Table 1 reports the proportions and travel times of particles arriving from Madagascar, Africa and India in SIM 1. Most particles (69%) originated from Africa, and had an average travel time of 3.5 months. Lagrangian streamfunctions were statistically integrated with particle trajectories to indicate general travel routes (Blanke & Raynaud, 1997; Döös, 1995). Most of the African particles moved south before their eastward transport towards Madagascar (Figure 2a; by definition, positive values indicate anticlockwise transport in backward streamfunctions). The fastest particles, at

extremely low numbers (0.07%), finished their journey in about 23 days. Closer examination of their trajectories, however, revealed that this travel time was severely underestimated. This was because, to derive the quantitative diagnostics using Ariane, the particles were released and arrested at the ocean faces of the model grid-cells (224×193 km) about 200 km from land, as can be seen from the initial and final positions in Figure 2a. To address these inherent deficiencies, we performed a second version of SIM 1 to estimate travel time more precisely. We released particles manually from 19 positions in the middle of the ocean grid-cells along Madagascar's west coast, about 110 km from the coastline, each month of a single climatological year (228 releases in total). Trajectories were computed backward until the particles eventually approached within ~ 100 km of the African coastline. For each release location, we selected the fastest particles to reach Africa, and we illustrate their backward trajectories in Figure 2b. The fastest particles landed in north-western Madagascar, and required 70 to 90 days to cross the channel. Hence, the minimal travel time for particles leaving Africa to reach Madagascar is 70 days, based on the mean monthly currents of our climatological year, even under the most conducive palaeogeographic conditions. A more extensive discussion of this correction is contained in Appendix S2.

The second transient Lagrangian simulation (SIM 2) was carried out continuously for 120 years to account for inter-annual current variations. Figure 3 shows the travel times of fast particles (i.e. shorter than 60 days' travel) according to the year and month they arrive in Madagascar. The most favourable currents occurred in the

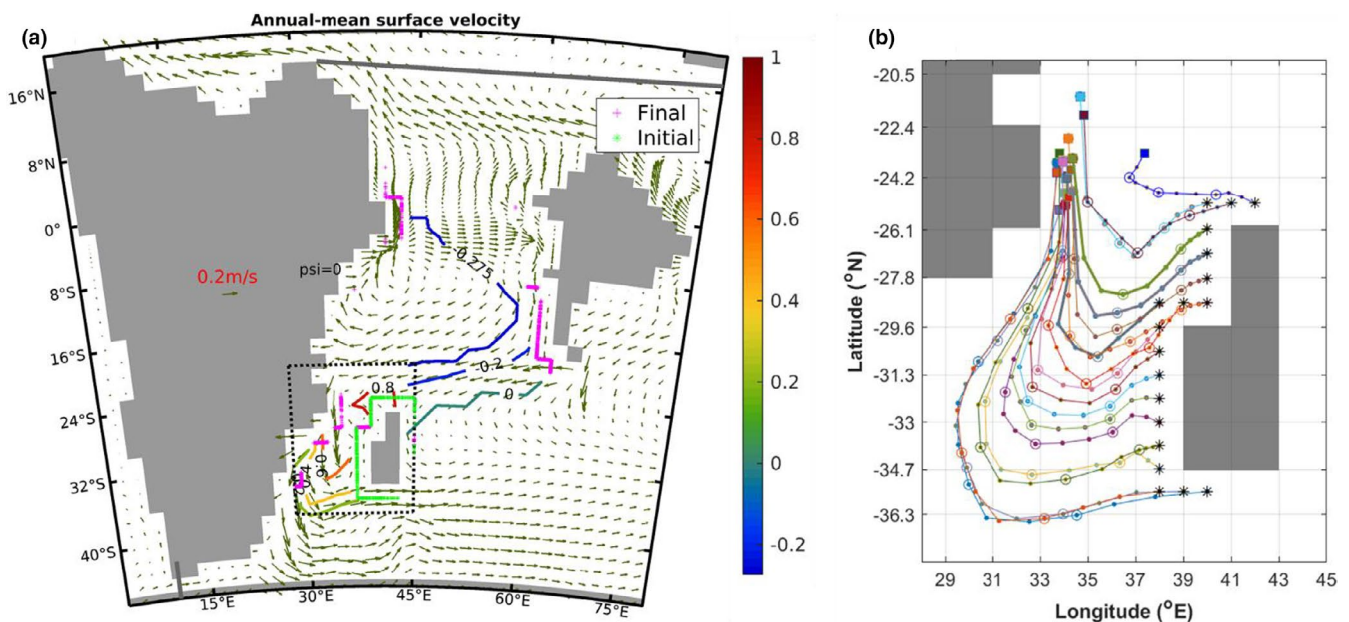


FIGURE 2 (a) Initial (*) and final (+) locations of particles in the first backtracking Lagrangian simulation (SIM 1). The Lagrangian streamfunction, integrated from particle trajectories, is indicated by coloured contours and shows transport in Sv units (1 Sverdrup = 10^6 m³/s). Positive values indicate anticlockwise transport. Annual mean surface velocities are shown as vectors, interpolated at the centre of temperature grid-cells. (b) Backward trajectories for the fastest particles across the Mozambique Channel in the enhanced SIM 1, plotting points every 10 days and circles every 30 days. The grid indicates the ocean model grid-cells, and grey shading represents land cells. Particles were released along Madagascar's west coast each month (black stars) and tracked backward in time until they reached East African coastal ocean cells (squares)

TABLE 1 Results of the first Lagrangian simulation (SIM 1) using climatological monthly currents: proportion of particles backtracked from Madagascar to three possible source continents, and travel times in days. Africa–Madagascar travel is shaded in grey

Particle source	Madagascar	Africa	Palaeo-India
Proportion of particles	7%	69%	24%
Minimum time (days)	2	23	140
Mean time (days)	40	106	229

austral summer, with arrivals in Madagascar from September to December and exceptionally in January, with travel times between 20 and 40 days. Some inter-annual variations in travel time occurred over these 120 years. For instance, relatively shorter travel times were seen in the years 20, 40 and 60–90, and longer travel times in the years 45 and 103–107. The fastest particles finished their journey in about 20 days in the year 96 (shown in blue in Figure 3), which is only slightly shorter than the 23 days found under the simulated mean monthly currents. As in SIM 1, these travel times must be corrected by the additional time needed to cross the coastal grid-cells on both the Malagasy and African coasts. The more accurate trajectories shown in Figure 2b indicate that the fastest particles took a minimum of 20 days to exit the coastal grid-cells of Madagascar, and probably a similar period close to Africa, leading to a minimum travel time of about 60 days in the most conducive year.

In summary, our Lagrangian analyses showed that very few particles (of tens of thousands) could cross the Mozambique Channel from East Africa to Madagascar within 70 days, given climatologically simulated mean monthly currents. Furthermore, accounting for inter-annual variations over a 120-year period only shortened the travel time by 3 days. These simulations did not consider the

influence of windage on floating objects (i.e. the effect of wind on the portion of an object above the surface). In our palaeoclimatic model results, average wind direction was eastward from Africa to Madagascar, with mean velocities up to 3 m/s. Including a crude estimate of windage (~1% of wind speed according to Allshouse et al., 2017; i.e. about 3 cm/s) reduced the travel time by a few days. Overall, our Lagrangian-based estimate of the fastest travel time between Africa and Madagascar is double that proposed by Ali and Huber (2010), despite similar palaeogeography and palaeocurrents. Hence, we believe that faith placed in this model to enhance the likelihood of sweepstakes dispersal from Africa to Madagascar (e.g. Samonds et al., 2012, 2013; Townsend et al., 2010) is unfounded.

Ali and Vences (2019, p. 2636) concluded their defence of long-distance over-water rafting with the words: "...rejection of the process necessarily requires causeways to explain the distributions.... What is the evidence for these physiographical features?" In the following section, we investigate this question.

5 | PALAEOGEOGRAPHY AND VERTICAL MOVEMENTS IN THE WESTERN INDIAN OCEAN: INDICATIONS OF CENOZOIC LAND BRIDGES

Past geological reconstructions of the evolution of the Mozambique Channel have focussed on horizontal displacements, essentially ignoring vertical movements. Earth's sediments, crust and mantle are in constant interaction with the oceans. Deep Earth and tectonic processes shape ocean structure and material transfer at the largest of scales. Subsidence and isostatic rebound, uplift, climatic variation and fluid escape are profoundly connected to the processes of erosion, sedimentary mass transfer and, ultimately, deposition and

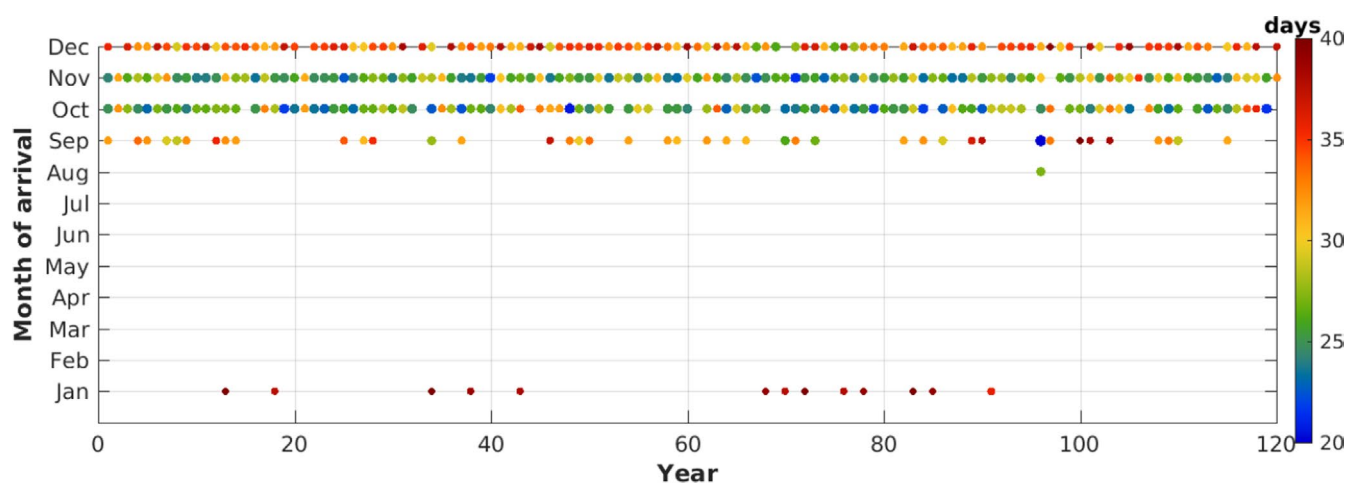


FIGURE 3 Monthly distribution of the fastest particles (i.e. those with a travel time shorter than 2 months) to reach Madagascar from Africa over the 120-year simulation (SIM 2), and their travel times (colour-coded to indicate numbers of days). Note that the day counts indicated by the colour spectrum are uncorrected for the additional time required for particles to cross the 200 km interval on either coast, so 2×20 days should be added to these figures; hence, a count of 20 days is in fact $20 + 20 + 20$ days. The month of arrival refers to the month particles reached Madagascar; their departure from Africa would have taken place 60–100 days prior to arrival

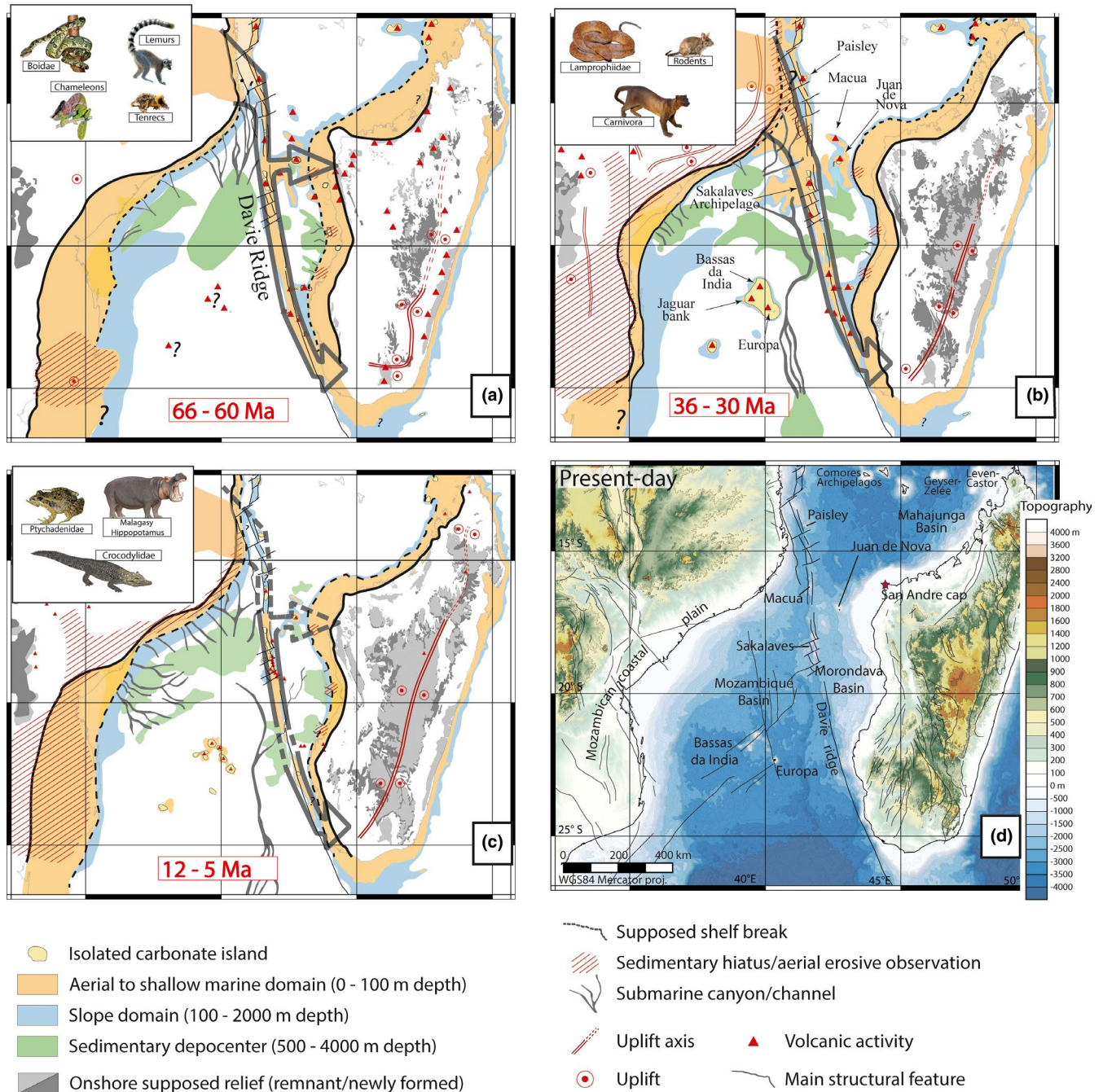


FIGURE 4 Past and present physiographic maps of the Mozambique Channel. The palaeomaps are compilations of recent studies (Baby et al., 2018; Courgeon et al., 2017; Delaunay, 2018; Leroux et al., 2020; Ponte, 2018; Ponte et al., 2019). Observations indicate three episodes of subaerial exposure: (a) Late Cretaceous–Early Palaeocene (66–60 Ma), (b) latest Eocene–Rupelian (36–30 Ma), (c) Late Serravallian–Messinian (12–05 Ma), while (d) shows present-day bathymetry. Animals portrayed in the top left hand corners of a, b and c may have colonized Madagascar at this time

storage of material in deep basins. These processes are at the heart of the sedimentary cycle, and comprise archives of Earth's past geodynamic activity and landform evolution. The sedimentary record is a consummate storyteller: even the absence of sedimentation (hiatuses) can yield information on uplifts and erosion, allowing us to reconstruct past environments and vertical movements.

Several magmatic events related to global kinematic changes affected the western Indian Ocean over time (Karoo ~180 Ma;

Movene-Bumeni ~145–135 Ma; Turonian traps ~95 Ma; completion of the Mascarene basin ~66 Ma; India-Eurasia collision ~50–45 Ma; second uplift of the East African margin ~40–23 Ma; magmatism around Madagascar ~10–7 Ma), producing bulges, uplifts and sea-mounts. To understand the effects of these events, the PAMELA (Passive Margins Exploration Laboratories) research programme undertook sedimentary, tectonic, volcanic, kinematic and palaeo-environmental studies of Mozambique and Madagascar, covering the

period from the opening of the Mozambique Channel to the present day. The project involved more than 100 researchers, including 12 PhD candidates and 10 post-doctoral fellows, and entailed eight oceanographic cruises between 2014 and 2017 (224 days at sea), and three onshore geological surveys in 2017 and 2018 (50 land days). It benefitted from collaborations with the Total and Schlumberger companies, which shared a large industrial dataset generated by drilling and tracking seismic lines. The PAMELA results present a far more complex and dynamic picture of the channel's bathymetric and topographic evolution than previously envisioned. Magmatic data were analysed by Courgeon et al. (2016, 2017, 2018) and Leroux et al. (2020), while other studies focussed on sedimentology (Baby et al., 2018; Delaunay, 2018; Ponte, 2018; Ponte et al., 2019), geodynamics and tectonics (Moulin et al., 2020; Thompson et al., 2019). We synthesized these results to reconstruct four palaeogeographic snapshots of the channel's evolution using the PLACA4D free-ware interactive tool for palinspastic reconstruction in 3D (Matias et al., 2005; Pelleau et al., 2015; Figure 4).

After the Madagascar plate stopped moving south, the Davie Ridge played a crucial role in the morphology of the domain. A consistently low record of sedimentation (low deposition and/or low preservation due to erosion) between 120 and 23 Ma (Delaunay, 2018; Ponte et al., 2019) indicates either the presence of a relatively consistent topographic high, or deposition–erosion sequences. Drowned Miocene carbonate platforms are characterized by well-developed karstic topographies, which suggest extended periods of subaerial exposure and include volcanoclastic deposits typified by armoured lapilli and carbonate fragments that indicate the occurrence of shallow to subaerial phreatomagmatic explosions (Courgeon et al., 2016, 2017, 2018). Evidence of general vertical movements attests to emergent land and/or very shallow areas creating land bridges between Africa and Madagascar at three well-defined periods separated by marine intervals. The width of the bridges is difficult to estimate precisely because of variations along the length of the ridge, but our data indicate that they were several to tens of km in extent.

These periods correspond to world-wide kinematic reorganizations, which drove or were associated with oceanic magmatism and continental flood-basalt eruptions, tectonic events (orogenesis, uplift or subsidence), abrupt changes in sea-floor spreading, ocean-anoxic and black-shale events, large evaporite deposits, mass extinctions and sea level lows (Leroux et al., 2018; Moulin et al., 2010). In reconstructing these palaeobathymetric maps, we did not consider sea levels; low sea levels would have extended the areas of subaerial exposure.

5.1 | Present-day situation

The modern physiography of the western Indian Ocean resulted from the break-up of western (South America and Africa) and eastern (Madagascar, India, Australia and Antarctica) Gondwana, which occurred in two phases: in the Late Triassic (165–155 Ma) and Early Cretaceous (135 Ma; Thompson et al., 2019). The southward motion

of the Madagascar plate relative to Africa (>155–120 Ma) produced a major transform zone called the Davie Fracture Zone or Davie Ridge: a 1,200-km-long topographic high with a N170 trend. It separates the Rovuma and Tanzania Basins, to the west; the Somali Basin, between Somalia and northern Madagascar (Mahajanga); and the Morondava Basin between the Davie Ridge and Madagascar's west coast to the east (Coffin & Rabinowitz, 1987; Davis et al., 2016; Heirtzler & Burroughs, 1971; Thompson et al., 2019). The southward motion of the Antarctica plate relative to Africa (>155–present-day) generated the Mozambique Basin, bounded to the west and north by the Mozambique coast, and to the east by the Davie Ridge (Thompson et al., 2019).

Figure 4d shows a present-day bathymetric map. Three volcanic seamounts (Paisley, Macua and Sakalaves) occur along the Davie Ridge (Bassias, 1992; Leclair et al., 1989). Buried carbonate terraces on some islands indicate that carbonate production took place in several phases: from 66 to 60 Ma (Sakalaves platform, Glorieuses, Juan de Nova Island, Leven-Castor highs); in Rupelian-Langhian times (36–30 Ma; Bassas da India, Hall Bank) and, more recently, in Messinian-Pliocene times (~5 Ma; Comoros archipelago; Courgeon et al., 2017; Leroux et al., 2020).

5.2 | Three potential short-lived land bridges

5.2.1 | Latest Cretaceous–Early Palaeocene (66–60 Ma): widespread continental uplift

This period (Figure 4a) coincided with a global mass extinction and wide-scale magmatism, including the outpouring of the Deccan flood basalts; the first uplift of the South African plateau (Baby et al., 2018); and volcanism in the Mozambique Channel and Madagascar (Bardintzeff et al., 2010; Delaunay, 2018; Ponte, 2018). A sedimentary hiatus on Madagascar's west coast between the uppermost Maastrichtian (66 Ma) and the basal Selandian (60 Ma; Delaunay, 2018) matches a hiatus along the Mozambican coast (Ponte, 2018), indicating broad exposures of coastal land on both sides of the channel. This period coincides with the end of the first uplift of the Malagasy plateau (Delaunay, 2018). The Davie Ridge was largely subaerial (Ponte, 2018), and land connections between Mozambique and Madagascar were possible in both the northern and southern parts of the Morondava Basin.

5.2.2 | Late Palaeocene–Early Eocene (60–50 Ma): general transgression, loss of land bridge

During the Palaeocene–Eocene transgression, sea levels rose and previously subaerial environments were submerged. Three small depocentres (i.e. deltaic deposits linked to fluvial outlets) were emplaced in the northern part of the Mozambique Basin, close to the Beira High and Limpopo Margin. By 57 Ma, ~200 m of largely hemipelagic sediments covered the deepest parts of



the basin (Ponte, 2018). This 10 Ma period embraced the Early Eocene Climatic Optimum (51–53 Ma; Zachos et al., 2001) and the Palaeocene-Eocene Thermal Maximum (~55 Ma; Zachos et al., 2008). This warm period led to the development of a shallow lagoon-reef carbonate system during the Palaeocene (Upper Grudja Fm.) and Eocene (Cheringoma Fm.; Salman & Abdula, 1995) in the shallowest parts of the basin. Carbonate formation would have occurred mostly on high points in the channel, often related to volcanism. Reef growth was inhibited near the deltaic outlets of the Zambezi and Save Rivers, with their large detritic inputs. A large, shallow carbonate platform (Tulear Carbonate Fm.) lies along Madagascar's south-west coast, except in the Cap Saint-André area, where the Palaeocene is not preserved (Delaunay, 2018). Maximum transgression also occurred in the Ypresian (52 Ma) on the western Malagasy margin, and led to the establishment of ramp-type carbonate (limestone) platforms on Madagascar's western periphery. Deposits 50–36 Ma correspond to a global highstand followed by a slow lowering of sea level in a cooling climate (Zachos et al., 2001). The sedimentary record indicates progradation of previous carbonate platforms, and mass transport of turbidites and contourites at greater depths.

5.2.3 | Late Eocene–Early Oligocene (36–30 Ma): very shallow marine corridors

The Eocene-Oligocene transition (Figure 4b) was the result of a major shift in global climates, coincident with the first occurrence of ephemeral ice sheets in Antarctica (Zachos et al., 2001). It saw the extinction of many northern hemisphere lineages that had flourished during the warm, humid Eocene, including the fossil relatives of Malagasy lemurs, and was termed “la Grande Coupure”. The physiography of the Mozambique Channel also changed in response to an episode of tectonic uplift that led to the bilateral re-emergence of carbonate platforms on both coasts. In Madagascar, this event is marked by a ~1.8 Ma sedimentary hiatus in the earliest Rupelian (Delaunay, 2018); in the Mozambique Basin, Oligocene deposits lie on a strong erosive surface incising the Late Eocene carbonate platform down to the upper slope (Ponte, 2018; Ponte et al., 2019).

At a regional scale, this event is coeval with the initiation of the East African Rift System (Chorowicz, 2005; Courgeon et al., 2017; de Wit, 2003; Ebinger, 1989; Macgregor, 2015), and the second uplift of the southern Africa plateau (38–16 Ma; Baby et al., 2018; Mougnot et al., 1986). As a consequence of this tectonism, the Davie Ridge emerged, together with the Sakalaves archipelago and Juan de Nova volcanic island, west of Cap Saint-André. Along the Mozambique Channel, other isolated islands experienced volcanic activity: Bassas da India, Europa, Jaguar Bank, Macua and Paisley. These islands were mostly subaerial 36–30 Ma, before being weathered and eroded, especially through wave activity, during the Late Oligocene-Miocene (Courgeon et al., 2017). During this time, the connections among the Davie Ridge, Rovuma and Madagascar may

not have been continuous, but interrupted by small (<50 km), shallow marine corridors between the topographic highs.

5.2.4 | Late Oligocene–Early-Middle Miocene (28–12 Ma): marine flooding, loss of land exposures

This interval is characterized by a fundamental change in sedimentary architecture from the low slope carbonate ramp system to a much more siliciclastic sedimentation with large prograding clinofolds along the Mozambique and Madagascar coasts (Delaunay, 2018; Ponte, 2018) and a clear shelf-slope-deep basin architecture (Ponte et al., 2019, fig. 6). Early Neogene sedimentation is characterized by several episodes of marine flooding during Langhian and Late Serravallian (16–12 Ma) times. In the Early to Middle Miocene, shallow platforms built up around isolated islands, at times affected by partial subaerial exposure with karstification (Courgeon et al., 2017).

5.2.5 | Late Serravallian–Messinian (12–5 Ma): non-continuous connections (stepping stones, shallow reefs, volcanic islands, shallow marine corridors)

Late Serravallian volcanism is recorded south of the Sakalave islands in the northern part of the Davie Ridge (Figure 4c), coeval with the third regional uplift of Madagascar (Delaunay, 2018), and causing exposure of Madagascar's continental platform in Serravallian-Tortonian time. Subaerial exposure in the Late Miocene-Pliocene is attested by presently drowned isolated platforms that preserve well-developed karstic topographies and fresh water diagenetic features (Courgeon et al., 2017). Subaerial volcanism, contemporaneous with extensional tectonic deformation, then covered the carbonate platforms, leading to their post-tectonic drowning in the Pliocene. Drowning of the southern part of the Davie Ridge is also evident from the Middle Miocene onwards, with the observation of deep-sea channels running from the Morondava Basin to the deep turbiditic system south of the Mozambique Channel (Delaunay, 2018). This north-south inundation is further attested by relatively thin sedimentary stack, <100 m in the northern Morondava Basin (a basal unconformity with a major hiatus of 14 Ma is observed in some wells), increasing in thickness to the south. Mean sedimentary accumulations of 300–800 m characterize the main river outlets in the central and southern parts. We therefore infer a non-continuous connection, interrupted by small (<50 km), shallow marine corridors between the Davie Ridge and the northern part of the Morondava Basin, during this period (Figure 4c).

This third bridge was followed by a general Late Miocene–Early Pliocene drowning of the Mozambique Channel. Many isolated carbonate platforms subsided to form guyots, and only a few are subaerial today (e.g. Juan de Nova, Comoros islands; Courgeon et al., 2017, 2018; Leroux et al., 2020). Tectonic and volcanic rejuvenation related to a world-wide Late Messinian geodynamic phase

(Leroux et al., 2018) led to the channel's present-day bathymetry (Figure 4d).

6 | DISCUSSION

Biogeographic mechanisms are generally dichotomized into vicariance (the earth moves) and dispersal (the organisms move). Vicariant taxa shared by Madagascar and Africa must have been present on the island by ~120 Ma, while taxa shared with India may be no younger than 84 Ma; hence, most researchers agree that lineages with Late Cretaceous–Cenozoic origins shared among Gondwanan landmasses must be the products of dispersal, which in turn is equated with transoceanic rafting, swimming or flying (Ali & Huber, 2010; Ali & Vences, 2019; Kappeler, 2000; Krause, 2010; Krause et al., 2020; Nagy et al., 2003; Vences et al., 2004; Yoder, 1996; Yoder et al., 2003; Yoder & Nowak, 2006). We agree with the first part of this conclusion, but propose that geodispersal along runways or corridors aided the dispersal of terrestrial vertebrates (Tattersall, 2006; Upchurch, 2008).

The possibility of short-lived land connections between Africa and Madagascar over the past 100 Ma has been widely rejected on two grounds: (a) the limited taxonomic representation of Madagascar's fauna, chiefly its mammals (Simpson, 1940); and (b) the absence of evidence for land bridges. Madagascar's living terrestrial mammals represent only four higher taxa: strepsirrhine primates, afrosericid tenrecs, euplerid carnivores and nesomyine rodents. If there had been a land bridge, authors argue, "a greater variety of animals would have crossed" (Ali & Huber, 2010), as "all clades of that antiquity would have had equally probable chances of colonizing Madagascar" (Yoder & Nowak, 2006), and "large-scale invasions [would] almost certainly have ensued" (Ali & Vences, 2019).

What might explain the taxonomically selective nature of Madagascar's extant mammal fauna? This is often (e.g. Ali & Vences, 2019) ascribed to a shared capacity to use heterothermy to survive adverse conditions. Our studies suggest that this interpretation is less likely than the alternative that heterothermy evolved in situ after the colonization events. Additionally, the small number of lineages known to have been present on Madagascar during the last 80 ka are unlikely to represent all of the taxa that colonized the island. Insular biotas are highly vulnerable to extinction and defaunation (Prendergast et al., 2016; Whittaker & Fernández-Palacios, 2007), particularly with respect to large-bodied animals, but the limitations of Madagascar's fossil record render most extinct taxa invisible. A more promising avenue of research to explain the limited taxonomic representation of successful colonists is the concept of habitat filtering: i.e. the fact that colonizers can only establish viable populations in habitats to which they are at least partially adapted. Dispersal filtering (van der Geer et al., 2010) describes the selective effects of vagility on migrants moving towards islands, but habitat filtering may impose more restrictions on biogeography than dispersal, even on remote oceanic islands (Carvajal-Endara et al., 2017). Land bridges

provide not only runways, but habitats as well; while rafting must occur within an individual's lifetime, geodispersal can occur over several generations. We propose that many of Madagascar's vertebrates arrived on the island with the aid of three short-lived (~5 Ma) land connections between Madagascar and Africa, which emerged during episodes of regional uplift, climate change and low sea level stands. Global cooling led to droughts in Madagascar and sub-Saharan Africa, associated with extinctions and subsequent radiations. Faunal and floral exchanges were facilitated by the presence of similar habitats on both sides of the channel, and need not have been unidirectional. Plants, such as crotons (*Croton*, Euphorbiaceae; Ngumbau et al., 2020) and baobabs (*Adansonia* spp.), and animals, such as the ancestors of loriform primates and Miocene tenrecids, may have colonized Afro-Arabia from Madagascar.

Our proposal indicates a different pattern of colonization from the near-random pattern predicted by sweepstakes dispersal. In Table 2, we list Malagasy faunal and floral taxa, the molecular divergence dates of which coincide with the presence of the three land bridges (data from Buerki et al., 2013; Crottini et al., 2012; Prum et al., 2015, and other authors cited in this study). We included birds despite their capacity for flight, as not all winged vertebrates are equally prone to dispersal across tracts of ocean. Furthermore, many plants (like the heather family Ericaceae; Schwery et al., 2015) and animals (like the Tenrecidae) belong to ancient lineages, but apparently reached Madagascar relatively recently. This implies that the island experienced long periods of isolation rather than continuous colonization by sweepstakes dispersal prior to the mid-Miocene.

6.1 | Early Palaeocene (66–60 Ma)

Only three early angiosperm families appear to have been present on Madagascar in the Late Cretaceous: the Hernandiaceae, Proteaceae and Winteraceae (Buerki et al., 2013; Callmander et al., 2011). The establishment of a continuous connection between Africa and Madagascar at the Cretaceous–Palaeocene boundary could have allowed the movement of tenrecs (related to African golden moles) and strepsirrhine primates (Poux et al., 2005; Yoder et al., 1996), as well as the ancestors of the cuckoo-rollers (*Leptosomus*), which form a clade with the mouse birds (Coliidae), now endemic to Africa but once more widespread (Prum et al., 2015). Other endemic birds likely to have colonized Madagascar at this time include the couas (Cuculidae) and the mesites (Mesitornithidae, Braun et al., 2019; Prum et al., 2015). At least three angiosperm families probably followed the first land bridge (Birkinshaw, 2001; Buerki et al., 2013). In two of these (Fabaceae, the diverse legume family) and Meliaceae (the mahogany family), early endemic genera (*Baudouinia* and *Quivisianthes*, respectively) had seeds dispersed by gravity, implying the existence of a continuous land bridge. The third family, Menispermaceae, was represented by *Burasaia*, which produces fleshy fruits and seeds dispersed by lemurs today. If this association is ancient, it suggests that primate–angiosperm coevolution may date back to the Early Palaeocene.



TABLE 2 Tempo of colonization of some plant and animal families (or sub-families) with Malagasy endemics, reconstructed on the bases of three hypothetical land bridges and available molecular divergence dates

	Cretaceous–Palaeocene boundary	Eocene–Oligocene boundary	Miocene–Pliocene boundary
Angiosperms ¹	Fabaceae Meliaceae Menispermaceae	Arecaceae Burseraceae ⁴ Didiereaceae Ericaceae ⁵ Euphorbiaceae ⁴ Gentianaceae Monimiaceae Myrticaceae Passifloraceae Rubiaceae Sapindaceae Simaroubaceae	Anacardiaceae ⁴ Asteraceae Brassicaceae (Capparoidae) ⁴ Combretaceae ⁴ Ebenaceae ⁴ Loganiaceae ⁴ Loranthaceae ⁴ Fabaceae (Mimosoideae) Malvaceae Salvadoraceae ⁴ Viscaceae ⁴ Poaceae ⁴ (except bamboos)
Fishes ²	Bedotiidae ^a Aplocheilidae Cichlidae		
Amphibians ²	Mantellidae ^a Microhylidae Hyperoliidae		Ptychadenidae
Reptiles ²	Boidae Chamaeleonidae Gekkonidae Gerrhosauridae Scincidae Typhlopidae Xenotyphlopidae	Lamprophiidae	Crocodylidae <i>Hemidactylus</i> (Gekkonidae) ^b
Birds ³	Leptosomatidae ^a Mesitornithidae ^a Cuculidae (Phaenicophaeinae ^a)	Brachypteraciidae ^a Upupidae Psittacidae	Eurylaimidae (Philepittinae ^a) Vangidae ^a
Mammals ²	Lemuridae ^a Tenrecidae ^a	Eupleridae ^a Nesomyidae	Hippopotamidae ⁴

Note: Dates from ¹Buerki et al. (2013) (angiosperm families with endemic genera); ²Crottini et al. (2012); ³Prum et al. (2015) or ⁴suggested by this study, and ⁵Schwery et al. (2015).

^aEndemic families or subfamilies.

^bPossible human introduction.

6.2 | Late Eocene–Early Oligocene (36–30 Ma)

Following the “Grande Coupure”, a second continuous or near-continuous land connection was established between Africa and south-western Madagascar as a result of regional uplift associated with the formation of the East African Rift System (de Wit, 2003; Delaunay, 2018). It may have assisted carnivores, rodents and the snake family Lamprophiidae (the ancestors of the bizarre *Langaha*, which has an extended rostrum) to colonize the island, along with vasa parrots (*Coracopsis*), ground rollers (Brachypteraciidae, related to true rollers) and the Madagascar hoopoe (*Upupa marginata*). The carbonate platforms and reefs that made up much of the bridge were probably dominated by mangroves, which are known to have spread throughout the Indian Ocean during the Eocene (Ellison et al., 1999). This would imply an environment much like the island of Zanzibar, which has indigenous carnivores (herpestids

and viverrids), murine rodents, primates and small afrotherians (hyraxes and sengis; Prendergast et al., 2016). Madagascar itself apparently experienced the spread of dry thicket, dominated by *Euphorbia* trees (Euphorbiaceae) and the Didieraceae (cactus-like trees long believed to be Malagasy endemics, but now allied with African genera; Applequist & Wallace, 2003; Table 2). Today, this vegetation type is endemic to the south of the island, but xerophytic relicts in the north and the north-east (such as the white-breasted mesite *Mesitornis variegata*, white-browed owl *Ninox superciliaris* and Madagascar hoopoe), suggest it was present throughout the island in the Oligocene, with the exception of a moist evergreen forest refuge in the south-east. Dispersal may have been aided by plant–animal diffuse coevolution: among the 12 angiosperm families that probably reached Madagascar during that time, all have species that are associated with lemurs, which serve either as pollinators (Didieraceae) or as seed dispersers (see Table 2,

particularly the speciose Rubiaceae; Birkinshaw, 2001; Bollen et al., 2004).

6.3 | Late Miocene (12–5 Ma)

The most recent connection occurred between two dry periods associated with the onset of modern climate, prior to the wet Early Pliocene. This period is associated with the formation of the north-western Sambirano moist evergreen forest subregion, which is connected to the eastern moist evergreen domain by means of a regional uplift that established the modern topography of the island. This last land bridge was established between the Davie Ridge and south-western Madagascar. It was probably discontinuous and consisted of two major deltas facing each other across the Mozambique Channel, separated by a narrow remnant of the old land bridge. Our reconstruction explains why the connection only allowed the dispersal of aquatic animals (crocodiles, hippopotamuses, one family of frogs), with one possible exception: the gecko *Hemidactylus*, which may have been a human introduction (Table 2). Again, seed dispersal by birds and lemurs probably assisted the colonization of Madagascar by plant families such as the Anacardiaceae, Brassicaceae (Capparoidae), Ebenaceae, Loganiaceae, Malvaceae [including Bombacoidae (baobabs, *Adansonia*) and Tilioidae (*Grewia*)], Salvadoraceae and mistletoes (Loranthaceae and Viscaceae; Génin & Rambeloarivony, 2018). At least two groups of birds are likely to have become established on Madagascar at that time: the endemic Vangidae, related to the African batises (Platysteiridae; Jønsson et al., 2012), and the asities, related to the African broadbills (Eurylaimidae; Prum et al., 2015). Finally, the spread of grasses (Poaceae) in Madagascar was limited to wetlands, forest and some high summits (Bossert, 1969; Paulian, 1961). The only grazers to follow them across the channel were hippopotamuses, which evolved dwarf forest forms, indicating that Madagascar's vegetation was considerably more woody than that of East Africa (Carlquist, 1974). Another example of insular woodiness concerns the African savanna Combretaceae (*Terminalia* and *Combretum*) and mimosoid Fabaceae, including the endemic genus *Alantsilodendron* (sister genus to *Dicrostachys*, also present on the island and shared with Africa) and acacias (*Senegalia* spp.); all of these woodland taxa became forest species on Madagascar (Buerki et al., 2013; Schatz, 2001). The Asteraceae family (*Io*), characterized by unusual anemochorous (wind-dispersed) seeds, may also have colonized the island during this period by discontinuous stepping stones, possibly from herbaceous ancestors (Buerki et al., 2013; Carlquist, 1974; Table 2).

7 | CONCLUSION

Our biogeographic reconstruction embraces a variety of mechanisms, including vicariance, geodispersal via land bridges, "island hopping" (Whittaker & Fernández-Palacios, 2007) and possibly

some limited rafting over short distances of brackish water by crocodiles, geckos and frogs. Long-distance transoceanic dispersal was restricted to plants producing minute seeds transported by wind (e.g. orchids) or floating seeds (coco palm, mangrove trees, perhaps *Strychnos* and *Adansonia*), bats and some birds, mostly of Eurasian or Australasian origin and distributed over many Indian Ocean islands (e.g. pigeons, drongos, warblers, magpie robins and white-eyes). The few Malagasy birds that migrate to Africa in winter are likely to have reached Madagascar in the Pleistocene (broad-billed roller, *Coracias glaucurus*; Madagascar bee-eater, *Merops superciliosus*; Madagascar lesser cuckoo *Cuculus rochii*; Madagascar squacco heron, *Ardea idea*).

We undertook this cross-disciplinary study to integrate information on Earth and life dynamics in an attempt to resolve a multi-dimensional problem that has remained intractable to less diverse approaches. We do not claim to have resolved this 200-year-old conundrum, but we present a new framework for investigation of the evolutionary history of the biota of this enigmatic island-continent. The details of our model are bound to change as more fossil and molecular data are recovered and applied to interrogate it. For this reason, we make explicit predictions that carry the possibility of disproof. Whatever its value for our colleagues, this study proved extremely educational for us, the authors. The data provided by the geologists and oceanographers were previously unknown to the biologists, and *vice versa*. When we combined our reconstructions, we were amazed by how much they informed one another. Surely, cross-disciplinary science is the future of biogeography.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The major part of the data employed in this study have been published, either in doctoral theses or widely available journals. We include a more extensive discussion of our test of the Ali-Huber model of Palaeogene currents as Appendix S2.

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BIOSKETCH

This synthesis germinated in 2017 at Nelson Mandela University, during the first meeting between JCM and DA. JCM is an evolutionary biologist focussing on strepsirrhine evolution. FG is an ecophysicist by training and a naturalist by calling. YZ is a palaeoceanographer and palaeo-climatologist. TH is a physical oceanographer with expertise in large-scale ocean modelling. PPAM is a vertebrate palaeontologist and taphonomist focussing on insular mammals, especially hippos. RP is a postdoctoral researcher who divides his time between France and South Africa, monitoring earth movements. MR is a sedimentologist with expert understanding of the late Miocene. DA is a geologist, geodynamicist, expert in plate tectonics and Director of the Laboratory of Geodynamics and Sedimentary Record at IFREMER. MD is a geophysicist, Director of AEON.

Author contributions: JCM and DA designed the project. JCM compiled the text. FG contributed the sections on heterothermy and much of the discussion. YZ and TH conducted the Lagrangian analysis and contributed Section 4.3. PPAM contributed Section 4.2 and Supporting Information. RP, MR and DA participated in the PAMELA project, supervised postgraduate projects and wrote Section 5. MD established the SA-France collaboration and kept the project on track.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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