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Introduction

Islands are a natural consequence of Earth's dynamic nature, and hundreds of thousands occur in our oceans. Most are classified as either continental (subaerial parts of continental shelves, connected to the mainland during sea level low-stands, and often inhabited by elements of the mainland biota) or oceanic (formed over oceanic plates and never connected to a continent, so that their biota arrives by dispersal) (Whittaker and Fernández-Palacios 2007). Madagascar comprises a large continental fragment (587,041 km^2) that shares attributes with both continental and oceanic islands. Today it has an oceanic level of isolation, separated by the Mozambique Channel from Africa's eastern shore by 420 km at its closest point. The channel is an extraordinarily ancient and formidable biogeographic barrier to the migration of terrestrial vertebrates, marking the first major rupture in the fragmentation of the Gondwana supercontinent (Reeves and de Wit 2000), 157 to 120 Mya. For most of its extent, its depth reaches 2000 to 3000 m; eustatic sea level changes of one to several hundred meters could not moderate its effectiveness by very much. The Agulhas Current which flows down this channel is one of the fastest flowing currents in the world.

Prior to this fragmentation in deep geological time, Madagascar was connected on all sides to the Gondwanan supercontinent, and undoubtedly hosted an ancient Gondwanan flora and fauna. With equal certainty, Madagascar's biotic composition has altered repeatedly in response to the tectonic and climatological upheavals that accompanied geological and organismal evolution on Earth. A comprehensive study of phylogenetic relationships among 188 living taxa of Malagasy vertebrates led Crottini et al. (2012) to reconstruct a complex scenario of biogeographic origins, including ancient (Cretaceous) elements, as well as a majority of Cenozoic (66 Mya-10 kya) colonists that have their closest relatives in either Africa or Asia. Phylogeographic investigations of the Malagasy flora show similar patterns (Buerki et al. 2013).

Biogeographic mechanisms are often viewed through a binary filter: either the organisms were in place before the landmasses sundered, or they arrived by dispersal. In the case of Madagascar, all organisms with African affinities that arrived after 120 Mya, and all those with Indian/Asian affinities that arrived after 83 Mya, are hence assumed to be products of long-distance dispersal; and dispersal is equated with "flying, swimming or rafting… across considerable marine barriers" (Krause et al. 2020). Comparable methods of dispersal are proposed for Madagascar's Cenozoic flora (Yoder and Nowak 2006; Buerki et al. 2013), although eolian transport has also been shown to be an effective long distance dispersal agent to faraway islands for a number of plants (Nathan 2006). There is a third alternative that has received insufficient consideration, in our view: i.e. geodispersal, or the expansion of floral and faunal ranges in response to the elimination of a prior biogeographic barrier (Lieberman 2000; Upchurch 2008). For Madagascar, this process implies the presence of episodic Cenozoic land connections between the island and eastern Africa, the elevation and submersion of which would yield a pattern of alternating periods of colonization and *in situ* diversification (Upchurch 2008).

The possibility of land bridges connecting Africa and Madagascar has been rejected repeatedly by scientists for a variety of reasons, primary among which is the limited and "unbalanced" higher-taxonomic composition of the island's biota relative to that of the mainland. In 1940, George Gaylord Simpson published a renowned and much cited paper on mechanisms of insular colonization by mammals, proposing that they involve three potential migration routes: (1) corridors; (2) filter-bridges; and (3) sweepstakes. Corridors are pathways devoid of any physical or ecological barriers; filter-bridges are perennially open to some species and not to others; and sweepstakes are routes of sporadic, accidental, and highly selective dispersal from continent to island by means of either stepping-stones or natural rafts. Simpson (1940) explained the fact that Madagascar's mammal fauna comprises only four terrestrial lineages with links to Africa (lemurs, tenrecs, euplerid carnivorans, and nesomyine rodents) in terms of sweepstakes dispersal. Because Simpson worked within a framework of fixed continents, the only way he could envisage for animals to cross the Mozambique Channel was by floating on rafts of vegetation. Late Miocene taxa including large carnivores, paenungulates (chiefly elephants), apes, and ungulates (other than hippos) were considered non-starters as colonists, whereas a major contributing factor to successful dispersal for earlier and smaller mammals was chance: being in the right place at the right time. Small-bodied canids and felids, monkeys, shrews, and most rodents were simply “unlucky” and missed the raft. This argument continues to be cited (e.g. Krause et al. 2020): If there had been a land bridge, then “a greater variety of animals would have crossed” (Ali and Huber 2010), as “all clades of that antiquity would have had equally probable chances of colonizing Madagascar” (Yoder and Nowak 2006), and “large-scale invasions [would] almost certainly have ensued” (Ali and Vences 2019).

These predictions place a high value on taxonomic filtering, but fail to acknowledge the significance the habitat filtering; i.e. colonizers can only establish viable populations in habitats to which they are at least partially adapted. 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 causeways, but habitats as well. This means that, while rafting must occur within an individual’s lifetime, geodispersal can occur over several generations. Another biological aspect that needs to be considered is the vulnerability of island biotas to extinction. The limited number of Malagasy clades alive today is unlikely to represent all of the lineages that ever colonized the island; but the absence of any Cenozoic fossils older than 26 kya renders them invisible to modern research.

Temporal (in)congruence

Despite the age and depth of the Mozambique Channel, bathymetric studies have revealed the presence of seamounts and submarine ridges comprising continental material topped by carbonates, that were probably exposed periodically during the Cenozoic (Courgeon et al. 2017). McCall (1997) proposed that the Davie Fracture Zone, the submarine ridge that marks the fault line that led to the Africa-Madagascar separation, was at least partially emergent between 45 and 26 Mya, and could therefore have assisted Cenozoic dispersal events. Poux et al. (2005) tested this hypothesis by estimating the colonization dates of Madagascar’s four terrestrial mammal lineages, and although their data, with its broad confidence intervals, could not refute the proposal, they demonstrated no particular pattern of congruence between the dates proposed for the land bridge and the separation ages of the African and Malagasy lineages. Furthermore, the colonization dates for lemurs and tenrecs differed by tens of millions of years from those estimated for the arrival of carnivorans and rodents (Yoder et al. 1996, 2003; Poux et al. 2005), and this asynchrony was also viewed as evidence in favor of sweepstakes dispersal (Yoder and Nowak 2006).

Looking More Deeply into the Mozambique Channel

Past geological studies of the Mozambique Channel have focused on horizontal movements, which form the crux of plate tectonics, whereas vertical movements – or the connection between deep (magmatic) and surface processes (subsidence, uplifts) – have largely been neglected. A major French-led project, PAMELA (Passive Margins Exploration Laboratories), has conducted sedimentary, tectonic, kinematic, and paleo-environmental studies of the history of the Mozambique Channel, involving eight oceanographic cruises (for a total of 224 days at sea) between 2014 and 2017, and three onshore geological surveys (for 50 land days) in 2017 and 2018. The results obtained from this intensive and extensive study, involving more than 100 researchers, present a much more complex and dynamic picture of the channel’s bathymetric topography (Courgeon et al. 2016, 2017, 2018; Delaunay 2018; Ponte 2018; Leroux et al. 2018, 2020; Ponte et al. 2019; Thompson et al. 2019; Moulin et al. 2020). We conducted a cross-disciplinary study of Madagascar’s Cenozoic biogeography using these new data (Masters et al. submitted), and concluded that there is strong evidence that geodispersal has contributed significantly to Madagascar’s standing (and recently extinct) biotas. Paleo-sedimentological maps (Figure 1) indicate three phases of regional uplift that affected connectivity between Africa and Madagascar during the Cenozoic.

A) Early Paleocene (66-60 Mya; exposure of the Sakalaves platform, Glorieuses and Juan de Nova Islands, and Leven-Castor highs);

B) Late Eocene – Early Oligocene (36-30 Mya; exposure of Bassas da India, and Hall Bank);

C) Late Miocene (12-5 Mya; worldwide Messinian crisis and origin of the Comoros archipelago).

These three periods reflect the three phases of uplift that led to Madagascar's modern topography (Delaunay 2018). They coincided with episodes of marked tectonic and climatic change: global cooling leading to droughts in Madagascar and sub-Saharan Africa, associated with mass extinctions and subsequent radiations, and low sea level stands. The fact that similar conditions are likely to have prevailed on both sides of the Mozambique Channel would have facilitated faunal and floral exchanges. This also suggests that some colonization events may have proceeded from Madagascar to Africa, as was recently proposed for *Croton* spp. (Euphorbiaceae; Ngumbau et al. 2020).

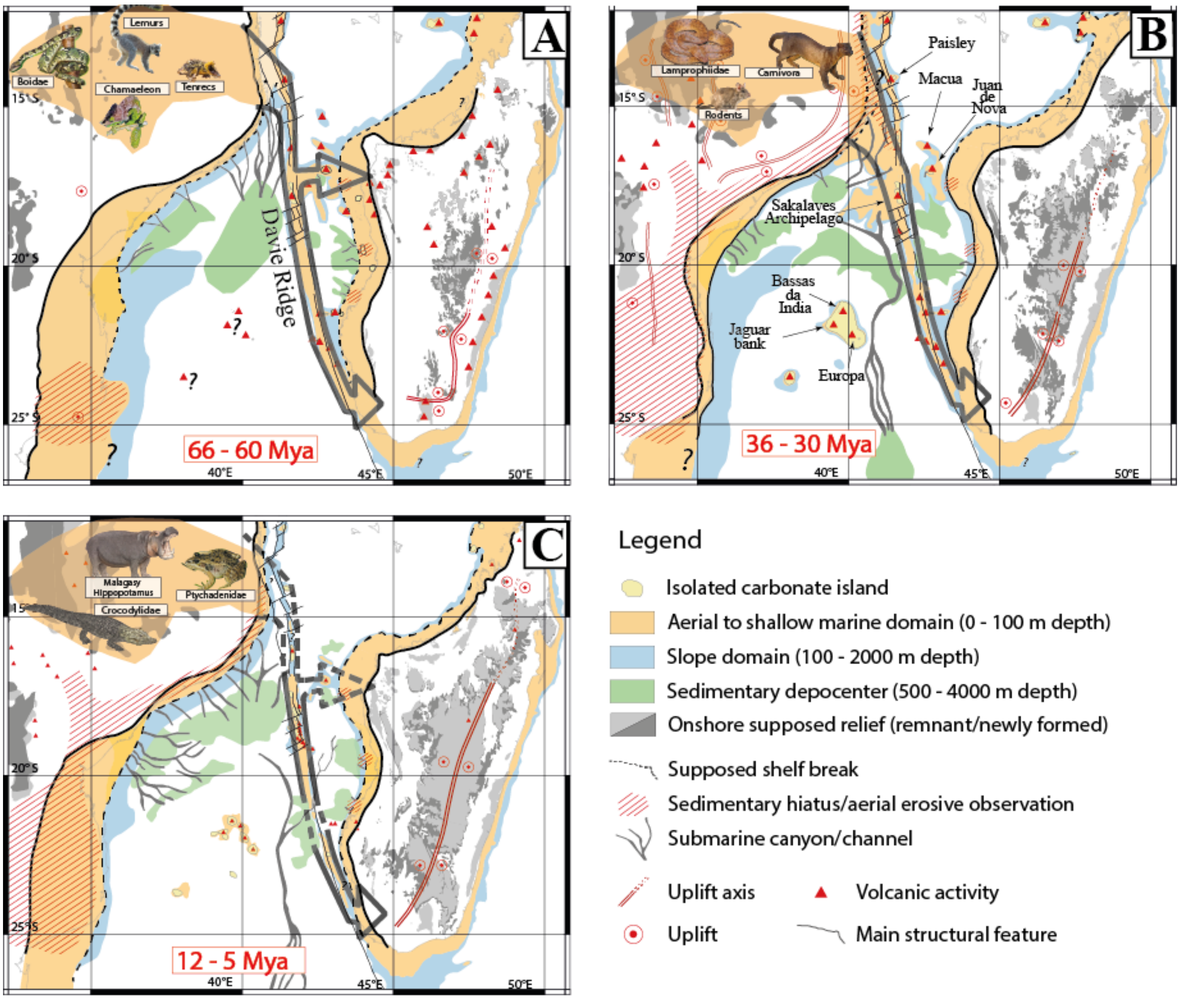

Figure 1. Paleo-sedimentological maps representing possible land bridges during three Cenozoic time frames, concomitant with the three phases of uplift of Madagascar's highlands: **A**) Cretaceous-Paleogene, **B**) Eocene-Oligocene, and **C**) Late Miocene.

Latest Cretaceous – Early Paleocene (66-60 Mya): Widespread Continental Uplift

This period is coincident with a global mass extinction and several major magmatic events, including the outpouring of the Deccan flood basalts and the collision of India with Asia; the first episode of 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 66 and 60 Mya (Delaunay 2018) corresponds to a hiatus along the Mozambican coast (Ponte 2018), indicating a general exposure of coastal land on both sides of the channel, and subaerial exposure of the Davie Ridge (Figure 1A). Faunal studies based on extinct and extant taxa link this period to a major biotic turnover on Madagascar, coincident with the worldwide K/P mass extinction: while some ancient reptilian taxa (iguanas, river turtles, boas) survived the environmental catastrophe (Noonan and Chippendale 2006; Crottini et al. 2012), forms known only from fossils (mammaliaform gondwanatheres, dinosaurs, and early birds; Krause et al. 1997, 2020; Sampson et al. 1998), succumbed.

At this time, both Madagascar and Africa were 10 – 15° (1100 – 1650 km) south of their present position. At such high latitude, Madagascar's landscape was probably dominated by low woodland, with only a few Cretaceous angiosperm families (Proteaceae, Hernandiaceae and Winteraceae) (Schatz 2001; Buerki et al. 2013). The two older mammal clades, lemurs and tenrecs, are likely to have dispersed during this period (Yoder et al. 1996; Poux et al. 2005). Other potential Paleogene colonists include angiosperm families (Fabaceae, Meliaceae, and Menispermaceae) (Buerki et al. 2013), freshwater fish (Bedotiidae, Aplocheilidae, and Cichlidae), amphibians (Mantellidae, Microhylidae, and Hyperoliidae), and reptiles (Chamaeleonidae, Gekkonidae, Gerrhosauridae, and Scincidae) (Crottini et al. 2012).

Late Eocene – Early Oligocene (36-30 Mya): Very Shallow Marine Corridors

The Eocene-Oligocene transition (EOT) (Figure 1B) is a well-known extinction event among students of lemur biology, as it caused the near-extinction of the Eocene relatives of modern tooth-combed primates (Fleagle 2013). Its devastation of Paleogene biotas led to it being termed "la Grande Coupure" ("the great cut"), and it marked a major shift in global climates, related to the first occurrence of ephemeral ice sheets in Antarctica (Zachos et al. 2001). The initiation and growth of ice sheets locked down water on land, causing a drop in global sea levels, and exposing coastal land. This was a dynamic time for Africa, coincident with the initiation of the East African rift system (Ebinger 1989; de Wit 2003; Chorowicz 2005; Macgregor 2015), and the second uplift of the southern Africa plateau (between 38 and 16 Mya; Mougenot et al. 1986; Baby et al. 2018). It also marked the second phase of uplift in Madagascar and affected the physiography of the Mozambique Channel, leading to the re-emergence of the carbonate platforms on the western and eastern shores, the Davie Ridge, the Sakalaves archipelago, and Juan de Nova volcanic island, west of Cap Saint-Andre. Other isolated islands (Bassas da India, Europa, Jaguar Bank, Macua, and Paisley) were also mostly subaerial between 36 and 30 Mya, before being weathered and eroded through wave activity during the Late Oligocene – Miocene (Courgeon et al. 2017). While connections between the Davie Ridge, Rovuma, and Madagascar may not have been continuous throughout this period, hiatuses between topographic highs would have consisted of short (< 50 km) and shallow marine corridors (1-100 m).

The EOT land bridge would have enabled the colonization of Madagascar by carnivorans, rodents, and the endemic snake family Lamprophidae. Comparison with continental-shelf islands on Africa's east coast, such as Zanzibar and Pemba (which do not have elephants, giraffes or lions, but do have primates, carnivorans, and rodents), suggests that this land bridge was probably dominated by mangroves, which were dispersed throughout the Indian Ocean (Ellison et al. 1999). Important plant colonists would have included Euphorbiaceae and the ancestors to the Didiereaceae, which form the matrix of Madagascar's dry spiny thicket biome. Today, this vegetation type is endemic to southern

Madagascar, but xerophytic relicts in the north and the west suggest that it once occupied the entire western region. The many plant families that probably colonized Madagascar at this time include Arecaceae (palms) and the speciose Rubiaceae (coffee family).

Late Miocene (12 - 05 Mya): Non-continuous Connections

Volcanism is recorded 12 Mya ago, south of the Sakalave islands (Figure 1C) in the northern part of the Davie Ridge, coeval with the final uplift of Madagascar (Delaunay 2018) and exposure of the Madagascar continental platform. Courgeon et al. (2017) identified Late Miocene – Early Pliocene subaerial volcanism covering previous carbonate platforms and extensional tectonic deformation, which led to the post-tectonic Pliocene drowning of the platforms, and to their present-day setting largely below sea level. Drowning of the southern part of the Davie Ridge occurred from the Mid-Miocene onwards, with the observation of deep-sea channels originating in the Morondava basin and reaching the deep turbiditic system south of the Mozambique Channel (Delaunay 2018). This north-south inundation is also attested by very low sedimentary accumulation (< 100 m) in the north of the Morondava Basin, and a mean sedimentary accumulation increasing from 300 to 800 m below the main river outlets and deltas in the central and southern parts.

We infer that this third bridge offered a non-continuous connection, interrupted by small, shallow marine corridors between the Davie Ridge and the northern part of the Morondava Basin (Figure 1C). Two major deltas faced each other across the Mozambique Channel, separated by a narrow remnant of the old land bridge. The narrow marine corridors are likely to have included various stepping-stones, such as shallow reefs and small volcanic islands; hence, this connection would have facilitated the dispersal of aquatic animals (crocodiles, hippopotamuses, and one family of frogs, Ptychadenidae), but not of terrestrial forms. The spread of grasses (Poaceae) was limited to wetlands, forest, and some high summits (Paulian 1961; Bosser 1969). The only ungulate grazers to follow them across the channel were hippopotamuses, which subsequently evolved dwarf forms. This last bridge was followed by a general drowning of the Mozambique Channel during the Late Miocene – Early Pliocene.

Conclusions

Recent research indicates that invoking geodispersal by means of short-lived land bridges to account for Madagascar's extant biota provides a new framework for understanding the evolution of life on the island.

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