Madagascar's endemism: demonstration of a holistic method

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The beginnings of the formation of the Indian Ocean are linked to the break-up of the Gondwana supercontinent, approximately 165 Ma ago: the southern part of Gondwana, a block made up of India, Australia, Antarctica and Madagascar, slides towards the South - South-East, in relation to its western part, a block made up of Africa and South America, giving rise to the ocean basins of Somalia and the Mozambique Channel. In the Valanginian (135 Ma), on the occasion of a global kinematic reorganization, these movements bend towards the South; in the western part, the Patagonian plate separates from Africa, slides along the Agulhas fracture zone and leads to the southern opening of the South Atlantic Ocean. The breakup of the eastern block of Gondwana is completed during the Aptian with, among other things, the cessation of the movement of Madagascar in relation to Africa and the beginning of the northward drift of the Indian plate, around 83 Ma, now dissociated from Madagascar, Australia and Antarctica. Thus, for about 120 million years, the island of Madagascar has been located more than 450 km from the African coast; over most of its extent the depth of the Mozambique Channel reaches 2000 to 3000 m and eustatic sea level changes of a hundred meters only slightly moderate these depths. Yet 80% of the fauna and flora of the island of Madagascar is endemic.

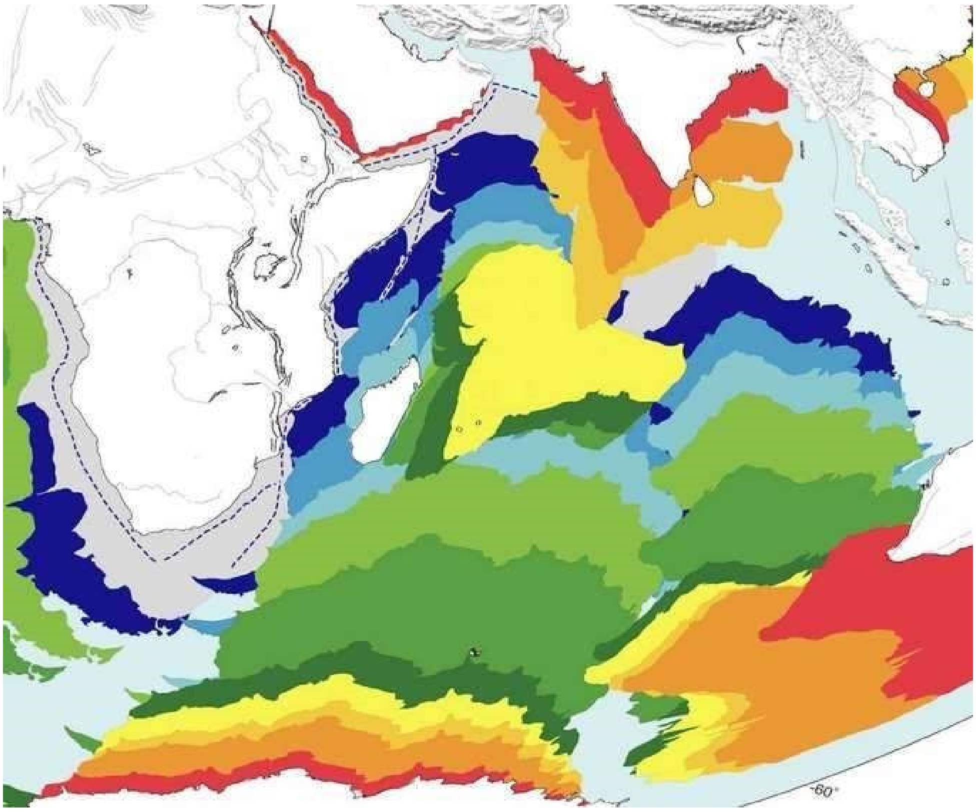

Figure 1: Breakup and fragmentation of Gondwana. Each color represents the position of the plates at the corresponding period in the geological time scale. The relative movements of each plate are calculated with respect to Africa, which is considered fixed here. The reliefs illustrated on the current plates (in white) are linked to the movements resulting from this dislocation. Hammer-Aïtoff projection.

The exhaustive study of the phylogenetic relationships between 188 living taxa of Madagascar vertebrates indeed draws a complex scenario of biogeographical origins, including 1) ancient elements (Cretaceous): before fragmentation, Madagascar, connected on all sides to the Gondwana, hosted ancient Gondwanan flora and fauna; 2) a majority of Cenozoic settlers at different periods of the Paleocene, Eocene and Miocene who have their closest relatives in Africa or Asia. Phylogeographic investigations of the Madagascar flora show similar patterns.

The presence of organisms with African affinity that arrived after 120 Ma, just like that of organisms with Indian/Asian affinity that arrived after 83 Ma, are therefore enigmatic in these conditions of distance between the continents and the depth of the basin separating them: they are assumed to be the products of long-range dispersal. Generally, this kind of dispersion, overcoming more or less considerable marine barriers, is connected to the airways (flight, transport by the wind) or marine (swimming or use of rafts). In the case of the Cenozoic colonization of Madagascar by vertebrates from Africa, the processes envisaged are the subject of controversy: swimming, for example, problematic for hippopotamuses, hibernation (even for mammals?) and the temporary presence of gas in the guts to increase the buoyancy of animals crossing more than 400 km of ocean, the competition of ocean currents, whose numerical models show complicated paths and whose course exceeds several months of progress, or even the transport on "floating rafts", torn from the African soil during extreme storm phases.

Figure 2: 80% of the species living on Madagascar are unique in the world. How did they get to the island?

There is an alternative that has not been sufficiently taken into account, in our opinion, it is geodispersion, or the expansion of the ranges of flora and fauna in response to the removal of a previous biogeographic barrier. For Madagascar, this process implies the presence of episodic Cenozoic land connections between the island and eastern Africa, the uplift and submersion of which would have produced a pattern of alternating periods of colonization and in situ diversification.

From: Washed up in Madagascar

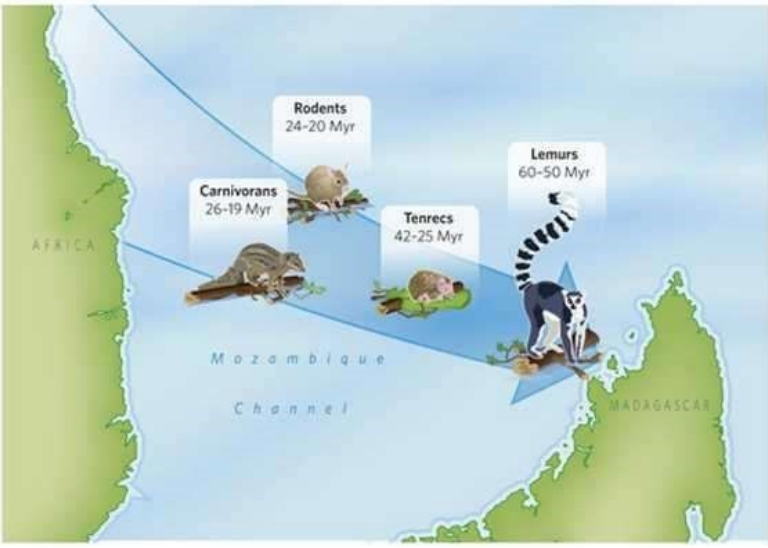

Figure 3: The so-called rafting hypothesis (Krause, Nature 2010). In this hypothesis, the crossing of the more than 450 km which separate the island of Madagascar from Africa is carried out on rafts, pieces of land and/or tree torn from the African continent during strong (and sporadic) storms.

Previous geological studies of the Mozambique Channel have focused on horizontal movements, which form the core of plate tectonics; vertical movements – ie the connection between deep (magmatic) and surface (subsidence, uplift) processes – have been largely neglected. During the PAMELA (Passive Margins Exploration Laboratories) project led by Ifremer and Total, 10 oceanographic campaigns were conducted (for a total of 224 days at sea) between 2014 and 2017, and three geological studies on land (for 50 terrestrial days) in 2017 and 2018. This project involved sedimentary, tectonic, kinematic and paleo-environmental studies of the history of the Mozambique Channel. 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. We conducted a cross-sectional study of the Cenozoic biogeography of Madagascar using these new data (Masters et al., 2021; Masters et al., 2022; Pellen et al., 2022; Aslanian et al., Submitted), and concluded that there is strong evidence for the intermittent presence of a land bridge through uplifts linked to global kinematic phases, suggesting that geodispersion has contributed significantly to the present (and recently extinct) biotopes of Madagascar. Paleo-sedimentological maps (Figure 4) indicate three phases of regional uplift that enabled connectivity between Africa and Madagascar during the Cenozoic.

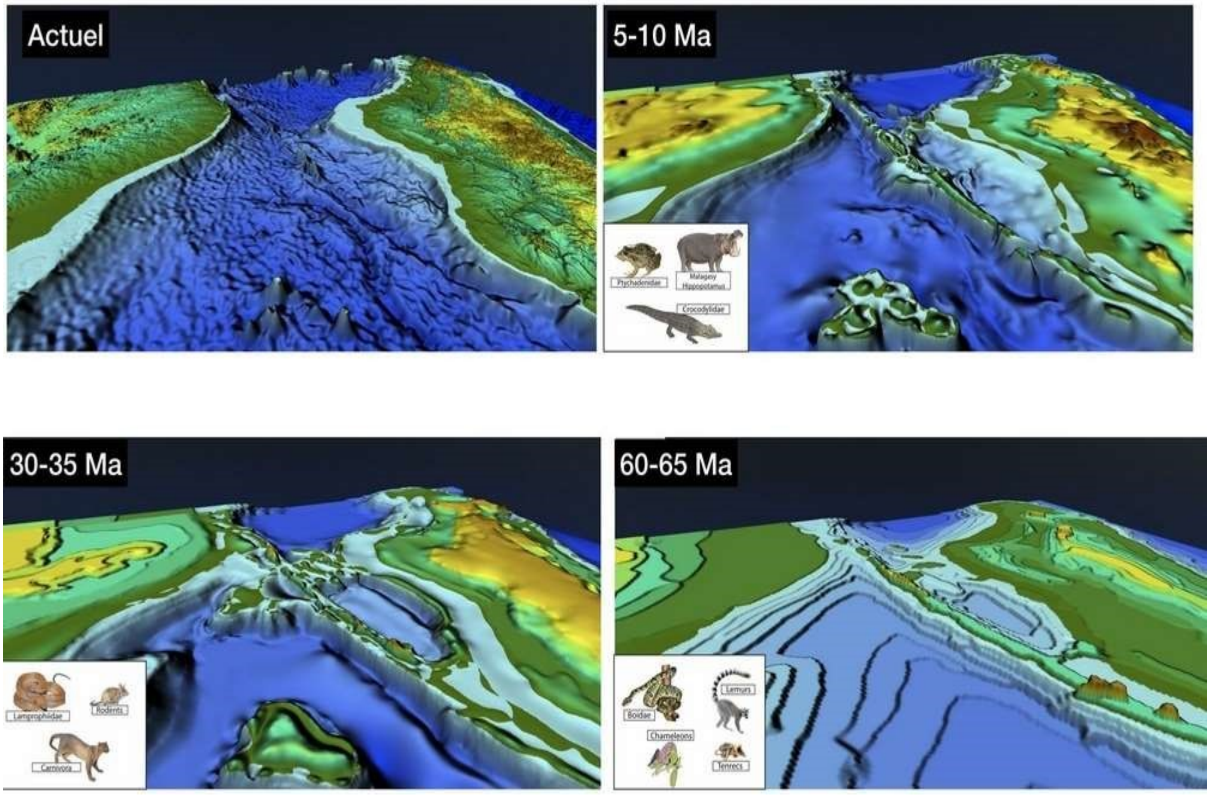

Figure 4: Relief views of the bathymetry of the Mozambique Channel and the topography of Africa and Madagascar at 4 periods, reconstructed from the compilation of data and results obtained during the PAMELA project (Baby, 2017; Baby et al., 2018; Courgeon et al., 2017; Delauney, 2018). Each box indicates the species that may have crossed during these periods (Master et al., 2021; Master et al., 2022) Early Paleocene - 66-60 Ma: exposure of the Sakalaves platform, the Glorious Islands and Juan de Nova , and the Leven-Castor Highlands) (Courgeon et al., 2017); Late Eocene - Early Oligocene - 36-30 Ma: exposure of Bassas da India, and Hall Bank); Late Miocene: 12-5 Ma: global crisis to which we link the Messinian Crisis in the Mediterranean (Leroux et al., 2018) and origin of the Comoros archipelago; Current.

Upper Cretaceous - Lower Paleocene (65-60 million years): widespread continental uplift

This period coincides with a global mass extinction and several major magmatic events, notably the emplacement of the Deccan basalts and the collision of India with Asia, the first episode of the emplacement of the Deccan basalts and the collision of India with Asia, the first episode of uplift of the South African shelf, and volcanism in the Mozambique Channel and Madagascar. Faunal studies based on extinct taxa link this period to a major biotic turnover in Madagascar, coinciding with the global mass extinction: while some ancient reptilian taxa (iguanas, river turtles, boas) survived the environmental catastrophe environmental catastrophe, forms known only from fossils succumbed. At that time, both Madagascar and Africa were both 10 - 15° (1100 - 1650 km) south of their present position. At such a high latitude, the landscape of Madagascar was probably dominated by lowland forests, with only a few families of Cretaceous angiosperms (Proteaceae, Hernandiaceae and Winteraceae). The two oldest mammalian clades, the lemurs and tenrecs, probably dispersed during this period. Other potential Paleogene colonizers include angiosperm families (Fabaceae, Meliaceae and Menispermaceae), freshwater fishes (Bedotiidae, Aplocheilidae, and Cichlidae), amphibians (Mantellidae, Microhylidae, and Hyperoliidae), and reptiles (Chamaeleonidae, Gekkonidae, Gerrhosauridae, and Scincidae).

The sedimentary hiatus on the west coast of the island of Madagascar between 66 and 60 Ma corresponds to the hiatus along the Mozambican coast, indicating a general exposure of coastal lands on both sides of the channel, and a subaerial exposure of the Davie Ridge, thus allowing a first Cenozoic phase of colonization, then of in situ diversification.

Late Eocene-Early Oligocene (36-30 Ma): very shallow marine corridors

The Eocene-Oligocene transition (EOT) is an extinction event well known to students of lemur biology, because it caused the near extinction of the Eocene relatives of modern comb-toothed primates. The devastation of the Paleogene biotopes earned it the nickname "The Great Divide" and marked a major shift in global climates, linked to the first appearance of ephemeral ice sheets in Antarctica. The appearance and growth of ice sheets has blocking water on land, causing sea levels to fall and exposing coastal lands. This is a dynamic period dynamic period for Africa, coinciding with the onset of the East African Rift System and the second uplift of the Southern African Plateau plateau (between 38 and 16 Ma). It is also marked by the second phase of uplift of Madagascar and affected the physiography of the Mozambique Channel, leading to the re-emergence of carbonate platforms on the western and eastern the Davie Ridge, the Sakalave Archipelago and the volcanic island of Juan de Nova, west of Cape Saint Andrew. of Cape Saint Andrew. Other isolated islands (Bassas da India, Europa, Jaguar Bank, Macua, and Paisley) were also mainly subaerial between 36 and 30 Ma, before being altered and eroded by wave activity during the Late Oligocene-Miocene. While connections between the Davie Ridge, Rovuma, and Madagascar may not have been continuous throughout this period, the gaps between these topographic highs remained shallow (1-100 m) on fairly short marine corridors (< 50 km). The EOT land bridge would thus have allowed the colonization of Madagascar by carnivores, rodents and the endemic snake family Lamprophidae. The comparison with islands of the continental shelf on the east coast of Africa, such as Zanzibar and Pemba (which do not have elephants, giraffes or lions, but which have primates, carnivores and rodents), suggests that this land bridge was probably dominated by mangroves that were scattered throughout the Indian Ocean. Important colonizing plants would have included the Euphorbiaceae and the ancestors of Didiereaceae, which form the matrix of the dry thorny thicket biome of Madagascar.

Today, this vegetation type is endemic to southern Madagascar, but xerophytic relics in the north and west suggest that it once occupied the entire western region. Among the many plant families that probably colonized Madagascar at this time are the Arecaceae (palms) and Rubiaceae (coffee family).

Late Miocene (12 - 5 Ma): non-continuous connections

In the northern part of the Davie Ridge, south of the Sakalave Islands, the last volcanic episode is dated at 12 Ma, coinciding with the last uplift of Madagascar and the exposure of the Madagascar continental shelf. A subaerial volcanism Late Miocene-Early Pliocene subaerial volcanism overlies the ancient carbonate platforms. The submergence of the platforms, and their current emplacement largely below sea level, corresponds to the extensional deformation, post-tectonic deformation of the Pliocene. The submergence of the southern part of the Davie Ridge occurred from the middle Miocene onwards, with the observation of deep channels starting from the Morondava Basin and reaching the deep turbidic system south of the Mozambique Channel. This south-northern flooding is also evidenced by a very low sedimentary accumulation (< 100 m) in the northern Morondava Basin, and an average sediment accumulation increasing from 300 to 800m under the main river outlets and deltas in the central and southern parts.

This third bridge thus provided a non-continuous connection, interrupted by small shallow marine corridors between Davie Ridge and the northern part of the Morondava Basin. Two major deltas face each other across the Mozambique Channel, separated by a narrow remnant of the ancient land bridge. It is likely that the narrow marine corridors have various stepping stones, such as shallow reefs and small volcanic islands; this connection would therefore have facilitated the dispersal of aquatic animals (crocodiles, hippos and a family of frogs, the Ptychadenidae), but not terrestrial forms. The spread of grasses (Poaceae) was limited to wetlands, forests, and some high peaks. The only ungulates to follow them across the channel were hippos, which later evolved into dwarf forms. This last bridge was followed by a general flooding of the Mozambique Channel during the early Pliocene.

These three periods thus reflect the three phases of Cenozoic uplift that led to the modern topography of Madagascar and to an alternation of colonization and dispersal phases explaining the endemic nature of the fauna and flora of flora of Madagascar (Master et al., 2021; Master et al., 2022). They coincided with episodes of marked tectonic and climatic changes: global cooling leading to droughts in Madagascar and sub-Saharan Africa associated with mass extinctions and subsequent radiation, and low-level marine levels. The fact that similar conditions probably prevailed on both sides of the Mozambique Channel would have facilitated faunal and floral exchange. This also suggests that some colonization events may have taken place from Madagascar to Africa from Madagascar to Africa, as recently proposed for Croton spp. (Euphorbiaceae). These periods of brief terrestrial connection (< 5 million years) have also given rise to continental phases, reflected in the in the chorology of Madagascar's vegetation by the phylogenetic harmonization of island and continental floras (Génin et al., 2022).

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Teams involved

This synthesis work, designed by DA and CWY, began in 2017 at Nelson Mandela University, Port Elizabeth, South Africa, during their first meeting.

Geodynamics and sedimentology team, Brest, France: DA is a geologist, geodynamicist, expert in plate tectonics at IFREMER.
MR is a sedimentologist, co-director of the UMR 6538 Geo-Ocean in Brest. MM is a geodynamicist and head of the GIPS team at UMR 6538. RP is a postdoctoral researcher who divides his time between France and South Africa, where he studies the movements of the earth movements.

JT was a PhD student at Ifremer under the supervision of MM and DA, with a topic focused on the kinematic evolution of the Indian Ocean; he is now a lecturer at the University of Accra in Ghana.

Geodynamics Team, Port Elizabeth, South Africa: MD and BL are researchers in geophysics and tectonics respectively at the Univ. Nelson Mandela University. MD heads the Earth Stewardship Science Research Institute (AEON).

Team Biologist South Africa: CM is an evolutionary biologist focusing on strepsirrhine evolution at the University of Fort Hare, Alice. FG is an evolutionary ecophysiologist and vocational naturalist at Nelson Mandela Univ, Port Elizabeth.

Paleontology Team Italy: PPAM is a vertebrate paleontologist and taphonomist specializing in island mammals, particularly hippopotamuses, at the Univ. of Florence.

Currentology team Brest, France: TH is a physical oceanographer specializing in large-scale ocean modeling and has supervised YZ, a paleoceanographer and paleoclimatologist, during his postdoctorate at the Laboratoire d'Océanographie Physique et Spatiale (LOPS, UMR 6523); she is now an assistant professor at Xiamen University, China.

PP is a research supervisor specialized in regional ocean dynamics at LOPS; he supervises, with TH, TLH who is currently doing his master's degree on the impact of the continental shelf on the formation of eddies along the coast of Mozambique.

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