

Mammals Insular Dispersal on Madagascar: Land Bridges and Rafting Theories, a Counterpoint Review¹

Daniel Aslanian,¹ Romain Pellen,¹ Marina Rabineau,¹ Maryline Moulin,¹ Estelle Leroux,¹ Eva Thicot,¹ Antoine Delaunay,² Guillaume Baby,³ Simon Courgeon,³ Bastien Linol,⁴ Jean-Pierre Suc,⁵ Speranta-Maria Popescu,⁶ Séverine Fauquette,⁷ Paul P. A. Mazza,⁸ Sébastien Couette,⁹ Massimiliano Delpero,¹⁰ Thierry Huck,¹¹ Pierrick Penven,¹¹ Théo Le Hir,^{1,11} and Yurui Zhang¹²

¹Geo-Ocean, Ifremer, Université de Bretagne Occidentale, CNRS, 29280 Plouzané, France

²Ali I. Al-Naimi Petroleum Engineering Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal 23955–6900, Saudi Arabia

³Université Bourgogne Europe, 6 bd Gabriel, 21000 Dijon, France

⁴AEON, Earth Stewardship Science Research Institute, Nelson Mandela University, Port Elizabeth 6001, South Africa

⁵Sorbonne Université, CNRS-INSU, Institut des Sciences de la Terre, IStEP UMR 7193, 75005 Paris, France

⁶GeoBioStrataData consulting, 385 Route du Mas Rillier, 69140 Rillieux la Pape, France

¹This article is dedicated to the memory of Judith Masters and Fabien Génin, whose insight, generosity, and scientific vision profoundly shaped the ideas developed here.

⁷Institut des Sciences de l'Évolution Montpellier (ISEM), Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France

⁸Department of Earth Sciences, University of Florence, Via La Pira 4, 50121, Florence, Italy

⁹EPHE - PSL, 75014 Paris & Biogéosciences, UMR 6282 CNRS, Université Bourgogne Europe, 6 bd Gabriel, 21000 Dijon, France

¹⁰Department of life sciences and systems biology, University of Turin, via accademia albertina 13 - 10123 Torino – Italy

¹¹Laboratoire d'Océanographie Physique et Spatiale (LOPS, UMR 6523), Univ Brest, CNRS, IFREMER, IRD, IUEM, Plouzané, France

¹²State Key Laboratory of Marine Environmental Science, College of Ocean & Earth Sciences, Xiamen University, Xiamen

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Abstract

Insular faunas and fossil assemblages result from a complex interaction of geodynamical (geological, climatic, eustatic) and biological, taphonomic and historical processes. The debate should not be framed as a contest between biology and geodynamics but rather as an effort to reconcile the two. Geodynamic reconstructions must remain independent of biological assumptions, yet they must also be consistent with biological evidence. If faunal dispersal patterns appear to contradict existing geological models to the extent that they require improbable explanations, then the fault likely lies in the geological reconstructions, which should be revisited. We present here how recent geophysical and geological data completely reshape out the view of the geodynamic evolution of the Mozambique channel and give a geodynamic and paleobiogeographical coherence, leading to more robust and coherent reconstructions of Earth's past.

1. INTRODUCTION

Islands arise through diverse geological processes, and most can be classed as either continental, retaining fragments of former landmasses, or oceanic, originating de novo on oceanic crust and requiring dispersal for colonization ([Whittaker and Fernández-Palacios 2007](#)). Madagascar, though continental in origin, now behaves biogeographically like an oceanic island. It is separated from Africa by the Mozambique Channel, a long-standing barrier formed during the earliest stages of Gondwana breakup (165–120 Mya: [Thompson et al. 2019](#)). For most of its length the channel is 2000–3000 m deep, glacio-eustatic sea-level changes of a few hundred meters could not meaningfully reduce its effectiveness. The Agulhas Current, one of the strongest in the world, further reinforces this isolation ([Lutjeharms 2006](#), [Penven et al. 2006](#)).

In their recent synthesis (2025), Ali & Hedges (A&H) review hypotheses concerning the arrival of terrestrial vertebrates on Madagascar. As noted earlier ([Aslanian et al. 2023](#)), such debate is scientifically vital; however, certain geological interpretations proposed by A&H are difficult to reconcile with recent geodynamic and sedimentological findings..

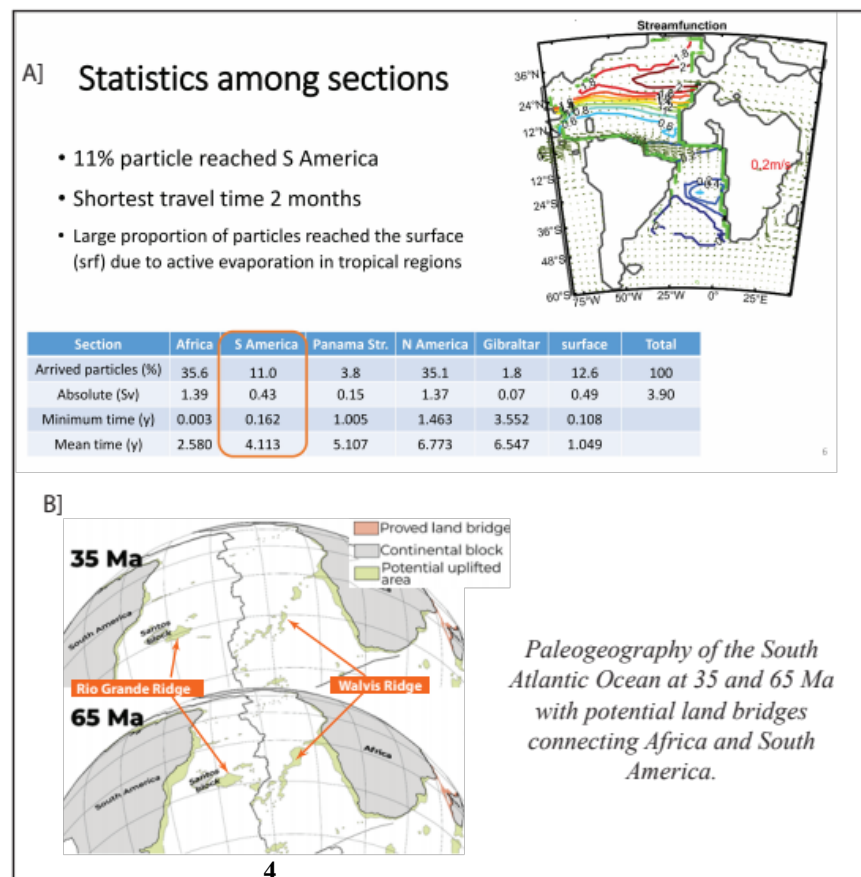
A clarified and updated review of the trans-disciplinary approach is provided here, integrating paleo-oceanography, geodynamic, coevolution, palynology and biostratigraphy and biology, with particular emphasis on hippopotamuses, whose dispersal represents a stringent test of biogeographic hypotheses. The strength of this integrative framework lies in the convergence of independent dating and correlation methods, including: (1) geophysical and tectonic chronologies tied to (2) global kinematic and climatic events; (3) fossil evidence; (4) molecular divergence estimates across multiple vertebrate clades; (5) paleoecological and coevolutionary indicators based on plant–animal associations ([Masters et al. 2021, 2022](#), [Génin et al. 2022](#)) and pollen/dinoflagellate assemblages from DSDP Site 242 ([Aslanian et al. 2023](#)).

This synthesis reveals coherent temporal patterns linking biological dispersal events with episodes of tectonic reorganization, magmatism, climatic disruption, and basin evolution, providing a robust foundation for evaluating alternative biogeographic models. It also reinforces the point raised by [Masters et al. \(2022\)](#): dispersal hypotheses should be evaluated in light of the full spectrum of geodynamic evidence, alongside biological inference. While [Ali & Hedges \(2022, 2023, 2025\)](#) incorporate geological data, our analysis of the recent data leads to different conclusions regarding its interpretation and implications.

2. PALEO-OCEANOGRAPHY – FEASIBILITY AND TIMESCALES OF RAFTING

Paleoceanographic models for ~40 Ma (late Middle Eocene) underpin the rafting hypothesis (Ali & Huber 2010), which assumes rare transient storms enabled Mozambique Channel crossings. They suggested trajectories with occasional eastward velocities of 0.20 m s^{-1} , enabling crossing times of approximately 25–30 days, later revised to 30–35 days in their 2025 update (Ali & Hedges 2025)—but Masters et al. (2021) questioned this duration. Relying simultaneously on maximum velocity (0.2 m s^{-1}) and shortest straight-line distance (~450 km) appears overly optimistic. Masters et al. (2021) provided more realistic probability and time estimates using Lagrangian trajectories using actual oceanic currents, revealing significant underestimation in A&H’ calculations. Currents cannot follow straight-line paths across the constrained channel with strong meridional flow and heterogeneous velocity fields (i.e., the maximum velocity is not achievable anywhere). These analyses indicate minimum travel times of at least 70 days for particles from Africa to Madagascar—twice the durations proposed by Ali & Huber (2010) and Ali & Hedges (2025). Similar analysis applies to the South Atlantic, where rafting has also been proposed (Box 1).

Figure 1 A] Lagrangian simulation conducted with the 55 Ma IPSL simulation and particle success rates and travel times from African coasts to South America. B] Paleogeography of the South Atlantic Ocean at 35 and 65 Ma, with potential land bridges.



To critically reassess these differences—given mesoscale eddies dominating circulation—two higher-resolution regional ocean model simulations were performed using CROCO (Auclair et al. 2022) at $1/12^\circ$ resolution over 2.5°W – 66°E , 46.75°S – 4.8°S , sufficient to resolve mesoscale eddies. The present-day simulation used GEBCO 2019 bathymetry (GEBCO Bathymetric Compilation Group, 2020), forced by GLORYS at open boundaries (Lellouche et al. 2018) and ERA5 at the surface (Hersbach et al. 2020, full description in Le Hir et al. 2025). The Eocene simulation was set-up on a region shifted 8° south and 3° east (centered over southern Africa, as plates were positioned farther southeast) using paleobathymetry from Poblete et al. (2021). This CROCO simulation was a downscaling of the IPSL-CM5A2 40 Ma 2XCO₂ paleoclimate model simulation (Toumoulin et al. 2021, Pillot et al. 2022a,b). In each simulation, 250 particles were released daily for 8 years at 1 km from the Mozambican coast (730,000 total), and their trajectories computed with 2-hour timestep using surface currents. Success was defined as reaching within 1 km of the Malagasy coast; particles hitting land were removed, as were those at sea for more than 100 days. Figure 2 shows particle positions at a key moment, successful trajectories to Madagascar, and travel-time distributions for present-day and 40 Ma simulations.

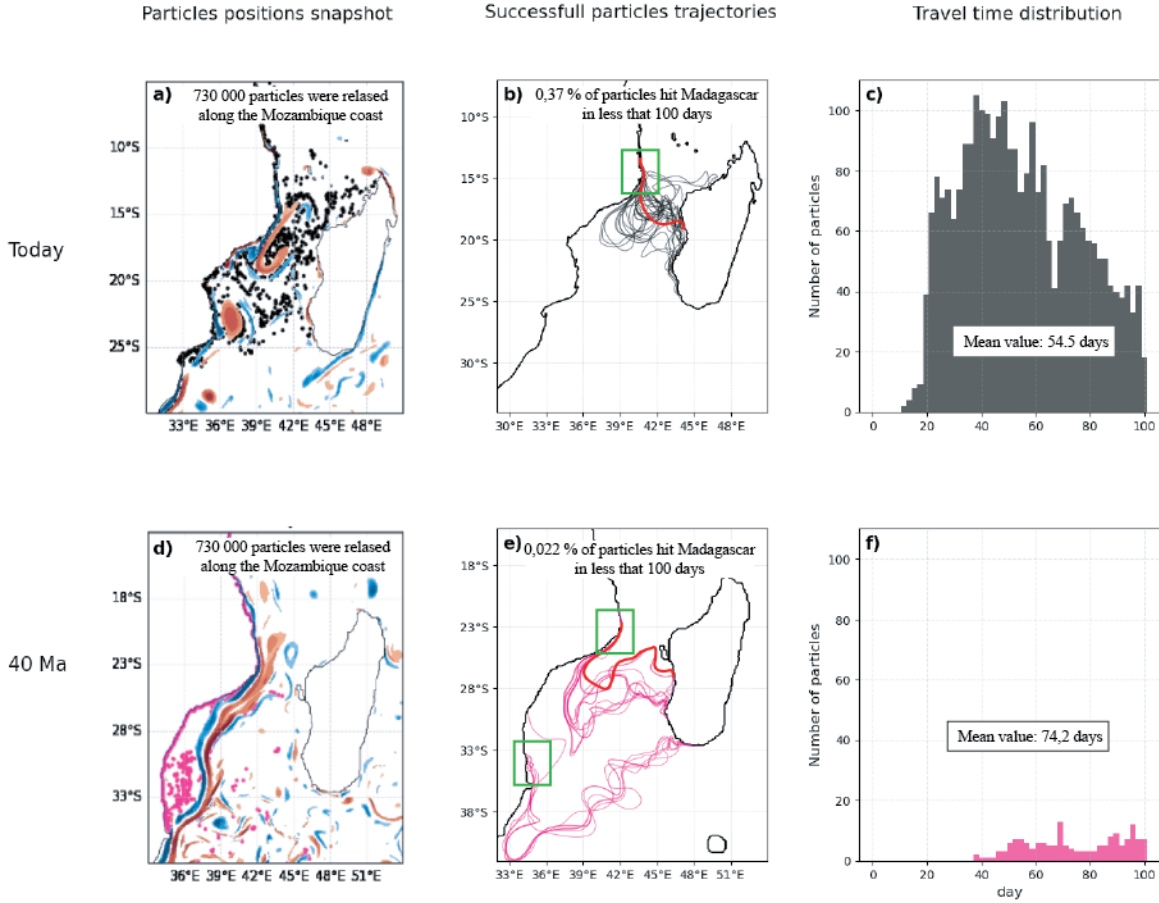


Figure 2 Lagrangian simulations from the Mozambique coast to Madagascar using ocean currents from eddy-resolving simulations. Panels a) and d) show a snapshot of particle positions after 14 months of running for the present-day (black particles) and 40 Ma (magenta particles) simulations. Relative vorticity is shown in the background, positive/negative values in red/blue correspond to anticyclonic/cyclonic rotation or shear of the surface currents (the blue/red ribbon on panel d is a typical signature of a noneddying western boundary current, while patches on panel a underlines the mesoscale eddies). Panels b) and e) Green rectangles represent the departure zones of particles passing through in less than 100 days with the trajectories of 20 randomly selected particles among them for each simulation. The red line shows the path of the particle with the fastest travel time. Panels c) and f) show the distribution of travel times for the particles that successfully reached Madagascar. (see the movie in the supplementary materials).

Figures 2b and **1e** show that 0.37% of particles (2731) reached the Malagasy coast in less than 100 days in the present-day simulation (mean travel time: 54 days), compared to the just

0.022% (162 particles) in the 40 Ma simulation (mean: 74 days).² These can be grouped by departure region. In the present-day simulation, successful particles originated from the Nampula region (NE Mozambique, near Matibane and Nacala; green rectangle in [Figure 2b](#)), crossing at the channel's narrowest point. In the 40 Ma simulation ([Figure 2e](#)), they came from two regions: Nampula (via longer, southwest trajectory) and Inhambane (with the longest travel times; green rectangles). [Figure 2a](#) and [2d](#) reveal that anticyclonic eddies characteristic of modern Mozambique Channel circulation (de Ruijter et al. 2002, [Halo et al. 2014](#)) were absent in the 40 Ma simulation. The South Equatorial Current was positioned farther north relative to Madagascar. In situ observations confirm eddies—and the jets between them—are crucial for eastward transport across the channel ([Hancke et al. 2014](#), [Penven et al. 2025](#)). Without eddies and a dominant western boundary Mozambique Current, particle in the 40 Ma simulation ([Figure 2d](#)) remained confined to the western channel, unlike the eddy-driven crossings in the present-day simulation. Madagascar's 8° southward shift relative to the South Equatorial Current likely reduced eddy activity ([Penven et al. 2006](#)).

3. GEODYNAMIC APPROACH

The Davie Ridge: A Transtensional Buffer Zone of Mixed Crustal Nature

The modern physiography of the western Indian Ocean resulted from the Gondwana's breakup, which occurred in two phases: Late Triassic (165–155 Ma) and Early Cretaceous (135–125 Ma). This breakup featured active seafloor spreading in the Western Somali and Mozambique Basins ([Figure 3A](#)), beginning in the early Kimmeridgian. It is identifiable from Mesozoic magnetic anomaly series, including the confidently dated oldest anomaly M25 (154 Ma) in the Mozambique, Somali basins (Western Indian Ocean) and Argo (NW Australia) basin ([Thompson et al. 2019](#)). In the Somali basin, Madagascar's southward motion relative to Africa (~155–125 Ma) created conjugate divergent margins fringed by a major transform Davie Fracture Zone (DFZ) or Davie Ridge—a 1200-km-long N170-trending topographic high (Coffin & Rabinowitz, 1987). Antarctica's southward motion relative to Africa (>155 to present) generated the Mozambique

²Particles were advected only in the surface layer (2D), excluding submersion.

Basin, bounded westward/northward by the Mozambique coast and eastward by the Davie Ridge (Thompson et al. 2019).

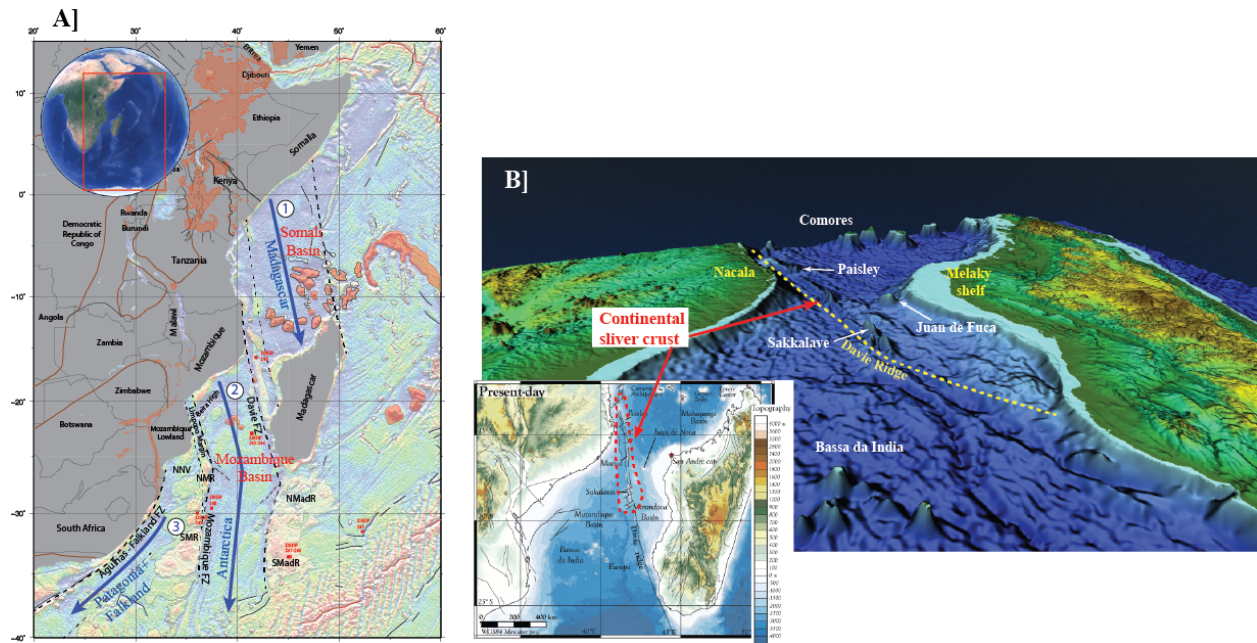


Figure 3 A] Free-air satellite-derived gravity anomaly of the Mozambique Channel by Sandwell et al. (2014). Segment 1 and 2 correspond respectively to the movement of the Madagascar and Antarctica tectonic plates, and the segment 3 corresponds to a later event involving the drifting of the Falkland and Patagonian plates. The Davie Ridge between Segments 1 and 2, is the result of the southwards movement of Madagascar respect to Africa. NNV = North Natal Valley, NMR = North Mozambique Ridge; SMR = South Mozambique Ridge; NMadR = North Madagascar Ridge; SMadR = South Madagascar Ridge. In red = Volcanism without distinction about the age (Mercator projection). After Thompson et al. 2019. B] 2D and 3D image of the bathymetry and topography around the Mozambique Channel and the Davie Ridge, with the location of the continental sliver crust (Vormann & Jokat 2021b).

The Davie Ridge was initially interpreted as a remnant transform fault controlling late Jurassic/early Cretaceous drift of Madagascar and Somali Basin opening (Heirtzler & Burroughs 1971, Lort et al. 1979, Rabinowitz et al. 1983, Scrutton 1978, Segoufin & Patriat 1981, Simpson et al. 1979), though its exact nature remained debated. Recent seismic data reveal structural variability along the shear zone: an elevated continental block in the south (14° – 20° S) transitioning northward to nonelevated basement buried under ≤ 6 -km-thick sediments (9° – 13° S) (Vormann et al. 2020, Vormann & Jokat 2021a). Rather than a narrow deformation zone, it features broad,

diffuse transtensional deformation with high-velocity lower-crustal bodies indicating underplating. Vormann & Jokat (2021b) identified a detached continental sliver forming the southern Davie Ridge, extending from north of the Paisley Seamount (near Mozambique's Nacala Coast) to the southern Sakalaves Seamounts—separated to the Melaky shelf offshore Madagascar by Juan de Nova Island (Figure 3B). This transtensional structure occupies a buffer zone (Box-2) with mixed crustal nature, akin to the Limpopo Margin (produced by Antarctic southward motion (Figure 3A), featuring thinned, altered continental crust intruded by intense magmatism (Evain et al. 2021), or the ~400-km-wide São Paulo Double Fracture Zone in the Equatorial Atlantic, which traps hyperextended continental crust ~500 km from South American (Schnurle et al. 2023). The Davie Ridge thus exemplifies a kinematic “buffer” zone (sensu Moulin et al. 2012), highly responsive to geodynamic changes through time.

McCall (1997) proposed that the Davie Ridge—the elevated topographic structure marking the shear zone between Africa and Madagascar—was at least partially emergent between 45 and 26 Ma and could have facilitated Cenozoic dispersals. This hypothesis was largely dismissed, due to 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). New precise geological, geophysical, and geodynamic data necessitated a reassessment of the Davie Ridge's vertical evolution.

Sediment, storyteller of the Earth: paleobathymetric marker and marker of vertical movements

Sediments record Earth's history: vertical movements are imprinted in their layers, and even their absence provides geodynamic insights (Rabineau 2014). Sediment-bare areas surrounded by thick deposits over a given period indicate either nondeposition or end-period erosion—both signaling subaerial conditions. Data quality is thus paramount.

At the end of the last century, seismic data in the Mozambique Channel were scarce and low-resolution: single-channel profiles (Lort et al. 1979, Mougénot et al. 1986, Mascle et al. 1987, Malod et al. 1991. Figure 4A-left), plus dredge and shallow piston-core sampling along the Davie Ridge between Paisley and Sakalaves Seamounts (Leclaire et al. 1989, Bassias & Leclaire 1990, Bassias, 1992). This yielded a blurred view of the ridge as small Cenozoic volcanic islands separated by wide open-water gaps, prompting Ali & Hubert (2010 Please check spellings of

Hubert) to deem overwater dispersal unavoidable and later sketch true dry land, low-elevation atolls, and impassable areas (Ali & Hedge 2022 Please check spellings of Hedge, 2025).

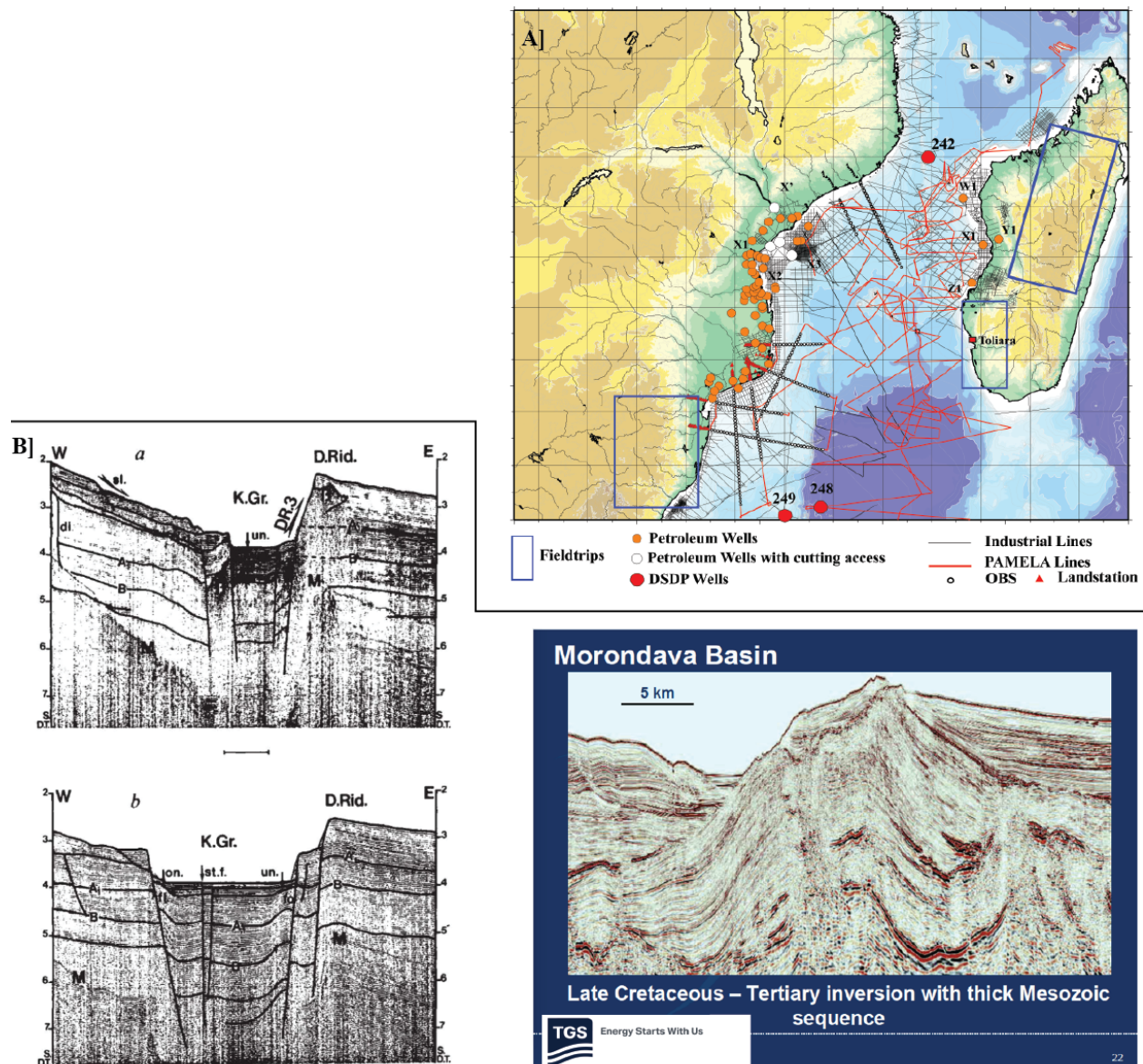


Figure 4 A] Academic and industrial data used in the PAMELA Project (Bourillet et al., 2013). Compilation after Baby (2017), Courgeon (2017), Delaunay (2018), Moulin et al. (2020), Ponte (2018). B] Comparison between an old single-channel seismic line along the Davie Ridge (Mougenot et al., 1986) and a multi-channel seismic line in the Morondava Basin, highlighting a tertiary inversion in the Mesozoic sequence (data presented with permission from TGS) used in the Pamela Project

In 2007 and 2014, new wide-angle seismic profiles revealed that the main Davie Ridge—between north of Paisley Island and south of the Sakalaves Islands, crossing the Mozambique Channel’s narrowest point—features continental crust (likely intruded and overlain by volcanoes; see above and [Figure 3B](#)), not isolated volcanic islands (Vormann and Jokat, 2021b).

The PAMELA project ([Bourillet et al. 2013](#)) led by Ifremer, Total and French Universities, involved 10 oceanographic campaigns (224 sea days) and three onshore studies in Madagascar and Mozambique (50 days). It acquired bathymetry, piston cores, water-column/sub-bottom profiles, gravity, magnetism, dredges, and wide-angle/reflection seismic data. Industry collaboration provided >100 PAMELA researchers access to high-definition onshore/offshore seismic lines and boreholes. [Figure 4B](#) compares single-channel profiles with PAMELA seismic lines. A large team of specialists processed this dataset to minimize interpretation errors. Results appeared in >100 specialized articles and supported 10 PhD theses (e.g., [Baby 2017](#), [Courgeon 2017](#), [Delaunay 2018](#), [Ponte 2018](#), Thompson 2018)—ideal for independently reassessing Mozambique Channel and Davie Ridge vertical evolution ([Masters et al. 2021](#), [2022](#)).

Methodology for Constructing Land-Sea Digital Terrain Models

The reconstruction methodology ([Pellen et al. 2022](#)) involved 5 steps. *Steps one and two* compiled and synthesized data on kinematics, structure, and sedimentary/morphological evolution of the Mozambique Channel, Madagascar, and Southern Africa. The Pamela project emphasized sedimentary layer attributes (e.g., age and thickness) and carbonate platforms, forming the basis for its maps; this work used free software QGIS and PLACA4D ([Pelleau et al. 2015](#)). *Step 3* applied subsidence corrections. In *Step 4*, paleodepth maps generated isohypse curves, which *Step 5* used to build XYZ grids in WGS84 format via Generic Mapping Tool (GMT) software. The resulting Land-Sea Digital Terrain Models (DTMs) are fully accessible on the SEANOE platform ([Pellen et al. 2022](#)).

On land, data on paleo-terraces and fluvial systems from [Guillocheau et al. \(2012\)](#), [Ponte \(2018\)](#) and [Delaunay \(2018\)](#) were incorporated. Once preserved paleo-surfaces are identified, paleo-relief estimates can be proposed for different periods (Cretaceous-Paleocene, Oligocene, and Upper Miocene). Seven generations of stepped flattening surfaces have been defined across East Africa and Madagascar, from Jurassic to Quaternary times. [Delaunay \(2018\)](#) and [Ponte \(2018\)](#) estimated average relief altitudes of 600 m, 800 m and 1100 m for the Late Cretaceous-

Paleocene, Oligocene and Upper Miocene, respectively. At sea, the compilation includes data from PAMELA oceanographic campaigns and studies by [Thompson et al. \(2019\)](#), [Delaunay \(2018\)](#), [Ponte et al. \(2019\)](#), [Moulin et al. \(2020\)](#), [Leprêtre et al. \(2021\)](#). PLACA4D software enabled comparison of data across geological periods, identifying phases of sedimentation and structural rupture. In the second step, this information was synthesized into a simple paleotopography classification: subaerial, shallow, continental slope (with submarine canyons), and deep environments at sea. Sedimentary depocenter limits informed deep-domain morphology. Potential magmatic edifices, reworked Mass Transport-Deposits were also highlighted.

On land, each break-up phase generated a new paleo-surface subject to fluvial erosion. Their inclinations, elevations, associated volcanic edifices, and activity periods indicated uplift directions and axes affecting Madagascar and Southern Africa. Normal thermal subsidence of oceanic crust was corrected using age models for each oceanic plate in PLACA4D. [Watts and Steckler's \(1981\)](#) law provided paleodepth estimates for offshore domains. Maximum marine domain extent along continental shelves followed [Ponte \(2018\)](#) and [Delaunay \(2018\)](#). Paleo-bathymetric reconstructions were adjusted for episodic magmatic events causing uplifts evident in sedimentary sequences (shallow carbonates, hiatuses, unconformities).

Several magmatic events impacted the region: Karoo (~180 Ma), Movene-Bumeni (~145–135Ma), Madagascar Turonian traps (~95 Ma), Lutetian, Oligocene, and Tortonian ([Moulin et al. 2020](#), [Leprêtre et al. 2021](#)), producing bulges, uplifts and seamounts. Consistently low sedimentation records (low deposition/preservation due to erosion) from 120 and 23 Ma ([Delaunay 2018](#), [Ponte et al. 2019](#)) suggest persistent topographic highs and/or deposition–erosion cycles. Carbonate platforms and terraces developed on structural highs (e.g., Hall Bank, Sakalaves platform, Glorieuses, Bassas da India and the Comores archipelago), documenting repeated phases of shallow-water carbonate production. Initiation of carbonate production on the Sakalaves plateau is dated to the Oligocene ([Courgeon et al. 2018](#)), rather than the Paleocene as previously stated. Rupelian–Langhian carbonate development is documented on Bassas da India and Hall Bank, while Messinian–Pliocene carbonate production characterizes parts of the Comores archipelago over volcanic basement ([Courgeon et al. 2017](#), [Leroux et al. 2020](#)). For Juan de Nova Island and the Leven–Castor highs, the timing of initial carbonate development remains less well con-

strained in the published literature. These carbonate systems reflect persistent bathymetric relief and episodic emergence–submergence of structural highs.

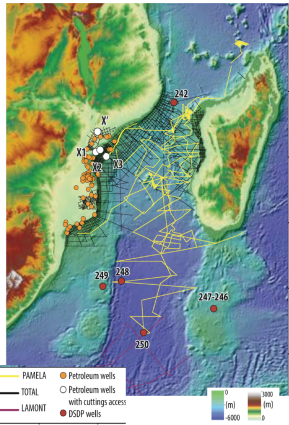
In line with global periodicity in biological and geological records (Box-3) and coherent with Pamela data, focus was on three periods: Maastrichtian-Paleocene Boundary (75–65 Ma), Paleocene-Eocene boundary (45–35 Ma), and late Miocene period (15–5 Ma). Evidence of these events appears, for example, on the Glorieuses Seamount (north of Madagascar) and in the surrounding Somali Basin (Leroux et al. 2020). The Glorieuses emerged from two Late Cretaceous magmatic pulses, with at least two Tertiary uplift phases—likely around the Eocene-Oligocene transition and Late Miocene. Basin sedimentation records an abrupt change in seismic facies in the Late Eocene, probably tied to major regional hydrodynamical shifts in the western Indian Ocean.

Late Cretaceous-Paleogene phase

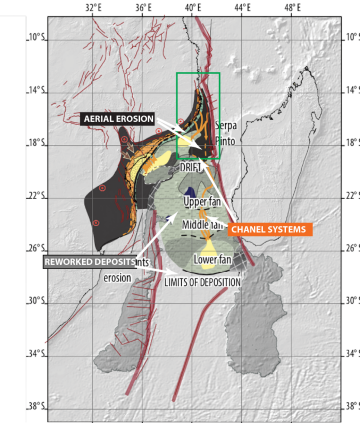
The K-Pg boundary marks synchronous biological and geological upheaval (Henehan et al. 2019), including the Chicxulub impact (Renne et al. 2013), global plate reorganization (Moulin & Aslanian 2010), Deccan volcanism (Courillot and Renne 2003), termination of spreading in the Mascarene Basin (Plummer & Belle 1995, Reeves 2014), Seychelles–India breakup (Collier et al. 2008), interruption of African-Eurasian plate convergence and subduction (Dewey et al. 1989, Fidalgo-Gonzalez 2001), and rapid exhumation of the South African Plateau (Gallagher & Brown 1999, Brown et al. 2014, Tinker et al. 2008). In Southern Africa, the Cretaceous-Paleogene boundary forms a regional unconformity of tectonic origin linked to plateau growth (Baby et al. 2018). Ponte et al. (2019) argue against a eustatic origin, noting that the boundary coincides with major warming and sea-level rise (Friedrich et al. 2012). In the Northern Mozambican Margin, the Paleogene features a shallow, mixed marine platform (Upper Grudja Fm. Ponte 2018, Ponte et al. 2019. Figure 5A). Wells X and Y21 near Madagascar reveal two erosional unconformities dated ~61–67 Ma and ~33.9–37.8 Ma (Delaunay 2018). The first represents a ≥6.5 Myr hiatus from uppermost Maastrichtian to basal Selandian, missing planktonic foraminiferal zones (*Pseudoguembelina hariaensis* through P4) in well X1 (Figure 4B). Large areas of reworked deposits occur along the Davie Ridge.

A]

Paleo-environments at ~65 Ma (after Ponte, 2018)
Note the Aerial erosion Ridge between Nacala and Sakalave aeras



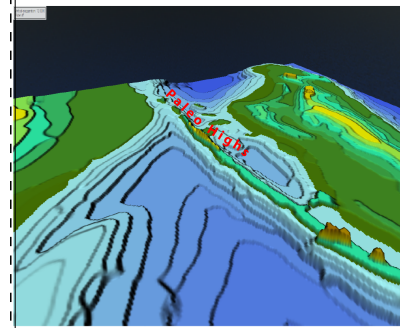
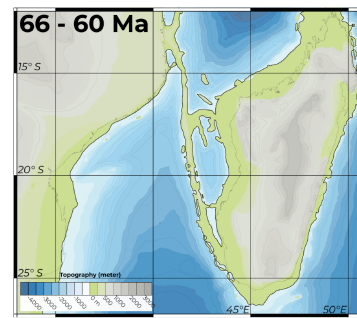
Dataset used in Ponte's work (2018) within the Pamela Project. Thin black lines (on shore and offshore) are industrial seismic profiles. Black dots represent the drill holes used for the stratigraphy analysis



Sedimentary deposits
Hemipelagic
Lobes
Delta
Silts - Sands
Erosion

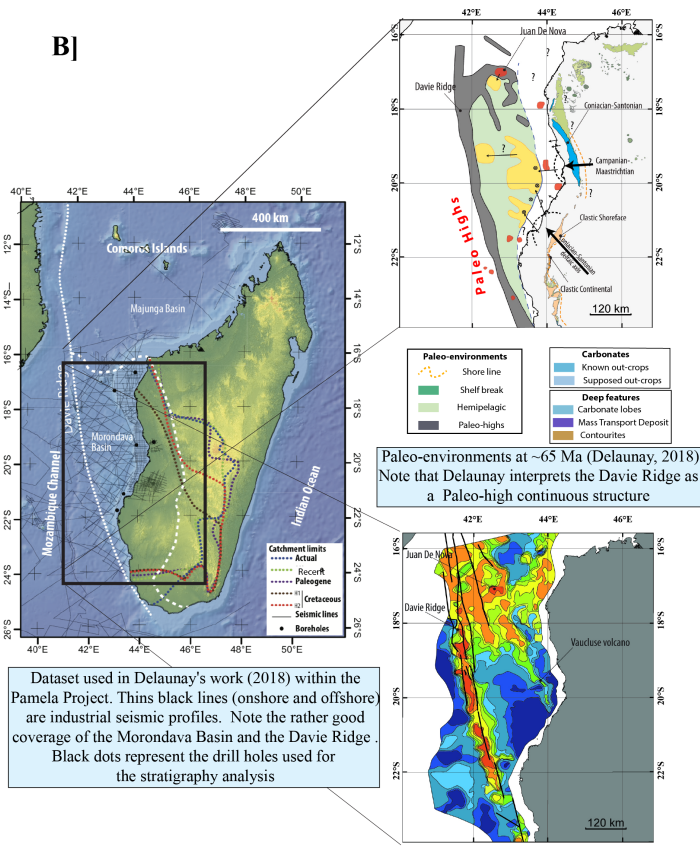
Main structures - Cinematic
Shelf break
Shoreline
Slope
Channel systems
Alluvial routing
Fracture Zone
Fault
Uplift
Subsidence

C]



2D and 3D view of the DTM build thanks to the PAMELA dataset at ~65Ma (Pellen et al., 2022)

B]



Paleo-environments at ~65 Ma (Delaunay, 2018)
Note that Delaunay interprets the Davie Ridge as a Paleo-high continuous structure

Dataset used in Delaunay's work (2018) within the Pamela Project. Thin black lines (on shore and offshore) are industrial seismic profiles. Note the rather good coverage of the Morondava Basin and the Davie Ridge. Black dots represent the drill holes used for the stratigraphy analysis

Sediment Thickness (isopachs) for the depositional sequence between 90Ma and 65Ma (After Delaunay, 2018)

Figure 5 Research including onshore-offshore industrial seismic profiles and drill wells conducted in the Mozambique Basin and the northeastern part of the Davie Ridge (A]) as well as in the Morondava Basin and the southern part of the Davie Ridge (B]) as part of the Pamela project for the Late Cretaceous-Paleogene phase. C] 2D and 3D views combining results of A] and B] of the DTM thanks to the Pamela dataset at 65Ma ([Pellen et al. 2022](#)).

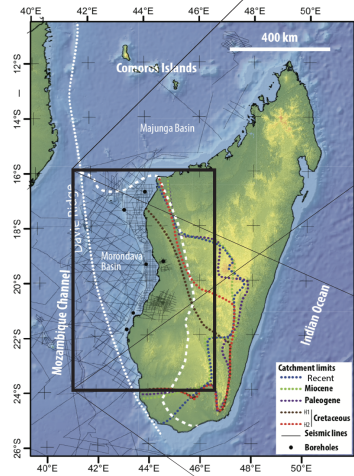
The dataset in the Morondava Basin and southern Davie Ridge ([Delaunay 2018](#)) enables a sediment thickness map revealing sediment-bare areas surrounded by thick deposits (**Figure 5B**)—indicating either 24 Ma nondeposition or end-period erosion, both suggesting aerial/subaerial conditions ([Aslanian et al. 2023](#)). The area also contains Mass Transport Deposits (MTDs), turbiditic carbonate systems (mainly disconnected slope lobes), and contouritic ridges to the north between the Davie Ridge and Juan de Nova Island. At the end of this period, carbonate platform extension positioned the paleoshelf break at the Davie Ridge—on the Mahafaly Plateau (south) and the Juan de Nova island (north; [Delaunay 2018](#)).

The Lutetian to Priabonian Phase

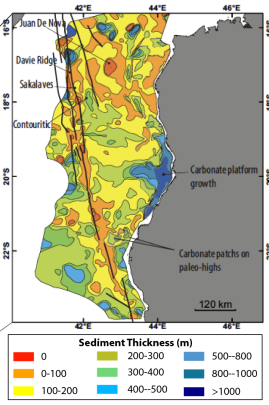
The Eocene–Oligocene transition features the “Grande Coupure” mass extinction—a major faunal turnover—coinciding with climatic change, intense volcanism, large meteorite impacts, and global plate reorganization. Afro-Arabian mammalian extinctions eliminated nearly two-thirds of late Eocene diversity by ~30 Ma ([de Vries et al. 2021](#)). Geodynamically, this phase includes Labrador Sea ridge jump to the Norwegian Sea, Pacific/Atlantic fracture zone reorientations, Emperor/Hawaii/Louisville alignment curvatures, Australia’s northward motion, and formation of three conjugate oceanic plateau pairs: Austral-Iquique, Tuamotu-Nazca, and Marquesas-Inca ([Gutscher et al. 1999](#)). The same methodology was applied to this phase using the full Pamela dataset (**Figure 6-Top**). Seismic facies analysis revealed depositional environments including carbonate shelf-edge platforms, isolated paleo-highs with patch reefs (e.g., Juan de Nova, Sakalaves, Morombe - [Delaunay 2018](#), [Courgeon et al. 2017](#)), and regionally variable slopes—gentler (ramp-like) to the south, steeper to the north ([Delaunay 2018](#)). [Delaunay \(2018\)](#) noted: *“the sediment thickness map shows two areas of minimal preservation along the Davie Fracture Zone and northward around Juan de Nova Island,”* suggesting nondeposition or end-period erosion. Two wells (X1 and Y21) near Madagascar exhibit a second unconformity—a significant erosional surface atop the underlying platform—marking a ≥ 1.8 Myr Rupelian-base hiatus with absent planktonic foraminiferal zone P18-O1 ([Delaunay 2018](#)). This regional unconformity ap-

pears westward along the Davie Ridge near the Mozambican coast (offshore Lacerda Basin; [Ponte 2018](#)) and across Africa, linked to mantle-driven continent-scale uplift ([Ponte et al. 2019](#), [Burke & Gunnell 2008](#)). The area also contains MTDs, disconnected turbiditic carbonate slope lobes, and northern contouritic ridges between the Davie Ridge and Juan de Nova Island.

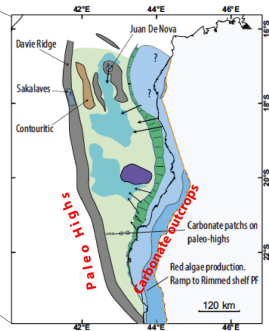
Lutetian to Priabonian Phase



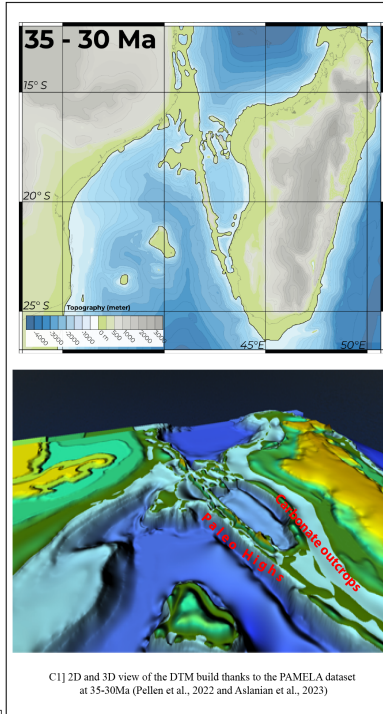
A) Dataset used in Delaunay's work (2018) within the Pamela Project. Thin black lines (onshore and offshore) are industrial seismic profiles. Note the rather good coverage of the Morondava Basin and the Davie Ridge. Black dots represent the drill holes used for the stratigraphy analysis.



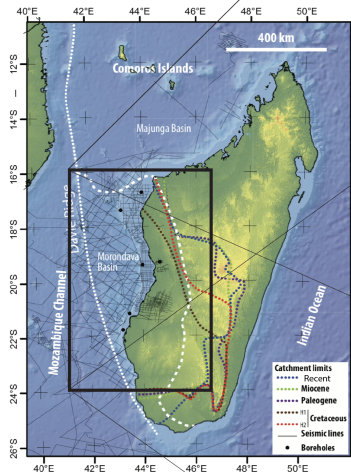
B1) Sediment Thicknesses (isopachs) for the depositional sequence between 66 and 33.9 Ma (after Delaunay, 2018)



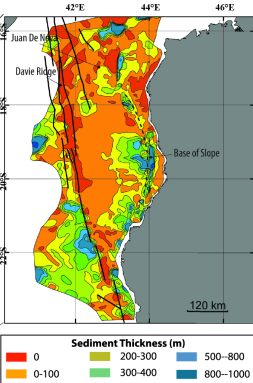
B2) Paleo-environments at ~33.9 Ma (after Delaunay, 2018). Note that Delaunay interprets the Davie Ridge as a Paleo-high continuous structure.



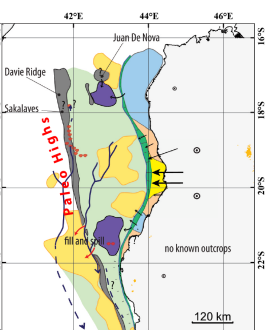
Late Miocene period



A) Dataset used in Delaunay's work (2018) within the Pamela Project. Thin black lines (onshore and offshore) are industrial seismic profiles. Note the rather good coverage of the Morondava Basin and the Davie Ridge. Black dots represent the drill holes used for the stratigraphy analysis.



B1) Sediment Thickness (isopachs) for the depositional sequence between 24 Ma and 12 Ma (After Delaunay, 2018)



B2) Paleo-environments at ~12 Ma (after Delaunay, 2018). Note that Delaunay interprets the Davie Ridge as a Paleo-high continuous structure.

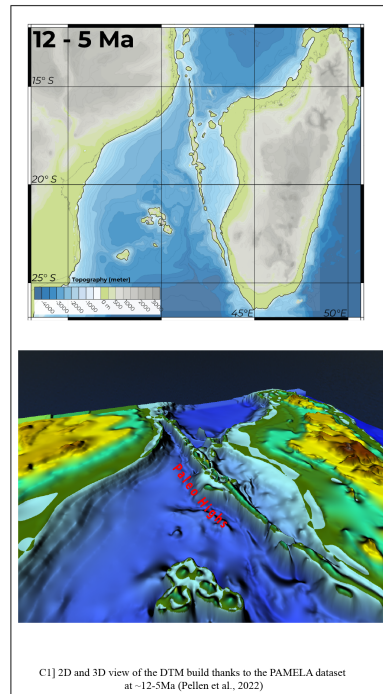


Figure 6 Research including onshore-offshore industrial seismic profiles and drill wells conducted in the Morondava Basin and the southern part of the Davie Ridge as part of the Pamela project for Lutetian to Priabonian Phase (top) and the Late Miocene period (bottom) Top: A] Dataset (industrial seismic lines and drill holes) used in [Delaunay \(2018\)](#); B1] Sedimentary thickness for the interval of ~32 My period between 66Ma and 33,9Ma; B2] Inferred paleo-environments at 33,9 Ma (after [Delaunay 2018](#)); C] 2D and 3D views of the DTM ([Pellen et al. 2022](#)). Bottom: A] Dataset (industrial seismic lines and drill holes) used in [Delaunay \(2018\)](#); B1] Sedimentary thickness for the interval of 12 My period between 24Ma and 12Ma (about the third duration than in the Lutetian-Priabonian thickness map, with the same thickness scale); B2] Inferred paleo-environments at 12 Ma (after [Delaunay 2018](#)); C] 2D and 3D views of the DTM ([Pellen et al. 2022](#))

Late Miocene Period (15–5 Ma)

In the Indian Ocean, the phase features major uplift causing Zambezi Channel bypass ([Guillocheau et al. 2018](#)). The end of this phase marks the Messinian revolution—last occurrence of a cyclic global event series ([Leroux et al. 2018](#)), that included magmatic reactivation of long-dormant volcan plateau worldwide ([Gutscher et al. 1999](#)), increased relief, accelerated basin sedimentation from heightened erosion in mountain belts, rare carbonatite occurrences, the Messinian Salinity Crisis in the Mediterranean, and a major global kinematic reorganization ([Briais et al. 2002](#), [Cande et al. 1995](#), [Ondreas et al. 2001](#), [Patriat & Larson 1989](#) - see [Leroux et al. 2018](#), for a review).

In the Mozambique Channel, Late Serravallian volcanism is recorded south of the Sakalaves seamounts along the northern Davie Ridge, coeval with Madagascar's third regional uplift ([Delaunay 2018](#)), which exposed its continental platform during Serravallian-Tortonian time. Carbonate production during the Messinian–Pliocene in the Comoros archipelago has been documented by [Leroux et al. \(2020\)](#). [Courgeon et al. \(2017\)](#) describe comparable carbonate development at Bassas da India south of the Davie Ridge. Subaerial exposure during the Late Miocene–Pliocene is evidenced by drowned isolated platforms preserving well-developed karstic topographies and freshwater diagenetic features ([Leroux et al. 2020](#)). Drowning of the southern Davie Ridge began in the Middle Miocene, as shown by deep-sea channels linking the Morondava Basin to the turbiditic system south of the Mozambique Channel ([Delaunay 2018](#)). This north-south inundation is further indicated by a thin sedimentary stack (<100 m) in the northern Morondava Basin—marked by a basal unconformity with a 14 Ma hiatus in some wells—that thickens southward, reaching 300–800 m at the central and southern river outlets. Non-

continuous connections can thus be inferred, interrupted by small (<50 km) shallow marine corridors between the Davie Ridge and the northern Morondava Basin ([Figure 6-Bottom](#)).

The global bathymetric grid from GeoMapApp ([Ryan et al. 2009](#); June 2022 update including the Southwest Indian Ocean Bathymetric Compilation) covers the Natal Valley, Mozambique Basin, and Ruvuma Basin but excludes the Davie Ridge and Morondava Basin. [Ali & Hedges \(2025\)](#) estimate that “~40,000 km³ of rock must have been removed since the Early Pliocene” posing two questions: 1) What mechanism stripped it away? 2) Where is the material now?”

Two straightforward answers emerge. First, their “rock” consists of sedimentary layers eroded in subaerial settings. Channel systems and strong bottom currents at the foot of bathymetric highs likely transported these sediments into deep basins, as [Ponte \(2018\)](#) notes: “A paleo-channel drained the system to the south along the Davie Ridge, even though the outlet to the Mozambique Channel deep-sea plain was not characterized.” Second, A&H claim that “none of the geophysical surveys of the Davie Ridge area (e.g., [Mougenot et al. 1986](#), [Mascle et al. 1987](#), [Malod et al. 1991](#), [Vormann & Jokat 2020](#)) have identified detritus piles that could be related to the feature.” This is unsurprising: the first three studies provide only schematic line drawings from low-resolution, single-channel seismic profiles, while [Vormann & Jokat \(2021a\)](#) focus on the northern Davie Ridge and Ruvuma-Kerimbas Basin using refraction profiles and one multi-channel seismic line far to the north—data inadequate for detailed sedimentary analysis. In contrast, PAMELA project data ([Delaunay 2018](#), [Ponte 2018](#)) reveal numerous reworked deposits and MTDs in deep basins across periods (see maps in [Figures 5 and 6](#)). Although not definitively linked to Davie Ridge erosion, these features plausibly account for the missing volume and are difficult to reconcile with Ali & Hedges’ interpretation.

3. TESTING THE HYPOTHESIS BY PALYNOLOGICAL STUDY

[Masters et al. \(2021\)](#) refined their methodology in follow-up study that used new data to test the land bridge hypothesis and propose a temporal-spatial model of African and/or Malagasy paleovegetation during plant and mammal migrations from Africa to Madagascar ([Génin et al. 2022](#)). Building on this, a palynological study was conducted at DSDP Site 242 (15°50.65’S, 41°49.23’E)—located eastward of and in proximal to the hypothesized Davie Ridge land bridge. The study aimed to (1) reconstruct the marine paleoenvironment using dinoflagellate cysts and

(2) infer land proximity from pollen grains and other continental palynomorphs (Aslanian et al. 2023). Messinian and Pliocene dinoflagellate cysts assemblages showed, in agreement with the global sea-level curves of Miller et al. (2011) and Ohneiser et al. (2015), sea-level changes from low sea-level at the beginning of biozone NN12, high sea-level at the end of biozone NN12 (~5.5 Ma) and finally a relatively low sea-level during biozone NN14 (~4 Ma) (Aslanian et al. 2023). Messinian (~5.5 Ma) pollen assemblages reveal vegetation belts ranging from coastal (mangroves) to high-elevation belts (montane forests) environments. The dominance of mangrove pollen indicates land proximity, as reported in other studies of ancient mangrove ecosystems (Popescu et al. 2021, Ponte et al. 2019) and supports a nearby island source more than an African or Madagascar coastline origin (Aslanian et al. 2023).

4. HIPPOPOTAMUSES, RAFTING, AND THE COLONIZATION OF MADAGASCAR

The colonization of Madagascar by its endemic vertebrates—including extinct hippopotamuses—has long relied on a rafting model. Early morphological studies traced Malagasy hippopotamuses to the common hippopotamus (*Hippopotamus amphibius*), proposing overwater dispersal from Africa by overwater routes (Weston & Lister 2009). The oldest reliably dated hippopotamus fossil currently known from Madagascar corresponds to *Hippopotamus laloumena* (Faure & Guérin 1990), dated to ca. 20 ka (Faure et al. 2010). This species is intermediate in size between *H. amphibius* and smaller, later species (*H. lemerlei* and *H. madagascariensis*), fitting an island-dwarfing scenario postcolonization.

This fits the prevailing view of Madagascar’s isolation since Gondwana breakup, leaving overwater travel as the sole option. Hippopotamus semiaquatic habits fuels notions of strong swimming or rafting across the Mozambique Channel (e.g., Ali & Huber 2010, Samonds et al. 2012, 2013, who modeled colonization by distance, currents, and ancestor traits).

Recent decades overturned this behavioral foundation. Biomechanical studies show hippopotamuses as bottom-walkers using underwater galloping, ill-suited to buoyant travel (Eltringham 1999, Fisher et al. 2007, Coughlin & Fish 2009, Mazza et al. 2013, Mazza 2014, 2015). Mazza (2014) deemed rafting untenable given poor swimming, strict ecology, and low drift success odds. He advocated a post-*Hippopotamus* African debut (~5 Ma) land connection—via sea-

level lowstands and emergent seafloor—urging geodynamic reevaluation via stratigraphy and bathymetry.

PAMELA (Passive Margins Exploration Laboratories) project geophysics confirm episodic Africa-Madagascar links at 66–60 Ma, 36–30 Ma, and 12–5 Ma, with bathymetric highs forming land corridors under uplift and lowstands (Masters et al. 2021, Génin et al. 2022, Aslanian et al. 2023). Rafting proponents persist. Van der Geer et al. (2015) rebutted Mazza (2014), citing neonate swimming, saltwater buoyancy, and natural rafts—echoing Ali & Huber (2010)—while Ali & Hedges (2023, 2025) favor rafting as the dominant colonization mechanism.

Here hippopotamuses are targeted as a rafting “extreme test case.” This paper (1) synthesizes locomotion/physiology data for overwater feasibility, (2) dissects van der Geer et al.’s (2015) claims, and (3) evaluates them against biomechanics, physiology, and geodynamics. Rafting fails realistic constraints; Neogene land connections offer a parsimonious alternative.

Comparative Case Studies: Lowstands, Island Bridges, and Insular Mammal Dispersal

A recurrent weakness in critiques of intermittent land-bridge scenarios is the implicit assumption that a transient emergence should necessarily leave a continuous and readily accessible vertebrate fossil record on the receiving landmass, and that failure to document such fossils at the expected ages falsifies dispersal. This reasoning conflates geodynamic feasibility with taphonomic visibility. Across many island systems, the physical existence of land connections is governed by the interaction of glacio-eustasy, regional isostasy, and vertical tectonics, whereas preservation and discovery of terrestrial vertebrates depends on contingent depositional settings, subsequent erosion, and sampling intensity. Consequently, “no fossils reported” is not equivalent to “no animals present,” particularly where depositional windows are narrow and later reworking is pervasive (see synthesis in Mazza et al. 2013). In the Mediterranean, repeated lowstands have been shown to generate transient connections across shallow sills and shelves. For the central Mediterranean, emergence of the Messina Strait threshold during major lowstands has been modelled as a time-limited land connection between Calabria and Sicily, with implications for terrestrial dispersal during the last ~40 kyr (Antonioli et al. 2012). More broadly, glacio-hydro-isostatic modelling of Mediterranean relative sea-level change since the LGM provides quantitative constraints on the magnitude and spatial variability of coastline migration and shelf exposure in tectonically stable sectors, reinforcing that connectivity windows are expected to be episodic

and regionally heterogeneous (Lambeck & Purcell 2005). In the Aegean domain, reconstructions of relative sea-level change and shoreline evolution since the Upper Palaeolithic likewise indicate that glacial–interglacial cycles repeatedly reorganized shelf areas, periodically exposing coastal plains and narrowing water gaps, thereby altering dispersal probabilities among today’s islands (Lambeck 1996). A second, globally important analogue comes from Southeast Asia. During Pleistocene lowstands, exposure of the Sunda Shelf repeatedly amalgamated much of present-day western Indonesia and Malaysia into emergent “Sundaland.” Classic cartographic reconstructions explicitly map shorelines, river systems and time-durations at different sea levels, and are widely used to evaluate dispersal corridors for terrestrial biota (Voris 2000). Stratigraphic records from Sunda Shelf cores document rapid late-glacial flooding, reinforcing the episodic nature of connectivity (Hanebuth et al. 2000). Complementary mapping of Holocene transgression and submerged landscapes on the Sunda Shelf further illustrates how quickly shelf areas can be inundated during sea-level rise and how former land surfaces may become submerged and inaccessible to conventional terrestrial sampling (Sathiamurthy & Voris 2006). Biogeographic syntheses of Southeast Asian mammals incorporate this history of shelf exposure and fragmentation to explain continental affinities in insular faunas, while also emphasizing the persistence of deep-water barriers across Wallacea (e.g., Heaney 1986). These examples illustrate a general principle relevant to hypotheses of island colonization: the absence of fossils in a given time slice is not, by itself, decisive against an earlier dispersal scenario, because preservation and sampling are strongly time- and environment-dependent, and many island records preferentially capture only the late phases of insular lineages (Mazza et al. 2013). This point is directly applicable when independent palaeogeographic reconstructions indicate repeated windows in which shelves and sills could have produced transient dispersal corridors.

Functional Constraints on Hippopotamus Dispersal

Biomechanical and anatomical evidence converge on one conclusion: hippopotamuses are not swimmers. Studies by Fish (1993, 2001, 2002), Coughlin & Fish (2009), and others reveal that *H. amphibius* propels underwater via low-frequency bounds off the substrate, not sustained strokes in neutral buoyancy. This bottom-walking reflects key traits. Barrel-shaped, unstreamlined bodies contrast with swimmers’ sleek profiles (Howell 1930, Eltringham 1999). Limbs lack webbing or propulsive modifications (Fish 1993, Coughlin & Fish 2009). High bone density—especially osteosclerosis in long-bone medullary cavities—raises specific gravity, lowers the

center of mass below buoyancy, and stabilizes substrate contact (Wall 1983, Fish & Stein 1991, Fish 2001, Coughlin & Fish 2009). These features persist in extinct hippopotamids (Mazza 2014).

Behavior aligns: hippopotamuses favor shallow water for bottom contact and shun deep, open areas (Klingel 1991, Eltringham 1999, Nowak 1999, Fisher et al. 2007). Adults surface every 3–5 minutes to breathe, juveniles every 2–3 minutes—even asleep (Eltringham 1999, Miller et al. 2025). Deep submergence under high hydrostatic pressure would disrupt this rhythm and thermoregulation.

Physiological demands compound the issue. Hippopotamuses require abundant fresh water and shade, being highly heat-sensitive (Wright 1987, Owen-Smith 1988, Calder 1984). Their “thick” skin features a thin epidermis over a vascular dermis with glands secreting cooling fluids (Luck & Wright 1964, Eltringham 1999, Miller et al. 2025). Anesthetized individuals need active cooling (shade, fans, water, ice) to avoid hyperthermia (Miller et al. 2025). Open marine exposure without relief proves intolerable. Sustained oceanic rafting would therefore entail prolonged exposure to saline and stormy conditions without reliable access to freshwater or shade. No demonstrated mechanism explains how sufficient freshwater could persist on drifting vegetative rafts during extended open-marine transit across the Mozambique Channel. Collectively, these traits define a shallow-freshwater bottom-walker, unfit for oceanic dispersal.

Van der Geer et al.’s (2015) Rafting Hypothesis

Van der Geer et al. (2015) directly rebutted Mazza (2014), defending overwater dispersal for island hippopotamuses (Madagascar, Crete, Cyprus) via rafting or swimming at glacial lowstands.

They redefine “swimming” to include bottom-walking and bounding, citing crossings of multi-kilometer rivers/lakes and inferring feasibility for shortened sea gaps. Cranial traits (sealable nostrils/ears) and extended dive times signal aquatic prowess, they claim, with saltwater buoyancy aiding—not impeding—movement.

Biogeographically, hippopotamuses on disconnected islands (Mediterranean islands, Zanzibar, Madagascar) demand overwater explanations; land bridges lack geological support. They

cite elephants and deer as rafting precedents for large mammals. Rafting aligns with geology and biology, they argue, while land bridges remain speculative without direct evidence.

Critical Evaluation

Van der Geer et al.'s (2015) claims clash with biomechanical and geodynamic data. Their cited aquatic traits (cranial valves, dive tolerance) coexist with antiswimming features: unstreamlined bodies, unmodified limbs, and osteosclerotic high-density bones that anchor to the substrate (Howell 1930, Wall 1983, Fish 1993, 2001, 2002, Fish & Stein 1991, Coughlin & Fish 2009, [Mazza 2014](#)).

Observationally, hippopotamuses hug shallows, avoiding deep seas; bottomless movement yields only brief ballistic bouts (Estes 1992, Coughlin & Fish 2009). No records show sustained, directional swims over tens of kilometers—let alone >300 km across the current-swept Mozambique Channel, even at glacial lowstands.

Lowstands would not shallow the channel sufficiently for bottom-walking, rendering periodic surfacing (every 3–5 min; Eltringham 1999, Nowak 1999) impossible without substrate. Rafting thus becomes mandatory: passive transport on vegetated platforms.

Yet rafting would require extreme and sustained conditions: founding populations surviving for weeks with raft-supplied shade, ~72 liters of fresh water per day per individual (Calder 1984), and tolerance to prolonged saline exposure under heat stress (Luck & Wright 1964, Wright 1987, Miller et al. 2025). No quantitative assessment has demonstrated the feasibility of such requirements under open-marine conditions.

By contrast, recent Mozambique Channel geophysical data challenge the long-standing assumption of continuous isolation since 160 Ma. [Masters et al. \(2021\)](#) and [Génin et al. \(2022\)](#) document persistent bathymetric highs and tectonic corridors, and [Aslanian et al. \(2023\)](#) identify emergent Africa-Madagascar connections during the Late Miocene (12–5 Ma), providing a geodynamically plausible interval for terrestrial dispersal.

Importantly, the currently oldest securely dated hippopotamus fossils from Madagascar (~20 ka: [Faure et al. 2010](#)) represent the youngest *preserved* occurrences rather than the timing of initial colonization. The Malagasy terrestrial fossil record is discontinuous and biased toward Late

Pleistocene deposits, and therefore cannot be interpreted as a first appearance datum for the lineage. In continental Africa, the earliest hippopotamids appear around the Miocene–Pliocene transition (Boisserie 2005), consistent with a Late Miocene dispersal opportunity.

Under this framework, a corridor model supported by geophysical evidence provides a parsimonious explanation relative to long-distance rafting under physiologically extreme conditions. Because hippopotamuses combine large body size, high freshwater dependence, and bottom-walking locomotion, they represent a stringent test case for rafting-based models.

Implications for the Malagasy Rafting Paradigm

Rafting plausibly explains dispersal of small mammals, reptiles, amphibians, and invertebrates over short-to-moderate distances (Ali & Huber 2010, Samonds et al. 2012, 2013). In contrast, the large body size, freshwater dependence, and bottom-walking locomotion of hippopotamuses raise substantial biomechanical and physiological constraints for sustained dispersal across hundreds of kilometers of deep ocean. Any rafting-based scenario for Malagasy hippopotamuses therefore requires explicit consideration of how locomotor, thermoregulatory, and hydration constraints could have been overcome during transit across the Mozambique Channel. At present, no quantitative feasibility framework has been proposed addressing these combined constraints.

PAMELA geodynamic reconstructions (Masters et al. 2021, Génin et al. 2022, Aslanian et al. 2023) provide an alternative mechanism: intermittent land connections during specific intervals of tectonic reorganization. These reconstructions are consistent with known hippopotamid evolutionary timing (Boisserie 2005) and offer a geologically plausible dispersal window. Under this framework, transient corridors provide a parsimonious explanation relative to prolonged oceanic rafting under physiologically demanding conditions.

4. CONCLUDING REMARKS AND FUTURE DIRECTIONS

Geological records strongly indicate the existence of intermittent Africa-Madagascar land bridges during three intervals coinciding with global geodynamic shifts. Their scale suggests significant biogeographic influence, including topographic steering of oceanic currents toward a west-to-east flow (Le Hir et al. 2025)—enhancing connectivity even without full emergence.

This does not preclude occasional short-distance rafting. However, given the Late Miocene timing inferred for hippopotamid dispersal and the documented geodynamic connectivity during 12–5 Ma, a corridor-based scenario provides a more parsimonious explanation for large mammals under these specific conditions. Dispersal models must integrate geology and biology for coherence.

Geodynamic reconstructions should remain independent of biological priors—yet align with faunal evidence. Where apparent discrepancies arise between biological and geological interpretations, both datasets warrant re-examination. Ultimately, the goal is not to force biological data to conform to geological models, nor to disregard geology in favor of biological assumptions. We advocate reciprocal refinement: geodynamics and paleobiogeography mutually informing robust Earth history.

Future research should strive for an integrative approach, as neither geology nor biology alone can fully resolve the complexities of island colonization. Recently, [Montheil et al. \(2026\)](#) show that a corridor between Asia and Balkanatolia became available, during the middle and late Eocene, when Asian terrestrial mammals dispersed to Europe, while primates and rodents dispersed across the 500-to-2000 km wide Neotethys Ocean to colonize Afro-Arabia. Comparative analyses of other island/Oceanic Plateaux systems (e.g., Galápagos, Greater Antilles, New Zealand, Walvis-Rio Grande Ridges - cf. [Box-1](#), Sri Lanka, Sulawesi..) may further illuminate how geodynamic evolution interacts with biogeographic models. In several of these systems (e.g., New Zealand and the Greater Antilles), debates over rafting versus tectonic connectivity have similarly required integration of geodynamic reconstruction with paleontological timing.

AUTHOR CONTRIBUTIONS

This synthesis germinated in 2017 at Nelson Mandela University, during the first meeting between DA (geologist, geodynamicist, expert in plate tectonics) and Judith Masters (evolutionary biologist focussing on strepsirrhine evolution). DA led the studies and compiled the text. TLH, YC, TH, PP (physical oceanographers with expertise in large-scale ocean modelling and palaeoclimatologists) contributed the sections on paleo-oceanography. PPAM (vertebrate palaeontologist and taphonomist) MP (geneticist with expertise in phylogenetics and primate evolution) and SC (palaeontologist with expertise in Cenozoic mammals paleo- biodiversity and morphological

variation) contributed the sections on Hyppothamuses. DA, MR, EL, RP, BL, MM, SC, GB, AD, ET (geodynamicists, geologists, structuralists, sedimentologists with expertises on stratigraphy, geomorphology, carbonate and sedimentary modeling) contributed the sections on sedimentology and geodynamic. JPS, SP, SF (Palynologist, Foraminiferist and paleoclimatologist) contributed to the section on palynology. JPS, SP, SF, EL, GB, SC, AD, RP, MM, MR, PP and DA participated in the PAMELA project.

DISCLOSURE STATEMENT

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

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BOX 1: CROSSING THE SOUTH ATLANTIC OCEAN

Like Madagascar, new primate fossil discoveries in South America—once considered devoid of primates ([Godinot 2020](#), [Marivaux et al. 2023](#), [Seiffert et al. 2020](#))—challenge explanations for Eocene crossings of the >2,000-km-wide South Atlantic. An extraordinary rafting journey from Africa to South America has been proposed. As with the Indian Ocean, Lagrangian simulations

were conducted with the 55 Ma IPSL simulation ([Figure 1-A](#)) to assess particle success rates and travel times from African coasts to South America. Results show few particles crossed the Atlantic, requiring more than 60 days—indeed extraordinary for mammals. [Figure 1-B](#) depicts South Atlantic paleogeographies at 65Ma and 35Ma, focusing on the Santos-Rio-Grande Rise-Walvis (S-RGR-W) system.

While the Santos block is continental ([Evain et al. 2015](#)), the nature of the Rio Grande Rise (RGR)—with an oceanic setting—remains debated, despite dredged crystalline continental rocks and crust-contaminated basalts from its crest and seamounts ([Santos et al. 2019](#)). Four competing hypotheses exist: 1) microcontinent overlain by basalts and sediments; 2) uplifted oceanic crust fragment; 3) hotspot/plume product 4) excessive magmatism controlled by oceanic fracture zones ([Hackspacher et al. 2022](#)). Regardless of crustal nature, the RGR experienced multiple uplifts since the late Cretaceous; red clays indicate sub-aerial exposure during the Eocene volcanic episode ([Srivastava et al. 2023](#)). The Brazilian portion of the S-RGR-W system appears to have acted as an intermittent composite land bridge. Irrespective of the Walvis Ridge’s (African) vertical evolution, these intermittent uplifts likely facilitated Africa-South America passages at various times—particularly during the Campanian–Maastrichtian, when more complex Antarctica-Ninetyeast route has been proposed ([Gobbo & Bertini 2025](#)).

BOX 2: SECOND-ORDER BOUNDARIES AND BUFFER ZONES

In 1984, Olivet et al. defined ‘second-order’ boundaries as ‘linear zones that are the site of small-amplitude, irregular, and/or slow horizontal movement compared to relative plate motions. Unlike diffuse intraplate deformation, this deformation is localized. Second-order boundaries naturally imply subplates, allowing major plates to be subdivided for coherent reconstructions.

[Moulin et al. \(2012\)](#) extended this to buffer zones—areas at intersections of kinematic systems, such as triple junctions (Azores plateau, Shastky rise, Ontong-Java plateau, Marquises, Kerguelen-Broken rise system,...), microblocks (e.g., the Danakil block: [McClusky et al. 2010](#), [Sichler 1980](#); the Jan Mayen microcontinent: [Talwani & Eldholm 1977](#), [Gaina et al. 2009](#); the Iberian subplate: [Olivet 1996](#)), or double fracture zones, strike-slip margins, and transitional zones with mixed materials: [Evain et al. 2021](#), [Pellen et al. 2016](#), [Schnurle et al. 2023](#)). These

features act as zones of weakness that respond readily to geodynamic changes. For instance, the subparallel Pacific oceanic plateaus (Austral, Tuamotu, Marquesas) formed on-axis during the mid-Miocene (Gutscher et al. 1999) and were reactivated during the Messinian global geodynamic revolution (Leroux et al. 2018).

BOX 3: INSERT EARTH CYCLICITY

Periodicity in biological and geological events has been recognized in numerous datasets, including biological extinctions (Lieberman & Melott 2007, Melott & Bambach 2010, 2013, 2017, Rampino & Caldeira 2020, Rampino et al. 2021, Raup 1984, 1985, Raup & Sepkoski 1984, Rohde & Muller 2005, Sepkoski 1989), terrestrial impact cratering (Matsumoto & Kubotani 1996, Rampino & Caldeira 2015), flood basalts and Large Igneous Province onsets (Rampino & Caldeira 1993, Rampino et al. 2021), climate shifts (Couvreur et al. 2021), sea-level oscillations (Boulila et al. 2021, Miller et al. 2005, Müller et al. 2008, Rampino & Caldeira 2020, Zachos et al. 2001), sedimentation rates (Meyers & Peters 2011), seafloor spreading changes (i.e., Cande et al. 1995, Labails et al. 2010, Thompon et al. 2019), magnetic reversals (Raup 1985), and oceanic anoxic events (Rampino & Caldeira 1992, 1993).

These events exhibit cyclicity potentially linked to geodynamic changes, as seen in Pangea's breakup in three main episodes: Triassic (195–185 Ma), Early Cretaceous (135–125 Ma) and Tertiary (75–65 Ma). These phases align with first-order patterns in Earth's magnetic field, suggesting connections between biological extinctions, magnetic reversals, large body impacts (Raup 1985), and global kinematic phases (Moulin & Aslanian 2010, Aslanian et al. 2022). Although exact cyclicity remains debated, the synchronicity of major geological (and some biological) events is striking (Raup 1985), and Earth's geological history exhibits several global revolutions. These revolutions affected the lithospheric stress field at very large wavelengths, exploiting tectonic heritage (old sutures, rifts, buffer zones) to drive large uplifts (e.g., South Africa), exhumation, break-up, erosion—impacting the sedimentary cycle. While the drivers of horizontal movements (subduction pull, ridge push, mantle convection, etc.) remain debatable, correlations between global revolutions and magnetic reversal patterns point to a deep origin. These revolutions appear cyclic, with the Messinian revolution as the latest in the series (Leroux et al. 2018).

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