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(Article begins on next page)

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Abstract

Madagascar's vertebrate fauna is the result of an intricate biogeographic history not considered in the models developed to explain colonisation on other islands. For 80 years popular opinion has held that most of Madagascar's terrestrial vertebrate fauna arrived via transoceanic dispersal (i.e., by rafting or swimming), chiefly from Africa. The alternative solution of recurrent uplifts of a land bridge connected with cyclic global kinematic revolutions, proposed in 2021, was recently challenged. The 2021 paper demonstrates the strength of a comprehensive holistic approach (sedimentary, tectonic, kinematic, and palaeo-environmental studies) based on the new, large-scale dataset provided by the PAMELA (Passive Margins Exploration Laboratories) research project. This episodic land bridges hypothesis was tested with divergence estimates of dispersal mechanisms of Madagascar's Angiosperm taxa. The present study includes preliminary palynological results obtained on the latest Miocene to earliest Pliocene material from DSDP Site 242. These pollen assemblages are illustrative of vegetation belts from the coastline to high relief, i.e., from mangrove up to montane forests including intermediate low altitude vegetation.

Introduction

The popularity that the transoceanic dispersal hypothesis has enjoyed over the past 80 years to explain how African terrestrial vertebrates colonized Madagascar led scientists to repeatedly - and often fiercely - reject the alternative view that most of these events were made possible by occasional physical connections through the Mozambique Channel. In a recent contribution, Masters et al. (2021) tested four hypotheses, three potentially supportive of the transoceanic model (i.e., passive transport of hibernating animals; swimming colonization never previously observed in hippopotamuses; action of the eastward Paleogene surface currents allowing rafts to reach Madagascar in 3–4 weeks, an hypothesis proposed by Ali & Huber in 2010, and the fourth, alternative to it, involving geodispersal via short-lived land bridges between Africa and Madagascar. The conclusions of Masters et al.'s (2021) study were that 1) hibernation was likely developed by adaptation to Madagascar's highly variable conditions, rather than being an effective means devised to overcome oversea dispersal challenges, 2) hippopotamuses are demonstrably unable to stay afloat self-propelling through water and 3) the Ali & Huber model (2010) does not survive experimental testing. As for the fourth option of their analysis, Masters et al (2021) reported the existence, based on new geological data, of three short-lived land bridges between Africa and Madagascar at 66–60 Ma, 36–30 Ma and 12–05 Ma, thereby concluding that Madagascar's extant biota was likely built up with the contribution of fauna dispersed following the three Cenozoic land bridges rather than through transoceanic rafting or swimming, although vicariousness, island hopping and limited rafting also possibly played a role.

Recently, Ali and Hedges (2022) proposed a refutation of Masters et al. (2021). In this paper, we first analyze this refutation showing the strength of sedimentary, tectonic, kinematic, and palaeo-environmental studies recently conducted in the Mozambique Channel by more than 100 re-searchers involved in the PAMELA (Passive Margins Exploration Laboratories) research project, which included 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 Early Oligocene to Early Pliocene material from DSDP Site 242 can be considered the first important contribution to more comprehensive understanding of the characteristics of the series of land bridge connections across the Mozambique Channel. The preliminary palynological results provide a new promising avenue to document the occurrence of periodic land bridge connections between the African mainland and Madagascar.

Analysis of a recent refutation by Ali and Hedges (2022, 2023)

Ali and Hedges (2022) proposed a refutation of Masters et al. (2021) that they claimed to have "falsified". Fair discussions and debates are the heart of good science, but the unfortunate use of the term is forcing us to examine the logical structure of their argument, before going back to the actual evidence that they provide. The criterion of falsifiability of a scientific theory was introduced by the philosopher of science Karl Popper, as best summarised in Popper (1963). His aim was a clear definition of science opposed to what is called pseudo-science. This, he argued, could not be the positive evidence because even religious dogmas are based on accepted facts that are no more than social conventions. Rather, a good scientific hypothesis should be falsifiable and offers ways of being tested *negatively* against *exclusive* alternatives. Clearly enough, the intermittent land bridge hypothesis is testable and falsifiable by new data acquisition, palaeoenvironment proxies (pollen grains, dinoflagellate cysts) or new, more detailed interpretation. Sweepstakes dispersal is not a falsifiable hypothesis but rather a *scenario* that could only be falsified through experimental verification (Stankiewicz et al. 2006, Mzilikazi

et al. 2006, Masters et al. 2007, Ali & Huber 2010, Masters et al. 2021). It is far more theoretical than the geological evidence of a physical land bridge. In Popper's view, a good theory is one that allows risky testing; in our particular case, a risky way of testing the Davie Land Bridge hypothesis would be analysing samples drilled in the Mozambique Channel in search for continental sediments, shallow palaeoenvironments, or erosion. Thomas Kuhn (1962) showed that scientists conform to conceptual paradigms that strongly drive their opinions (model-dependent analysis). Scientists can thus operate within a paradigm as if in a closed system and go to great lengths to defend it against falsification by adding *ad hoc* assumptions to existing theories. Supporters of sweepstakes dispersal try to accommodate criticisms using what Popper called "conventional twists", i.e., *post hoc* additions (such as, in our case, rafting in hibernation, eddies reversing the main currents, etc.) in such a way that it escapes refutation.

In their most recent study, Ali and Hedges (2023) overlooked the hard geological evidence available from the Mozambique Channel (Masters et al., 2021, 2022). They also seem once again to omit the numerous specific biological, physiological, physical, and oceanographic controversies raised the oversea dispersal theory (e.g., capacity of rafters to deal with stresses from food and water deprivation, temperature and humidity excursions, high salt intake; the need to transfer sufficiently high numbers of healthy colonizers; water drag resistance of the natural rafts; amount of wind- and sea current-generated propulsive power needed to move the animal transporting flotsam with sustained and appropriately directed thrust) remarked by various authors (Mazza et al., 2013, 2019; Masters et al., 2021, 2022). In contrast, the two authors reject the geodispersion theory based on molecular-clock age-dated phylogenetic reconstructions and reiterate their preference for the oversea dispersal alternative. Molecular-clock age-dates and phylogenetic trees, however, generally rest on very subjective interpretations, and molecular-clock age-dates often have temporal resolutions of many millions of years.

Trans-oceanic crossings by terrestrial mammals
To the writers' knowledge, the only case of an open sea rafted land mammal is that of a jackrabbit, *Lepus californicus,* reported by Prescott (1959). The animal was observed on a raft of giant kelp near one of the three Channel Islands off the coast of San Clemente, California: despite their proverbial fertility and their inhabiting western North America for over 1.5 million years, these lagomorphs apparently never made it to those relatively close islands. Ali et al. (2021) reported the presence of howler monkeys (*Alouatta seniculus*) on a free - floating island on a river of Colombia. They indicated that the presence of animals on such islands support the over-water colonization hypothesis for the colonization of Madagascar. However, they could not really indicate a drift distance for the floating-island nor attest that the island will reach the open sea and continue its course.

Transoceanic crossings by terrestrial mammals can only be transposed to a particular case *by analogy*. Ali and Hedges (2022) wrote "Resistance [to the sweepstakes] view is rooted in the belief that land vertebrates, especially the land-locked mammals, cannot survive such journeys, which would take a few to several weeks (Ali & Huber, 2010), due to a lack of food and an absence of freshwater." Ali and Huber (2010) was a response to Stankiewicz et al. (2006). Despite Mozambique Channel currents are generally directed south-westward, Ali and Huber (2010, p. 654) wrote that "trajectories starting in the northeast region of Mozambique and Tanzania sporadically experience enhanced eastward velocities of > 20 cm/s and could therefore have crossed the necessary distance in 25-30 days". Masters et al. (2021) tested these conclusions. Lagrangian simulations used to determine the proportion of particles moving from the African coast to Madagascar, with accurate tracking of their trajectories, as well as the time they required to do so, revealed that the time estimated by Ali and Huber (2010) was severely underestimated due to the size of the model grid-cells (224*193 km) (Masters et al., 2021). Corrected simulations presented by Masters et al. (2021) found a minimum crossing time of 70

through 90 days, even under the most conducive palaeogeographic conditions, which is more than twice the time estimated by Ali and Huber (2010). This leads to conclude that over-water dispersal "assisted by ocean currents" may indeed be conceivable for floating seeds, but is not empirically supported for the colonisation of Madagascar by land mammals.

Geological information

Overall, Ali and Hedges' (2022) is a « reinterpretation » of the geological information used by Masters et al. (2021). Based on only limited information from Delaunay's thesis, Ali and Hedges (2022) wrote: "One possibility for the mis-portrayal by Masters et al. is that they misunderstood Delaunay's maps." The authors then refer to a « newly-developed topological schema », without further mention or supplementary information of it in the article, to claim the issue to be well-resolved. Ali and Hedges (2022) seem unaware of the volume and quality of new data analysed in the PAMELA (Passive Margins Exploration Laboratories) project and the expertise of the co-authors of Masters et al (2021). Three of them are a geologist, a sedimentologist and a geodynamicist, who designed, organised, and led part of the PAMELA project, and had access to all data (Fig. 1). This new article is also co-authored by Antoine Delaunay, Guillaume Baby [who worked on both South African shores (Baby et al., 2020), and not only on the western one as indicated in Ali and Hedges' (2022) Fig. 2], Simon Courgeon, Estelle Leroux and Maryline Moulin, who acquired valuable knowledge through their experiences in the area thanks to the PAMELA project.

Quite expectedly, Ali and Hedges (2022) come to different conclusions from those reached by Masters et al. (2021), because they worked on only a small and simplified excerpt of the data used by the latter authors, as will be explained below. They mainly base their « newly-developed topological schema » on an outdated set of data obtained from a low-resolution, mono-channel seismic profiles (e.g. Mascle et al., 1987; Mougenot et al., 1986). Ali and Hedges (2022) seem to interpret the lack of information in their sparse and low-resolution dataset as evidence of absence of uplift, thus implicitly equating "No data" with lack of movement. By doing this, they seem to neglect and minimise that the PAMELA project led by Ifremer, Total and French Universities, that involved 10 oceanographic campaigns including 224 days at sea (2014 and 2017), and three onshore geological studies (50 days in 2017 and 2018, in Madagascar and Mozambique). The fruitful collaboration with the industry granted over 100 researchers involved with the PAMELA project access to a dense set of industrial onshore and offshore seismic lines and boreholes (Fig. 1). The results of this intensive and extensive study were presented in more than hundred specialised articles published in the following years and enabled the implementation of ten PhD projects (e.g., Baby, 2017; Courgeon, 2017; Delaunay 2018; Ponte, 2018; Thompson, 2018).
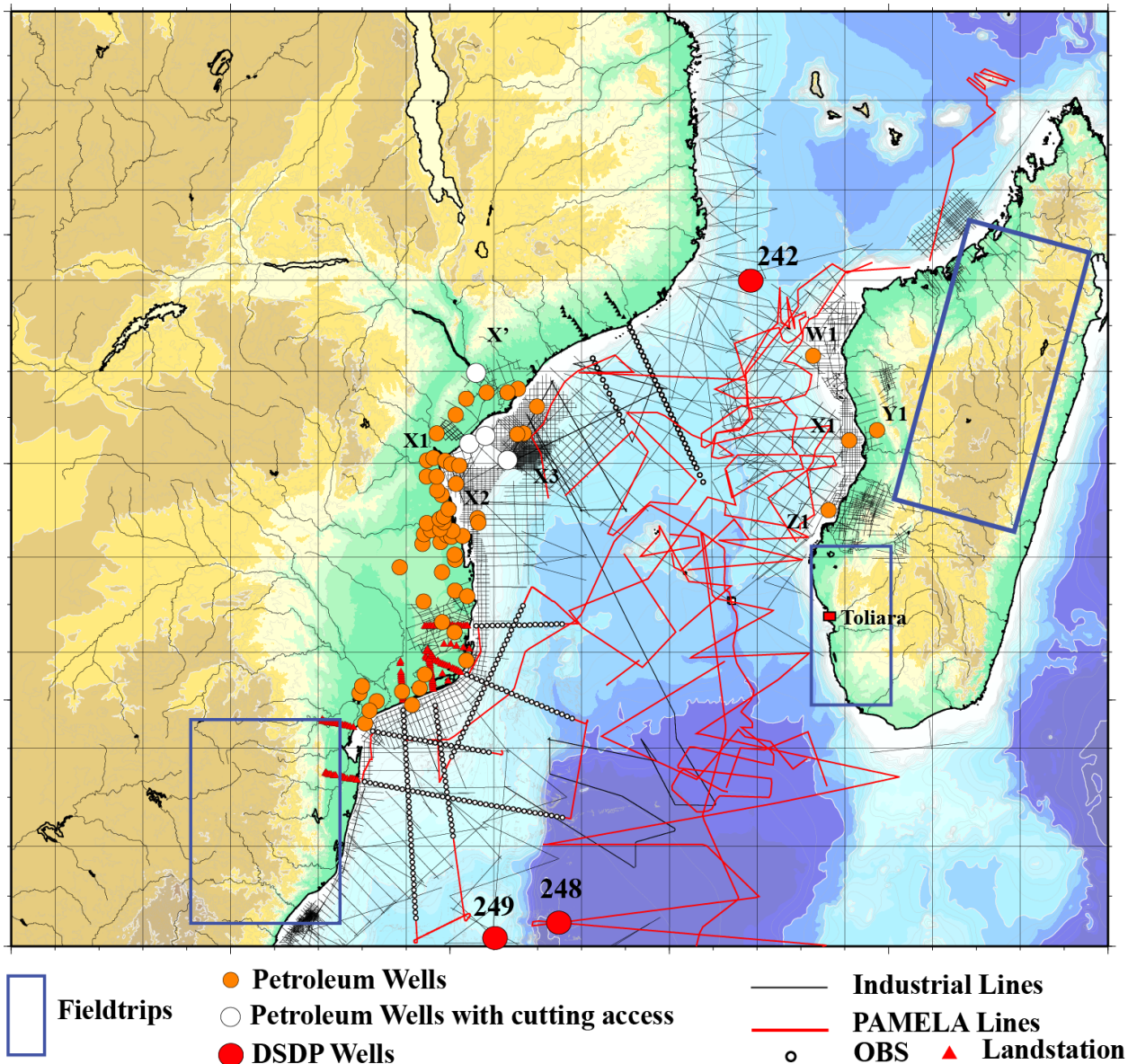
Figure 1 : Data used in the PAMELA Project used to reconstruct the palaeobathymetries of Masters et al. (2021). Compilation after Ponte (2018), Moulin et al. (2020), Delaunay (2018).

Ali and Hedges' (2022) exhibited an inadequate understanding of the interconnections between Madagascar and the Davie Ridge, as well as of the ascertained uplift events recorded in the latter. Their erroneous interpretation stemmed from a partial use of Delaunay's (2018) results and maps. Delaunay (2018) meticulously emphasised sedimentary layer attributes, such as age and thickness, alongside carbonate platforms, which was the basis for his maps. Figure 2 presents a comprehensive synthesis of those maps for the 66-60Ma land bridge, as documented in Masters et al. (2020). This illustrative figure stands as a representative illustrating Ali and Hedges' (2022) deviations from an accurate interpretation, akin to what philosopher Karl Popper (1963) would term "conventional twists".

The thickness of the sediments is shown on the left of Figure 2-A, while the palaeobathymetric interpretation is presented on the right; the reconstructions are based on the dense set of industrial and academic seismic lines and boreholes reported in Figure 1 for the time period ranging from the Late Turonian (90 Ma) through the KT boundary (66 Ma). Red spots indicate sediment-free areas. Sediments tell Earth's history: even their absence provides geodynamic insight (Rabineau, 2014). The areas bare of sediment in Figure 2-A, surrounded by areas covered

by thick sediment, may either result from 24 Ma lack of deposition, or erosion at the end of the considered period; both indicate aerial/subaerial conditions. The KT boundary is a time of global geodynamic revolution on Earth (see below Geodynamical insights). In the light of this, the lack of sediment on the Davie Ridge likely marks its late uplift at 66 Ma, rather a generalised, 26 Ma-long (late Turonian—KT boundary) starvation of sediment supply.

Figure 2-B shows the extension of the carbonate platform just after that time. According to Ali and Hedges (2022), "*Using Delaunay (2018), we surmise that the* [Tolaria] *area* [« 22.5°S-24.4°S gap »] *was under deep water during each of the purported land bridge periods*". In reality, the palaeoshelf break reaches the Davie Ridge on the Mahafaly Plateau during the Eocene and Oligocene. Further north, lack of sediment on the Davie Ridge in the « Betsileo-22.5°S gap » (Fig. 2-A]) leads Ali and Hedges (2022) to conclude again that "*Using Delaunay (2018), it can be inferred that during the various causeway windows this stretch of the Davie lineament was covered by deep ocean*", in contrast to all observations. The authors say the same for the *Sakalaves-Betsileo gap* where, according to Delaunay's (2018) map, no sediments are reported.
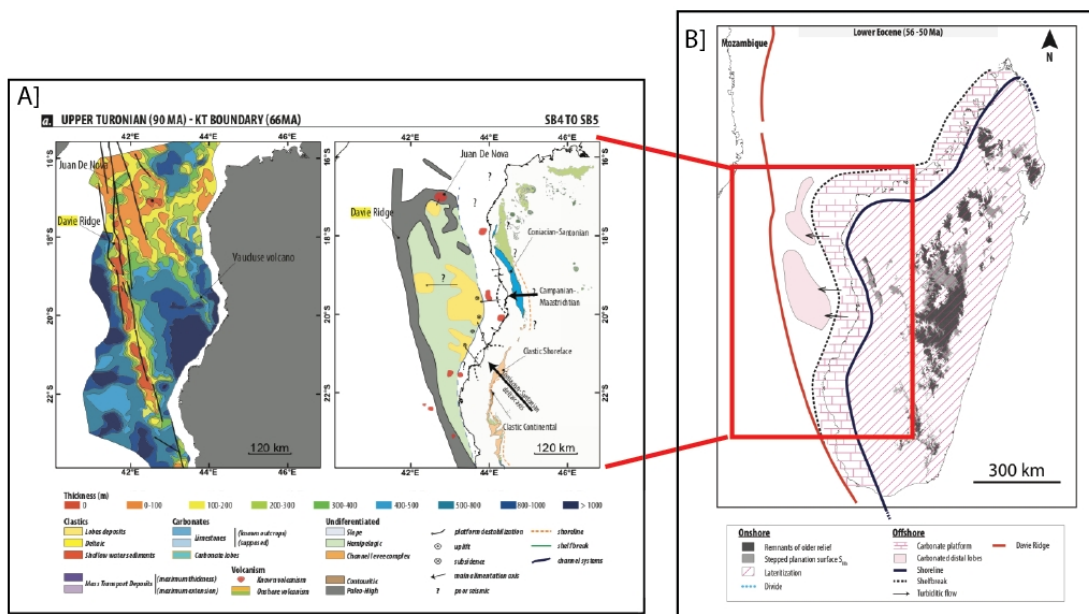
Figure 2 — A] Sediment thickness (isopach) maps and facies (palaeogeographic) map for the Upper Turonian (90Ma) - KT boundary (66Ma) depositional sequence. B] Synthetic map of the extension of the Lower Eocene (56-50Ma) carbonate (after Delaunay, 2018). Net of other problems, note the difference between Delaunay's (2018) original interpretation of a highly continuous «palaeo-high » in the Sakalaves area and that of a strongly disrupted « seabed high », in the same area, given in Ali and Hedge's (2022) figure 11 and allegedly attributed to Delaunay (2018).

West of the Davie Ridge and relatively to its northern part, Ali and Hedges (2022) neglect Ponte's (2018) conclusions with regards to an area extended from the Limpopo Margin, at west, to the Davie Ridge, at east, as opposed to what is displayed by Ali and Hedges' (2022) Figure 2, which restricts this area to the Zambezi Basin. Ali and Hedges (2022, see their figure 5) rely strongly on Vormann and Jokat (2021), arguing, quite surprisingly for a review article, that « *it is worth noting that Phethean et al. (2016) presented an ostensibly identical scenario, indicating a general consensus* ». To the writers' knowledge, the only recent comparative study

of Indian Ocean evolution is from Thompson et al. (2019) who, by comparing all published models (for the full set of comparisons, see Thompson, 2017), report long gaps, extensive overlaps and misfits of major structural and cratonic bodies in their proposed reconstructions, as well as misplaced tectonic blocks, inconsistent with field observations, « *a phenomenon sustained by inadequate data, long standing debates and a lack of consensus on the nature of major structures and basins in the ocean* » (Thompson et al., 2019). This is particularly true for the Mozambique Coastal Plain (MCP) and the North Natal Valley (NNV), where Vormann and Jokat's (2021) model (and before that, Muller and Jokat's, 2017 and all the models based on Leinweber and Jokat, 2012) produces an overlap (Ali and Hedges', 2022, Figure 5 at the Late-Early Jurassic) that Ali and Hedges (2022) explain « due to « young » sedimentary deposits in southern Mozambique » and to the presence of oceanic crust in the Natal Valley (Leinweber & Jokat, 2011). In contrast, Thompson et al. (2019) propose a new model that they claim consistent with current data interpretations of major structures across the Indian Ocean.

The Moz3-5 cruise carried out in 2016 as part of the PAMELA project acquired new geophysical and geological data (bathymetry, piston cores, water column, sub-bottom profiles, gravity, magnetism, dredges, wide angle and reflection seismic) that include a total of 193 Ocean Bottom Seismometer (OBS) records from over 7 wide-angle seismic profiles across the southern-Mozambique margins (Moulin et al., 2020 - Fig. 1). Four of these profiles were extended on-land through the deployment of 125 additional land seismic stations. At present and as far as we know, this is one of the most explored areas in the world with the densest deep wide-angle seismic coverage and with several crossing profiles performed to prevent over-interpretation on individual profiles. The PAMELA Team was granted access to a vast number of industrial seismic profiles over the entire study area as a result of a close collaboration with the oilfield service company Schlumberger and with Total-Energy Company. This huge dataset was processed by a team of specialists to avoid interpretation pitfalls and errors that might otherwise be committed by single individuals working on multiple profiles (Moulin et al., 2020; Lepretre et al, 2021 ; Evain et al., 2021 ; Watremez et al., 2021 ; Aslanian et al., 2021 ; He et al., 2021; Schnürle et al., in press). The data collected by the PAMELA-MOZ3 (Moulin & Aslanian, 2016) and PAMELA-MOZ5 (Moulin & Evain, 2016) cruises are archived and referenced at SISMER and accessible on request at https://doi.org/10.17600/16009500 and https://doi.org/10.17600/16001600). In short, Moulin et al. (2020) provided an overview of the Pamela-MOZ3-5 results, which reveal the presence of a 35-km-thick continental crust in the MCP and that of a 30-km-thick crust in the NNV. Vormann et al.'s (2021) hypothesis of Antarctic plate overlap, referred to by Ali and Hedges (2022), is contradicted this large volume of data and results.

Geodynamical insights
All the previous analyses of the possible origins of the Malagasy biota focussed on the vicariousness versus trans-oceanic dispersal dichotomy based on Gondwana breakup reconstructions, and only considering horizontal, tectonic movements (see for instance Vidal et al. 2010). Vertical movements were only considered in relation to the hot spot theory and regarded as local events.
The new paradigm used by Aslanian et al. (2022) is based on the consideration of cyclic kinematic revolutions concomitant with mass extinctions, sea-level lows, continental flood-basalt eruptions, mountain-building events, abrupt changes in seafloor spreading, ocean-anoxic and black-shale events, vast evaporite depositions, major magmatic events associated with global uplifts and connected to sedimentary cycles, production of carbonate plate-forms and climate evolution. Although the mechanisms underlying these events are poorly known, their occurrences are well-documented at a global level, and often associated with tectonic movements and volcanism (for instance: Raup & Sepokoski, 1984; Raup, 1985; Rhode & Muller, 2005 ;

Moulin & Aslanian, 2010 ; Rampino, 2015 ; Baby, 2017; Boulila et al, 2018 ; Leroux et al.,2018 ; Rampino & Caldeira, 2020 ; Moulin et al., 2020; Rampino et al., 2021 ; Aslanian et al., 2022). These events present a cyclicity which may be related to the geodynamic changes related to the disruption of Pangea during three main episodes (Moulin & Aslanian, 2010): Triassic (195–185 Ma), Early Cretaceous (135–125 Ma), and Cenozoic (75–65 Ma). These were also times of major global events, such as biological extinctions, magnetic reversals, impacts by large extra-terrestrial bodies (Raup 1985), and global kinematic phases (Moulin & Aslanian 2010; Aslanian et al., 2022). Possible causes of horizontal movements remain debatable (subduction pull, ridge push, mantle convection, etc.) but correlation between global kinematic revolutions and changes in magnetic reversal patterns suggest a very deep origin of these dislocations. The latest, episodic land bridge connection proposed by Masters et al. (2021) occurred in correspondence with the last of these 30 Ma-cyclic major geodynamic events: the Messinian revolution (Leroux et al., 2018).

During the 75–0 Ma time period considered by Masters et al. (2021) there were three global revolutions:

   • at the Cretaceous-Paleogene boundary, marked by various events, among which a mass extinction, a faunal turnover, the Deccan magmatic event, a rapid ocean acidification (Henehan et al., 2019), the Chicxulub impact (Renne et al., 2013), and global plate reorganisation (Moulin & Aslanian, 2010)

   • at the Eocene–Oligocene transition, when the mass extinction known as the "Grande Coupure", a faunal turnover, co-occurred with a major climatic change, intense volcanic activity, several large meteorite impacts, and global plate reorganisation. Recently, Rossini et al. (2022) argue that the *Gomphotherium* corridor, globally accepted as a temporary land bridge between Africa and Asia, must be postdated to the Eocene–Oligocene (albeit suggesting "routine transoceanic dispersal events" for the colonisation of Madagascar from Africa at the same period).

   • during the Messinian, when the severe ecological disruptions during the extremes of the Messinian Salinity Crisis led to the almost complete desiccation of the Mediterranean Basin, but also faunal changes, global rejuvenation of volcanism, increase in sedimentary influx, global plate reorganisation manifested by the reorientation of transform fracture zones, carbonate deposition, and significant relief change (Leroux et al., 2018).

Evidence of these three revolutions have been traced on the Glorieuses Seamount (North Madagascar) and in the surrounding deep Somali Basin (Leroux et al., 2020). The Glorieuses volcanic Seamount emerged from two successive Late Cretaceous magmatic pulses, and, at least two further uplift phases occurred during the Tertiary, likely around the Eocene—Oligocene transition and during the Late Miocene. Basin sedimentation also recorded an abrupt change (seismic facies change) probably related to major regional hydrodynamical changes in Late Eocene times in the Western Indian Ocean.

The kinematic revolutions produced changes in the lithospheric stress field on very large wavelengths. Tectonic heritage played a major role, with the reactivation of old sutures and rifts, large uplifts (as in South Africa), exhumations, break-ups, erosion, and strong impacts on sedimentary cycles. These effects were increased in the areas called the "second-order intraplate boundaries » by Olivet et al. (1984) and Olivet (1996). These pre-existing crustal zones of weakness are the most affected by deformations (Moulin et al., 2010). The Davie Ridge is a second-order intraplate boundary initially produced by the southward motion of the Madagascar-India plate that opened the Somali Basin between 165 and 120 Ma (Thompson et al., 2019). This N-S, 1200-km-long, strike-slip and complex structure (Vormann et al., 2020), a typical kinematic "buffer" zone *sensu* Moulin et al. (2012), are likely to react vigorously to any geodynamic

change through time. This was the hypothesis that was intended to be tested through the analysis of the huge set of data collected for the PAMELA project, independently of biological and palaeo-oceanographic factors.

In short (for details, reference should be made to Pellen et al., 2022), data and results on kinematics, structures, as well as on the sedimentary and morphological evolution of the Mozambique Channel, of Madagascar and of southern Africa, collected through the implementation of the PAMELA Project, were all recorded on a map. The information was then summarised and compiled into a set of palaeo-topographic submarine settings (subaerial, shallow, continental slope with submarine canyon systems, and a deep environment), while subsidence was corrected by applying Watts and Steckler's law (1981) to the oceanic plates. The palaeo-bathymetric reconstructions were then corrected in consideration of episodic magmatic events that produced the uplifts revealed by the sedimentary sequences (presence of shallow carbonates, hiatuses, discordances). Land-sea Digital Terrain Models (DTMs) were thus produced through the interpolation of contour curves (in xyz WGS84 format) over the entire area, for each time-slice (Pellen et al., 2022) and are fully available in free access on the SEANOE site (Pellen et al., 2022).

Back to Biology

Remarkably, Ali and Hedges (2022, 2023) addressed a biological issue clearly aimed at the community of biogeographers but published it in a geological journal. Indeed, the idea of the supremacy of hard geology over soft biology has so far always dominated the debate on Madagascar colonization. Masters et al. (2021) took a different approach, considering that biological information can also feed geological debates. They used geological studies that did not address any biological questions, and in particular Delauney (2018) and Ponte (2018) that they interpreted in a biogeographical context.

This trans-disciplinary approach led to the most convincing argument developed by Masters et al. (2022), regrettably ignored by Ali and Hedges (2022, 2023): the modes of temporal distribution revealed by independent dating techniques, including: (1) dates corresponding to known global events including the coincidence of kinematic revolutions, climatic events, mass-extinction events, closely followed by major radiations; (2) dates provided by geophysical studies and using a combination of relative (stratigraphic) and absolute (isotopes, etc.), based on both academic and industrial data; (3) dates provided by the fossil record; (4) dates provided by molecular dating in a variety of taxa; (5) and finally, dates secondarily suggested by the study of coevolved plants and animals (Masters et al., 2021, 2022; Génin et al., 2022).

Studies reporting molecular divergence dates rarely provide amounts of statistical error on accompanying figures, and generally relegate alternative estimates and confidence intervals to the supplementary information. By relying perhaps too heavily on the official dispersal dates, biogeographers are little inclined to consider alternatives, thereby proposing overwater dispersal solutions to otherwise apparently intractable conundrums. Masters et al. (2021) called attention to the considerable uncertainties in these time estimates and showed that most of the temporal variation generally overlaps the hypothetical events of land connection. A larger dataset is used in this study to account for the uncertainties through consideration of the temporal distribution frequencies of the Malagasy taxa.

The combination of the geological and biogeographical methods led a breakthrough overlooked by Ali and Hedges (2022, 2023). Other authors, and in particular McCall (1997), had already identified the Davie Ridge as a possible geodispersal pathway but could conceive that this possible land bridge had only emerged once and then sunk forever. This hypothesis predicts a single temporal event of phylogenetic divergence of lineages distributed in Madagascar,

whereas over-water dispersal allows for a uniform distribution.

Biologically, the three successive land bridge connections described by Masters et al. (2021) would give rise to three distinct immigration episodes punctuated in time, and thereby to three pulses of accelerated phenotypic evolution and phylogenetic divergence of taxa distributed in Madagascar from the African ones. Hence, a discrete, non-uniform distribution of Malagasy taxa would give immediate biological feedback to the land bridge connections across the Mozambique Channel, against overwater dispersal whereby faunal distributions would result from more uniformly and randomly scattered events through time.

In their evaluations of the multiple land-bridge model, Ali and Hedges (2023) base their conclusions on a set of probabilistic calculations of summations of taxa through time. However, Mayr's (1954) renown founder-effect and the model of coevolutionary organization of biodiversity (Genin et al., 2022) over time teach us that complex, interacting biological systems cannot be translated into mere mathematical expressions. The ancestral stocks of new immigrants and the origins of new ecosystems are virtually invisible to the fossil record, as well as to molecular tracking. It is only when new ecosystems grow more mature, radiate, and eventually consolidate, in intervals of time of geological extent, that they have more chances to be detected. The various taxa therefore first appear only when their populations stabilise reaching a considerable size. Figure 3 is built on first occurrences of phylogenetic divergences within endemic lineages reconstructed based on molecular data and fossils. Strictly monophyletic taxa were considered for this analysis: they largely include the first endemic taxa to diverge after each suspected event of colonisation.A total of 79 endemic taxa were analysed. First occurrence dates were compiled from 81 articles and chapters found in the literature and presented in Supplementary files. A taxa is considered as endemic when the entire clade is endemic, or when one of the subclades is endemic. In the latter case, the first occurence retained for the taxa is the one corresponding to the subclade, not to the entire taxa..

Although transoceanic, pendel-route dispersal by good swimmers (such as crocodiles) and flyers (birds and bats) is not excluded in this study, the results document five modes of divergence, all consistent with geodispersal (Fig. 1). These include vicariance (circa 120 Ma), a connection to Antarctica (circa 90 Ma), and the three surfacing events of the Davie Ridge proposed by Masters et al. (2021). Figure 3 also reveals a 5 Ma-lag in the origination of the endemic lineages. This average timing of delay between each first colonisation of the island and lineage divergences is a strong argument in favour of physical land connections, habitat continuity and coevolutionary diversification. In this interpretation, endemism only emerges after isolation.

The Malagasy biome was modified through time by repeated injections of new ecosystems introduced by the land bridges that connected Madagascar to the African mainland. From a co-evolutionary viewpoint, Génin et al. (2022) claim that the – largely mangrove – ecosystems diverged in isolation on the land bridges during the time when the latter were surfacing to finally connect with the island. These exclusive ecosystems, but perhaps also the dynamics of the land bridges, likely exercised a strong filtering function preventing any biotic interchange between Africa and Madagascar.

The overwater dispersal hypothesis highly relies on the capacity of animals for hypothermy or torpor, an important prerequisite for animal survival during the journey. Considering torpor as an advantage for sea crossing is probably a misunderstanding. Daily torpor is used by animals to reduce their heat loss and compensate the energy used for growth or reproduction in non-exceptional conditions. The amount of energy animal use is close to their basal needs in normal conditions. Daily torpor is a physiological strategy animals resort to setting a – fragile – balance between energy production and energy requirements in case of deficits (Vuarin et al., 2013; Jastroch et al., 2016), and it cannot be seen as a means to endure extreme conditions. Moreover, daily torpor is a mechanism used by small-bodied animals, with

body mass lower than 1 kg (Geiser, 2013). If we can imagine that the ancestors of Malagasy Tenrecidae and Nesomyidae rarely reached this body mass limit, probably the same does not apply to the ancestral Lemuroidea nor Eupleridae (Masters et al., 2014; Meador et al., 2019). Compelling evidence is provided, for example, by African lorisiforms and Malagasy lemuriforms. Although these primates share common ancestry and many lifestyle features, daily torpor exists in Malagasy mouse lemurs but it is absent among African lorisiforms, despite it is relatively common among Africa's small-bodied mammals (Hallam & Mzilikazi, 2011; Mzilikazi & Lovegrove, 2004).

Another option is travelling in states of hibernation (multiday torpor) to avoid energy loss in harsh (e.g., dry, cold) conditions. Hibernation is an adaptive response to climatic stress and it has been observed only among animals of Palaearctic origin living in cold regions, such as bats and dormice (Geiser & Stawski, 2011; Mzilikazi et al., 2012; Nowack et al., 2020). In contrast to daily torpor, hibernation is rare in Africa; it most unlikely that African ancestors of Malagasy taxa were capable to hibernate to survive the multiple stresses and hazards entailed in travelling from Africa to Madagascar via oversea dispersal. The Malagasy mouse and dwarf lemurs (Cheirogaleidae) are the only living primates known to hibernate. Considering the Miocene origins of these lineages (Herrera & Dávalos, 2016), hypothermy is likely to be a derived character evolved in association with phyletic dwarfing after, and not prior to, the colonisation of Madagascar (Génin & Masters, 2016; Masters et al., 2014, 2020, 2021).

Some bird species also resort to daily torpor, primarily to make up for energy loss during the night. Heterothermy is present in eight bird families, but none of them is included in Madagascar's avifauna (MacKechnie & Mzilikazi, 2011). It seems highly improbable that bird species that survived the stresses imposed by oversea dispersal by making use of daily torpor then lost this capability after adapting to Madagascar.

If overwater dispersal and geodispersal were submitted to a stress test, we would find that the former raises many more problems than it solves. It cannot convincingly explain how heterothermic mammals and birds, but also freshwater fishes or amphibians, could survive the countless hazards they would be subjected to crossing the Mozambique Channel towards Madagascar (Mazza et al., 2013, 2019). Conversely, most (if any) of those hazards and stresses are not an issue for geodispersal through land bridges.

While daily torpor and hibernation, and floating mats of vegetation can be invoked to possibly explain oversea dispersal, they can by no means be imagined for hippopotamuses. In fact, hippopotamuses provide smoking-gun evidence in support of the geodispersal model of colonization of Madagascar. These pachyderms are notorious non-swimming animals (Eltringham, 1999; Fisher et al., 2007; Coughlin & Fish, 2009; Mazza et al., 2013; Mazza, 2014). Other factors mitigating against any kind of oceanic crossing by hippopotamuses are that 1) they naturally avoid deep water, 2) adult hippopotamuses are far too heavy – 1.5 to 3 metric tons - to be supported by a tangled mat of vegetation acting as a seaworthy raft, and 3) in order to ensure a successful colonization, several individuals of this size need to be transferred all at one time or through successive rafting events. Despite the acknowledgement of hippopotamuses' pronounced sensitivity to solar radiation, a paramount consideration lies in their imperative requirement for substantial daily water consumption (Calder 1984).

Three hippopotamuses are known from Madagascar, the relatively large sized, but poorly documented *Hippopotamus laloumena*, and two better represented, smaller species, *H. lemerlei* and *H. madagascariensis*. They are all radiocarbon dated to the Holocene (Burney et al., 1997, 2004; Samonds et al., 2010), with the only exception of *H. laloumena* from Belobaka XVII which is Late Pleistocene in age, dating approximately to 20 ka (Faure et al., 2010). Because of the very recent age of these remains, scientists had no alternative but to identify the ancestor of the Madagascan hippopotamuses with the extant *H. amphibius* (e.g., Stuenes, 1989; Weston & Lister, 2009). Samonds et al. (2013), personally interpreting Boisserie's (2005) study, added that

H. madagascariensis is more closely related to *Choeropsis* (or *Hexaprotodon*) *liberiensis*. This implies that hippopotamuses needed not only one (Vences, 2004), but possibly a minimum of two recent overwater crossings to reach Madagascar from Africa (Samonds et al., 2013).

The fossil record that documents the earliest evolution of Hippopotamidae is extremely poor up until the latest Miocene when, probably around 8.5 Ma or between 8.5 and 7.5 Ma, large sized, advanced hippopotamids started appearing, marking what is known as the 'hippopotamine event' (Boisserie, 2006, 2020; Boisserie et al., 2010, 2011; Orliac et al., 2010). The subfamily Hippopotaminae is first recorded in Lothagam, Kenya, eastern Africa by *Archaeopotamus harvardi* (Weston, 2003), as well as in Toros-Ménalla, Chad, central Africa, by *Hexaprotodon garyam* (Boisserie et al., 2005). The subfamily subsequently diversified into distinct lineages: *Archaeopotamus* ended in the Early Pliocene; *Hexaprotodon*, from which aff. *Hippopotamus* branched off sometime during the Late Miocene; and *Hippopotamus*, which is documented from the earliest Pleistocene, but which presumably appeared sometime during the Pliocene.

By indicating that non-volant and non-swimming mammals had a last chance to cross the Mozambique Channel through a land bridge connecting Madagascar with mainland Africa from around 12 to about 5 Ma, Masters et al. (2021) placed the colonization of the island in a new light and opened promising new directions for research. In the particular case of hippopotamuses, the study demonstrated 1) how little importance has been given to the unusual mixture of *Hexaprotodon* and *Hippopotamus* characters repeatedly highlighted by those who have succeeded in the study of Madagascan hippopotamuses (Stuenes, 1981, 1989; Harris, 1991; Boisserie, 2005) and 2) that, despite having reached the island at a minimum of 5 Ma, hippopotamuses are entirely absent from the fossil record of Madagascar, which inevitably leads to considerable underestimation of their times of appearance, but also opens the way to any sort of speculation.

Palaeontologists are well-aware that fossils should only provide minimum stratigraphic ages; unfortunately, dispersalists are not as much aware of this. Hence, an incomplete fossil record can easily convince that the earliest available fossil-calibrated ages are maximum rather than minimum ages of stratigraphic distribution (Heads, 2015; Masters et al., 2022). By doing so, one should assume that hippopotamuses reached Madagascar approximately at the time indicated by *Hippopotamus laloumena* from Belobaka XVII, and therefore during the latest Pleistocene, or shortly before. This makes the only possible candidate for the role of ancestors of the Madagascan hippopotamuses the extant *Hippopotamus amphibius*, if there was a single immigration event, or both *Hippopotamus amphibius* and *Choeropsis* (or *Hexaprotodon*) *liberiensis*, if there were at least two arrivals, as posited by Samonds et al. (2013). In either cases, the morphological differences separating the three species indicate that soon after their arrival in Madagascar hippopotamuses underwent an explosive radiation. A further complication, however, far more difficult to explain, is that, either with a single immigration event, or with two or more, the radiation entailed the transversal distribution of *Hippopotamus* and *Hexaprotodon* characters among the species that were emerging. Masters et al.'s (2021) reconstruction, which proposes the arrival of hippopotamines in the 12-5 Ma time window, opens to a more parsimonious solution; the only difficulty would be admitting that behind presently known Madagascan hippopotamuses there is a long, antecedent history which is totally unrecorded.
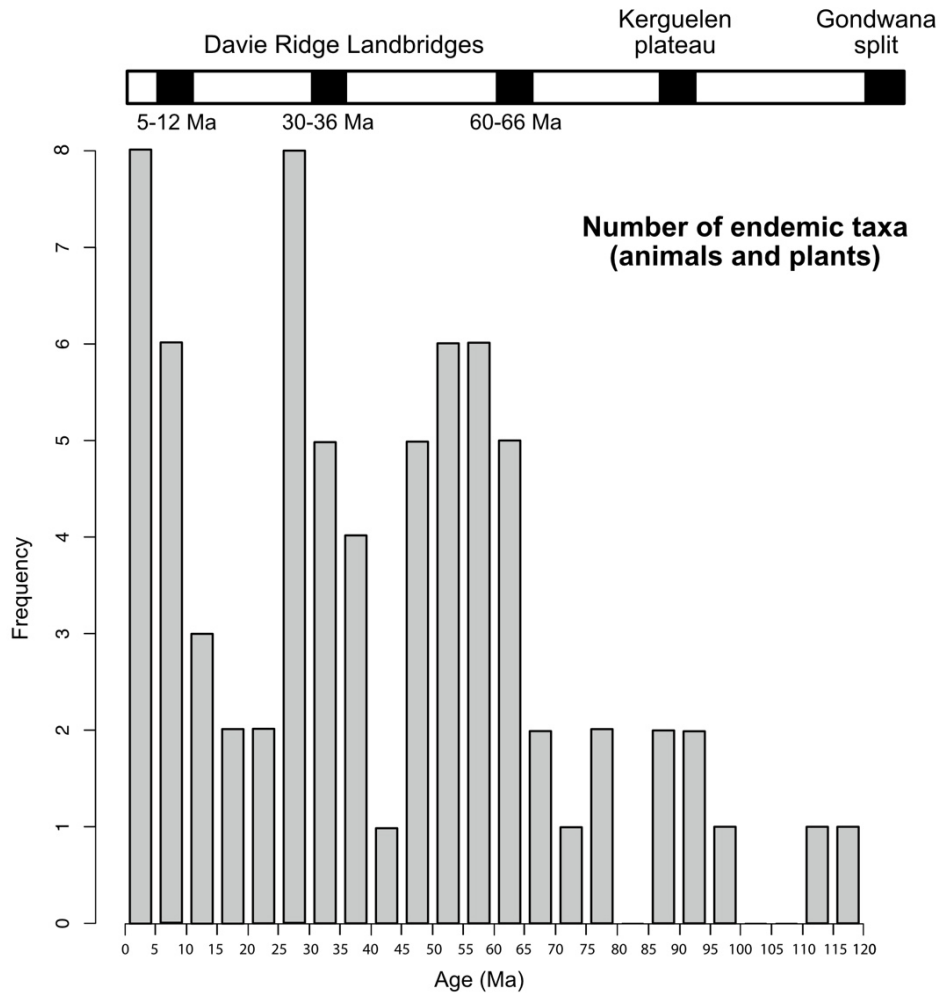
Figure 3. Histogram showing the frequency distribution of the first occurrence of monophyletic endemic taxa in Madagascar through time. Data are given in supplementary material (Table 1).

Real test of the land bridge hypothesis

The methodology used by Masters et al. (2021) was improved in a second contribution which, also based on new data, directly tested the land bridge hypothesis and proposed temporal and spatial dynamics of African and/or Malagasy palaeovegetation in the course of combined plant and mammal migration from Africa to Madagascar (Génin et al., 2022).

DSDP Site 242 (15°50.65'S, 41°49.23'E; Fig. 1) was cored eastward and very near the proposed land bridge along the Davie Ridge (Masters et al., 2021). These marine deposits were intermittently cored and their sediment records are therefore weak: some 103 m of recovered sediments vs. 134 m of coring along the 676 m of drilled sediments (Simpson et al., 1974). However, this borehole benefits from a reliable biostratigraphy for the Late Eocene – Early Pliocene time-interval (Müller, 1974; Zobel, 1974). More specifically, two of the time-intervals (36–30 Ma, 12–5 Ma; Masters et al., 2021) suggested for land bridge occurrence, can be investigated within this discontinuous sedimentary record.

The first palynological research reported in this paper concerns five samples from the clayey interval 155.31–151.31 mbsf (metres below sea floor), ascribed to the calcareous nannoplankton

zone NN12, and another one clayey sample at 135.29 mbsf, ascribed to the calcareous nannoplankton zone NN14 (Müller, 1974), i.e., to the periods 5.59–5.12 and 4.13–3.92 Ma (Anthonissen & Ogg, 2012; Hilgen et al., 2012), respectively (Fig. 4).

This study aims (1) to specify the marine environmental context using dinoflagellate cysts and (2) to identify the potential vicinity of some land on the basis of the occurrence of pollen grains and, secondarily, of some other palynomorphs of continental origin (spores, freshwater microalgae, reworked palynomorphs, etc.). About 30 grams of sediment were processed per sample using the classical method (acid digestions with HCl and HF, concentration in $ZnCl_2$ at density 2 and sieving at 10 μm). More than 120 dinoflagellate cysts were counted per sample in parallel to a maximum of pollen grains when present in enough quantity.
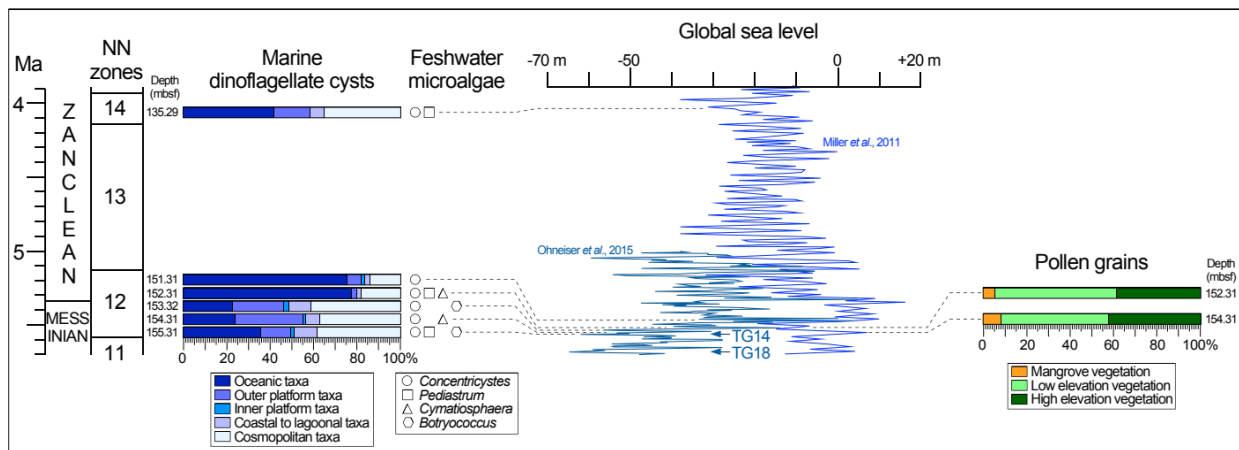

Figure 4. DSDP Site 242: summary diagrams of marine dinoflagellate cyst and pollen grain assemblages grouped according to their origin and/or significance, including occurrence of four freshwater microalgae, and chronostratigraphically distributed with respect to biostratigraphy (calcareous nannoplankton) and global sea-level fluctuations (Miller et al., 2011 Vs. Ohneiser et al., 2015).

Twenty-four taxa were identified among the marine dinoflagellate cysts (Table 1). They are arranged into five groups according to their ecological significance (Table 1). Four freshwater microalgae come from land (*Concentricystes*, *Pediastrum*, *Cymatiosphaera*, and *Botryococcus*). The marine context of the studied samples evidenced by Müller (1974) and Zobel (1974) is also supported by the abundance of marine dinoflagellate cysts. However, the three oldest samples (155.31–153.32 mbsf) show a markedly lower number of oceanic taxa and thus may correspond to the global sea-level falls of the beginning of biozone NN12 (Fig. 4; Miller et al., 2011; Ohneiser et al., 2015). On contrary, samples at 152.31 and 151.31 mbsf, characterized by large amounts of oceanic taxa, may correspond to the higher global sea level of biozone NN12 (Fig. 4). The sample at 135.29 mbsf (biozone NN14), with a moderate abundance of oceanic taxa, may correspond to a relatively lower global sea level than that inferred from the previous samples (Fig. 4; Miller et al., 2011).

Depth (m) Taxa	135.29	151.31	152.31	153.32	154.31	155.31
Oceanic taxa:						
Impagidinium aculeatum	32	44	70	20	16	27
Impagidinium patulum	27	49	32	8	15	10
Impagidinium sp.	1	5	6	4	3	1
Nematosphaeropsis labyrinthus	1	5		1		4
Operculodinium janduchenei	2	9	5	2	1	2
Pyxidinopsis sp.	1	3			1	
Outer platform taxa:						
Invertocysta tabulata	2	7	2		2	1
Spiniferites mirabilis	5		2	16	9	4
Spiniferites membranaceus	4	1			4	4
Spiniferites hyperacanthus	15	2		21	32	8
Inner platform taxa:						
Spiniferites bentorii				2	2	1
Brigantediniup sp.		2		2		1
Coastal to lagoonal taxa:						
Lingulodinium machaerophorum	6	1		14	8	11
Homotryblium sp.	4			1		2
Tuberculodinium vancampoae		3	3	1		
Polysphaeridium zoharyi					2	
Cosmopolitan taxa:						
Spiniferites spp.	17	8	12	11	15	20
Spiniferites ramosus	10	3		15	13	8
Spiniferites bulloideus	8	1		20	7	2
Edwarsiella sexispinosa	12	5	12	2	9	14
Operculodinium centrocarpum	3	1	2	13	5	3
Cyst of Pentapharsodinium dalei	3	2		2	6	
Melitasphaeridium choanophorum				1	1	
Hystrichokolpoma sp.	1	1				
Reworked marine dinoflagellate cysts	1	4	30		15	
Freshwater microalgae:						
Concentricystes		6	2	7	3	2
Cymatiosphaera		2	6		4	7
Pediastrum	1		2			8
Botryococcus				P		P
Analysed slide surface (mm²)	800	1600	3440	800	600	3440

Table 1. Number of individuals of marine dinoflagellate cysts and freshwater microalgae recorded in the six studied samples from DSDP Site 242. P = present. Analysed slide surface is indicated (the surface of a microscope slide = 960 mm².).

Samples at 155.31, 153.32, 151.31 and 135.29 mbsf are extremely poor in Pteridophyte spores and pollen grains mainly represented by *Podocarpus* (Table 2), the bisaccate pollen of which is easily (air-water) transported on long distance (Suppl. mat. Plate 1, Figs. 8–9). Only the samples at 154.31 and 152.31 mbsf are rich enough in Pteridophyte spores and pollen grains indicating a suitable plant diversity to be considered as representative of terrestrial vegetation (Fig. 4; Table 2). Thanks to accurate examination of the morphological characters of fossil pollen grains and their comparison with modern pollen grains stored within remarkable collections (ISEM, GEOBIOSTRATDATA) and illustrated in several iconographic databases, botanical identification is performed at least at the family level and very often at the genus level. Twenty-one and twenty taxa have been identified in the pollen floras of samples 154.31 and 152.31 mbsf, respectively.

These pollen assemblages are illustrative of vegetation belts from the coastline to high relief (Fig. 4; Table 2), i.e., from mangrove (ca. 5–8% of the pollen sum; *Avicennia* (Suppl. mat. Plate 1, Fig. 1), Rhizophoraceae (Suppl. mat. Plate 1, Figs. 5–6), *Nypa* (Suppl. mat. Plate 1, Fig. 3), *Sonneratia* (Suppl. mat. Plate 1, Fig. 11), *Xylocarpus* (Suppl. mat. Plate 1, Fig. 14) up to montane forests (ca. 39–42% of the pollen sum; *Podocarpus*, *Casuarina*, *Olea* (Suppl. mat. Plate 1, Fig. 4), Ericaceae, *Myrica*, etc.), including intermediate low altitude vegetation (ca. 50–55% of the pollen sum; forests: Arecaceae including cf. *Calamus* (Suppl. mat. Plate 1, Figs. 2, 7), Lythraceae, Moraceae, *Trichocladus* (Suppl. mat. Plate 1, Fig. 13), etc.; open landscapes

including marshes: Acanthaceae (Suppl. mat. Plate 1, Fig. 12), Convolvulaceae, Poaceae, Cyperaceae (Suppl. mat. Plate 1, Fig. 10), etc.). In addition, these samples reveal a large quantity of reworked pollen grains that, as the high amount of Pteridophyte spores, points out an intense continental water run-off and/or river transport. This assumption is supported by abundance of fungal spores and mycelium fragments in the palynological slides and by large amount of reworked dinoflagellate cysts in the two samples rich in pollen grains.

Depth (m) / Taxa	135.29	151.31	152.31	153.32	154.31	155.31
Mangrove taxa:						
Avicennia					2	
Nypa			1		1	
Rhizophoraceae			3		1	
Sonneratia					1	
Xylocarpus			2		1	
Low elevation taxa:						
cf. Calamus					3	
Arecaceae		1	5		3	
Buxus			1			
Lythraceae			1			
Moraceae			1			
cf. Stachyothyrsus					1	
Cupressaceae					1	
Borassus			1			
Acanthaceae			2			
Alafia					1	
Convolvulaceae	1		1		4	
Pistacia			1		2	
Leucas-type			1			
Poaceae		1	10		5	
Sesuvium			1			
Aizoaceae			1			
Cyperaceae	1	2	34		11	3
Trichocladus			2		4	
Ranunculaceae					3	
High elevation taxa:						
Artemisia					1	
Ericaceae					2	1
Olea			2		1	
Casuarina			2			
Myrica					7	
Podocarpus	5	3	39	2	20	4
Unidentified pollen grain					1	
Reworked pollen grains	10	1	8	4	32	
Spores of Pteridophytes:						
Polypodiaceae		3				1
Monolete spores	7	5	60	4	51	7
Trilete spores	6	2	41	6	17	1
Other spores	12	1	33		51	
Analysed slide surface (mm²)	920	920	3520	920	4560	920

Table 2. Number of pollen grains and Pteridophyte spores recorded in the six studied samples from DSDP Site 242. Analysed slide surface is indicated (the surface of a microscope slide = 960 mm²).

Which inference in terms of occurrence of some neighbouring land? The terrestrial palynomorphs (pollen grains, spores, freshwater microalgae) preserved in significant quantity and diversity at depths 154.31 and 152.32 mbsf from Site 242 came from a land area. As they are indistinctly recorded from sediments deposited during relatively low and high sea levels (Fig. 4), it is suggested that sea-level fluctuations did not influence the presence/vicinity of this land. The observed irregularity in such records might be controlled by some variability in fluvial transport and/or marine currents. The major question concerns the location of the piece of land at the origin of these terrestrial palynomorphs: SE Africa? Madagascar Island? an island in-between?

The record of mangrove pollen grains is of major importance, even if they are in low quantity, because it demonstrates the closeness of land as discussed by Popescu et al. (2021) and Ponte et al. (2019) for past mangroves. Among the mangrove taxa, *Nypa* and *Xylocarpus* are always underrepresented in modern pollen records where their presence thus supports the existence of land in the immediate vicinity (Somboon, 1990; Phuphumirat et al., 2016). Similar observations and conclusions are expressed by Popescu et al. (2021) from past mangrove pollen records. These data document the origin of mangrove pollen grains from a nearby island rather than from the Africa and Madagascar far coastlines. The plants from high elevation biotopes are mostly constituted by *Podocarpus* in the pollen record from Site 242. These plants are reported in very low percentage in the Late Miocene sediments drilled from the offshore Zambezi Delta, the nearest African source of their pollen being distant of at least 1500 km (Ponte et al., 2019). A transport of these pollen grains from Madagascar relief appears more acceptable with respect to the Malagasy drainage system proposed by Delaunay (2018) and Pellen et al. (2022) for the Late Miocene. This is also consistent with suggested Malagasy detrital inputs for the Glorieuses surrounding basin at that time (Leroux et al., 2020: Fig. 12). However, there is no objection for the development of such a vegetation belt on a nearby island all the more so since the modern species *Podocarpus madagascariensis*, for example, inhabits today an elevation extent ranging from the coastline to the highest summits (>2000 m; White 1983). In addition, it is also possible to hypothesize a land with elevated relief as it can be observed today in the Comoro Archipelago (Andilyat et al., 2022). The Site 242 is very close to the Macua Seamount which can thus be considered as a good candidate for such an island constitutive of a discontinuous land bridge between Africa and Madagascar. According to Ali and Hedges (2022), the Macua Seamount was submerged during the interval 12–5 Ma on the basis of a reconstructed global sea level higher (Miller et al., 2011) than that proposed by Ohneiser et al. (2015) (Fig. 4). In addition, this area is one of the rejuvenated volcanic hotspots at 6 Ma (see for details: Leroux et al., 2018), an event ignored by Ali and Hedges (2022). These glacio-eustatic and geodynamic data both matches with momentarily emerged lands as supported by our pollen records

A first attempt of climatic quantification based on the sum of these two pollen spectra (depths 154.31 and 152.32 mbsf) has been made using the Climatic Amplitude Method (CAM; Fauquette et al., 1998). This method, after comparison with more than 6,000 present-day pollen records distributed worldwide, relies on the relationship between the relative abundance of each individual taxon and the climate. The estimated mean annual temperatures (MAT), mean temperatures of the coldest (MTC) and warmest (MTW) months and mean annual precipitation (MAP) concern low-elevation vegetation because the meso-microthermal taxa *Podocarpus* which may live today at higher elevations (although, as mentioned just above, *P. madagascariensis* may inhabit at low elevation) was excluded from the calculation to avoid a cold bias linked to transport from higher elevations. In this method, the estimates for each climatic parameter are given as an interval (minimum and maximum values of the parameter) and a most likely value (MLV) corresponding to a weighted mean. The mean annual temperature (MAT) is estimated between 21 and 27°C with a most likely value around 26.5°C, the mean temperature of the coldest month (MTC) between 15 and 20°C with a MLV around 19°C, the mean temperature of the warmest month (MTW) between 27 and 29°C with a MLV around 28.4°C and mean annual precipitation (MAP) are estimated between 1300 and 2200 mm with a MLV around 1650 mm. These reconstructed values are relatively like modern values at the same latitude than Site 242 (for example MAT 26.1°C, MTC 24.1°C, MTW 27.2°C and MAP 1290 mm at Besalampy, Madagascar; MAT 25.6°C, MTC 23.2°C, MTW 27.5°C and MAP 970 mm at Island of Mozambique, Mozambique, https://fr.climate-data.org). However, it should be noted that this region was certainly located a little further south than it is today (Vrielinck & Bouysse, 2003).

Accordingly, this preliminary palynological study must be considered as a promising approach to document the occurrence of periodic string of islands between the Eastern Africa and Madagascar Island. This research will be pursued on the available material of Site 242 from the Early Oligocene to Early Pliocene.

Cross-disciplinarity and biogeography

The transdisciplinary approach adopted by Masters et al. (2022) provided particular strength to the arguments that they presented; unfortunately, they were not appropriately appreciated by Ali and Hedges (2022). Independent dating techniques permitted to assess modes of temporal distribution of Malagasy taxa. Particularly noteworthy were: (1) dates of known global events tuned with kinematic revolutions, climatic events, mass-extinction events, closely followed by major radiations; (2) geophysical dates and dates obtained from a combination of relative (stratigraphic) and absolute (isotopes, etc.) methods, based on both academic and industrial data; (3) fossil record-based dates; (4) molecular-based dates from a variety of taxa; and (5) dates secondarily provided by coevolving plants and animals (Masters et al., 2021, 2022; Génin et al., 2022).

It is likely that since the 1830s every geology student was imbued with Lyell's mantra: "The present is the key to the past". Forces currently in operation have driven the evolution of Earth from her fiery beginnings. Nevertheless, the past cannot simply be read from the present situation. For instance, if we took the fossil record at face value, we should conclude that none of Madagascar's living vertebrate species can be older than 80,000 years. Evolution is change, the only certainty in an uncertain world. Change often destroys the evidence of what went before – in genes, morphology, or geology. Genome dynamics include deletions, insertions, replications, substitutions and transpositions of anything from single nucleotides to entire gene sequences, without considering the impacts of epigenetic modification on the gene expression. The growth and development of plant and animal bodies involves a complex interaction of the genomic system and the environment, which may lead to similar or dissimilar structures, rapid changes in body size or form, and the loss or reinvention ancestral morphology. Like living forms, Earth's surface is continually being re-sculpted by deposition, erosion, eruption, faulting, and uplift. Understanding the co-evolution of Earth and its biota requires extensive study of biological and geological processes, and active reconstruction of past events based on disparate fragments of largely cryptic evidence. Reconstructions of the past require more than just data; observations must be fitted into logically sound and testable models of process. Biogeographic models are even more complex, as they require expertise in both Earth and life dynamics, and crosstalk among experts with different priorities, academic cultures and languages, and approaches to problem solving. Hence, despite the necessity of interdisciplinary research in this increasingly specialised age, it is far harder than it looks.

Conclusion

The transdisciplinary approach adopted by Masters et al. (2022) provided particular strength to the arguments that they presented, a view evidently not shared by Ali and Hedges (2022). The temporal distribution of Malagasy taxa was determined using a combination of independent dating techniques. Several of these bioevents appear to be tuned with (1) kinematic revolutions, climatic changes, mass-extinction events, all closely followed by major radiations, (2) geophysical dates and dates obtained from a combination of relative (stratigraphic) and absolute (isotopes, etc.) methods, based on both academic and industrial data, (3) fossil record-based dates, (4) molecular-based dates from a variety of taxa, and (5) dates secondarily provided by coevolving plants and animals (Masters et al., 2021, 2022; Génin et al., 2022). The preliminary palynological results reported in this study provide a new promising avenue to document the

occurrence of periodic land bridge connections between the African mainland and Madagascar. The Early Oligocene to Early Pliocene material from DSDP Site 242 can be considered the first important contribution to more comprehensive understanding of the characteristics of the series of land bridge connections across the Mozambique Channel. The geological records therefore show that intermittent land bridges existed between Madagascar and Africa at three specific dates that correspond to global geodynamic revolutions. It seems highly unlikely that these land bridges didn't play a significant geodispersive role in the colonisation of Madagascar. Because the presence of these land bridges limits inter-basin exchanges of the ocean water masses and radically modifies the parameters used for palaeocurrent modelling, these modifications are presently analysed using coupled global simulations at low resolution (2°) at the LSCE and regional oceanographic models at higher resolution (1/12°). The impacts of possible oceanographic modifications will be tested against changes in the sediment architecture inferred from seismic data as well as from foraminifera, most sensitive to changes in salinity and temperature, studied from borehole sediments.

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Supplementary material.
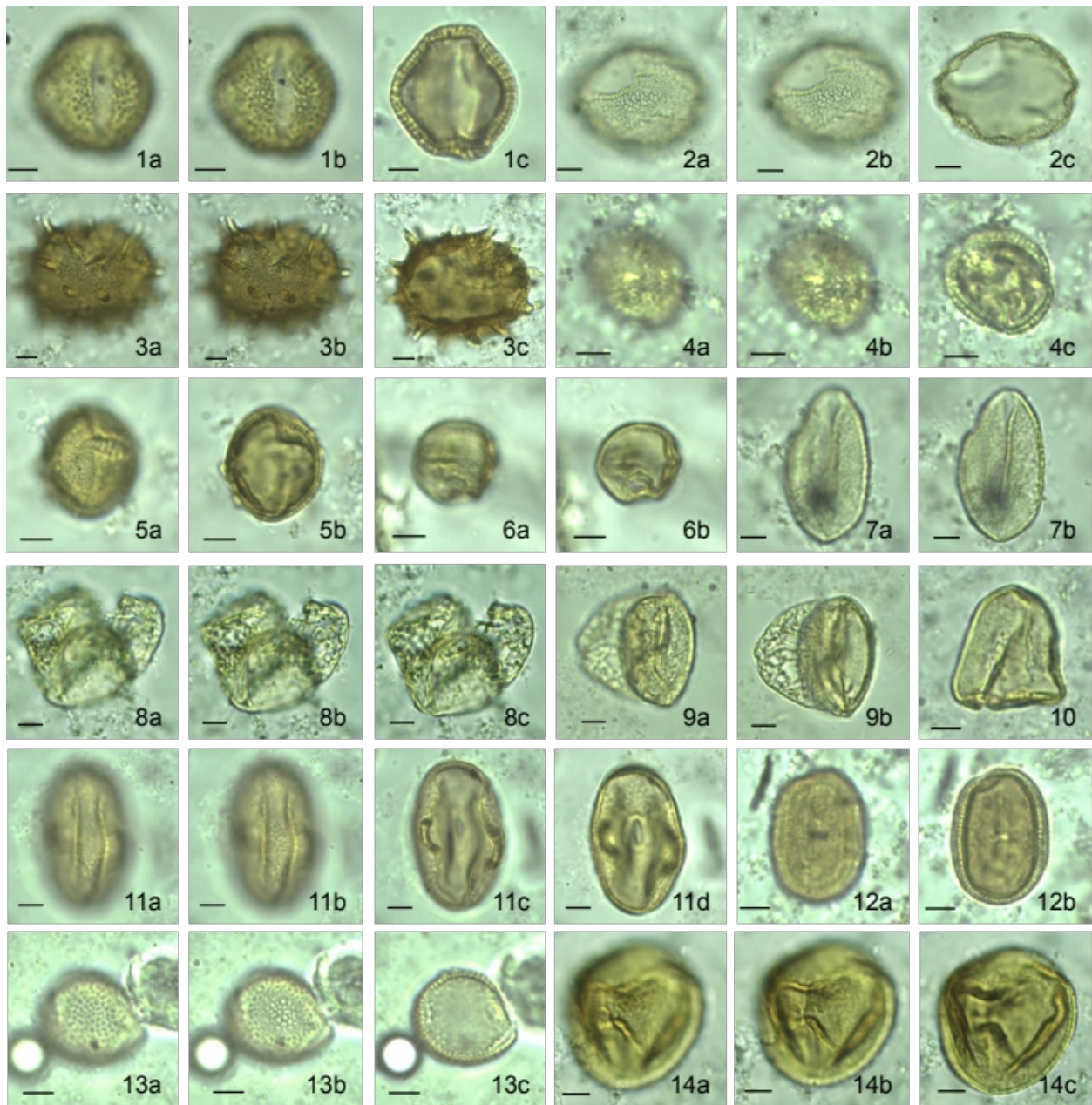
Plate 1. Photographs of some remarkable fossil pollen grains from Site 242 at light microscope. Scale bar = 5 μm.

Fig. 1. *Avicennia* (Acanthaceae), 154.31 mbsf, in equatorial view (aperture facing). LO-analysis: a, reticulate ornamentation and ectoaperture (colpus); b, focus on base of columellae; c, optical section.

Fig. 2. Cf. *Calamus* (Arecaceae), 154.31 mbsf, in equatorial view (aperture facing). LO-analysis: a, reticulate ornamentation and aperture (colpus); b, focus on base of columellae; c, optical section.

Fig. 3. *Nypa* (Arecaceae), 152.31 mbsf, in polar view. LO-analysis: a, echinate and reticulate ornamentation; b, focus on base of spines and base of columellae; c, optical section.

Fig. 4. *Olea* (Oleaceae), 152.31 mbsf, in polar view. LO-analysis: a, reticulate ornamentation; b, focus on base of columellae; c, optical section.

Fig. 5. Rhizophoraceae, 152.31 mbsf, in equatorial view (aperture facing). LO-analysis: a, reticulate ornamentation and aperture (colporus); b, optical section.

Fig. 6. Rhizophoraceae, 154.31 mbsf, in equatorial view (aperture facing). LO-analysis: a, microreticulate ornamentation and aperture (colporus); b, optical section.

Fig. 7. Arecaceae, 152.31 mbsf, in equatorial view (aperture facing). LO-analysis: a, reticulate ornamentation and aperture (colpus); b, optical section.

Fig. 8. *Podocarpu*s (Podocarpaceae), 152.31 mbsf, in profile view. LO-analysis: a, focus on alveoli of the sacci; b, optical section.

Fig. 9. *Podocarpu*s (Podocarpaceae), 154.31 mbsf, in proximal view. LO-analysis: a, focus on alveoli of the sacci; b, optical section.

Fig. 10. Cyperaceae, 154.31 mbsf, optical section showing pseudoapertures.

Fig. 11. *Sonneratia* (Sonneratiaceae), 154.31 mbsf, equatorial view (intercolpium). LO-analysis: a, verrucate ornamentation and meridional ridge; b, apertures (pori); c, optical section and aperture (porus).

Fig. 12. Acanthaceae, 152.31 mbsf, equatorial view (aperture facing). LO-analysis: a, scabrate ornamentation with circular islets and aperture (porus); b, optical section.

Fig. 13. *Trichocladus* (Hamamelidaceae), 154.31 mbsf, in equatorial view (intercolpium). LO-analysis: a, reticulate ornamentation; b, focus on base of columellae; c, optical section and apertures (colpi).

Fig. 14. *Xylocarpus* (Meliaceae), 152.31 mbsf, in equatorial view (aperture facing). LO-analysis: a, scabrate ornamentation and aperture (colporus); b, focus on endoaperture; c, optical section and aperture.

Table 1. Dataset used for Figure 3. Taxa are named at the family taxonomic level in order to homogenize the compilation of datasets, however, in many cases, the families are not fully endemic but some of the subclades are. In that case the first occurrence age is the one corresponding to the time divergence of the subclades.

Group	Vernacular name	Taxa	Age	References
Amphibians	Hyperoliid frogs	Hyperoliidae	46.33	Mean value from Vences et al. 2003; Crottini et al. 2012
Amphibians	Microhylid frogs	Microhylidae	66.63	Mean value from Van der Mejden et al. 2005; Van Bocxlaer et al. 2006; Crottini et al. 2012
Amphibians	Mantellid frogs	Mantellidae	87.92	Crottini et al. 2012
Amphibians	Grassland frogs	Ptychadenidae	10	Crottini et al. 2012
Angiosperms	Asterales	Asteraceae	7.5	Mean value from Strijk et al. 2012
Angiosperms	Proteales	Proteaceae	9	Zanne et al. 2014
Angiosperms	Canellales	Canellaceae	25	Wikströme et al. 2001
Angiosperms	Canellales	Winteraceae	56	Mean value from Magallón et al. 2015; Tank et al. 2015; Zanne et al. 2014; Wikström et al. 2001; Müller et al. 2015
Angiosperms	Cucurbitales	Cucurbitaceae	30	Schaefer et al. 2009
Angiosperms	Malvales	Malvaceae	16.7	Koopman & Baum, 2008
Angiosperms	Malvales	Sarcolaenaceae	41.5	Mean value from Wikström et al. 2001; Zanne et al. 2014
Angiosperms	Malvales	Buxaceae	47.4	Zanne et al. 2014
Angiosperms	Malvales	Sphaerosepalaceae	71.2	Zanne et al. 2014
Angiosperms	Caryophyllales	Didiereaceae	30	Mean value from Ocampo & Columbus 2010; Arakaki et al. 2011; Magallón et al. 2015; Tank et al. 2015; Zanne et al. 2014
Angiosperms	Caryophyllales	Asteropeiaceae	71	Mean value from Wikström et al. 2001; Zanne et al. 2014
Angiosperms	Caryophyllales	Barbeuiaceae	59	Mean value from Wikström et al. 2001; Tank et al. 2015; Zanne et al. 2014
Angiosperms	Solanales	Convolvulaceae	55.1	Zanne et al. 2014
Angiosperms	Solanales	Montiniaceae	27.9	Zanne et al. 2014
Angiosperms	Apiales	Torricelliaceae	62.7	Mean from Magallón et al. 2015; Tank et al. 2015
Angiosperms	Ericales	Sapotaceae	61	Bartish et al. 2011
Angiosperms	Sapindales	Burseraceae	9.9	Federman et al. 2015
Angiosperms	Laureales	Monimiaceae	35.8	Renner et al. 2010
Angiosperms	Buxales	Buxaceae	93.1	Mean value from Wikström et al. 2001; Tank et al. 2015; Zanne et al. 2014
Birds	Bullbuls	Pycnonotidae	1	Warren et al. 2005
Birds	Sunbirds	Nectariniidae	5.1	Mean value from Warren et al. 2003
Birds	Vangas	Vangidae	24	Mean value from Beresford et al. 2005; Fuchs et al. 2006; Reddy et al. 2012; Jönsson et al. 2012
Birds	Malagasy songbirds	Bernieridae	25.2	Bresford et al. 2005

Birds	Ground rollers	Brachypteraciidae	34	Prum et al. 2015
Birds	Elephant birds	Aepyornithidae	50	Mitchell et al. 2016
Birds	Parrots	Psittaculidae	56.6	Mean value from Wright et al. 2008
Birds	Mesites	Mesitornithidae	54	Prum et al. 2015
Birds	Cuckoo rollers	Leptosomidae	63	Prum et al. 2015
Birds	Asities	Philepittidae	19	Prum et al. 2015
Birds	White-eye songbirds	Zosteropidae	0.44	Warren et al. 2005
Crocodiles	Crocodiles	Crocodylidae	3	Mean value from Crottini et al. 2012
Decapods	Freshwater crayfish	Parastacidae	147	Toon et al. 2010
Decapods	Freshwater crabs	Potamonautidae	76.2	Daniels et al. 2006
Ferns	Cyatheales	Cyatheaceae	21.06	Mean value from Janssen et al. 2008
Fish	Madagascar rainbowfish	Bedotiidae	46.5	Crottini et al. 2012
Fish	Cyprinodontiform fish	Aplocheilidae	47	Crottini et al. 2012
Fish	Cichlid fish	Cichlidae	76.31	Mean from Azuma et al. 2008; Vences et al. 2008; Crottini et al. 2012; Matschiner et al. 2016
Snails	Caenogastropoda	Pachychilidae	25.5	Köhler & Glaubrecht, 2010
Insects	Swallowtail butterflies	Papilionidae	0.5	Clark & Vogler 2009
Insects	Termites	Termitidae	13.2	Nobre et al. 2010
Insects	Diving beetles	Dysticidae	14.5	Bukontaite et al. 2015
Insects	Butterflies	Nymphalidae	23	Kodandaramaiah et al. 2010
Insects	Carpenter bees	Apidae	25.37	Mean value from Schwartz et al. 2006; Chenoweth & Schwartz 2011; Rehan et al. 2010
Insects	Millipede assassin bugs	Reduviidae	30	Forthman & Weirauch, 2016
Insects	Ants	Formicidae	52	Brady et al. 2006
Insects	Whirligig beetles	Gyrinidae	61.2	Mean from Gustafson et al., 2017
Insects	Dung beetles	Scarabaeidae	64	Mean from Gunter et al. 2016, Wirta et al. 2010
Insects	Water scavenger	Hydrophilidae	91.6	Toussaint et al. 2016
Spiders	Golden orb weaver spiders	Nephilidae	5.2	Kuntner & Agnarsson 2011
Spiders	Pelican spiders	Archacidae	154	Wood et al. 2015
Mammals	Sportive lemurs	Lepilemuridae	20.21	Mean value from Yoder and Yang 2004; Chatterjee et al. 2009; Horvath et al. 2008; Perelman et al. 2011; Springer, 2012; Kistler et al. 2015; Herrera & Davalos, 2016
Mammals	Lemurs	Lemuridae	24	Mean value from Yoder and Yang 2004; Chatterjee et al. 2009; Horvath et al. 2008; Perelman et al. 2011; Springer, 2012; Kistler et al. 2015; Herrera & Davalos, 2016

Mammals	Indrids	Indriidae	24.42	Mean value from Yoder and Yang 2004; Chatterjee et al. 2009; Horvath et al. 2008; Perelman et al. 2011; Springer, 2012 ,Kistler et al. 2015; Herrera & Davalos, 2016
Mammals	Cheirogaleus	Cheirogaleidae	25.57	Mean value from Yoder and Yang 2004; Chatterjee et al. 2009; Horvath et al. 2008; Perelman et al. 2011; Springer, 2012; Kistler et al. 2015; Herrera & Davalos, 2016
Mammals	Tenrecs	Tenrecidae	53	Mean value from Doudy et al. 2002; 2003; Poux et al. 2005, 2008; Crottini et al. 2012; Everson et al. 2016
Mammals	Bats	Myzopodidae	52	Teeling et al. 2005
Mammals	Bats	Pteropodidae	0.06	Mean value from Gunnell 2010*; Samonds 2007*
Mammals	Bats	Hyposideridae	0.08	Samonds 2007*
Mammals	Bats	Emballonuridae	0.01	Mean value from Sabatier & Legendre 1985; Gunnell 2010*
Mammals	Bats	Mollosidae	0.01	Mean value from Sabatier & Legendre 1985, Gunnell 2010*
Mammals	Bats	Vespertilionidae	0.01	Samonds 2007*
Mammals	Carnivores	Eupleridae	22.98	Mean value from Yoder et al. 2003; Poux et al. 2005; Crottini et al. 2005; Zhou et al. 2017
Mammals	Rodents	Nesomyidae	32	Mean value from Poux et al. 2005; Crottini et al. 2012
Flatworms	Monogenean flatworms	Polystomatidae	116.2	Verneau et al. 2009
Squamata	Elapoid snakes	Pseudoxyrhophiinae	30.8	Mean value from Nagy et al. 2003; Crottini et al. 2012
Squamata	Leaf-tailed gekos	Gekkonidae	41.05	Mean value from Raxworthy et al. 2008; Crottini et al. 2012
Squamata	Plated lizards	Gerrhosauridae	50.3	Mean value from Raselimanana et al. 2009; Crottini et al.2012; Blair et al. 2015
Squamata	Blindsnakes	Typhlopidae	51.5	Mean value from Vidal et al. 2010; Crottini et al. 2012
Squamata	Chameleons	Chamaeleonidae	55.5	Mean value from Crottini et al. 2012; Tolley et al. 2013
Squamata	Boas	Boidae	66.66	Mean from Noonan & Chippindale 2006; Crottini et al. 2012
Squamata	Blindsnakes	Xenotyphlopidae	86.66	Mean value from Crottini et al. 2012; Vidal et al. 2013
Squamata	Madagascan iguanas	Opluridae	111	Mean value from Noonan & Chippindale 2006; Okajima & Kumazana 2009; Crottini et al. 2012; Townsend et al. 2011
Testudines	Tortoises	Testudinidae	31.875	Mean value from Caccone et al. 1998; Crottini et al. 2012; Palkovacs et al., 2012
Testudines	Turtles	Podocnemididae	91.6	Mean value from Noonan & Chippindale 2006; Crottini et al. 2012; Vargas-Ramirez et al. 2008

BIOSKETCHES

The initial synthesis germinated in 2017 at Nelson Mandela University, during the first meeting between JCM and DA, who designed the project.

JCM was an evolutionary biologist focussing on strepsirrhine evolution. FG was an ecophysiologist by training and a naturalist by calling.

Evolutionary primatology tragically lost one of its liveliest intellects when Judith Masters, with her partner and scientific collaborator Fabien Génin, died during a robbery at their home in South Africa in October 2022.

PPAM is a vertebrate palaeontologist and taphonomist focussing on insular mammals, especially hippos.

SebC is a palaeontologist with expertise in Cenozoic mammals paleobiodiversity and morphological variation.

MD is a geneticist with expertise in phylogenetics and primate evolution.

YZ is a palaeo-oceanographer and palaeo-climatologist.

TH is a physical oceanographer with expertise in large-scale ocean modelling.

TLH is a physical oceanographer PhD student.

PP is a physical oceanographer with expertise in regional ocean modelling.

DA is a geologist, geodynamicist, expert in plate tectonics.

RP is a postdoctoral researcher who divides his time between France and South Africa, monitoring earth movements.

MR is a sedimentologist with expert understanding of the late Miocene and deputy director of Geo-Ocean.

MM is a geologist, geodynamicist and co-leader of the Geo-Ocean/GIPS.

EL is a sedimentologist expert in stratigraphic modelling.

GB is a geologist with expertise in stratigraphy and geomorphology.

SimC is a geologist with expertise in stratigraphy and carbonate.

AD is a geologist with expertise in stratigraphy and geomorphology.

BL is a Geologist, at AEON, Nelson Mandele University.

JPS is a Geologist at CNRS (ISTeP, Sorbonne University), specialist in pollen grain analysis.

SMP is a Geologist, CO of the GEOBIOSTRATDATA Company, specialist in dinoflagellate cyst and pollen grain analysis.

SF is a paleoclimatologist at CNRS (ISEM, Montpellier University) working on climate reconstructions based on pollen data.

JPS, SP, SF, EL, GB, SC, AD, RP, MM, MR and DA participated in the PAMELA project.