



GEODISPERSAL AS A BIOGEOGRAPHIC MECHANISM FOR CENOZOIC EXCHANGES

the island and eastern Africa, the elevation and submersion of which would yield a pattern of alternating periods of colonization and in situ diversification (Upchurch 2008).

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

These predictions place a high value on taxonomic filtering but fail to acknowledge the significance the habitat filtering; in other words, colonizers can only establish viable populations in habitats to which they are at least partially adapted. Habitat filtering may impose more restrictions on biogeography than dispersal, even on remote oceanic islands (Carvajal-Endara et al. 2017). Land bridges provide not only causeways but habitats as well. This means that, while rafting must occur within an individual's lifetime, geodispersal can occur over several generations. Another biological aspect that needs to be considered is the vulnerability of island biotas to extinction. The limited number of Malagasy clades alive today is unlikely to represent all of the lineages that ever colonized the island, but the absence of any Cenozoic fossils older than 26,000 years renders them invisible to modern research.

TEMPORAL (IN)CONGRUENCE

Despite the age and depth of the Mozambique Channel, bathymetric studies have revealed the presence of seamounts and submarine ridges comprising continental material topped by carbonates, which were probably exposed periodically during the Cenozoic (Courgeon et al. 2017). McCall (1997) proposed that the Davie

Fracture Zone, the submarine ridge that marks the fault line that led to the Africa-Madagascar separation, was at least partially emergent 45–26 Mya, and could, therefore, have assisted Cenozoic dispersal events. Poux et al. (2005) tested this hypothesis by estimating the colonization dates of Madagascar's four terrestrial mammal lineages, and although their data, with its broad confidence intervals, could not refute the proposal, they demonstrated no particular pattern of congruence between the dates proposed for the land bridge and the separation ages of the African and Malagasy lineages. Furthermore, the colonization dates for lemurs and tenrecs differed by tens of millions of years from those estimated for the arrival of carnivores and rodents (Yoder et al. 1996, 2003; Poux et al. 2005), and this asynchrony was also viewed as evidence in favor of sweepstakes dispersal (Yoder and Nowak 2006).

LOOKING MORE DEEPLY INTO THE MOZAMBIQUE CHANNEL

Past geological studies of the Mozambique Channel have focused on horizontal movements, which form the crux of plate tectonics, whereas vertical movements—or the connection between deep (magmatic) and surface processes (subsidence, uplifts)—have largely been neglected. A major French-led project, PAMELA (Passive Margins Exploration Laboratories), has conducted sedimentary, tectonic, kinematic, and paleoenvironmental studies of the history of the Mozambique Channel, involving eight oceanographic cruises (for a total of 224 days at sea) between 2014 and 2017, and three onshore geological surveys (for 50 land days) in 2017 and 2018. The results obtained from this intensive and extensive study, involving more than 100 researchers, present a much more complex and dynamic picture of the channel's bathymetric topography (Courgeon et al. 2016, 2017, 2018; Delaunay 2018; Ponte 2018; Leroux et al. 2018, 2020; Ponte et al. 2019; Thompson et al. 2019; Moulin et al. 2020). We conducted a cross-disciplinary study of Madagascar's Cenozoic biogeography using these new data (Masters et al. 2020) and concluded that there is strong evidence that geodispersal has contributed significantly to Madagascar's standing (and recently extinct) biotas. Paleosedimentological maps (Figure 2.20) indicate three phases of regional uplift that affected connectivity between Africa and Madagascar during the Cenozoic.

- A. Early Paleocene (66–60 Mya; exposure of the Sakalaves platform, Glorieuses and Juan de Nova Islands, and Leven-Castor highs);
- B. Late Eocene to early Oligocene (36–30 Mya; exposure of Bassas da India, and Hall Bank);
- C. Late Miocene (12–5 Mya; worldwide Messinian crisis and origin of the Comoro archipelago).

These three periods reflect the three phases of uplift that led to Madagascar's modern topography (Delaunay 2018). They coincided with episodes of marked tectonic and climatic change: global cooling leading to droughts in Madagascar and sub-Saharan Africa, associated with mass extinctions and subsequent radiations, and low sea level stands. The fact that similar conditions are likely to have prevailed on both sides of the Mozambique Channel would

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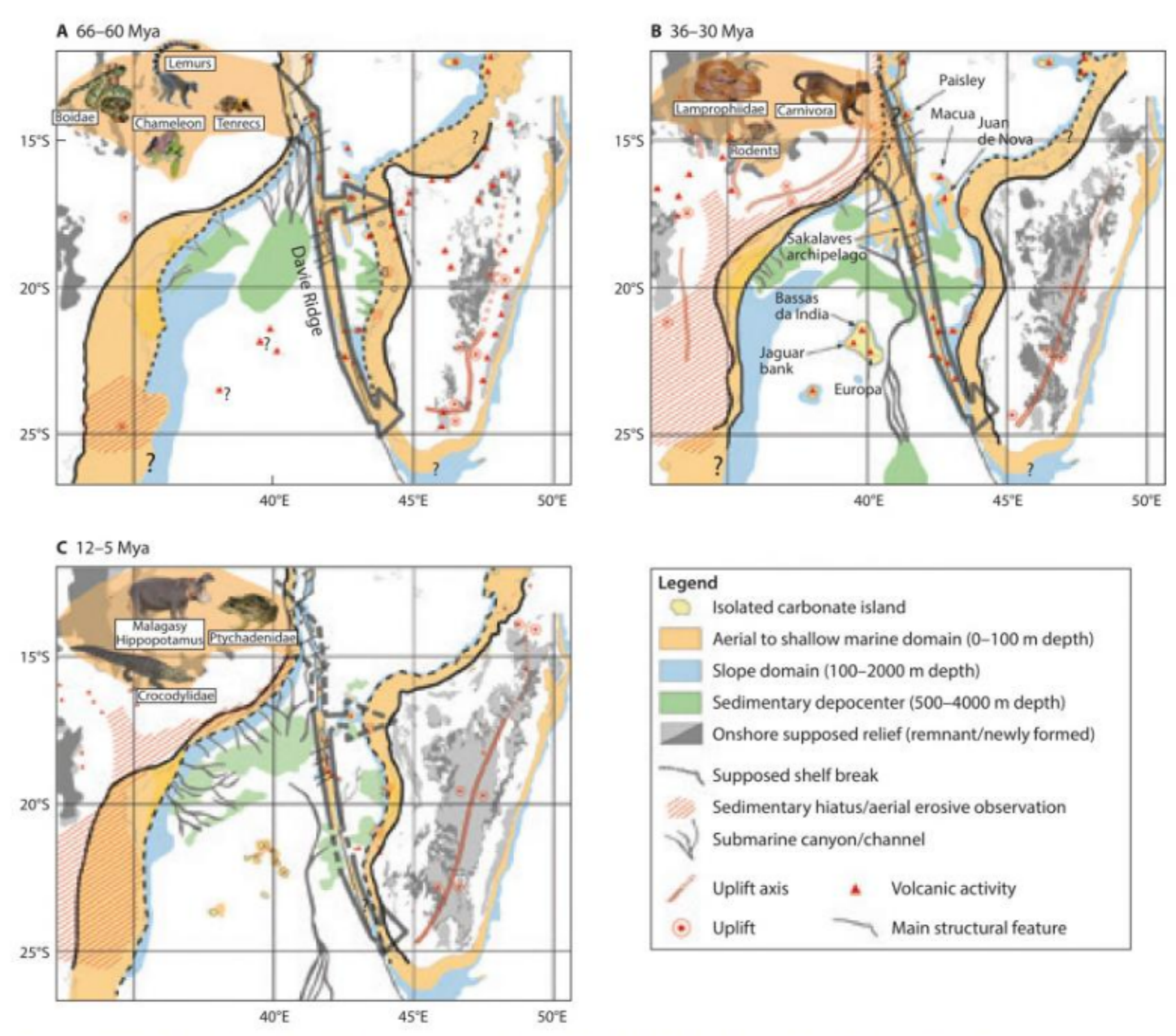


FIGURE 2.20 Paleosedimentological maps representing possible land bridges during three Cenozoic time frames, concomitant with the three phases of uplift of Madagascar's highlands: A) early Paleocene, B) late Eocene to early Oligocene, and C) late Miocene.

have facilitated faunal and floral exchanges. This also suggests that some colonization events may have proceeded from Madagascar to Africa, as was recently proposed for *Croton* species (Euphorbiaceae; Ngumbau et al. 2020).

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

This period is coincident with a global mass extinction and several major magmatic events, including the outpouring of the Deccan flood basalts and the collision of India with Asia; the first episode of uplift of the South African plateau (Baby et al. 2018); and volcanism in the Mozambique Channel and Madagascar (Bardintzeff et al. 2010; Delaunay 2018; Ponte 2018). A sedimentary hiatus on Madagascar's west coast 66–60 Mya (Delaunay 2018) corresponds

to a hiatus along the Mozambican coast (Ponte 2018), indicating a general exposure of coastal land on both sides of the channel, and subaerial exposure of the Davie Ridge (Figure 2.20a). Faunal studies based on extinct and extant taxa link this period to a major biotic turnover on Madagascar, coincident with the worldwide Cretaceous–Paleogene mass extinction: While some ancient reptilian taxa (iguanas, river turtles, boas) survived the environmental catastrophe (Noonan and Chippendale 2006; Crottini et al. 2012), forms known only from fossils (mammaliaform gondwanatheres, dinosaurs, and early birds; Krause et al. 1997c, 2020; Sampson et al. 1998) succumbed.

At this time, both Madagascar and Africa were 10–15° (1100–1650 km) south of their present position. At such high latitude, Madagascar's landscape was probably dominated by lowland woodland, with only a few Cretaceous angiosperm families (Proteaceae,

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Hernandiaceae, and Winteraceae) (Schatz 2001; Buerki et al. 2013). The two older mammal clades, lemurs and tenrecs, are likely to have dispersed during this period (Yoder et al. 1996; Poux et al. 2005). Other potential Paleogene colonists include angiosperm families (Fabaceae, Meliaceae, and Menispermaceae) (Buerki et al. 2013), freshwater fishes (Bedotiidae, Aplocheilidae, and Cichlidae), amphibians (Mantellidae, Microhylidae, and Hyperoliidae), and reptiles (Chamaeleonidae, Gekkonidae, Gerrhosauridae, and Scincidae) (Crottini et al. 2012).

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

The Eocene–Oligocene transition (EOT) (Figure 2.20b) is an extinction event well-known among students of lemur biology as it caused the near-extinction of the Eocene relatives of modern tooth-combed primates (Fleagle 2013). Its devastation of Paleogene biotas led to it being termed “la Grande Coupure” (“the great cut”), and it marked a major shift in global climates, related to the first occurrence of ephemeral ice sheets in Antarctica (Zachos et al. 2001). The initiation and growth of ice sheets locked down water on land, causing a drop in global sea levels, and exposing coastal land. This was a dynamic time for Africa, coincident with the initiation of the East African rift system (Ebinger 1989; de Wit 2003; Chorowicz 2005; Macgregor 2015), and the second uplift of the southern Africa plateau (38–16 Mya; Mougnot et al. 1986; Baby et al. 2018). It also marked the second phase of uplift in Madagascar and affected the physiography of the Mozambique Channel leading to the reemergence of the carbonate platforms on the western and eastern shores, the Davie Ridge, the Sakalaves archipelago, and Juan de Nova volcanic island, west of Cap Saint André. Other isolated islands (Bassas da India, Europa, Jaguar Bank, Macua, and Paisley) were also mostly subaerial 36–30 Mya, before being weathered and eroded through wave activity during the late Oligocene and Miocene (Courgeon et al. 2017). While connections between the Davie Ridge, Rovuma, and Madagascar may not have been continuous throughout this period, hiatuses between topographic highs would have consisted of short (<50 km) and shallow marine corridors (1–100 m).

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

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

### Late Miocene (12–5 Mya): Noncontinuous Connections

Volcanism is recorded for 12 Mya ago, south of the Sakalaves archipelago (Figure 2.20) in the northern part of the Davie Ridge, coeval with the final uplift of Madagascar (Delaunay 2018) and exposure of the Madagascar continental platform. Courgeon et al. (2017) identified late Miocene to early Pliocene subaerial volcanism covering previous carbonate platforms and extensional tectonic deformation, which led to the post-tectonic Pliocene drowning of the platforms, and to their present-day setting largely below sea level. Drowning of the southern part of the Davie Ridge occurred from the mid-Miocene onward, with deep-sea channels originating in the Morondava Basin and reaching the deep turbiditic system south of the Mozambique Channel (Delaunay 2018). This north–south inundation is also attested by very low sedimentary accumulation (<100 m) in the north of the Morondava Basin, and a mean sedimentary accumulation increasing 300–800 m below the main river outlets and deltas in the central and southern parts.

We infer that this third bridge offered a noncontinuous connection interrupted by small, shallow marine corridors between the Davie Ridge and the northern part of the Morondava Basin (Figure 2.20). Two major deltas faced each other across the Mozambique Channel, separated by a narrow remnant of the old land bridge. The narrow marine corridors are likely to have included various stepping-stones, such as shallow reefs and small volcanic islands; hence, this connection would have facilitated the dispersal of aquatic animals (crocodiles, hippopotamuses, and one family of frogs, Ptychadenidae), but not of terrestrial forms. The spread of grasses (Poaceae) was limited to wetlands, forests, and some high summits (Paulian 1961; Bosser 1969). The only ungulate grazers to follow them across the channel were hippopotamuses, which subsequently evolved dwarf forms. This last bridge was followed by a general drowning of the Mozambique Channel during the late Miocene and early Pliocene.

## CONCLUSIONS

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

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- Abdala, F., Ribeiro, A. M., and Schultz, C. L. 2001. A rich cynodont fauna from Santa Cruz do Sul, Santa Maria Formation (Middle–Late Triassic), southern Brazil. *Neues Jahrbuch für Geologie und Paläontologie* 11: 669–687.
- Abdala, F., Martinelli, A. G., Soares, M. B., de la Fuente, M., and Ribeiro, A. M. 2009. South American Middle Triassic continental faunas with amniotes: Biostratigraphy and correlation. *Palaentologia Africana* 44: 83–87.
- Aduse-Poku, K., Brattström, O., Kodandaramiah, U., Lees, D. C., Brakefield, P. M., and Wahlberg, N. 2015. Systematics and historical biogeography of the Old World butterfly subtribe Mycalesina (Lepidoptera: Nymphalidae: Satyrinae). *BMC Evolutionary Biology* 15: 167.
- Agnarsson, L., and Kuntner, M. 2012. The generation of a biodiversity hotspot: Biogeography and phylogeography of the Western Indian Ocean islands. In *Current Topics in Phylogenetics and Biogeography of Terrestrial and Aquatic Systems*, ed. K. Anamthawat-Jönsson, pp. 33–82. Rijeka: InTech Europe.
- Agnolin, F. L. 2012. New Calyptrorhynchidae (Anura, Neobatrachia) from the Upper Cretaceous of Patagonia, Argentina, with comments on its systematic position. *Studia Geologica Salmanticensis* 48: 129–178.
- Alberti, M., Arabas, A., Fürsich, F. T., Andersen, N., and Ziolkowski, P. 2019. The Middle to Upper Jurassic stable isotope record of Madagascar: Linking temperature changes with plate tectonics during the break-up of Gondwana. *Gondwana Research* 73: 1–15.
- Alessio, B. L., Collins, A. S., Siegfried, P., Glorie, S., De Waele, B., Payne, J., and Archibald, D. B. 2019. Neoproterozoic tectonic geography of the south-east Congo Craton in Zambia as deduced from the age and composition of detrital zircons. *Geoscience Frontiers* 10: 2045–2061.
- Ali, J. R., and Aitchison, J. C. 2008. Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Science Reviews* 88: 145–166.
- . 2009. Kerguelen Plateau and the Late Cretaceous southern-continent bioconnection hypothesis: Tales from a topographical ocean. *Journal of Biogeography* 36: 1778–1784.
- Ali, J. R., and Huber, M. 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* 463: 653–656.
- Ali, J. R., and Krause, D. W. 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: Refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography* 38: 1855–1872.
- Ali, J. R., and Vences, M. 2019a. Mammals and long-distance over-water colonization: The case for rafting dispersal; the case against phantom causeways. *Journal of Biogeography* 46: 2632–2636.
- . 2019b. Novel summary metrics for insular biotic assemblages based on taxonomy and phylogeny: Biogeographical, palaeogeographical and possible conservation applications. *Journal of Biogeography* 46: 2735–2751.
- Alvarez-Carretero, S., Goswami, A., Yang, Z., and Dos Reis, M. 2019. Bayesian estimation of species divergence times using correlated quantitative characters. *Systematic Biology* 68: 967–986.
- Andrianavalona, T. H., Ramihangihajason, T. N., Rasoamiaramana, A., Ward, D. J., Ali, J. R., and Samonds, K. E. 2015. Miocene shark and batoid fauna from Nosy Makamby (Mahajanga Basin, Northwestern Madagascar). *PLoS One* 10: e0129444.
- Anisimova, M., ed. 2019. *Evolutionary Genomics: Statistical and Computational Methods*. New York: Humana Press.
- Archibald, D. B., Collins, A. S., Foden, J. D., Payne, J. L., Holden, P., Razakamanana, T., De Waele, B., Thomas, R. J., and Pitfield, P. E. 2016. Genesis of the Tonian Imorona-Itsindro Magmatic Suite in central Madagascar: Insights from U-Pb, oxygen and hafnium isotopes in zircon. *Precambrian Research* 281: 312–337.
- Archibald, D. B., Collins, A. S., Foden, J. D., Payne, J. L., Macey, P. H., Holden, P., and Razakamanana, T. 2017. Genesis of the Stenian–Tonian Dabolava Suite of west central Madagascar: Implications for the evolution of the Mozambique Ocean and the formation of Rodinia. *Journal of the Geological Society*, London 175: 111–129.
- Archibald, J. D. 2003. Timing and biogeography of the eutherian radiation: Fossils and molecules compared. *Molecular Phylogenetics and Evolution* 28: 350–359.
- Argus, D. F., Gordon R. G., and DeMets, C. 2011. Geologically current motion of 56 plates relative to the no-net-rotation reference frame. *Geochemistry, Geophysics, Geosystems* 12: Art. No. Q11001.
- Armistead, S. E., Collins, A. S., Payne, J. L., Foden, J. D., De Waele, B., Shaji, E., and Santosh, M. 2018. A re-evaluation of the Kumta Suture in western peninsular India and its extension into Madagascar. *Journal of Asian Earth Sciences* 157: 317–328.
- Armistead, S. E., Collins, A. S., Meredith, A. S., Payne, J. L., Cox, G. M., Foden, J. D., Razakamanana, T., and De Waele, B. 2019. Evolving marginal terranes during

## REFERENCES

- Neoproterozoic supercontinent reorganization: Constraints from the Bemarivo Domain in northern Madagascar. *Tectonics* 38: 2019–2035.
- Asher, R. J., and Krause, D. W. 1998. The first pre-Holocene (Cretaceous) record of Anura from Madagascar. *Journal of Vertebrate Paleontology* 18: 696–699.
- Averianov, A. O., Archibald, J. D., and Martin, T. 2003. Placental nature of the alleged marsupial from the Cretaceous of Madagascar. *Acta Palaentologica Polonica* 48: 149–151.
- Baby, G., Guillocheau, F., Morin, J., Ressonche, J., Robin, C., Broucke, O., and Dall'Asta, M. 2018. Post-rift stratigraphic evolution of the Atlantic margin of Namibia and South Africa: Implications for the vertical movements of the margin and the uplift history of the South African Plateau. *Marine and Petroleum Geology* 97: 169–191.
- Bardintzeff, J. M., Liégeois, J.-P., Bonin, B., Bellon, H., and Rasamimanana, G. 2010. Madagascar volcanic provinces linked to the Gondwana break-up: Geochemical and isotopic evidences for contrasting mantle sources. *Gondwana Research* 18: 295–314.
- Battail, B. 1991. Triassic terrestrial ecosystems and the biogeography of the Triassic. In *Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota* (extended abstracts), eds. Z. Kielan-Jaworowska, N. Heintz, and H. A. Nakrem, pp. 3–4. Oslo: University of Oslo Palaentological Museum.
- Battail, B., Beltan, L., and Dutuit, J.-M. 1987. Africa and Madagascar during Permo-Triassic time. The evidence of the vertebrate faunas. In *Gondwana six: Stratigraphy, sedimentology, and paleontology*, ed. G. D. McKenzie. *Geophysical Monograph* 41: 147–155.
- Bell, P. R., Fanti, F., Hart, L. J., Milan, L. A., Craven, S. J., Brougham, T., and Smith, E. 2019. Revised geology, age, and vertebrate diversity of the dinosaur-bearing Grimpan Creek Formation (Cenomanian), Lightning Ridge, New South Wales, Australia. *Palaogeography, Palaeoclimatology, Palaeoecology* 514: 655–671.
- Beltan, L. 1993. Overview of systematics, paleobiology, and paleoecology of Triassic fishes of northwestern Madagascar. In *Mesozoic Fishes: Systematics and Paleoecology*, eds. G. Arratia and G. Viohl, pp. 479–500. Munich: Dr. Friedrich Pfeil.
- Besairie, H. 1936. Recherches géologiques à Madagascar, première suite; la géologie du nord-ouest. *Mémoires de l'Académie Malgache* 21: 1–259.
- . 1956. Carte géologique [Majunga, No. 2], 1:500,000. Antananarivo: Service Géologique de Madagasikara.
- . 1969. Carte géologique [Majunga, No. 3], 1:500,000. Antananarivo: Service Géologique de Madagasikara.
- . 1972 (also dated 1971). Géologie de Madagascar, 1. Les Terrains Sédimentaires. *Annales Géologiques de Madagascar* 35: 1–463.
- Besairie, H., and Collignon, M. 1972. Géologie de Madagascar—les terrains sédimentaires. *Annales Géologiques de Madagascar* 35: 1–553.
- Betancur-R., Wiley, E. O., Arratia, G., Acero, A., Bailly, N., Miya, M., Lecointre, G., and Ortí, G. 2017. Phylogenetic classification of bony fishes. *BMC Evolutionary Biology* 17: 162.
- BGS-USGS-GLW. 2008. République de Madagascar Ministère de l'énergie et des Mines (MEM/SG/DG/UCP/PGRM). British Geological Survey Research Report. Bindellini, G., and Dal Sasso, C. 2019. Sauroptid teeth from the Middle Jurassic of Madagascar, and the oldest record of Titanosauriformes. *Papers in Palaentology* 2019: 1–25. doi:10.1002/spp2.1282.
- Bininda-Emonds, O.R.P., Beck, R.M.D., and MacPhee, R.D.E. 2012. Rocking clocks and clocking rocks: A critical look at divergence time estimation in mammals. In *From Clone to Bone: The Synergy of Morphological and Molecular Tools in Palaeobiology*, eds. R. J. Asher and J. Müller, pp. 38–82. Cambridge: Cambridge University Press.
- Boger, S. D., Hirdes, W., Ferreira, C.A.M., Schulte, B., Jenett, T., and Fanning, C. M. 2014. From passive margin to volcano-sedimentary forearc: The Tonian to Cryogenian evolution of the Anosy Domain of southeastern Madagascar. *Precambrian Research* 247: 159–186.
- Boger, S. D., Maas, R., Pastuhov, M., Macey, P. H., Hirdes, W., Schulte, B., Fanning, C. M., Ferreira, C.A.M., Jenett, T., and Dallwig, R. 2019. The tectonic domains of southern and western Madagascar. *Precambrian Research* 327: 144–175.
- Bonaparte, J. F. 1986a. The early radiation and phylogenetic relationships of the Jurassic sauroptid dinosaurs, based on vertebral anatomy. In *The Beginning of the Age of Dinosaurs*, ed. K. Padian, pp. 247–258. Cambridge: Cambridge University Press.
- . 1986b. History of the terrestrial Cretaceous vertebrates of Gondwana. *IV Congreso Argentino Paleontología Biostratigrafía* 2: 63–95.
- Bosser, J. 1969. *Graminées des pâturages et des cultures à Madagascar*. Antananarivo: ORSTOM.
- Brochu, C. A. 2007. Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zoological Journal of the Linnean Society* 150: 835–863.