

Sunken continents inferred from divergence dating based on molecular phylogeny of terrestrial animals

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Abstract. Based on the results of molecular phylogenetics, this paper attempts to explain the migration of mainly terrestrial animals between continents and islands by land bridges. The possibility of the existence of the land bridges are based on the sea-level rise curve since the end of the Jurassic period, which is inferred from deep-sea drilling and the deposition mechanism of stratigraphic formation, and is derived from the considerably low sea-level position in the past. Organisms inhabit and extend their ranges within those natural environments. The migration of terrestrial animals and segregation of their distribution should be based on this idea. Based on this idea, this paper estimates the land bridges in the past crossed by terrestrial animals that existed on the ocean floor. These land bridges include the Scotia Arc from the Africa to Antarctica, the Pacific-Antarctic Ridge - the East Pacific Rise from New Zealand to South America, the Davie Ridge between Africa and Madagascar, the Carnegie Ridge from South America to the Galápagos Islands, and the Mid-Atlantic Ridge from Africa to South America.

Keywords: biogeography, land bridge, sea-level rise, migration of terrestrial animals, Molecular phylogenetics

Introduction

Molecular phylogenetics, the analysis of genetic information, has made remarkable progress and now reveals the genetic information of almost all living organisms. This has been used to estimate the order of divergence of their ancestral lineages and the age of their divergence. These results show that the ages of continental break-up and collision, which have been used as the basis for vicariance theories, often do not correspond to the age of divergence of terrestrial animals, and that these divergences cannot be explained by a single separation of the continents. Many biogeographers, while not rejecting the theory of plate tectonics, which has little credibility in explaining the distribution of terrestrial animals, have begun to change their minds to the theory of oceanic dispersal, in which they moved across the oceans in an 'unlikely, rare, strange and miraculous' way.

The oceanic dispersal theory explains the movement of animals to islands by the swimming ability of elephants and deer and by the sweepstake dispersal by natural rafts (Simpson, 1965). Terrestrial animals that are thought to disperse to the ocean include not only mammals, but also reptiles, amphibians and freshwater fish. However, the likelihood of reptiles, amphibians and freshwater fish dispersing to the ocean is very low. Sweepstake dispersal, which relies on 'miraculous coincidences', is an unscientific idea and should not be believed by biologists, who are scientists.

Biologists can now infer branching order and branching age of organisms from genetic phylogeny. Rather than relying on unreliable theories of continental drift or plate tectonics, or easily adopting the theory of oceanic dispersal, biologists should consider the distribution and paleogeography of organisms without regard to current landforms, based on the idea of the natural dispersal of organisms, i.e. that they live and expand their ranges within those natural environments. This would allow biologists to consider a unified understanding of the evolution of life and the history of the ocean floor, the reality of which is still largely unknown.

This paper considers the distribution and evolution of terrestrial animals, based on the divergence dating from genetic phylogenetics, as they migrated using land bridges in their habitats. The land bridges that con-

nected the different continents are then estimated, assuming that the lineages diverged when the land bridges were submerged and the habitat fragmented. The bathymetric data presented in this paper was obtained from the Bathymetric Data Viewer of NOAA: <https://www.ncei.noaa.gov/maps/bathymetry>.

Sea-level rise and continental submergence

The author assumed that the sea-level position 430,000 years ago during the late Middle Pleistocene was 1,000 m lower than the present, and that subsequent land uplift and sea-level rise formed the present landform (Shiba, 2017a, 2017b). It was then inferred that the land area, which had low uplift relative to the sea-level rise after 430,000 years ago, subsided and became a seafloor, thereby separating the island from the continent, and that isolated organisms became endemic to the island (Shiba, 2020, 2021).

For the position of the sea-level before the late Middle Pleistocene, the depths of sites where volcanic and plutonic rocks and other rocks indicating shallow water or terrestrial deposits were recovered during DSDP and ODP deep-sea drilling were examined. And the sea-level rise or subsidence were estimated from the sea-level rise or subsidence curves (Haq et al., 1987) based on deposition mechanism of stratigraphic formation (Shiba, 2022a, 2022b).

The position of the sea-level since the end of the Jurassic, determined from the depth distribution of rocks recovered during deep-sea drilling that indicate shallow water or land, was 6 km lower than the present day at the end of the Jurassic and 3 km lower at the end of the Miocene. The horizontal distribution of shallow-water or land rocks suggests that most of the continental margin areas and ocean platforms in the Atlantic, Indian and Pacific Oceans were once continents, and that most of the seafloor shallower than 3 km depth was terrestrial until the Eocene or Oligocene, becoming deeper after the Miocene (Shiba, 2022a, 2022b). And those former continents are thought to have sunk into the sea in stages caused by the uplift of the seafloor due to micro-expansion of the earth (Hoshino, 1991, 2014).

The deposition mechanism of stratigraphic formation (Haq et al., 1987), based on petroleum exploration, proposed that strata are formed by sea-level fluctuations and crustal subsidence, while also showing the amount of sea-level rise (coastal onlap) and proposing a sea-level change curve for the Triassic period and beyond. The author examines the sea-level curve of Haq et al. (1987) from the standpoint of not accepting crustal subsidence and considers that the sea-level fall of this coastal onlap curve can be interpreted as the amount of uplift at the continental margin as a phenomenon and that the amount of sea-level rise is a cumulative increase (Shiba, 2022a, 2022b). The cumulative coastal onlap volume since the end of the Jurassic of Haq et al. (1987) is proposed as the sea-level rise curve shown in Fig. 1 (iv), based on the position of the sea-level at the end of the Miocene, which was 3 km lower than the present based on deep-sea drilling results (Shiba, 2022a, 2022b). This sea-level curve shows that the sea-level was 12 km lower at the end of the Jurassic than at present, and that the sea-level has been rising toward the present. This relative subsidence or sea-level rise of 12 km since the Latest Jurassic is also consistent with the depth of burial of the Jurassic evaporate layer in the Gulf of Mexico (Sheridan et al., 1981).

Estimated continents from gene divergence dating

Early placentals and the Late Cretaceous sea-level rise

DNA genome sequencing suggests that the mammalian placentals split almost simultaneously into three groups 90-88 Ma (million years ago): the Afrotheria which lived in Africa, South American Xenarthra and the Boreotheria which lived in Laurasia (Hasegawa, 2020). This cannot be attributed to the division of the three continents according to the continental drift theory, nor to the island-borne passage of early placental ancestors across the Atlantic Ocean between South America and Africa, which were not yet very far apart.

For the divergence of placentals between 90-88 Ma, it should simply be assumed that the land bridge

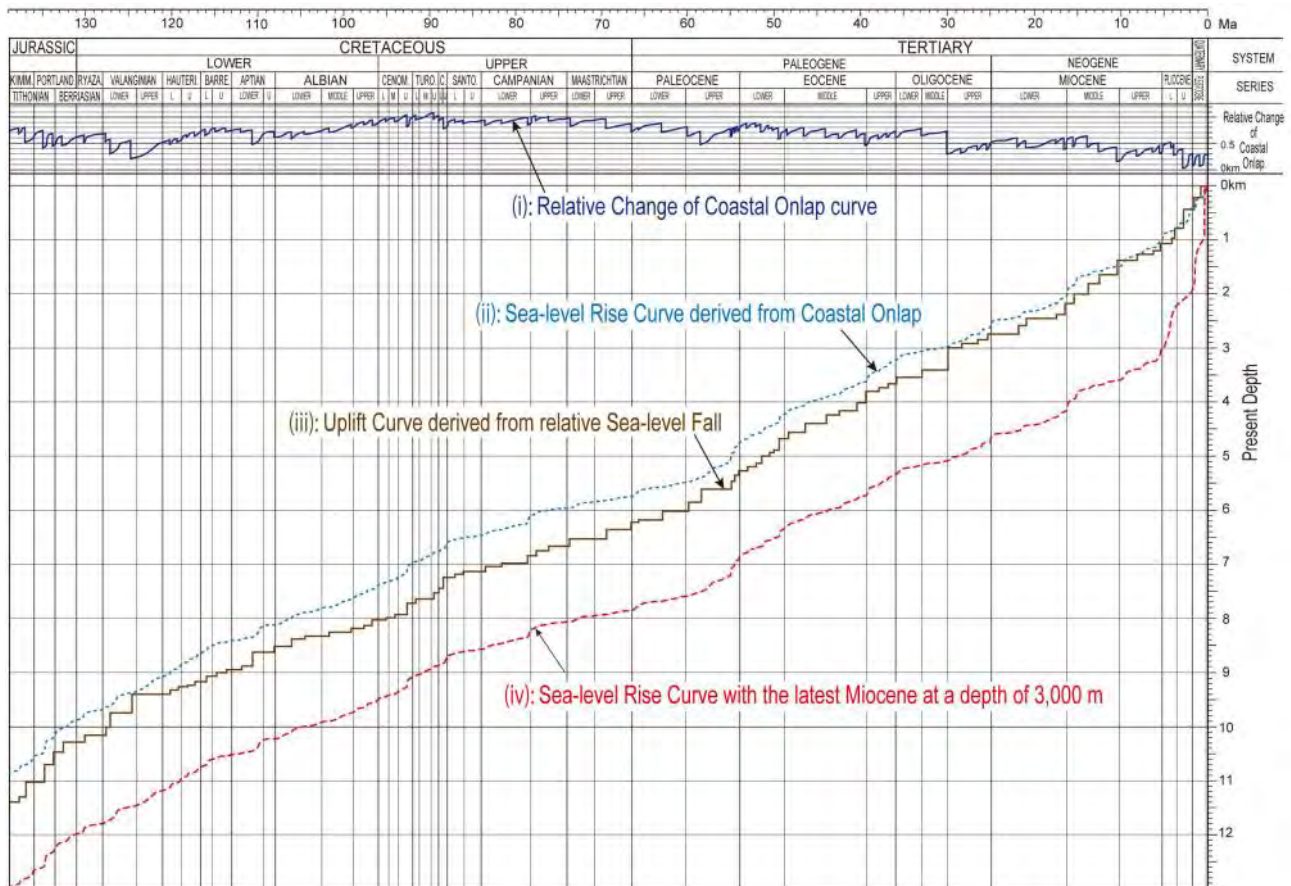


Fig. 1 Post-Jurassic sea-level rise (ii) and uplift curves (iii) based on the relative sea level curves from the relative change of coastal onlap (i) by Haq et al. (1987). The fourth curve (iv) is a sea-level rise curve with a depth of 3,000 m at the latest Miocene (After Shiba, 2022a, 2022b).

connecting the three continents was submerged. The period when these three continents ceased to be connected by land was around the Turonian to Coniacian ages of the Late Cretaceous. As can be seen from the coastal onlap curve of Haq et al. (1987) and the author's sea-level rise curve (Fig. 1), relatively large sea-level rise continued to occur during this period. The amount of sea-level rise over that period of time alone is about 300 m. It is not known specifically where the land bridges connecting these three continents were located. However, the connection between Laurasia and South America was between what is now North America and South America and between Eurasia and Africa. In addition, there was a land bridge connecting African and South America.

Possible candidates for a land bridge connecting Africa and South America are the relatively shallow part near the equator of the current Mid-Atlantic Ridge region (Fig. 2-(1)), or a route connecting the Walvis Ridge off the Africa with the Rio Grande Rise off South America (Fig. 2-(2)). There is also a route from the Cape at the southern tip of Africa to the Falkland Islands (Fig. 2-(3)) via the Agulhas Ridge and the Mid-Atlantic Ridge at around 45°S.

The equatorial Mid-Atlantic Ridge regional route (1) crosses the Atlantic Ocean where the seafloor shallower than 5,000 m east to west between 0° and 10°N, from the Sierra Leone Plateau off Guinea, Africa, through the Mid-Atlantic Ridge to the Ceará Ridge off Guiana, South America, to Guiana or northern Brazil, South America. In this area, rocks constituting continental crust such as granite, granodiorite and iron gabbro have been collected in the Doldrums Fracture Zone of the Mid-Atlantic Ridge (Kepezhinskas and Dmitriev, 1992). The western top of the Romanche Fracture Zone, along the equator, is covered by the Miocene shallow-water limestone (Gasperini et al., 2001). An unconformity surface is found in its eastern part, and the coarse-grained, angular quartz grains that make up the overlying the Middle to Late Eocene siltstone layer suggest the presence of a granitic continent in close proximity (Bonatti et al., 1996).

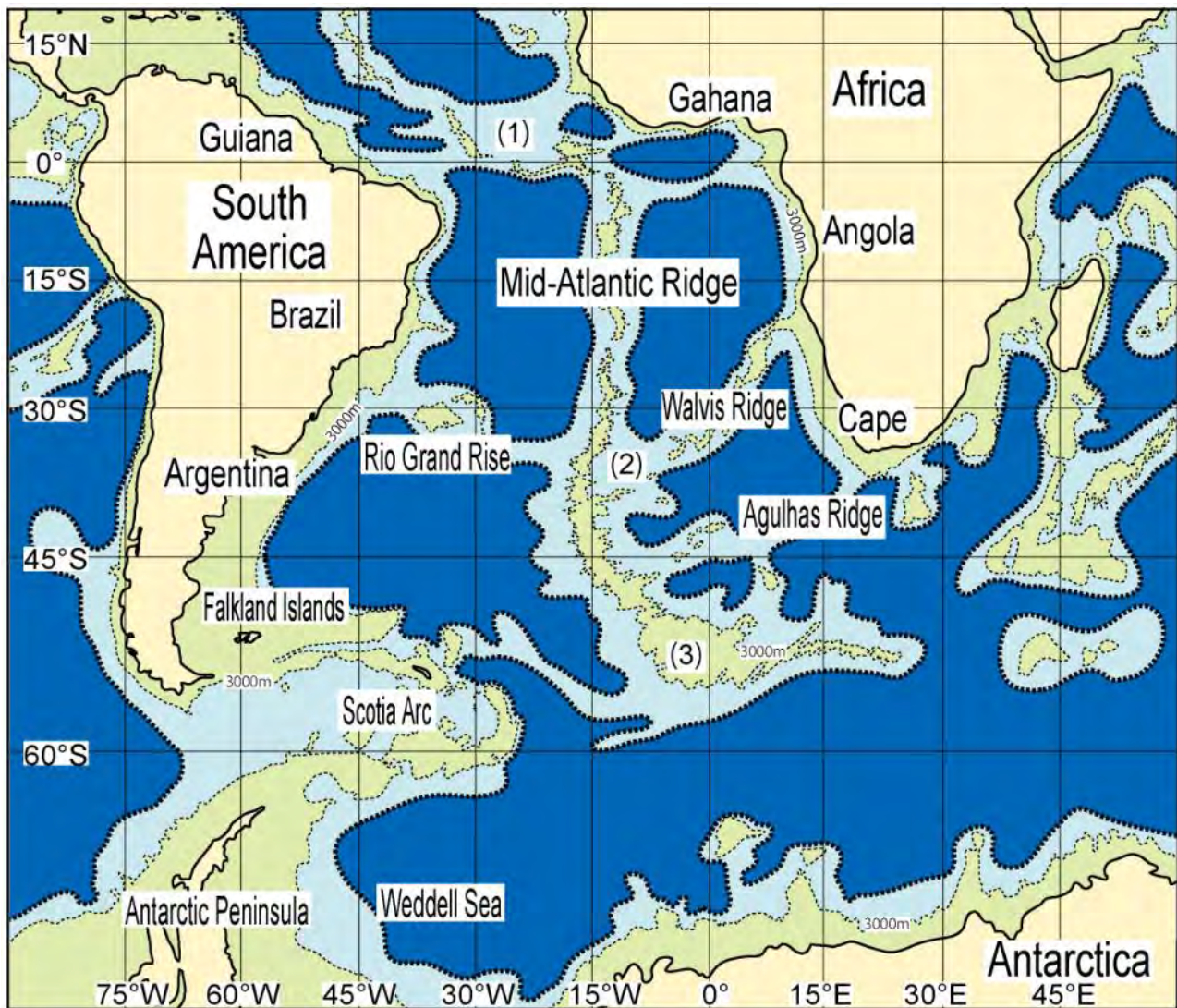


Fig. 2 Location of land bridges connecting the Africa and South America. (1)-(3): Route of the overpass in the text. Drawn along isobaths at a depth of approximately 4,000 m. Yellow and green is land, light blue is land or shallow sea and blue is deep sea.

The Walvis Ridge-Rio Grande Rise route (2) runs from the Walvis Ridge off Namibia in Africa via the Mid-Atlantic Ridge at 30°-40°S to the Rio Grande Rise to South America. An unconformity between the Early Oligocene and Miocene strata has been found at deep-sea drilling site 526 in the Walvis Ridge (Shipboard Scientific Party, 1984), and granite outcrops have been found in the Rio Grande Rise (Kitazato, 2014). In the Rio Grande Rise, the plutonic and metamorphic rocks from a further 22-540 Ma have been dredged, indicating that they were uplifted during the Eocene and their tops were eroded on land (Santos et al., 2019).

The route (3) from Cape at the southern tip of Africa to the Falkland Islands via the Agulhas Ridge and the Mid-Atlantic Ridge at around 45°S. There, at the southern end of the Mid-Atlantic Ridge, in the central axis near the Bouvet triple junction, a continental base of the Archean to the Early Proterozoic age has been inferred (Kamenetsky et al., 2001). On the Falkland Plateau, deep-sea drilling has yielded basaltic lava that consists of the Proterozoic basement rocks and was erupted onshore during the Late Cretaceous (The Shipboard Scientific Party and Burns, 1973; Shipboard Scientific Party, 1988). However, there is so far no evidence of terrestrial deposits without the Falklands Plateau.

Australian marsupials

At present, marsupials are found on South America and Australia and are broadly divided into two

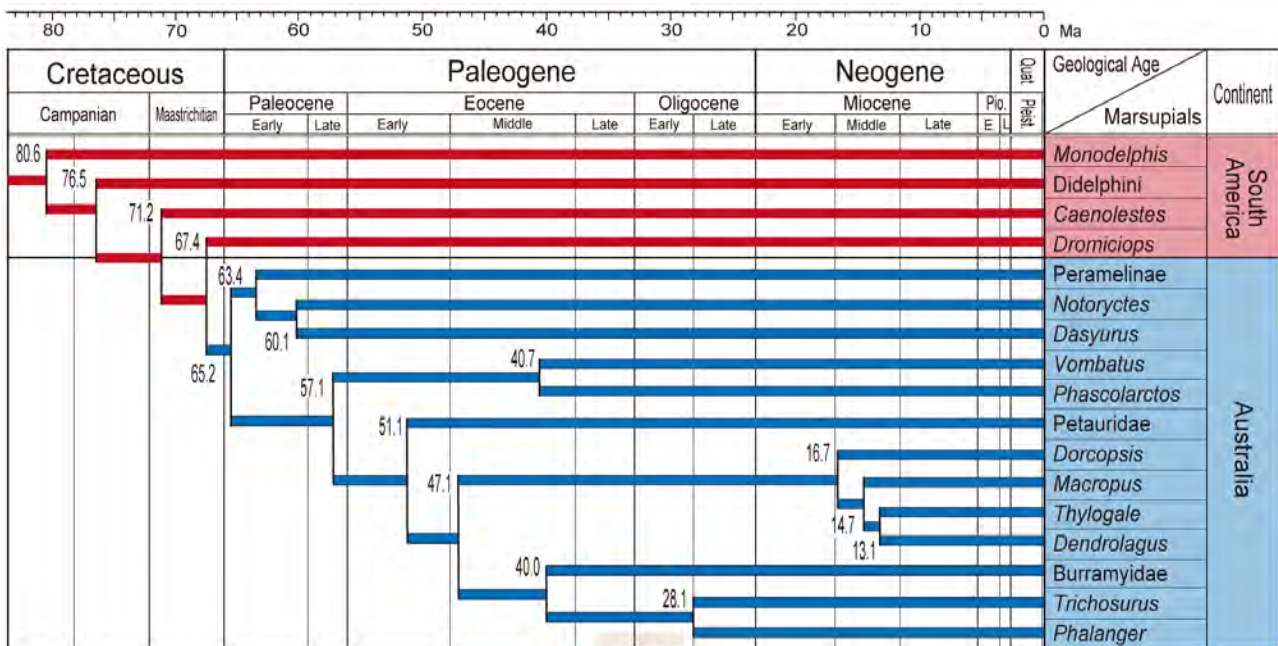


Fig. 3 Molecular phylogeny and divergence age of marsupials (After Beck, 2008).

Number is divergence age (Ma).

groups, the American marsupials (Ameridelphia) and the Australian marsupials (Australidelphia), based on the divergent phylogenies of the fossil assemblages and the molecular phylogenetic analysis of the present assemblages. According to Endo (2018), the divergence age from molecular genetics between Metatheria (marsupials) and Eutheria (placentals) is 220-180 Ma (the Jurassic period), with a shallow estimate of 135 Ma (the Early Cretaceous period). Fossils of older lineages include the oldest metatherians, *Sinodelphis* 125 Ma, *Holoclemensia* 110 Ma, the North American-Asian lineage *Kokopekllia* distributed until 98 Ma in the North America, and Eutherians from 160 to 110 Ma, The age from molecular genetics appears to be too old compared to the fossil evidence.

These suggest that Metatheria and Eutheria coexisted during the Cretaceous period. Fossil evidence suggests that marsupials evolved in North America, and that the North and South America were land-locked at some point during the Late Cretaceous, when the North American marsupials migrated and dispersed to South America.

In the evolutionary sequence of marsupials, the South American lineage emerged first, with the Australian marsupials occurring in South America (Beck, 2008, Fig. 3). It is then believed to have subsequently migrated from South America to Australia between the Late Cretaceous and Early Paleocene (67 to 63.4 Ma). And fossil Australian marsupials are thought to have passed through Antarctica, as fossil Australian marsupials have been recovered from the Eocene strata in Patagonia, South America, and from the Antarctic Peninsula (Beck, 2008).

Therefore, the arrival of Australian marsupials via Antarctica occurred near the boundary between the Cretaceous and Paleocene (Paleogene), the so-called K-Pg boundary. The absence of marsupial exchange between South America and Australia after that time suggests that South America and Antarctica, or Antarctica and Australia, were completely separated by an ocean. Australian marsupials subsequently dispersed within the Australia or Antarctica, with the diversification of grassland groups such as kangaroos occurring on Australia, particularly with the emergence of grasslands during the Middle Miocene continental climate change (Martin, 2006).

When was Antarctica isolated?

Between South America and Antarctica is the so-called Scotia Arc, a group of islands in the Drake Passage that runs from Fuego Island at the southern tip of South America to Georgia Island and the South

Sandwich Islands on its eastern side, and then turns west to the Orkney Islands and the Antarctic Peninsula. This island arc has long been thought to have been a former land bridge, also known as the Scotia land bridge. On the other hand, the ridge between Antarctica and Australia extends in a northwesterly direction from the western side of the Ross Sea in Antarctica, intersects the southwestern extension of the Pacific-Antarctic Ridge and reaches the south of the Tasman Rise on Australia. The uplifted zone is only continuous with the Tasman Rise at depths of 4,500-5,000 m, but marsupials probably crossed the land bridge that existed here (Fig. 4).

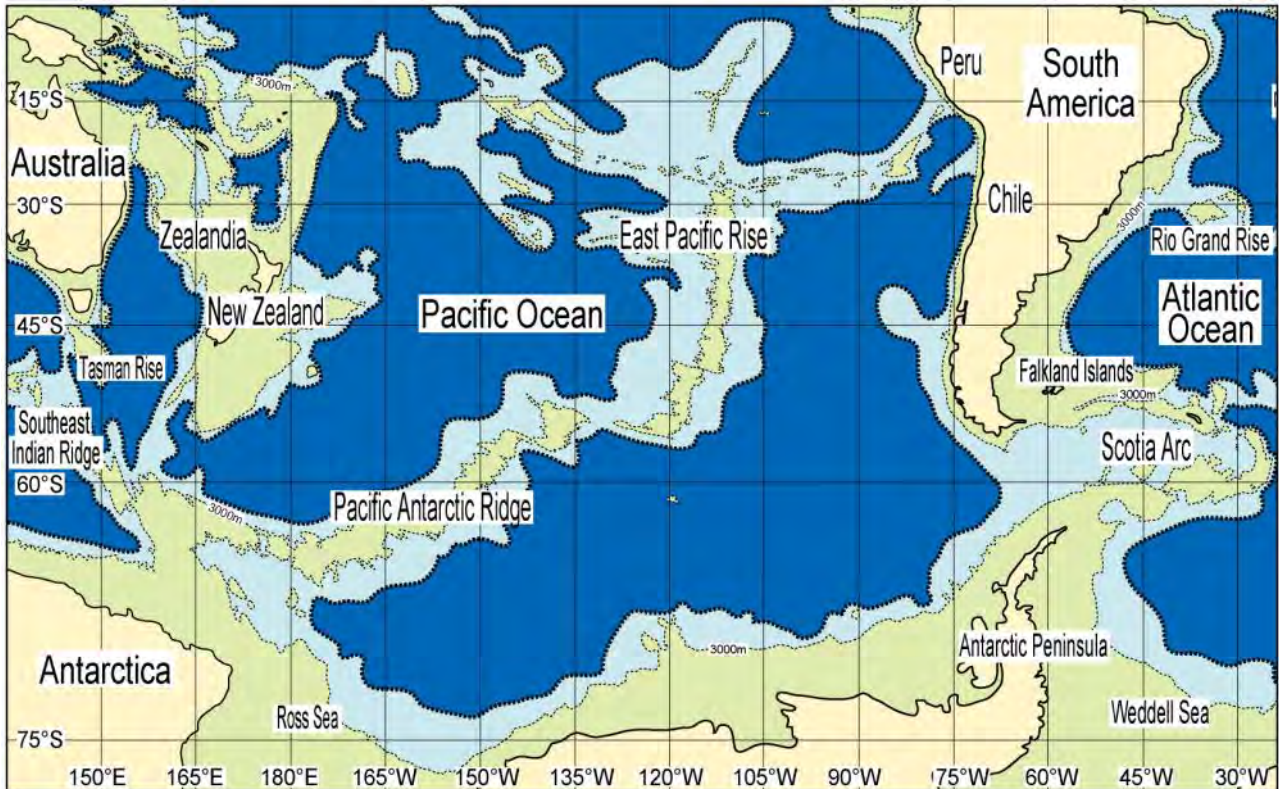


Fig. 4 Submarine topography around Antarctica and location of land bridges connecting South America and Australia in the latest Cretaceous. Drawn along isobaths at a depth of about 4,000 m. Yellow and green is land, light blue is land or shallow sea and blue is deep sea.

Antarctica is currently an ice continent covered by a thick ice sheet, but the first ice sheets, and mountain glaciers, were formed in Antarctica during the Middle Eocene, and a major cooling event occurred at the boundary between the Middle and Late Eocene (Prothero, 1994). According to Prothero (1994), this is the time when the first shallow ocean circulation appeared in the Tasman Sea between Antarctica and Australia. In addition, the Early Oligocene was marked by a rapid cold snap (Shackleton and Kennett, 1975; Wolfe, 1978), and large continental ice sheets are estimated to have developed during 14 million years before the Middle Miocene (Kennett, 1982). This large-scale cooling at the beginning of the Late Eocene (about 37.8 Ma) is thought to have been caused by the Antarctic Circumpolar Current that began to form around Antarctica as Antarctica and Australia were no longer completely connected by land, and Antarctica became an isolated ice continent after that time.

Why aren't penguins in the Arctic?

All penguins are currently found in Antarctica and the Antarctic Circle, with the exception of the Galápagos penguin, which lives in the Galápagos Islands near the equator in the Pacific Ocean, and on the islands of South America, Africa, the southern tip of Australia and New Zealand around Antarctica.

The closest living bird group to the penguin order is the order Petreliformes, to which albatrosses and other birds belong, and penguins and albatrosses are thought to share a common ancestor dating from about

71 Ma (during the Maastrichtian age in the Late Cretaceous). The oldest fossils of penguins have been found in New Zealand from the lower Paleocene series, approximately 62 Ma (Slack et al., 2006), and their skeletons are very similar to those of present-day penguins. Most of the Paleocene fossils are known from New Zealand, but some are also known from Antarctica (Pelegrin et al., 2022), suggesting that New Zealand and Antarctica shared the same coastline during the Paleocene and Eocene.

Subsequently, penguins are thought to have evolved mainly on Antarctica during the Middle Eocene and then expanded outside Antarctica as the global climate cooled. The reason why penguins are not found in the Arctic Circle is thought to be that they originally adapted to the cold climate of the Antarctic Circle, which allowed them to benefit from the rich biological productivity of the Antarctic Ocean and allowed them to evolve and thrive in a cold region where other predators, their natural enemies, could not adapt. When penguins dispersed from the Eocene to the Miocene, the southern and northern continents were not contiguous at that time (Prothero, 1994), which may have also contributed to their absence from the northern continent.

Molecular phylogenetic studies of present-day penguins (Baker et al., 2005) indicate a divergence age of 37.7 Ma (the Late Eocene) between the genera of the King penguin (*Aptenodytes*) and Gentoo penguin (*Pygoscelles*) living in Antarctica and other genera living in the Antarctic Circle outside Antarctica (Fig. 5). This coincides with the aforementioned formation of the Antarctic Circumpolar Current and the complete

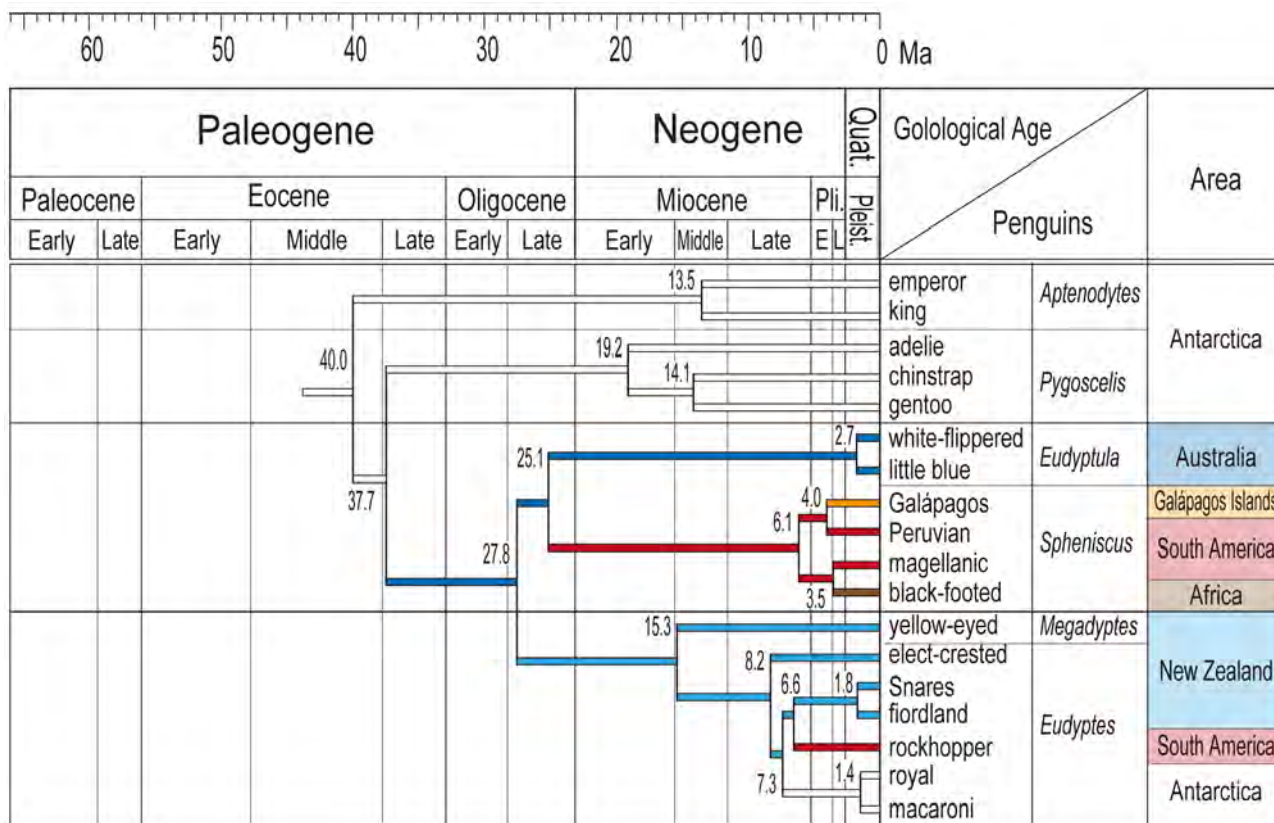


Fig. 5 Molecular phylogeny and divergence age of penguins. (After Baker et al., 2005). Number is divergence age (Ma).

isolation of the Antarctic continent (37.8 Ma). In other words, the ancestors of the penguins living on Antarctica today and those living elsewhere are thought to have been separated by the complete isolation of Antarctica from the other continents and the complete formation of the Antarctic Circumpolar Current.

Data on the age of divergence of penguin species from molecular genetics (Baker et al., 2005) are used to infer the subsequent evolution of penguins and the history of their habitat fragmentation by the sea. As penguins are swimmers, one might expect them to be able to disperse anywhere, but as each species of penguin without a few species such as the macaroni penguin (*Eudyptes chrysolophus*) is almost exclusively distrib-

uted over a range of areas (isolated distribution), they are unlikely to be able to disperse over long distances over the ocean without some degree of terrestrial or island and drift ice succession (Fig. 6).

Penguins distributed outside Antarctica, including the Royal penguin (*Eudyptes*), which also has a distribution on the Antarctic Peninsula, diverged into two groups 27.8 Ma (the Late Oligocene), one group inhabiting mainly New Zealand and the Antarctic islands, the other inhabiting Australia and South America (including Galápagos and African penguins). The latter group of Australia and South America were then separated 25.1 Ma (the Late Oligocene).

The phylogeny of penguins suggests that those from Antarctica and the rest of the world (Australia and New Zealand) may have been continuous until the Eocene. This suggests that the land bridge that was submerged when the Australian marsupials were isolated from South America (63.4 Ma) was the Scotia land bridge that connected South America and Antarctic. And the land bridge connecting Antarctica with

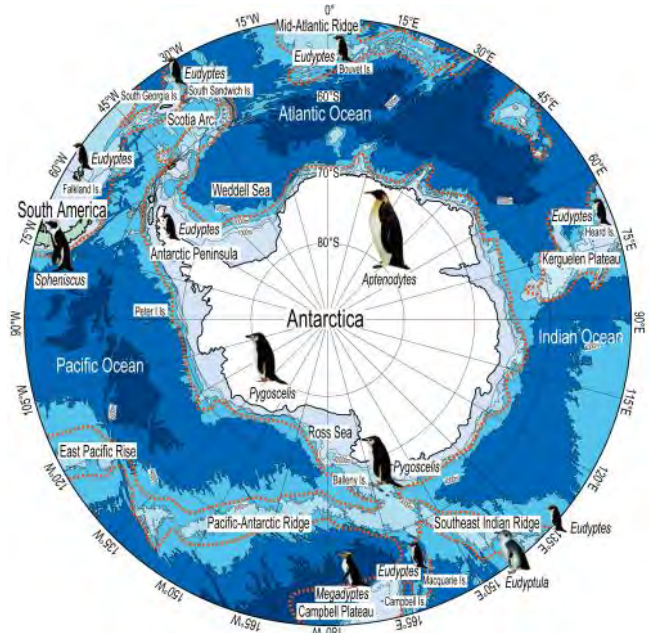


Fig. 6 Bathymetry and distribution of major penguins around Antarctica. The thick orange dashed line is the estimated continental coastline up to the Middle Eocene, drawn by isobaths at depths of 4,000-3,000 m. The submergence at the beginning of the Late Eocene is thought to have caused the phylogenetic divergence and distribution dispersal of penguin species with the formation of the Antarctic Circumpolar Current.

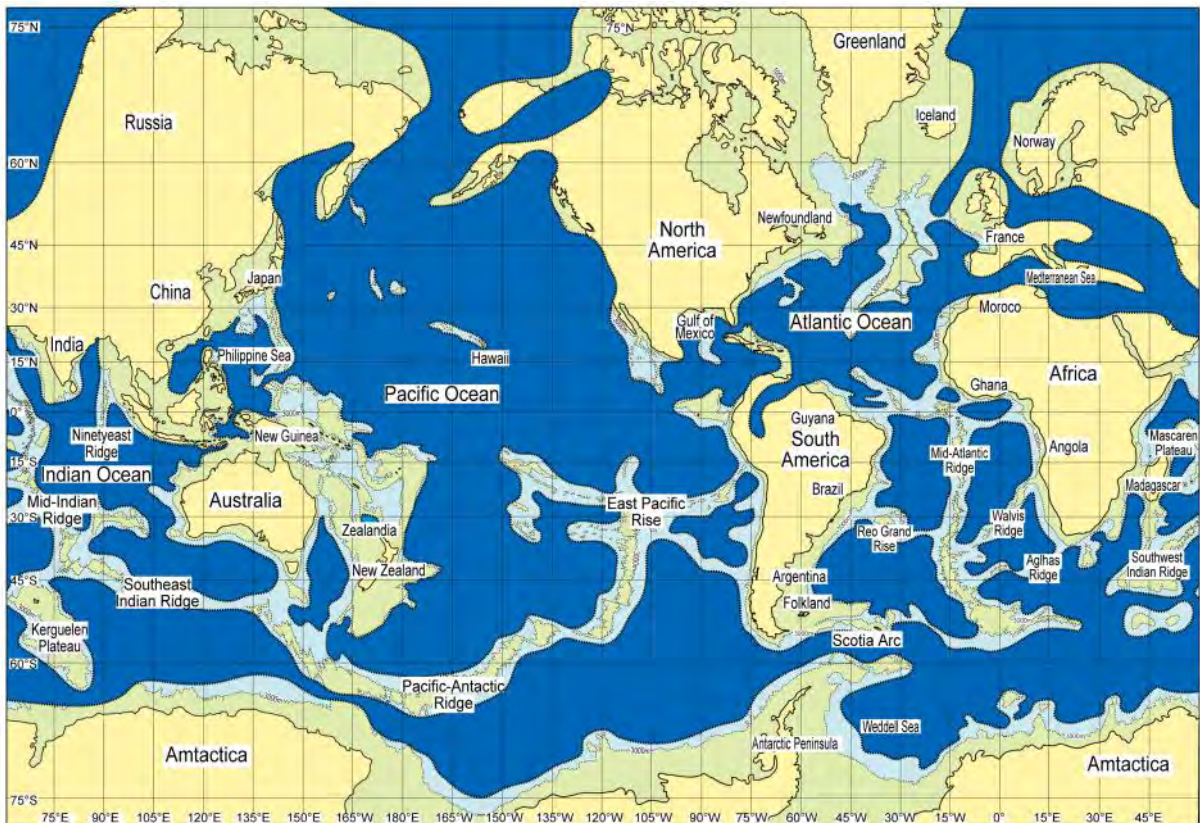


Fig. 7 The Late Eocene to Early Oligocene (37.8-28.1 Ma) continents and oceans. The light blue and yellow-green area enclosed by the thick dotted line is the land or shallow water, and the blue area is the ocean. With age, terrestrial areas submerge and diminish, while some areas of the sea rise and become terrestrial.).

the Australia or New Zealand is thought to have been completely submerged 37.8 Ma, when Antarctica was isolated (Fig. 7). The Antarctic-facing land bridge connecting the Australian continent with New Zealand is thought to have been submerged between 27.8 and 25.1 Ma.

The ancestors of the penguins that now inhabit Australia and South America diverged 25.1 Ma. The land bridges that played a role in the dispersal from Australia to South America were probably not accessible to animals other than penguins, and dispersal may have moved along the island like stepping stones, possibly due to the ecology of swimming penguins. The Pacific-Antarctic Ridge from the south of the Australian continent and the contiguous East Pacific Rise are candidates for such a route. Since the author's sea-level rise curve (Fig. 1 (iv)) assumes that the sea level was about 5,000 m lower in the Late Oligocene, it is possible that those uplift zones existed as a continuous land area or a series of islands in the Late Oligocene.

During the Eocene, there was a marked diversification of New Zealand lineages and many fossils have been found, and their close relatives have been found in the Eocene of Peru in South America. Their fossils indicate a closely related penguin fauna between New Zealand and Peru, a relationship that continued into the Late Miocene (Pelegrin et al., 2022). That is, the land bridges connecting New Zealand and Peru during that period were assumed to be land bridges or islands that were on the East Pacific Rise. However, there is a chronological discrepancy between the fossil divergent lineages and the molecular genetic divergence of the present-day inhabitants, and further study is required.

After the Late Pliocene to Pleistocene, penguins became dispersed and distributed on Africa and the islands of the Antarctic Circle. This may be partly due to stepping islands and drift ices migration in association with the rapid cooling around Antarctica during the so-called Pleistocene glaciation and the dramatic development of the Antarctic Circumpolar Current.

Biologists often refer to drifting ocean currents as a method of oceanic dispersal of island endemics, but when did ocean currents as we know them exist? Ocean currents are formed by temperature and density differences in surface seawater and prevailing winds over the sea. The present-day climate zones and ocean circulation systems of the Earth began to form after the Late Eocene, when the sinking of the land bridge between the Faroes and Shetland Islands in the North Atlantic caused the cold waters of the Arctic Ocean to move southwards through the Atlantic as deep water, while the Antarctic Circumpolar Current was born around Antarctic. Such an ocean circulation system is thought to have manifested itself in the Late Miocene, particularly in the Late Pleistocene, when the distinct climatic zones and ocean currents of the present day were formed. It is therefore unlikely that during the Eocene, Oligocene or Middle Miocene there were currents exactly like those of the present day.

Evolution of ratites and Antarctic

Groups of flightless birds such as Ostriches (*Struthio*: Struthionidae) are known as ratites, and are classified as Palaeognathae, including Tinamou (*Tinamus*: Tinamidae) of South America, and are distinguished from the Neognathae, to which all other present-day birds belong. The birds of this Palaeognathae are found in their current distribution on Africa for *Struthio*, on South African for Rheas (*Rhea*: Rheidae) and Tinamou in Australia for Emu (*Dromaius*: Dromaiidae) in Australia and New Guinea for Cassowaries (*Casuaris*: Casuariidae) and in New Zealand for Kiwi (*Apteryx*: Apterygiidae). Madagascar and New Zealand were also home to the giant extinct ratites Aepyornis (Aepyornithidae) and Moa (Dinornithidae), respectively, until the time humans arrived there.

Nuclear genome fragments have been recovered from these currently inhabiting Palaeognathae birds and from extinct Aepyornis and Moa, and a reliable phylogenetic tree of Palaeognathae has been reconstructed (Yonezawa et al., 2017). According to this, the ancestor of the Palaeognathae was a small flightless bird, distributed in Laurasia, where the first divergence of lineages linked to the present Palaeognathae occurred between an Ostrich's ancestor and others approximately 79 Ma (the Coniacian age in the Late Cretaceous).

The Ostrich's ancestors subsequently became larger and more flightless birds in Eurasia, and then moved into Africa, which became land-locked 20 Ma, becoming recently extinct in Eurasia. The other group is

called the Southern Palaeognathae because their descendants are distributed on the continents and islands of the Southern Hemisphere derived from Gondwana. The common ancestor of the Southern Palaeognathae migrated from North America to South America by about 70 Ma, and speciation exploded during the period around the Cretaceous-Paleogene boundary, dispersing to the continents and islands of the Southern Hemisphere (Fig. 8).

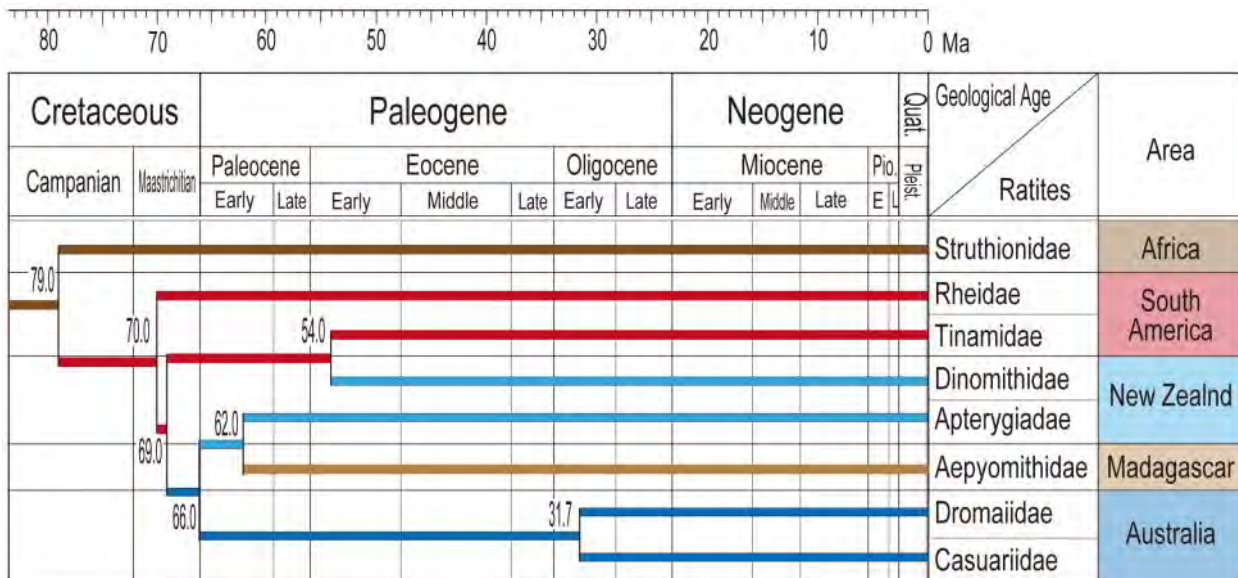


Fig. 8 Molecular phylogeny and divergence age of ratites (After Yonezawa et al., 2017). Number is divergence age (Ma).

The ancestors of Rhea of South America first diverged about 70 Ma, and among the remaining ones the ancestral group of Tinamou + Moa and the ancestral group of Emu + Cassowaries + Kiwi + Aepyornis diverged 69 Ma. The ancestors of the South American Tinamou and the New Zealand Moa of the former group diverged 54 Ma, the ancestors of the Australian Emu and Casuarii from the latter group diverged 66 Ma, and from the rest the ancestors of the New Zealand Kiwi and the Madagascar Aepyornis were estimated to have diverged around 62 Ma.

The separation of the ancestors of the southern Palaeognathae, the Australian continental Emu and Casuarii and New Zealand Kiwi, around the Cretaceous-Paleogene boundary 69 Ma, coincides with the sinking of the land bridge that brought Australian marsupials from South America to Australia via Antarctica. In other words, the ancestors of the Australian marsupials and Australian and New Zealand ratites are thought to have migrated from South America to Australia and New Zealand via the same Antarctic route as the Australian marsupials.

The ancestors of the South American Tinamou and the ancestors of the New Zealand Moa separated 54 Ma, which means that the link between New Zealand and South America continued until the Early Eocene. A possible route is the Pacific-Antarctic Ridge-East Pacific Rise and its continuous ridge from south of New Zealand to Peru in South America, which was used by the penguins in the Oligocene. The author's sea-level rise curve assumes that the sea-level was about 7,000 m lower in the Early Eocene, so it is possible that these uplift zones were on land. It is also thought that the ancestors of these ratites originally had a certain degree of flight ability and were unable to fly after being isolated on islands, so they may have been able to disperse along the islands, where other animals could not cross, in the same way as the penguins.

The divergence of the ancestors of Kiwi (Apterygiidae) of New Zealand and Aepyornis (Aptomyomithidae) of Madagascar approximately 62 Ma (the Early Oligocene) suggests that New Zealand and Madagascar may have been land-locked before that time. The route may have been a land bridge from New Zealand via the Southeast Indian Ridge, the Mid-Indian Ridge and the Mascarene Plateau to Madagascar Island.

Lemurs of Madagascar and the Lemurian Continent

Madagascar is the fourth largest island in the world, located in the western Indian Ocean southeast of Africa, separated from the African continent by the Mozambique Channel, which is about 400 km long (Fig. 9). Madagascar is a continent composed of a Proterozoic granite base, inhabited by lemurs belonging to the Primates suborder of Prosimii (Strepsirrhines). Lemurs closely related to these lemurs live not only on Madagascar, but also on the Asian islands of Sri Lanka and Sumatra, 5,000 km east of Madagascar, and the wide area from Madagascar to Southeast Asia where lemurs are distributed was once known as the "Lemurian Continent".

The earliest Primates are known as fossils from the Paleocene series of Europe and North America, and molecular genetics suggests that the divergence of Primates from other Mammal dates back to the middle of the Cretaceous (Endo, 2002). The Strepsirrhine are not only lemurs on Madagascar, but also their closest relatives, lorises in Asia and galagos and pottos on Africa. Molecular divergence studies (Purvis, 1995) place the divergence of lemurs, including

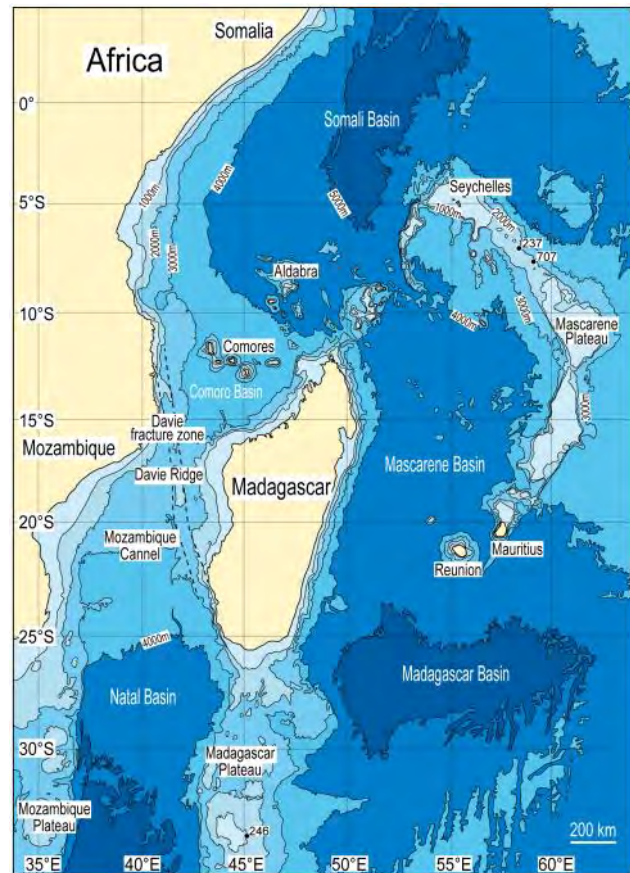


Fig. 9 Submarine topography around Madagascar Island. The dotted line is the Davie Ridge zone connecting Africa and Madagascar. Small black circles and numbers are points of deep-sea drilling site.

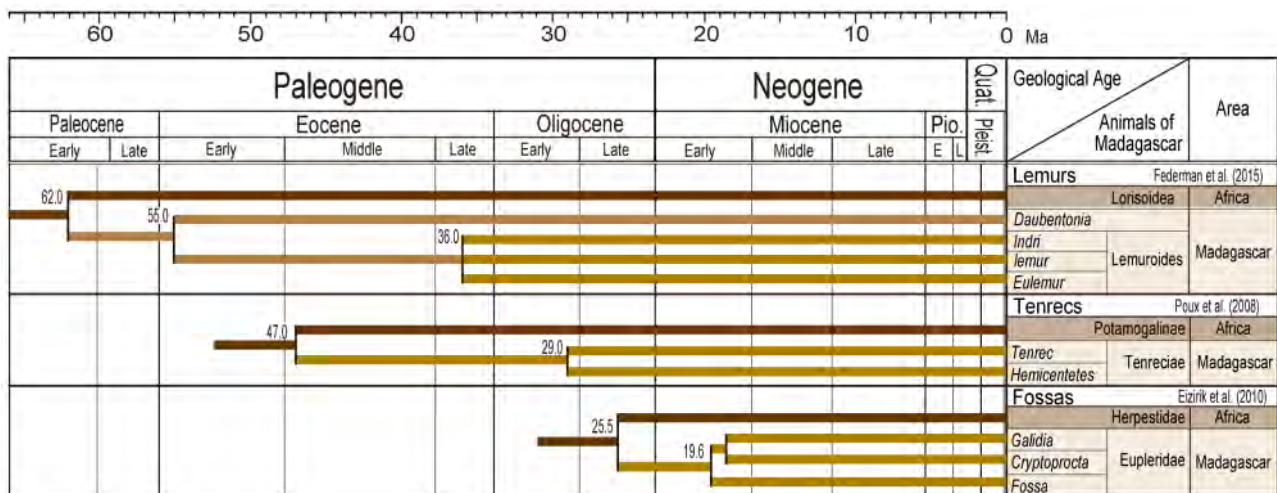


Fig. 10 Molecular phylogeny and divergence age of lemurs (Federman et al., 2015) and tenrecs (Poux et al., 2008), fossas and other carnivores (Eizirik et al., 2010). Number is divergence age (Ma).

aye-ayes of Madagascar, from other regional Strepsirrhine such as galagos and lorises at about 40-20 Ma. However, recent molecular divergence studies (Federman et al., 2015) suggest that lemurs and lorises diverged around 62 Ma (the Early Eocene), aye-ayes and lemurs around 55 Ma (the Early Eocene) and at 36.5 Ma (the Late Eocene). Lemurs on Madagascar Island diverged in three major groups (Fig. 10). This suggests that lemurs, including aye-ayes, migrated to Madagascar between 62 Ma and 55 Ma, or 55 Ma and 36.5 Ma.

According to the plate tectonics theory, Madagascar separated from Africa when the Gondwana continent broke-up about 120 Ma during the Early Cretaceous. However, the age of this continental break-up is considerably older than the age of molecular divergence of the Strepsirrhine, and the theory of plate tectonics cannot explain the isolation of lemurs on Madagascar.

The Davey Ridge in the Mozambique Channel consists of basement rocks such as gneisses and arkose sandstones, the crest of which underwent land erosion from the Middle Eocene (about 45 Ma) to the Late Oligocene (26 Ma), during which time this ridge may have served as a land bridge (McCall, 1997). Lemurs on Madagascar probably came to the island between about 40 and 26 Ma, across a land bridge at the Davy Ridge in the Mozambique Channel.

Other mammals of Madagascar

In addition to lemurs, the island of Madagascar is currently home to endemic mammals such as tenrecs, fossa and other carnivores, rodents, pygmy hippopotamuses and bats. There are also other elephant tortoise and, in the past, ratites of *Aepyornis*.

For the tenrecs, the divergence between the subfamily Tenreciidae of Madagascar and the subfamily Potamogalinae of Africa is estimated to be about 47 Ma, and the oldest divergence within the Madagascar tenrecs is estimated to be 29 Ma (Poux et al., 2008). Therefore, the ancestors of the tenrecs of Madagascar arrived on the island between 47 and 29 Ma (the Middle Eocene to Early Oligocene), the period that coincides with the arrival of lemurs. It should be noted that the already extinct Madagascar aardvark is recently

considered to have evolved from an ancestor of the subfamily Tenreciidae, rather than belonging to the Tubulidentata.

Madagascar has carnivores such as fossa, the ring-tailed vontsira and the malagasy civet. These carnivores are phylogenetically grouped into one group, the Eupleridae, the most closely related of which is the Mongoose family (Herpestidae). The divergence of the Herpestidae and the Eupleridae is dated to 25.5 Ma (the Late Oligocene) (Eizirik et al., 2010). It coincides with the last time the Davy Ridge was a land bridge.

Galápagos Islands and elephant tortoise

The Galápagos Islands comprise 13 islands and lie on the Cocos Ridge, which extends from Central America in the eastern equatorial Pacific (Fig. 11). The Cocos Ridge, on which the Galápagos Islands are situated, is considered by the plate tectonics theory to be the upwellings of the present-day plates (Hay, 1977), and the oldest islands are said to have been formed 3-5 Ma (Cox, 1983). The Galápagos Islands have marine and land iguanas, the Galápagos elephant tortoises, monitor lizards, geckos and snakes and endemic terrestrial animals such as bats, mice and Darwin's finches, as well as endemic flora. Each animal is also differentiated into species and subspecies on each of the several islands.

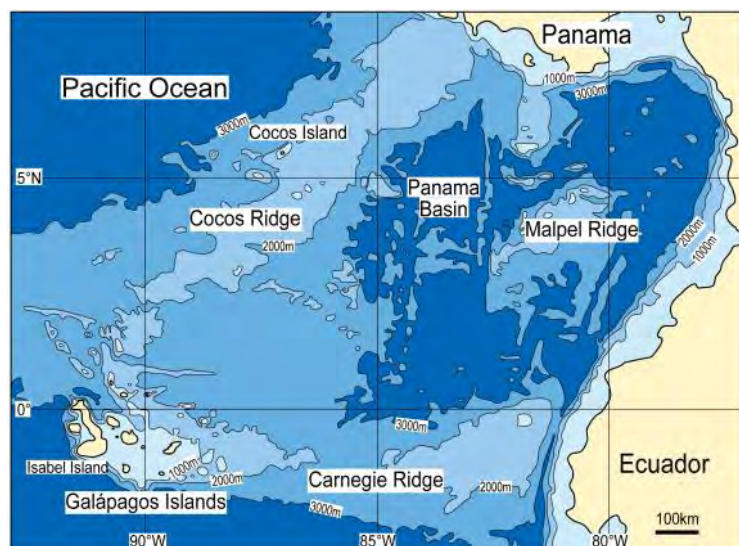


Fig. 11 Submarine topography of the Galápagos Islands and their surroundings. The South America and the Galápagos Islands are contiguous at a depth of 3,000 m isobath.

Of these, the elephant tortoises are found in South America and the Bahamas, the African continent, the island of Madagascar, the Seychelles Islands and the southern Mauritius Islands in the Mascarene in the western Indian Ocean (Vries, 1984), in addition to the Galápagos Islands. Fifteen subspecies of the Galápagos tortoise have been identified in *Chelonoidis niger*, with those of the same genus occurring in South America and the Bahamas (Kehlmaier et al., 2023).

Three endemic genera of rodents have also been recognized in the Galápagos Islands, which are considered to be an extremely diversified group of rodents from North, Central and South America (Clark, 1984). The flora of the Galápagos Islands is very different in its composition from that of the nearby continents, indicating that a number of important flora families of the nearby continents are absent from the archipelago and are not recent drifters (Eliasson, 1984).

Geologists use the plate tectonics theory to explain that the Galápagos Islands are recently formed volcanic islands (Hay, 1977), while biologists explain that the ancestors of such relict species drifted to the

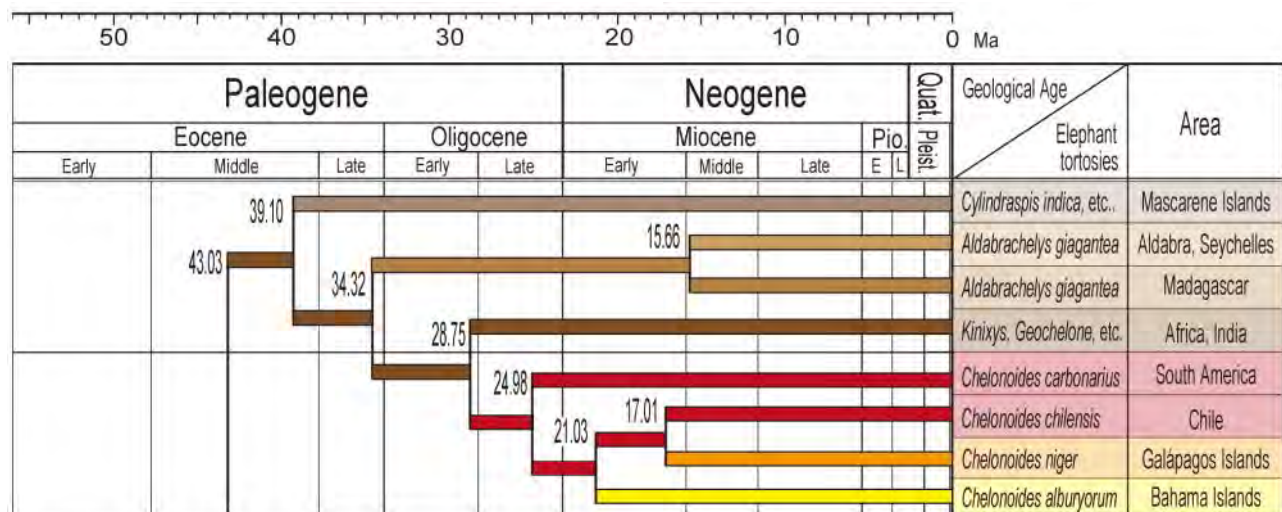


Fig. 12 Molecular phylogeny and divergence age of the elephant tortoises (After Kehlmaier et al., 2023).

Number is divergence age (Ma).

Galápagos Islands recently on rafts (Perry, 1984). The author considers these geologist's and biologist's explanations of the Galápagos Islands and their inhabitants' origins totally implausible because of the ancient origins of the ancestors of the Galápagos inhabitants.

Elephant tortoises in the islands of the western Indian Ocean

Recent results from a mitochondrial analysis of elephant tortoise genes (Kehlmaier et al., 2023) indicate that elephant tortoises diverged from closely related species on Africa about 43.03 Ma (the Middle Eocene). And the first elephant tortoise (genus *Cylindraspis*), which first inhabited the southern Mascarene islands of Mauritius, Rodrigues and Reunion, first diverged 39.10 Ma (the Middle Eocene) with the following diverse tortoise genus groups. The genus *Cylindraspis* diverged first with other African, Madagascar, Seychelles, Aldabra Atoll, India, South America, Galápagos Islands and Bahamas tortoises (Fig. 12).

The next group to diverge was the *Aldabrachelys* group, mainly from Madagascar-Aldabra Atoll-Seychelles Islands, which diverged at the end of the Eocene, 34.32 Ma, from sisters group including tortoises from Africa, India, South America, the Galápagos Islands and the Bahamas. The first and second divergences coincide with the divergence of lemurs and other mammals on Madagascar, already mentioned, and may be the result of submergence of the land bridge connecting the east coast of Africa and the Mascarene Islands with Madagascar due to sea-level rise.

The elephant tortoises of Madagascar, Aldabra Atoll and the Seychelles Islands diverged as endemic species on each island during the Middle Miocene, 15.66 Ma. This indicates that Madagascar, Aldabra At-

oll and the Seychelles Islands were connected by a land bridge until the Middle Miocene. According to the author's sea-level rise curve, sea-level during the Middle Miocene was approximately 3,800 m below present-day sea-level, suggesting that these islands may have been connected by land until that time.

The presence of frogs in the Comoros, Madagascar and Seychelles Islands is thought to be the result of multiple oceanic dispersals from Africa to Madagascar and from Madagascar to the Seychelles Islands during the Oligocene to Miocene (Vences et al., 2003). However, for the distribution of the frogs, a land bridge from Africa through Madagascar to the Seychelles Islands should be considered. The frog overpass would have existed during the Eocene to Middle Miocene period when the elephant tortoises passed through.

Elephant tortoises in South America and the Galápagos Islands

The results of a genetic analysis of elephant tortoises (Kehlmaier et al., 2023) place the divergence of Africa and Indian tortoises from South America and the Galápagos Islands at 28.75 Ma (the late Early Oligocene). The divergence between the tortoises of South America and those of the Galápagos Islands and the Chilean - Bahamas are dated to 24.98 Ma (the Late Oligocene). This indicates that elephant tortoises migrated from Africa to South America between 28.75 and 24.98 Ma during the Oligocene period. This inter-continental migration, i.e. the Atlantic land bridge, will be discussed in the sections on “New world monkeys and Cabimorpha rodents across the Atlantic Ocean”, which crossed the Atlantic around the same time.

The elephant tortoises that migrated to South America were divided 24.98 Ma into two groups: the ancestral group of tortoises from the Galápagos Islands, Chilean and the Bahamas, and the rest of the tortoises. It then diverged into the Galápagos and Chilean groups and the Bahamas group 21.03 Ma (the Early Miocene). The divergence between the Galápagos and Chilean groups occurred 17.01 Ma (the Early Miocene) (Kehlmaier et al., 2023). This means that the Galápagos Islands were isolated from South America when the Galápagos tortoises diverged from the Chilean group, which is thought to have occurred during the Early Miocene, 17.01 Ma.

The Galápagos Islands lie at the southern end of the Cocos Ridge, which extends from Costa Rica in

Central America, but also at the western end of the Carnegie Ridge, west of Ecuador, from South America. Presumably, the Galápagos Islands were connected to South America by land at the top of the Carnegie Ridge until the Early Miocene, and the ancestors of Galápagos tortoises crossed that land to the Galápagos Islands. Then, the sea-level rise at the end of the Early Miocene submerged the area between South America and the Carnegie Ridge, and the elephant tortoises are thought to have been isolated on the Galápagos Islands (Fig. 13). Tortoises that lived on land at the top of the Carnegie Ridge or Cocos Ridge in the Early Miocene were displaced by rising sea-level to higher, restricted areas, which became islands, and where they remained islands due to their uplift and volcanic activity against a gradually rising sea-level, they survived. It is therefore

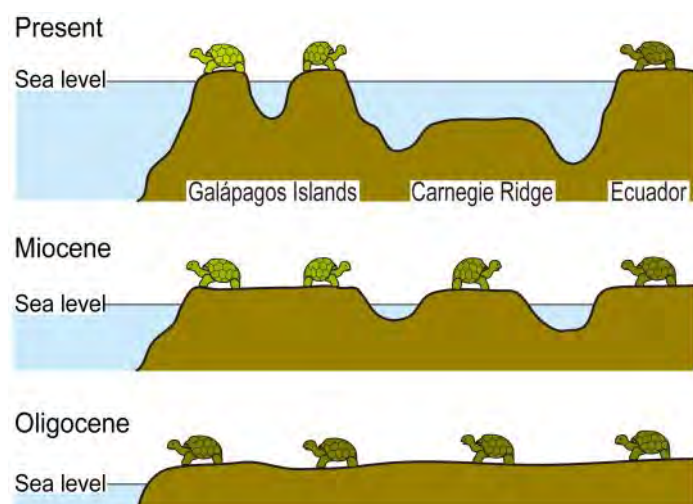


Fig. 13 Land bridges crossed by ancestors of Galápagos elephant tortoises and their submergence.

considered that subspecies have arisen on each island. In other words, the topographic section of the Galápagos Islands is also the very phylogenetic tree of the organisms that inhabit it.

A tortoise in the Bermuda Islands

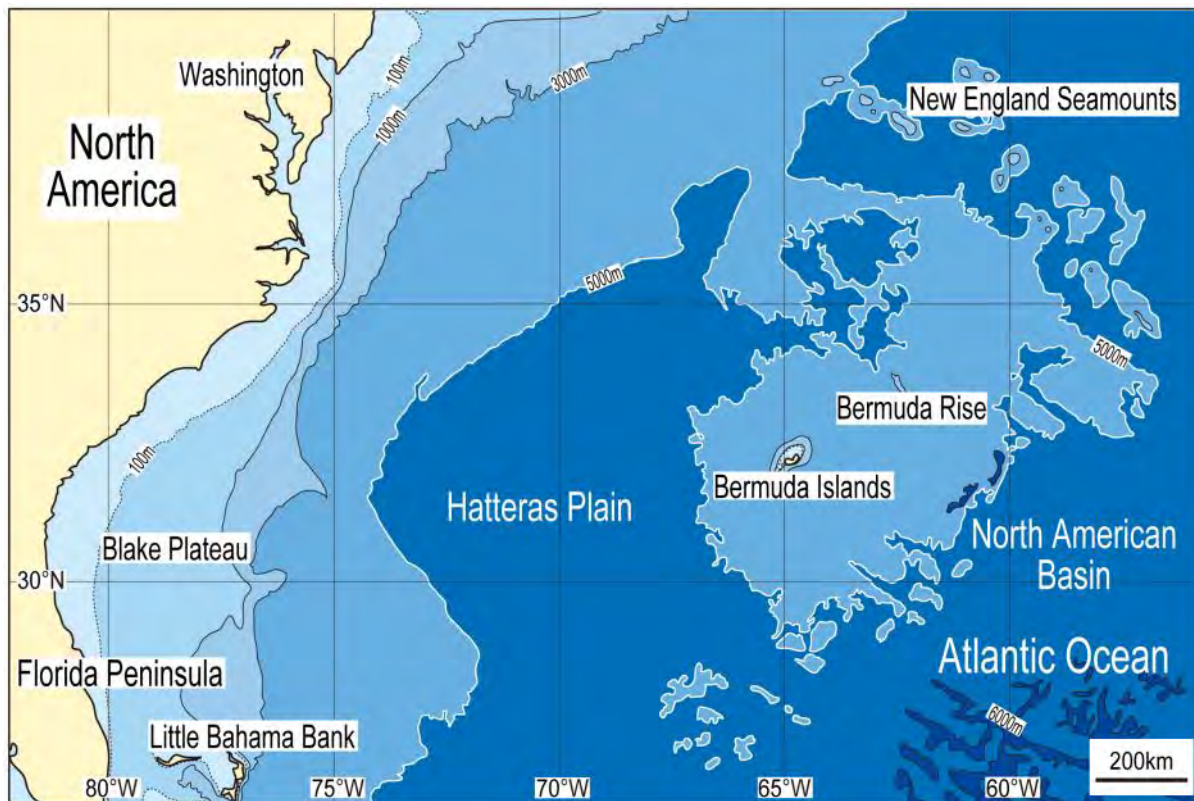


Fig. 14 Submarine topography around the Bermuda Islands. An isobath (white line) at a depth of 5,000 m connects the Bermuda Islands to the North American continent.

The Bermuda archipelago consists of approximately 150 coral reefs and reefs and is isolated in the ocean, 1,200 km from the North American continent. The Bermuda Islands are surrounded by a deep sea-floor that can only be connected to the North American continent by an isobath at a depth of 5,000 m (Fig. 14). A tortoise fossil (Testudines) have been found in Pleistocene strata in the Bermuda Islands, and this tortoise is considered to be a new species of the extinct North American genus of *Hesperotestudo* (Meylan and Sterrer, 2000). The genus *Hesperotestudo* is an extinct tortoise native to North and Central America from the Early Miocene to Late Pleistocene, with a carapace length larger than that of some extant elephant tortoise.

Researchers who found this fossil of land tortoise in the Bermuda Islands concluded that this tortoise reached the islands through oceanic dispersal (Meylan and Sterrer, 2000). However, the probability of a land animal being preserved as a fossil is very low, and the presence of fossils means that this tortoise was very abundant on the island. Van der Gree et al. (2010) reject land bridge migration as the fauna of the islands is characterized by heterogeneity and poverty, which had a strong filtering effect on migration to the islands. However, this is thought to have been due to the short time that land bridges were formed that allowed migration to the islands, the limited natural environment of the islands and, furthermore, the limited number of species that were able to adapt due to island shrinkage and environmental changes after isolation on the islands and the formation of endemic species within them through the composition of new niches (Shiba, 2020, 2021).

The author's sea-level rise curve shows that the sea-level at the beginning of the Late Oligocene to Early Miocene is in the range of 5,100-4,800 m. Therefore, the possibility that the ancestors of the Bermuda tortoise crossed the land bridge from the North American continent to the islands at this time cannot be ruled out.

New world monkeys and Cabimorpha rodents across the Atlantic Ocean

The ancestors of new world monkey (the Platyrrhini) and the Cabimorpha rodents, which are now wide-

spread in South America, are thought to have crossed the Atlantic Ocean from Africa to South America during the Eocene and Oligocene periods (Takai, 1995). The primates presently living can be divided into two suborders: the Prosimii, consisting of lemurs and tarsiers, and the Anthropoidae, consisting of the Platyrrhini and the Catarrhini. The Platyrrhini (Broad-nosed macaques) comprise members of the macaque family, so named because their nostrils spread to the left and right, and are known as new world monkeys because they are found only on South America.

New world monkey fossils have been found in South America since about 25 Ma, when there were no primate fossils at all in South America. This is why the origin of new world monkeys has been a mystery. There is a theory that new world monkeys originated in North America, but this theory has not been adopted because, although there are fossils of the Prosimii in North America, there are no fossils of the Anthropoidae, and the North and South American continents were not connected by land at the time the new world monkey was born. Another theory, now considered a strong contender, is that primitive Anthropoidae from Africa may have crossed the Atlantic Ocean (Takai, 1995).

On the other hand, the Cabimorpha rodents are found on South America. The rodents include guinea pigs and capybaras, which are included in the suborder Hystricomorpha. This suborder, which includes these rodents, is divided between South America and Africa, suggesting that the ancestors of these rodents migrated from Africa to South America and diversified.

Studies of the fossil record and genetic analyses of the present species (Poux et al., 2006) suggest that the Platyrrhini migrated across the Atlantic Ocean from Africa between 37 and 16.8 Ma (the Late Eocene to Early Miocene), while the Cabimorpha rodents migrated between 45.4 and 36.7 Ma (the Middle to Late Eocene), and it is estimated that they dispersed, and it is possible that they both arrived in South America at the same time.

When these the new world monkeys and the Cabimorpha rodents arrived in South America, South America is thought to have been isolated from all other continents, and they migrated across the Atlantic Ocean, where the distance between the two continents was shorter than now, on floating island-like rafts of driftwood (de Queiros, 2017). However, as we have seen, terrestrial animals cannot cross oceans, so this theory of oceanic dispersal cannot explain the migration of new world monkeys and the Cabimorpha rodents to South America.

Atlantic land bridge crossed by new world monkeys

If new world monkeys and the Cabimorpha rodents reached South America from Africa at the same time, the divergence age of both inferred from genetic analysis studies (Poux et al., 2006) would place their range between 37 and 36.7 Ma during the Late Eocene, when they overlapped. Similarly, the age of divergence of the elephant tortoises from Africa to South America, i.e. the age range of their arrival in South America, is between 28.8 and 24.95 Ma (the Early to Late Oligocene) (Kehlmaier et al., 2023). A discrepancy between these two dates has occurred.

Although the branching order of each taxon of an organism can be determined for the estimation of branching ages based on molecular genetic analysis, the age of the branching of these taxa depends on the fossil detection date of the lineage and the method of branching age analysis, which can differ greatly if they are different. Fossils are not found anywhere, at any age, of any kind, and the probability of an organism remaining in strata as a fossil is small, and the discovery of well-preserved fossils is rare. Therefore, the fossil record is incomplete, and the accuracy of the branching chronology must be rough if fossils of importance for the consideration of branching have not been found.

With regard to the period of existence of the land bridge, it is considered that, depending on the amount of uplift and sea-level rise in the area of the land bridge, the land bridge may have been partially submerged and disconnected or reconnected at certain times. For land bridges connecting the Africa and South America, the following routes are mentioned in Fig. 2: (1) the present-day equatorial Mid-Atlantic Ridge region route, (2) the Walvis Ridge-Rio Grande Rise route to its south, and (3) the Agulhas Ridge-Falkland Plateau

route. All of these are contiguous areas on the seafloor shallower than 5,000 m deep today, and the author's sea-level rise curve indicates that the sea-level from the Late Eocene to the end of the Oligocene was in the range 5,700-4,700 m lower than today, so it is possible that a transatlantic land bridge existed around the Paleogene period.

At present, the exact location of the transatlantic land bridge crossed by the new world monkeys and the Cabimorpha rodents, as well as the elephant tortoises, is unknown. However, it is certain from the present distribution of organisms that during the Eocene to Oligocene, a land bridge across which these terrestrial animals crossed existed in the Atlantic Ocean.

Submerged continents in the Caribbean Sea

The Caribbean Sea lies to the east of Central America and is surrounded by the West Indies (Fig. 15). The West Indies consists of the Bahamas, the Greater and Lesser Antilles (Fig. 15). The Greater Antilles mainly comprises the islands of Cuba, Hispaniola, Jamaica and Puerto Rico, while the Lesser Antilles consists of the Leeward Islands in the north and the Windward Islands in the south, also known as the Eastern Caribbean. Other islands in the Caribbean include the Yucatan Peninsula and a number of islands off the coast of Venezuela in northern South America.

The Greater Antilles was once home to five species of new world monkeys, all of which are now extinct primates. Other fossil Antilles terrestrial mammals, such as the Cabimorpha rodents, large sloths and solenodonts, are thought to have already been present on one or more of the Antilles islands by the Early Miocene.

Fossils and their DNA analysis reveal that one of the already extinct the new world monkeys from the

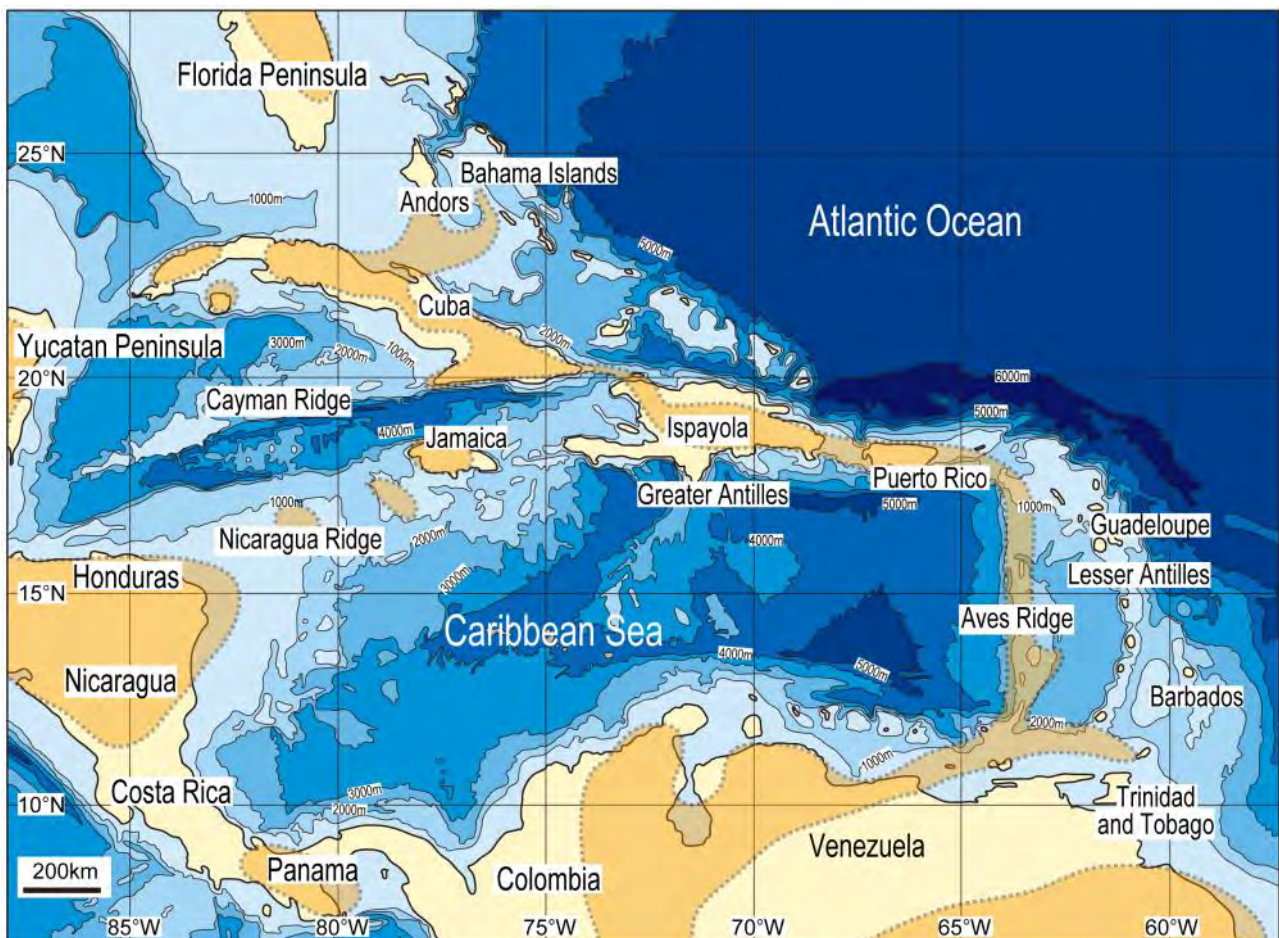


Fig. 15 Caribbean islands and bathymetry. The Light orange areas enclosed by dotted lines are the Eocene to Oligocene land area assumed by Macphée and Iturralde-Vinenta (2000).

island of Jamaica in the Greater Antilles inhabited the Caribbean region during the Early Miocene, 18.5-17.5 Ma (Woods et al., 2018). They reveal that the northern Greater Antilles was land-locked to the north-east of South America during the Eocene to Oligocene, and that the new world monkeys crossed the land from South America. This land mass is thought to have been temporarily connected to the peninsular land mass that includes the Aves Ridge, which parallels the western side of the Lesser Antilles, and is known as GAARlandia (Ituralde-Vinent and MacPhee, 1999).

The Greater and Lesser Antilles are home to over 120 species of anole lizards, as well as elephant tortoise. The elephant tortoise of the Bahamas diverged from the Galápagos and Chilean groups 21.03 Ma during the Early Miocene (Kehlmaier et al., 2023). Given the distribution of these elephant tortoise, GAARlandia probably existed in the Caribbean until the Early Miocene. However, many unanswered questions still remain about the biology of the Caribbean islands, especially the origin and ecology of their terrestrial fauna, making them a hotspot of biogeography.

Distribution of terrestrial animals and sunken land bridges

As we have seen, the distribution of terrestrial animals, especially during the Cenozoic Era after 66 Ma, is considered to be closely related to past changes in the position of the sea-level, or, to an approximation, to the present bathymetric distribution. Most of the seafloor shallower than 3,000 m depth on the continental margins in the Atlantic, Indian and Pacific Oceans were terrestrial until the Eocene or Oligocene, and became deep after the Miocene. Therefore, it is possible that large areas of the present seafloor were land (continents) during the Paleocene and the Late Cretaceous. The former continents are thought to have sunk into the sea in stages due to the uplift of the earth's crust, i.e. the rise in sea-level caused by the micro-expansion of the earth as described by Hoshino (1991, 2014).

The fact that large parts of the present-day seafloor were land (continents) means that if the present-day amount of seawater on the Earth had remained the same, then either parts of the present-day continents would have been seafloor or the seafloor would have been deeper to meet that amount of seawater. As for the deep seafloor in the past, the Pacific Ocean probably played a large part of the role, especially the deep seafloor of the north-east Pacific Ocean, where sediments from the Neogene period onwards hardly cover the seafloor (Vasiliev, 2006), which was once quite deep.

Some areas of the seafloor rise as much as on land, others less so, and the timing of these rises varies, and the relationship between the timing of the rises and the position of the sea-level at the time determines whether the area was on land or on the seafloor. In some cases, volcanic activity is accompanied by uplift, and volcanic activity creates landforms such as volcanic islands that are topographically higher than the sea-level, and some relict species are lucky enough to continue to live there, such as the Galápagos Islands.

Based on recent results in molecular phylogenetics, this paper attempts to explain the migration of terrestrial animals between continents and islands by land bridges, rather than by continental break-up based on the plate tectonics and oceanic dispersal by rare chance. The possibility of the existence of this land bridge is based on the sea-level rise curve since the end of the Jurassic period, which is inferred from the results of deep-sea drilling and the deposition mechanisms revealed by petroleum geology, and the fact that the past sea-level position was considerably lower. Organisms expand their distribution within the natural environment of their respective home ranges. The migration of organisms and the segregation of their distribution should be based on this idea, and the land bridges crossed by terrestrial animals on the ocean floor are estimated in this paper.

They include the Scotia land bridge, which was crossed to Antarctica by Australian marsupials and ratites in the latest Cretaceous, and the land bridge, which was crossed from Antarctica to Australia. The land bridge connecting Antarctica and Australia was used by penguins until the Middle Eocene, after which Antarctica was completely surrounded by the sea and isolated. The Pacific-Antarctic Ridge-East Pacific Rise land bridge, over which New Zealand penguins crossed to South America during the Eocene, was apparently also used by the South American ratites when they crossed to New Zealand during the Eocene.

The land bridge between the African continent and Madagascar is thought to be the Davie Ridge in the Mozambique Channel, which was land during the Middle Eocene and Late Oligocene, and which was used by the respective ancestors of lemurs, tenrecs, fossa and other carnivores, rodents and elephant tortoises. The ancestors of the Galápagos tortoises are thought to have migrated using the Carnegie Ridge, which until the Early Miocene connected South America with the Galápagos Islands by land. The respective ancestors of new world monkeys and Cabimorpha rodents are thought to have migrated from Africa to South America across a land bridge on the Mid-Atlantic Ridge between the Eocene and Oligocene.

References

- Baker, A. J., S. L. Pereira, O. P. Haddrath and K.-A. Edge (2005) Multiple gene evidence for expansion of penguins out of Antarctica due to global cooling. *Proc. R. Soc. B*, 273, 11-17.
- Beck, R. M. D. (2008) A dated phylogeny of Marsupials using a molecular supermatrix and multiple fossil constraints. *Jour. Mammalogy*, 89, 175-189.
- Bonatti, E, M. Ligiet, A. M. Boresetti, I. Gasperini, A. Negri and R. Sartori (1996) Lower Cretaceous deposits trapped near the equatorial Mid-Atlantic Ridge. *Nature*, 380, 518-520.
- Clark, D. A. (1984) Native land mammals. In: Perry, R. (ed) *Galápagos: Key Environments*, Pergamon Press, Oxford, 225-231.
- Cox, A. (1983) Ages of the Galápagos Islands. In: Bowman, R. I., M. Berson and A. E. Leviton (eds) *Patterns of Evolution in Galápagos Organisms*, American Association for the Advancement of Science, Pacific Division, 11-24.
- de Queiroz, A. (2017) *The Monkey's Voyage, How improbable journeys shaped the history of life*. Misuzu Shobo, Tokyo, 412p. [de Queiroz, A. (2014) *The Monkey's Voyage, How improbable journeys shaped the history of life*. Basic Books, New York, translated by Shibata, Y. and M. Hayashi, in Japanese]
- Eizirik, E., W. J. Murphy, K.-P. Koepfli, W. E. Johnson, J. W. Dragoo, R. K. Wayne and S. J. O'Brien (2010) Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Mol. Phylogenet. Evol.* 56, 49-63.
- Eliasson, U. (1984) Native climax forest. In: Perry, R. (ed) *Galápagos: Key Environments*, Pergamon Press, Oxford, 101-114.
- Endo, H. (2002) *Evolution of the Mammals*. University of Tokyo Press, 383p. [in Japanese]
- Endo, H. (2018) *Natural History of Marsupials*. University of Tokyo Press, 272p. [in Japanese]
- Federman, S., A. Dornburg, D. C. Daly and A. L. Baden (2015) Implications of lemuriform extinctions for the Malagasy flora. *Proc. Natl. Acad. Sci.* 113, 5041-5046.
- Gasperini, L., D. Bernoulli, E. Bonatti, A. M. Boresetti, M. Ligi, A. Negri, R. Sartori and S. Kalis (2001) Lower Cretaceous to Eocene sedimentary transverse ridge at Romanche Fracture Zone and the opening of the equatorial Atlantic. *Marine Geology*, 176, 101-119.
- Haq, B. U., J. Hardenbol and P. R. Vail (1987) Chronology of fluctuating sea levels since the Triassic. *Science*, 235, 1156-1166.
- Hasegawa, M. (2020) *Evolution: Coincidence and necessity during 3.8 billion years*. Kokusho, Tokyo, 415p. [in Japanese]
- Hay, R. (1977) Tectonic evolution of the Cocos-Nazca spreading center. *Geol. Soc. America Bull.*, 88, 1404-1420.
- Hoshino, M. (1991) *The Basaltic Stage: Basic Concepts of Geological Science*. Tokai University Press, Tokyo, 456p. [in Japanese with English abstract]

- Hoshino, M. (2014) *The History of Micro-Expanding Earth. History of the Earth from viewpoint of Sea Level Rise*. E. G. Service, Sapporo, 234p.
- Iturralde-Vinent, M. A. and R. D. E. MacPhee (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull. Amer. Muse. Natu. Hist.* 238, 1-95.
- Kamenetsky, V. S., R. Mass, N. M. Sushchevskaya, M. D. Norman, I. Cartwright and A. A. Peyve (2001) Remnants of Gondwanan continental lithosphere in oceanic upper mantle: Evidence from the South Atlantic Ridge. *Geology*, 29, 243-246.
- Kehlmaier, C., E. Graciá, J. R. Ali, P. D. Campbell, S. D. Chapman, V. Deepak, F. Ihlow, N.-E. Jalil, L. Pierre-Huyet, K. E. Samonds, M. Vences and U. Fritz (2023) Ancient DNA elucidates the lost world of western Indian Ocean giant tortoises and reveals a new extinct species from Madagascar. *Science Advances*, 9 (2), doi: 10.1126/sciadv.abq2574
- Kennett, J. (1982) *Marine Geology*. Prentice-Hall, Inc., Hoboken, 813p.
- Kepezhinskas, P. and D. Dmitriev (1992) Continental lithospheric blocks in Central Atlantic Ocean. *Ophioliti*, 17, 19-35.
- Kitazato, Y. (2014) *Deep Sea, Another Universe - The birthplace of life as seen by the Shinkai 6500*. Iwanami, Tokyo, 176p. [in Japanese]
- MacPhee, R. D. E. and M. A. Iturralde-Vinenta (2000) Short History of Greater Antillean Land Mammals: Biogeography, Paleogeography, Radiations, and Extinctions. *Tropics*, 10, 145-154.
- Martin, H. A. (2006) Cenozoic climatic change and the development of the arid vegetation in Australia. *Jour. Arid. Environments*, 66, 533-563.
- McCall, R. A. (1997) Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. *Proc. R. Soc. London, B, Biol. Sci.*, 264, 663-665.
- Meylan, P. A. and W. Sterrer (2000) *Hesperotestudo* (Testudines: Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. *Zoolog. Jour. Linnean Soc.*, 128, 51-76.
- Pelegrín, J. S. and C. A. Hospitaleche (2022) Evolutionary and biogeographical history of penguins (Sphenisciformes): Review of the dispersal patterns and adaptations in a geologic and paleoecological Context. *Diversity*, 14, 255, doi: org/10.3390/d14040255
- Perry, R. (1984) *The Islands and their history*. In: Perry, R. (ed) *Galapagos: Key Environments*, Pergamon Press, Oxford, 1-14.
- Poux, C., P. Chevret, D. Huchon, W. W. de Jong and E. J. P. Douzery (2006) Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. *Syst. Biol.*, 55, 228-244.
- Poux, C., O. Madsen, J. Glos, W. W. de Jong and M. Vences (2008) Molecular phylogeny and divergence times of Malagasy tenrecs: Influence of data partitioning and taxon sampling on dating analyses. *BMC Evolutionary Biology*, 8, 102.
- Prothero, D. R. (1994) *The Eocene-Oligocene Transition, Paradise Lost.*, Columbia University Press, New York, 291p.
- Purvis, A. (1995) A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond. B*, 348, 405-421.
- Santos, R. V., C. E. Ganade, C. M. Lacasse, I. S. L. Costa, I. Pessanha, E. P. Frazao, E. L. Dantas and J. A. Cavalcante (2019) Dating Gondwanan continental crust at the Rio Grande Rise, South Atlantic. *Terra Nova*, 31, 424-429.
- Shackleton N. J. and J.P. Kennett (1975) Paleotemperature history of the Cenozoic and initiation of Antarctic glaciation: Oxygen and carbon isotope analyses in DSDP Sites 277, 279, and 281. *Init. Rep. DSDP*,

29, 743-755.

- Sheridan, R. E., J. T. Crosby, G. M. Bryan and P. L. Stoffa (1981) Stratigraphy and structure of southern Blake Plateau, northern Florida Straits, and northern Bahama Platform from multichannel seismic reflection data. *AAPG, Bull.*, 65, 2571-2593.
- Shiba, M. (2017a) Formation of Suruga Bay - Large-scale uplift of arc and sea level rise. Tokai University Press, Hiratsuka, 406p. [in Japanese]
- Shiba, M. (2017b) Geology of the island arcs in the northwestern margin of the Pacific Ocean and their formation by a large-scale uplift and sea level rise - the formation of Suruga Bay. *New Concepts in Global Tectonics Journal*, 5, 532-548.
- Shiba, M. (2020) Distribution of island endemic animals and the late Middle Pleistocene land bridges as evidence of sea level rise of 1,000 m since the late Middle Pleistocene. *Jour. Fossil Research*, 53, 1-17. [in Japanese with English abstract]
- Shiba, M. (2021) Distribution of island endemic animals and the late Middle Pleistocene land bridges as evidence of sea level rise of 1,000 m since 430 ka. *New Concepts in Global Tectonics Journal*, 9, 60-78.
- Shiba, M. (2022a) Shallow-water sediments discovered by deep-sea drilling and sea-level rise since the Jurassic -Location of sea-level in the Basaltic Stage-. *Collection of Memorial Papers for Professor Michihei Hoshino*, 21-76. [in Japanese with English abstract]
- Shiba, M. (2022b) Distribution of shallow-water sediments founded in the records of deep-sea drilling and sea-level rise since the Jurassic period. *New Concepts in Global Tectonics Journal*, 10, 123-157.
- Shipboard Scientific Party (1984) Site 526. *Init. Rep. DSDP*, 74, 64-235.
- Shipboard Scientific Party (1988) Site 698. *Proc. ODP, Init. Rep.*, 114, 87-150.
- Simpson, G. G. (1965) *The Geography of Evolution*. Capricorn Book, New York, 249p.
- Slack, K. E., C. M. Jones, T. Ando, G. L. Harrison, R. E. Fordyce, U. Arnason and D. Penny (2006) Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Mol. Biol. Evol.*, 23, 1144-1155.
- Takai, M. (1995) Current evolutionary and phylogenetic classification of Platyrrhini. *Anthropological Science*, 103, 429-446. [in Japanese]
- The Shipboard Scientific Party and D. Burns (1973) Site 698. *Init. Rep. DSDP*, 21, 333-367.
- Van der Geer, A., G. Lyras, J. De Vos and M. Dermitzakis (2010) *Evolution of Island Mammals. Adaptation and Extinction of Placental Mammals on Islands*. Wiley-Blackwell, A John Wiley & Sons, Ltd, Publication, West Sussex, 479p.
- Vasiliev, B. I. (2006) Geological structure and origin of the Pacific Ocean. *Earth Science*, 60, 185-196. [in Japanese with English abstract]
- Vences, M., D. R. Vieites, F. Glaw, H. Brinkmann, J. Kosuch, M. Veith and A. Meyer (2003) Multiple overseas dispersal in amphibians. *Proc. Biol. Sci.*, 270, 2435-2442.
- Vries, T. J. (1984) The giant Tortoises: A natural history disturbed by man. In: Perry, R. (ed) *Galápagos: Key Environments*, Pergamon Press, Oxford, 145-156.
- Wolfe, J. A. (1978) A Paleobotanical interpretation of Tertiary climates in North hemisphere. *American Science*, 66, 694-703.
- Woods, R, S. T. Turvey, S. Brace, R. D. E. MacPhee and I. Barnes (2018) Ancient DNA of the extinct Jamaican monkey *Xenothrix* reveals extreme insular change within a morphologically conservative radiation. *Proc. Natl. Acad. Sci.*, 115, 12769-12774.
- Yonezawa, T., T. Segawa, H. Mori, P. F. Campos, Y. Hongoh, H. Endo, A. Akiyoshi, N. Kohno, S.

Nishida, J. Wu, H. Jin, J. Adachi. H. Kishino, K. Kurokawa, Y. Nogi, H. Tanabe, H. Mukoyama, K. Yoshida, A. Rasoamiaramanana, S. Yamagishi, Y. Hayashi, A. Yoshida, H. Koike, F. Akishinomiya, E. Willerslev and M. Hasegawa (2017) Phylogenomics and morphology of extinct paleognaths reveal the origin and evolution of the Ratites. *Curr. Biol.*, 27, 68-77.