The Aegeanman Hypothesis I

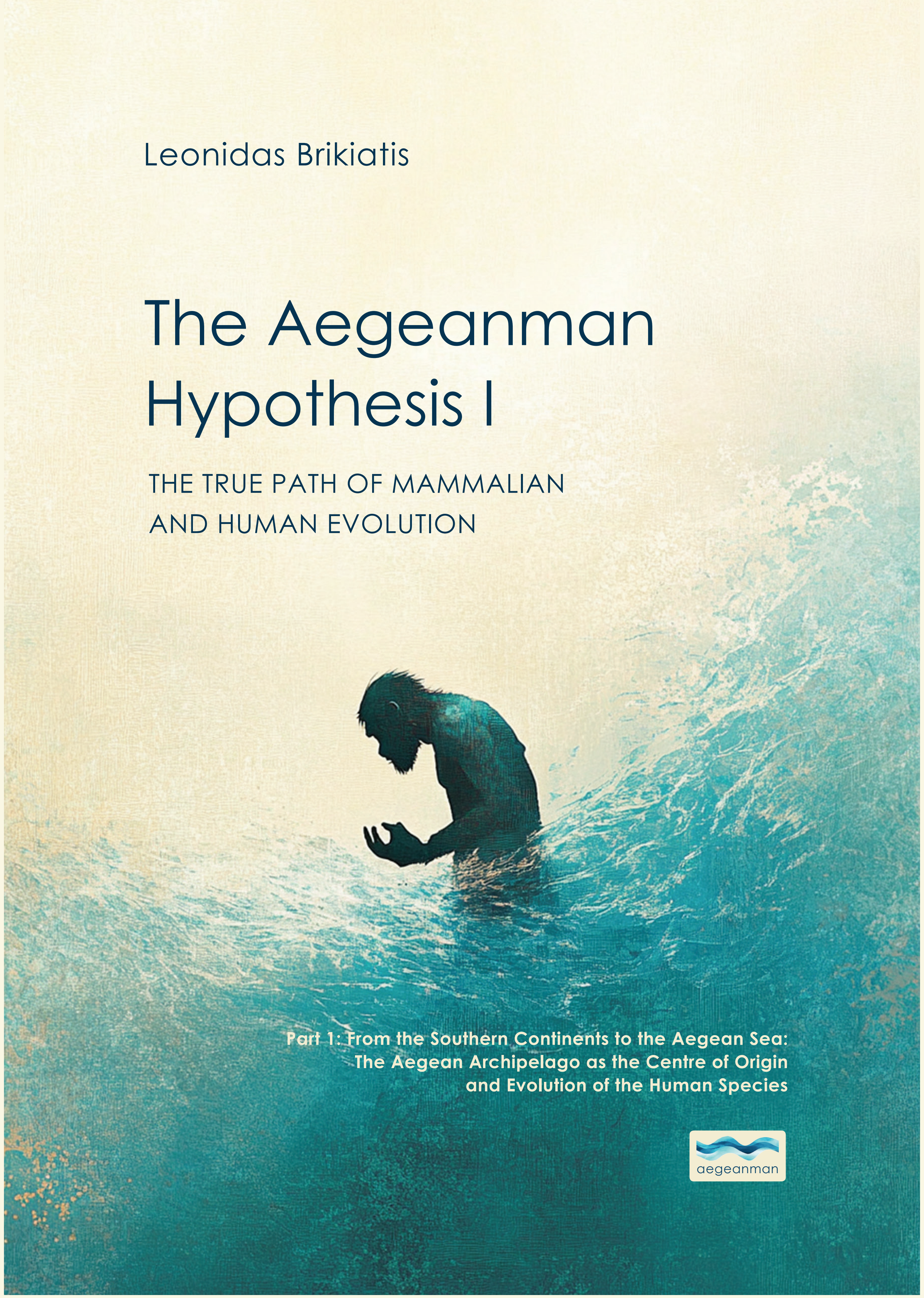
This innovative monograph proposes a unified biogeographic framework for understanding the evolution of boreoeutherian mammals, with an emphasis on primates and hominins. Challenging the prevailing vague and generalised paradigm of mammalian evolution, the author, Leonidas Brikiatis, reconstructs in detail the vicariant biogeographical processes and palaeogeographical events that generated the major boreoeutherian lineages.

The author then narrows his focus and applies the above framework to analyze the speciation and distribution of major primate clades, focusing on classical biogeographic mechanisms and avoiding *ad hoc* dispersal hypotheses. Notably, this biogeographic approach explains the extended Miocene hominoid diversity by linking ape and human speciation to repeated episodes of palaeogeographical fragmentation and reconnection in Central Eurasia.

Within the author's unique biogeographic perspective, a new model emerges in which the human lineage followed an evolutionary trajectory centered in the Eastern Mediterranean, distinct from that of African apes. This "Aegeanman Hypothesis" offers independent support for waterside models of human evolution and explains the later dispersal of early hominins into Africa.

Essential reading for researchers, students, and enthusiasts of biological and anthropological sciences, this book offers a unifying perspective for answering longstanding questions in mammalian evolution, particularly that of primate and human lineages, combining rigorous scholarship with accessible prose.

Leonidas Brikiatis   The Aegeanman Hypothesis I



Leonidas Brikiatis

The Aegeanman Hypothesis I

THE TRUE PATH OF MAMMALIAN AND HUMAN EVOLUTION

Part 1: From the Southern Continents to the Aegean Sea:
The Aegean Archipelago as the Centre of Origin
and Evolution of the Human Species

aegeanman

THE AEGEANMAN HYPOTHESIS I

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without the use of Artificial Intelligence.

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CONTENTS

Abstract

Theories about the evolution of life on Earth, including human evolution, have been primarily based on phenotypes as understood through the study of fossils. For this reason, the views of palaeontologists have had a dominant role in shaping ideas about the phylogenetic and chronological context of evolution. Although the phylogenetic framework has been enriched and upgraded in recent years by molecular evidence, the chronological context has remained a hostage to palaeontological views. This is because the “molecular clock” needs to be correctly calibrated to “show the correct time,” which traditionally has relied on age estimates derived empirically from palaeontological views of phenotypic evolution. Palaeontological views are influenced by the chronological conclusions of molecular clocks, however, creating and maintaining a dead-end circular argument.

Phenotypic change is the result of evolution, but it may say nothing about the cause of evolution. The causes of evolutionary transitions are linked to speciation events that remain unstudied by palaeontologists. For this reason, despite great efforts, the study of morphological evolution in the fossil record is not able to capture the big picture of evolution because phenotypic change is just part of the story.

The big picture of evolution is closer to the subject of a different kind of scientific analysis, that is, biogeography. While palaeontology deals with the effects of evolution, biogeography deals with the causes. Biogeographical analysis is focused on finding multidimensional answers to how, where, when, and why new species emerged and dispersed. To achieve this, biogeographical analysis uses mechanisms from evolutionary biology, cladistic classifications from palaeontology, chronological dating from molecular biology, and knowledge from other sciences such as ecology and geology that sheds light on not only the organisms that evolved but also the palaeoenvironment of their evolution. The biogeographer thus takes the small picture of morphological evolution and places it within a big picture

constructed with bits of knowledge from many other scientific disciplines, like pieces of a puzzle. From this perspective, ideas about the evolutionary history of life should be formulated by biogeographers, not palaeontologists.

In this book, the entire course of early human evolution, including that of the primates and the boreoeutherian mammals (i.e. the group of Northern Hemisphere mammals to which the primates belong), is re-examined from a biogeographical standpoint. More specifically, the evolutionary ancestry of humans is examined not in terms of how species evolved morphologically—which could be the job of a palaeontologist—but in terms of how species became differentiated and distributed in space and time. The conclusions overturn the vague and generalised evolutionary framework that has been reconstructed on the basis of morphological considerations, and they rewrite in detail—and from scratch—the history of early mammalian, primate, and human evolution.

In this book, the reader will find::

1. Hypotheses for the vicariant phylogeny of the primates and the rest of the boreoeutherian orders, explaining where, how, when, and why their evolution took place.
2. The routes followed in the dispersals of the primates (and the rest of the boreoeutherian clades) from the southern continents (Indo-Madagascar and Antarctica) to the Northern Hemisphere, where some diverged lineages resumed contact with one another during the thermal maximum of the Palaeocene/Eocene boundary.
3. The vicariant phylogeny of the early catarrhines, the scenario of their dispersal to Africa through Asia, and the true divergence dates of their main phylogenetic clades.
4. The exact palaeogeographical events that led to the divergence of the great apes and humans, as well as their fossilised ancestors.
5. Answers to where, how, when, and why the decisive step in early human evolution towards bipedalism took place.

Preface

Historical biogeography is the science that studies the current and past geographical distributions of living organisms, as well as the environmental causes and conditions that led to these distributions. This book is the result of more than 20 years of research on the historical biogeographical evolution of life and the Earth's environment. It contains accumulated knowledge and information that will enable the reader to gain a deep understanding of the mechanisms and environmental conditions that led to the evolution of modern mammals, including humans.

The author brings forth innovative conclusions, reached using simple and understandable biogeographical mechanisms, which have been overlooked by the scientific community for various reasons. No ideas or conclusions are drawn arbitrarily; all questions are asked and answered with evidence and explained in a simple and understandable way so the reader becomes a sharer of the conclusions drawn. By understanding these biogeographical mechanisms in light of the available evidence, the reader will become the possessor of knowledge and ideas that the academic community has only begun to suspect.

Through this book, the author aspires to set in order the important field of historical biogeography, which in the last 25 years seems to have derailed from the lines of classical consideration, largely due to a massive influx of data and raw conclusions from the relatively new science of genetics and, particularly, one of its branches, phylogeography. This imposition of order makes it necessary to overturn some widespread theories and opinions, essentially rewriting from scratch the early history of the evolution of modern mammals and humans.

Although the content of this book is primarily addressed to specialists in mammalian and human evolution, special efforts have been made to make it understandable to readers from all disciplines of science. Such a goal is difficult to achieve, so the author humbly asks the forgiveness of specialists and non-specialists alike for the oversimplification of certain concepts and the brief presentation of some subjects.

Introduction

How do different forms of life come to exist? This is a question that must have occupied, at some point, even fleetingly, all the great thinkers of humankind. The scientific answer to this question is called the Modern Synthesis, and it combines the principles of evolution formulated by Charles Darwin with knowledge of the role of DNA in heredity. Today, we know that new species can emerge when long-term geographic isolation leads to genetic (i.e. reproductive) isolation of populations. In other words, when geographic barriers arise and prevent separate populations of the same species from interbreeding and exchanging genetic material, the populations become genetically divergent and eventually become separate species.

Surprisingly, although the science of palaeontology is considered to be the most competent discipline when it comes to formulating scenarios for the evolution of mammals in general and humans in particular, its representatives have shown no inclination or intention to explain how the fossilised species they recover from the ground came into being. This is especially true when the species are sympatric, meaning they are recovered from the same geographic location. For example, although it is widely believed that gorillas, chimpanzees, and humans each originated in Africa, no attempt has been made to explain how these three genera of hominines diverged from a common ancestor. How was the condition of reproductive isolation met? Difficult questions of this kind have been systematically avoided by scientists who study hominoid evolution. In fact, no palaeontologist today has any idea how the divergence (speciation) of the major hominoid lineages could have even taken place. The few existing hypotheses do not seem to have convinced much of the scientific community of their plausibility.

Another persistent view in the field of palaeontology is that the mammals of the Northern Hemisphere (boreoeutherians) evolved in situ in the Northern Hemisphere. In other words, the centre of their development and dispersion is identified with the wider area they inhabit today. More specifically, according to the fossil record, undoubted representatives of all the modern mammalian orders first appeared within just a few million years of each other, at a time marked by the most rapidly developing climatic warming event ever recorded: the Palaeocene/Eocene thermal maximum (PETM), which occurred ~56 million years ago (Mya). During this relatively short period, which lasted around 50,000 years, the average temperature on the Earth's surface was around 15°C hotter than it is today. This resulted in the dispersal of tropical ecosystems from the equatorial zone to higher latitudes, which is where the modern orders of boreoeutherian mammals first appear in the fossil record. Evidence derived from DNA sequences (i.e. the "molecular clock") indicates that ancestors of the boreoeutherian mammals must have existed much earlier, however, living in the shadow of the dinosaurs. From this point of view, the absence of early representatives of the modern mammalian orders from the fossil record of the Northern Hemisphere is one of the greatest mysteries in historical biogeography. Where were the ancestors of the modern mammals before the Palaeocene Epoch (~60 Mya), and why have they not been found in the fossil record? The answer to the latter part of this question is that we have been looking in the wrong place. The ancestors of the modern mammalian orders came from the Southern Hemisphere, not the Northern Hemisphere. Therefore, the search for them should be directed to Antarctica, India (formerly a continent of the Southern Hemisphere), and South America, not Asia and Africa.

This book explains in a simple and comprehensible way how the boreoeutherians, and particularly the primates (including humans), came to exist. It also explains how humans, our hominine relatives (the other great apes), and their extinct ancestors, known only from the fossil record, diverged and speciated.

Chapter 1

From Fish to Anthropoids

1.1. GETTING OUT OF THE WATER AND OBSERVING THE WORLD FROM SOMEWHERE HIGHER

Our story begins about 430 Mya (the Silurian Period), when some species of fish that evolved in the deep ocean began to inhabit shallow coastal waters. This change of habitat from open ocean to coastal waters was most likely the result of certain species taking advantage of nutritional resources provided by the relatively recent development of terrestrial ecosystems. As all life on Earth originally developed in the sea, the land was first colonised by invertebrates and plants millions of years before the fish species in question made an appearance.

Over a few million years, some fish species became able to live in fresh water, rather than the salt water of the ocean, and eventually left the water entirely to colonise the land (**Figure 1**). By recognising the close similarities between fossils of these early land colonisers and their living relatives, the lungfish, we can make assumptions about the special characteristics that the land colonisers must have possessed. Lungfish can breathe both in and out of water, which is why they are taxonomically classified as Dipnoi (a name that refers to their capacity for two types of breathing). Lungfish live exclusively in freshwater environments, and some have the advantage of being able to survive droughts by hibernating in wet cavities in the soil. These characteristics would have enabled the ancient colonisers to disperse onto land, not only through rivers that flowed into the oceans but also through the transient currents of fresh water that form during rainy seasons.

Another special characteristic of lungfish is the structure of their fins. Whereas most fish have fins with a radial arrangement of bony spines (ray-finned fish, or Actinopterygii), lungfish have two pairs of fins (front and back) with a special bony joint and muscle system (lobe-finned fish, or Sarcopterygii). These two conjugated pairs of muscular fins enable out-of-water locomotion based on leverage. In some of the ancient Sarcopterygii, the two pairs of muscular fins evolved into legs, marking the appearance of the first four-legged (quadrupedal) vertebrates in the fossil record. One such organism that existed 375 Mya was *Tiktaalik roseae*, a fossil of which was found in the Canadian Arctic in 2004[1] (**Figure 1**).

As you might expect, these first quadrupeds were amphibians, meaning they still spent part of their life in the water. Four-legged amphibians took their first steps out of the water about 400 Mya (the Devonian Period), setting them on an evolutionary path separate from that of the lungfish. This is confirmed by the 398-million-year-old fossilised tetrapod footprints found on the site of an ancient coast in Poland[2]. The next evolutionary step took place a few tens of millions of years later, ~350 Mya (the Carboniferous Period), when some early amphibians managed to adopt a purely terrestrial life cycle, setting them on their own evolutionary path separate from that of the other amphibians.

Nothing in nature happens by magic, so it is important to understand some facts about the mechanisms that drive the evolution of species. Evolution, at least as it is understood by science today, is the result of the complementary actions of a phenomenon and a process. The phenomenon is the occurrence of errors as DNA is repeatedly copied to transfer hereditary characteristics from generation to generation. These errors are called mutations, and they very rarely become permanently embedded, or fixed, in the DNA of an entire species (e.g. once every thousand generations). The molecular clock hypothesis is based on the fact that this rate of mutational change is very stable in the long term.

Figure 1. A virtual depiction of the first land colonisation by vertebrates. In the middle is the 375-million-year-old Tiktaalik, which, with its flattened head and body, represents an important intermediate step in the evolutionary transition from fish to vertebrates that walk on land.

Because DNA contains information about an organism's structure and functions, mutations can lead to variation in the organism's morphology and physiology in relation to not only its parents but also its entire lineage. Because morphological and physiological variation can be either harmful, beneficial, or neutral, for it to benefit species in the long term, there needs to be a process to accurately evaluate it, maintaining and spreading beneficial variants while rejecting harmful ones. This process is called natural selection and was first described by the great biologist Charles Darwin in the seminal work *On the Origin of Species* in 1859. The gist of the theory of evolution by natural selection is that certain characteristics provide benefits for survival and reproduction, and individuals that happen to possess these characteristics have an inherent advantage over individuals that do not have them. Thus, certain individuals tend to produce more offspring than others, and the beneficial characteristics that provide a reproductive advantage eventually become present in the entire population. In this way, a novel characteristic that arises by chance in a single individual can become a key trait for an entire species. The time that it takes for this to happen depends on the size of the population, but according to some calculations, a mutation that confers an additional 1% advantage on an organism can spread throughout the entire population within 100 generations. In the opposite case, where a novel characteristic confers a disadvantage, the characteristic is less likely to spread in the population, as individuals that do not possess it have an inherent competitive advantage over those that do.

Under constantly changing environmental conditions, the evolution of new characteristics that help a population to survive and prevail over competitors is called adaptation. Since the theory of evolution set the general framework within which species should be understood, the concept of adaptation has acquired fundamental importance, as the phenotypic and genetic composition of a species is considered to be largely the result of adaptation.

Returning to our story of the evolution of terrestrial vertebrates, we were at an age ~350 Mya when the only quadrupedal land-dwelling vertebrates were a few amphibian species, as well as a single reptile-like amniote* species that had managed to adopt a purely terrestrial life cycle. At this time, most of the land on the Earth's surface was accreted into a single continent called Pangaea (or Pangea, from the Greek words *παν* + *γαία* meaning "everywhere land"), which would eventually break apart into separate geographic and biogeographic territories.

The geological breakup of Pangaea is very important to our story because it drove an equally important biological process called cladogenesis, that is, the creation of different species of life. Cladogenesis is one of two fundamental processes in the evolution of life. The other is anagenesis. Anagenesis refers to the evolution of a particular lineage (species) over time, whereas cladogenesis refers to the evolution of different lineages from a single ancestral lineage through speciation. When Pangaea broke apart into different land areas separated by seas, populations of terrestrial organisms were likewise broken up into non-communicating (and therefore non-interbreeding) subpopulations, which subsequently evolved in isolation for millions of years. During this time, these subpopulations acquired many random and different mutations, which caused them to evolve different traits and morphologies, essentially becoming different organisms. When some of the land masses were eventually reunited through continuous palaeogeographical rearrangements, ancestrally related populations that had evolved in isolation for millions of years had accumulated so many differences that they could no longer interbreed** and thus constituted new species. This manner of speciation through the long-term geographic isolation of related populations is called vicariant, or allopatric*,* speciation and is today the most widely accepted and understood mechanism for the creation of new species (**Figure 2**).

The parallelism between biological evolution and palaeogeographical changes was highlighted in a 2020[3] study showing how successive formations of a marine corridor in the Ural Mountains region of Russia bisected the terrestrial continuity of Pangaea, leading to the evolution of multiple new species of amniotes that all had as their common ancestor the terrestrial vertebrate *Protoclepsydrops* (**Figure 3**). The first occurrence of this marine corridor took place ~320 Mya and led to the evolution of the two most basic clades of terrestrial tetrapods: the synapsids (Synapsida), which include the extant mammals, and the sauropsids (Sauropsida), which include the extant reptiles and birds as well as the dinosaurs. It is interesting to note that birds are considered to be a branch of dinosaurs that survived the extinction event that wiped out the other dinosaurs.

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* Amniotes are a large group that comprises the vast majority of living terrestrial and semiaquatic tetrapod vertebrates, including mammals, birds, and reptiles.

** Actually, the genetic distance between two closely related species can vary. When it is not too large, the two species might be able to produce hybrid offspring through crossbreeding, but the hybrid offspring are infertile.

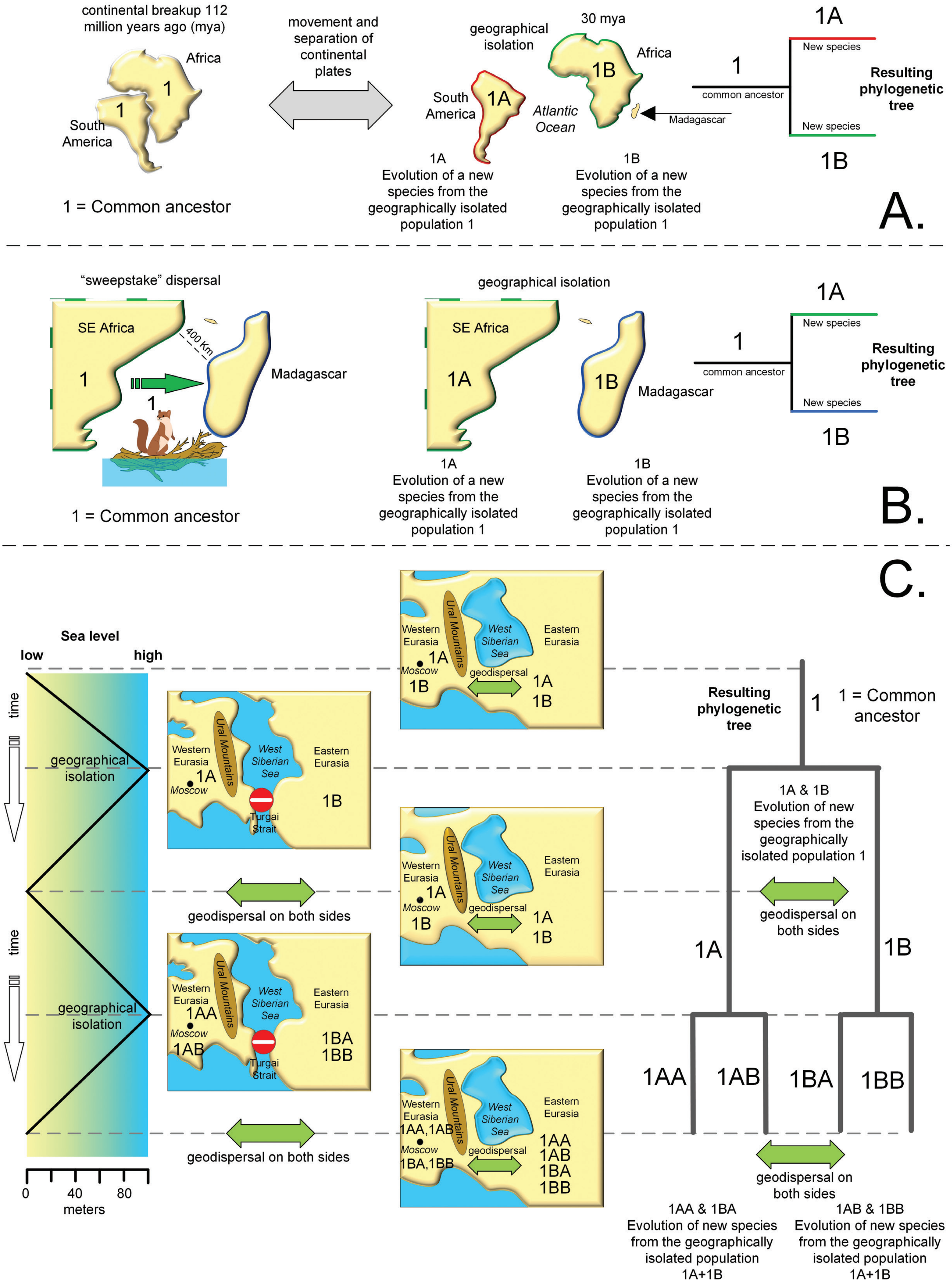
1.2. RETRIEVING FOSSILISED INFORMATION

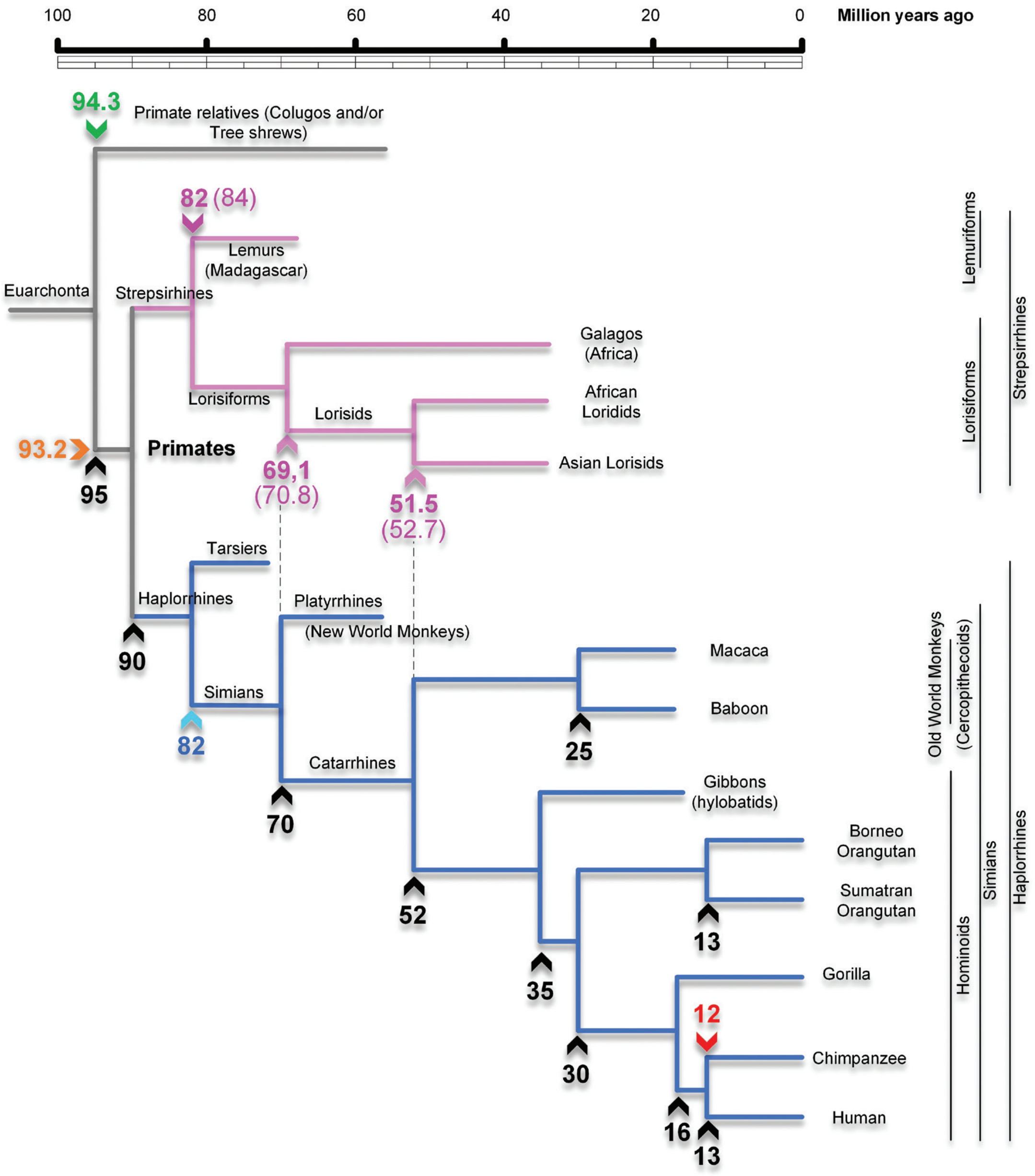
Under specific and ideal conditions, the hard tissues of some organisms, including vertebrates, can be buried and preserved for thousands, even millions, of years. These preserved remains make up the fossil record, and studying them can give us information about the evolution of life on Earth. In practice, absolute continuity in the fossil record is rare, and the available record presents temporal and spatial gaps. The main cause of gaps in the fossil record is erosion of the soils that house the fossils. Another reason for these gaps is that the chemical and physical composition of some soils is inappropriate for the preservation of fossils.

The methodology of cladistics was developed to show the phylogenetic relationships among different—fossilised and living—organisms. According to this methodology, the study of fossil morphologies should identify specific and unique features (synapomorphies) for each fossil morphotype, the number and type of which will clarify the relative relatedness of a given morphotype to other morphotypes. This information is used to compile a phylogenetic tree that records and describes the relationships among the discovered fossils. In this way, fossil morphotypes are classified into various groups, species, genera, subfamilies, families, orders, and so on, depending on the number and type of synapomorphies that characterise them. Each group is called a taxon (plural taxa) and has a particular taxonomic rank.

Because life on Earth evolves over time, determining a fossil's age is equally as important as assessing its phenotype (i.e. morphology). Most of the rocks we see around us are, for the most part, sediments that were deposited on the bottom of ancient oceans and later resurfaced through tectonic rearrangements. These sediments contain microfossils of marine organisms that have been identified and dated, so their presence in any particular area on the Earth's surface is evidence of

Figure 2. (Pages 20-21) Geographic isolation, speciation, and dispersal. There are three common ways in which formerly undivided and communicating populations can become geographically isolated and evolve into separate species. A) Movement of continental plates (i.e. vicariance; for example, from the breakup of Africa and South America 112 Mya). B) Random "sweepstake" dispersal of a founder population to an already geographically isolated area (for example, the random dispersal of carnivorous mammals from Africa to Madagascar). C) Sea level rise due to melting of the polar ice caps. When the sea level subsequently drops and the water barrier is removed, the new species can disperse over the entire land mass. Repeating this cycle will lead to more geographic isolation and thus more species.


continental breakup 112 million years ago (mya)
Africa
1
1
South America
1 = Common ancestor
movement and separation of continental plates
geographical isolation
30 mya
South America
1A
1B
Africa
Atlantic Ocean
Madagascar
1A
Evolution of a new species from the geographically isolated population 1
1B
Evolution of a new species from the geographically isolated population 1
1A
1
common ancestor
New species
New species
1B
Resulting phylogenetic tree
A.
"sweepstake" dispersal
SE Africa
1
400 Km
1
Madagascar
1 = Common ancestor
geographical isolation
SE Africa
1A
1B
Madagascar
1A
Evolution of a new species from the geographically isolated population 1
1B
Evolution of a new species from the geographically isolated population 1
1A
1
common ancestor
New species
New species
1B
Resulting phylogenetic tree
B.
C.
Sea level
low
high
time
geographical isolation
time
geographical isolation
0
40
80
meters
Western Eurasia
Moscow
Ural Mountains
West Siberian Sea
Eastern Eurasia
geodispersal
Turgai Strait
1A
1B
1AA
1AB
1BA
1BB
1AA,1AB
1BA,1BB
geodispersal on both sides
geodispersal on both sides
Resulting phylogenetic tree
1
1 = Common ancestor
1A & 1B
Evolution of new species from the geographically isolated population 1
geodispersal on both sides
1A
1B
1AA
1AB
1BA
1BB
geodispersal on both sides
1AA & 1BA
Evolution of new species from the geographically isolated population 1A+1B
1AB & 1BB
Evolution of new species from the geographically isolated population 1A+1B



be true; however, the inferred vicariant topology is compatible with both versions. In any case, the phylogenetic trees depicted in **Figure 16B and 16C** are consistent with current knowledge of the phylogenetic relationships of Primates with the other orders of Euarchonta and may even help resolve some problematic relationships among the primates.

One problematic relationship is that of the strangest primate, the aye-aye (*Daubentonia madagascariensis)* of Madagascar. Competing hypotheses based on molecular or morphological data have given either simians, prosimians, or the other Malagasy lemurs as the closest relatives of the aye-aye. This relationship is unequivocally resolved in our vicariant phylogenetic tree, which shows the aye-aye as a sister clade to the clade formed by simians and tarsiers (the validity of this latter clade is widely accepted). The aye-aye therefore does not belong to the Malagasy lemur clade, which explains why molecular studies have failed to link it to that group with strong statistical probability. Another problematic relationship is that between dermopterans and primates. In some molecular analyses, dermopterans appear to branch within the order Primates, as shown in **Figure 16B**. What is remarkable, however, is that the divergence ages in the vicariant phylogenetic tree in **Figure 16** are identical to those of the tree shown in **Figure 13**. That is, the divergence ages derived from the palaeogeographical events of the vicariance scenario are identical to those based on molecular evidence. This cannot be a coincidence.

Figure 17 shows the routes that the members of the various primate lineages must have taken from the Southern Hemisphere to the Northern Hemisphere, where they met again during the PETM ~56 Mya. Because the fossil evidence left behind by these dispersals is very poor, the methodology and reasoning behind this biogeographic scenario are based on indirect evidence. For example, Professor Judith Masters and colleagues[27], using the age of the final separation of India from Madagascar (~84 Mya) as a reference for the divergence of lorisiform primates

Figure 13. Phylogenetic tree of the order Primates and the divergence ages of its clades. The diagram describes the phylogenetic relationships among the different clades that compose the order Primates and the ages of their divergence. The divergence ages are based on the original publication by Prof. Arnason's team in 2000[20] (indicated in black) or on more recent results from other publications. Dates indicated in magenta are based on reference[27] (these ages have undergone a slight correction/reduction based on a final India-Madagascar separation age of 82 Mya rather than the 84 Mya of the original reference, which are given in parentheses). The date indicated in green is based on reference[158] and refers to the divergence age of the tree shrews (Scandentia). The date indicated in blue is based on reference[53]. The date indicated in red is based on reference[21]. The date indicated in orange is based on reference[166]. From the diagram, it becomes apparent that the original calculations of Professor Arnason's team[20] are supported by a variety of independent studies.

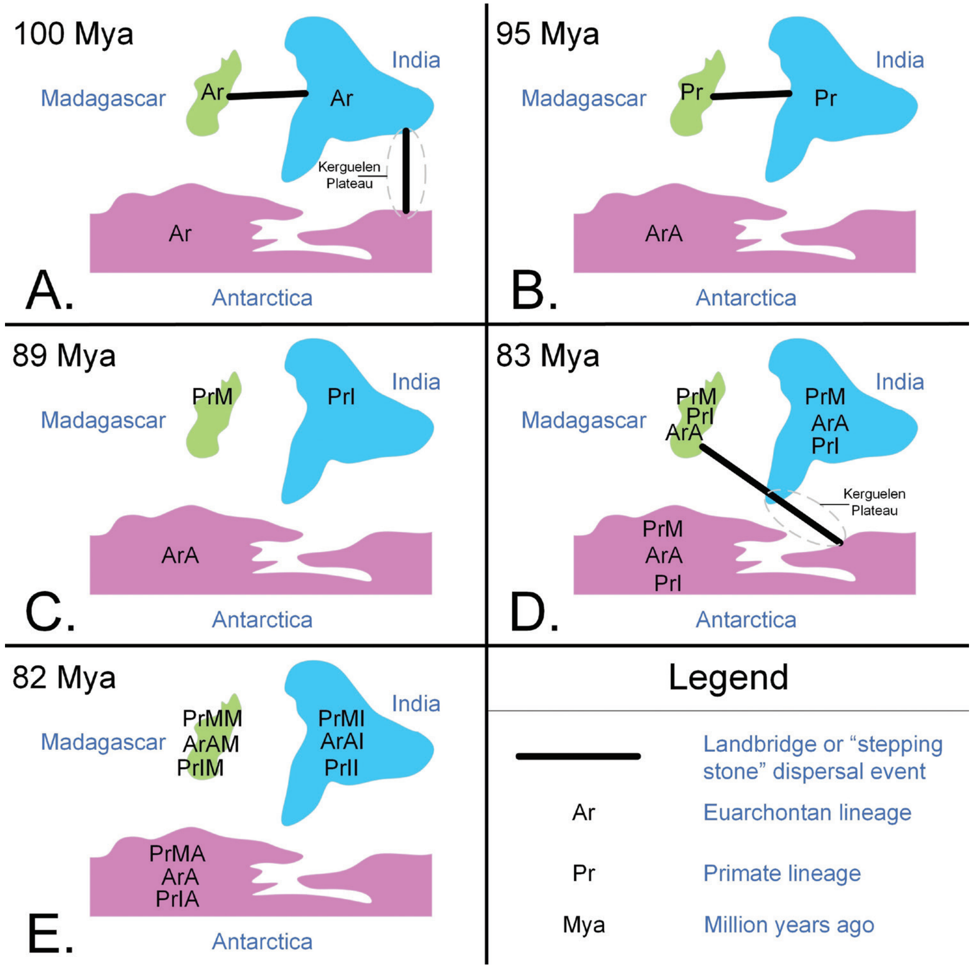


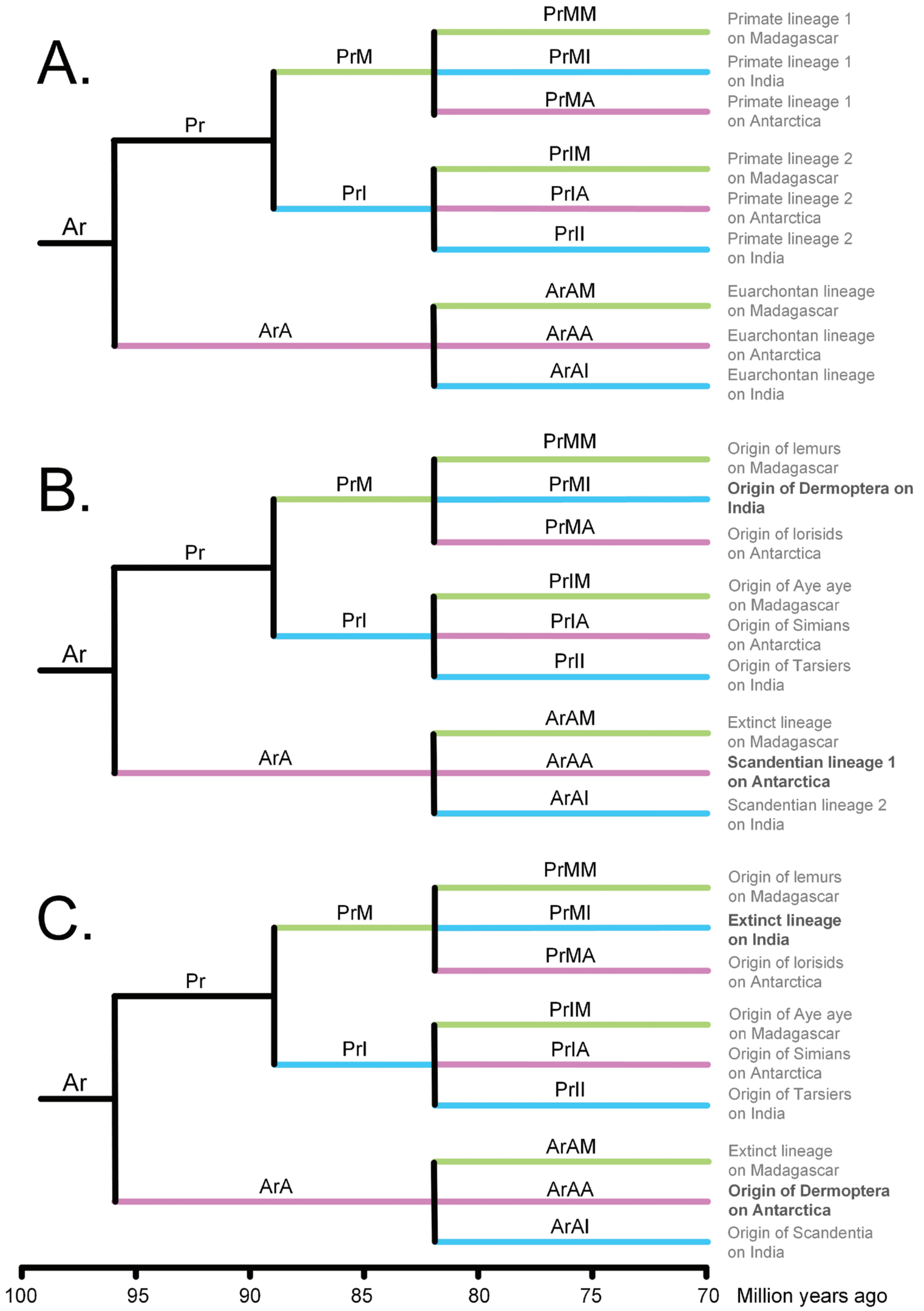
Figure 15. Sequence of terrestrial junctions and disjunctions of India-Madagascar-Antarctica during the breakup of the single continental block. The Euarchonta refers to a taxonomic group that includes the primates and their close relatives, the colugos (flying lemurs) and the tree shrews. Around 100 Mya, when the sequence of palaeogeographical divisions begins, primates had not yet diverged from the ancestral Euarchonta. Therefore, the vicariant scenario begins with the assumption that 100 Mya, the common ancestor of the Euarchonta is scattered throughout the Indo-Madagascar and Antarctic blocks, which were still connected through the Kerguelen Plateau. Primates, as a separate clade, arose 95 Mya, when the Kerguelen Plateau land bridge subsided, causing the ancestor of the primate clade to become geographically isolated on the Indo-Madagascar block. The letters on the continents refer to the creation of different Euarchontan lineages after the successive events of geographic isolation (vicariance) and dispersals. Thus, during the first split 95 Mya, the original population of Euarchonta (*Ar*) split into a population that gave rise to the primates (*Pr*), which evolved in Indo-Madagascar, and a population of Euarchonta that evolved separately into the *ArA* clade in Antarctica. The subcontinents of Madagascar and India separated for the first time 90–89 Mya, resulting in the splitting of the primates into two clades, one of which (*PrM*) was isolated and continued to evolve in Madagascar, while the other (*PrI*) was isolated and continued to evolve in India. Continued movement of the Indian plate caused a temporary reconnection of all three land masses ~85–83 Mya, aided by a low sea level (83 Mya) and continued volcanic activity north of the central Kerguelen Plateau. The previously isolated lineages of *PrM*, *PrI*, and *ArA* were each dispersed across all three land masses but had become genetically incompatible with one another after millions of years of isolation. In this way, after the final separation of the three continents 82 Mya, the lineages *PrMM*, *PrIM*, and *ArAM* evolved on Madagascar, *PrMI, PrII*, and *ArAI* evolved in India, and *PrMA, PrIA*, and *ArAA* evolved in Antarctica. Note that because geographically isolated lineages are constantly evolving, this evolution is depicted in the lettering, which denotes the successive areas in which the evolution takes place (*M* for Madagascar, *I* for India, and *A* for Antarctic). Also note that this change in lettering is essential and mandatory. For example, the original lineage of Euarchonta (*Ar*) that became isolated in Antarctica was not biologically the same as the one that had evolved after a few million years (*ArA*) because it had accumulated genetic changes that made it genetically distinct from its ancestor.

of all the modern orders of boreoeutherians during the PETM in the Northern Hemisphere ~56 Mya can be explained by the biogeographic scenario developed here.

But do palaeontologists today believe that the primates originated from the southern continents? And what is the evidence in the fossil record?

1.14. EVALUATING THE NEW EVIDENCE

The prevailing view today is that the boreoeutherians originated in the Northern Hemisphere, despite the conspicuous absence of their ancestors from the fossil record of the Northern Hemisphere. Because North America and Europe are relatively well explored, researchers expect to discover fossil evidence of boreoeutherian ancestors in the less-explored regions of Asia and Africa in the future, whereas they think the southern continents were inhabited exclusively by other primitive forms of mammals. For example, in contrast to the palaeogeographical scenario that traces the origin of the Malagasy lemurs back to the India-Madagascar split, most scientists currently believe that the last common ancestor of the Malagasy lemurs colonised Madagascar via sweepstake dispersal from Africa. That is, the ancestor somehow managed to cross the ~400 km of sea that separates Madagascar from Africa and colonise the island. Not all palaeontologists are in favour of this view, however. One such example is Professor of Anthropology Robert Martin, who has long suggested that early primate diversification could have taken place on the southern continents[29], and the divergence of the Malagasy lemurs resulted from the separation of India from Madagascar[30].

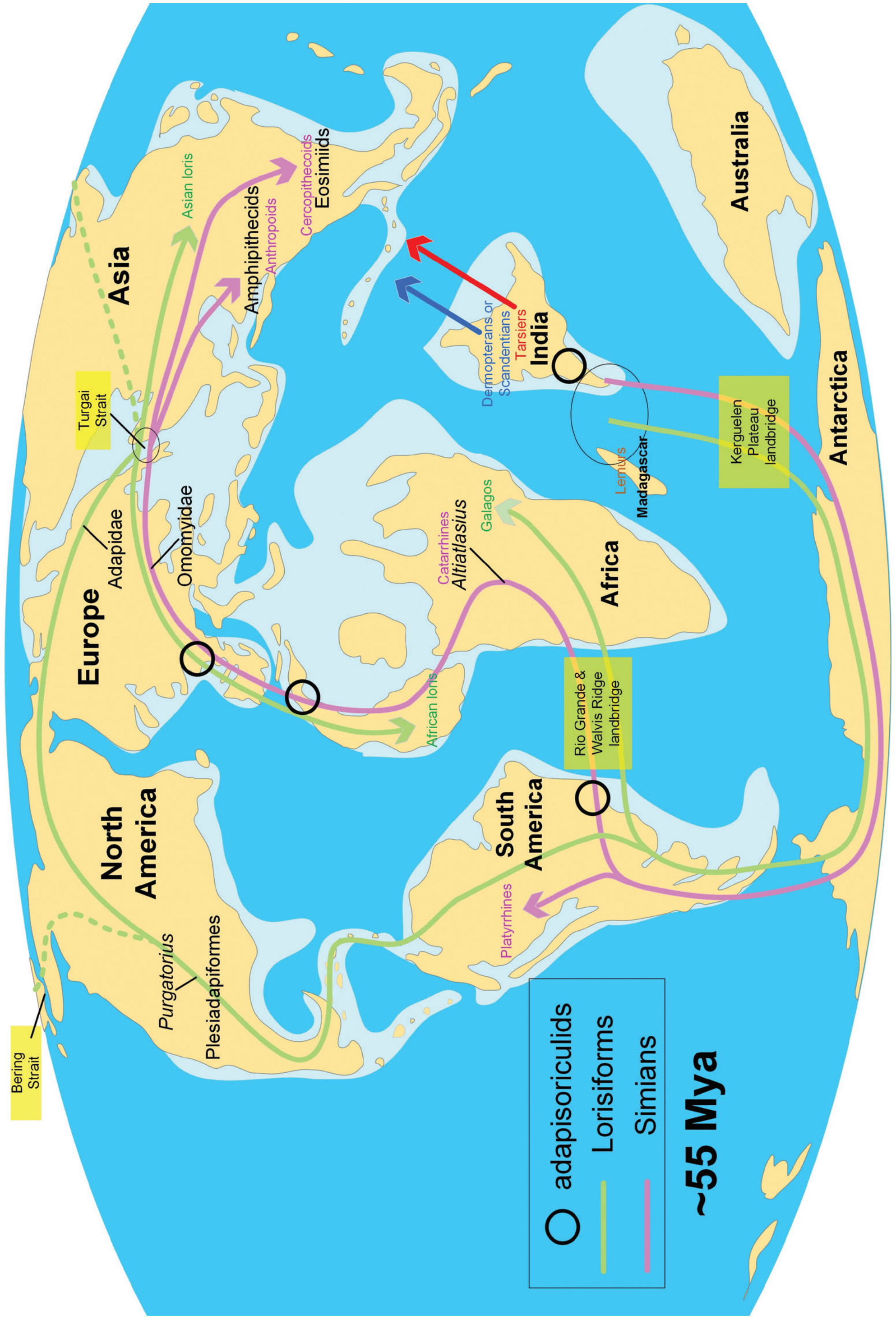


Indeed, some efforts have been made in recent years to overturn old, outdated beliefs, either by presenting new evidence or by taking a second look at pre-existing evidence[31]. For example, it was recently shown that ancestors of modern marsupials and placental mammals (tribosphenic mammals) lived during the Early Jurassic period on the continents of the Southern Hemisphere, 50 million years before they appear in the fossil record of the Northern Hemisphere[32]. This means that the ancestors of placental mammals were living in the Southern Hemisphere when the palaeogeographical rearrangements described in **Figure 14** and **Figure 15** took place. This new fossil evidence of early mammalian evolution supports the hypothesis that the early mammals first evolved on the southern continents.

The next question is whether there is any fossil evidence that documents the biogeographic scenario of the dispersal of primates (and boreoeutherians in general) from the southern continents to the northern continents by the routes indicated in **Figure 17**. As it happens, such evidence does exist, and it has to do with the appearance in the fossil record of a mysterious lineage called the adapisoriculids. Indeed, the adapisoriculids appear in the fossil record of both the Southern Hemisphere and the Northern Hemisphere exactly at the time and place predicted by the biogeographic scenario (**Figure 17**).

The adapisoriculids are a family of primitive eutherian mammals that are somewhat similar to modern insectivorous mammals. Although there is currently a debate as to how they should be classified taxonomically, the most “optimistic” opinion is that they represent a euarchontan lineage[33] that includes the primates and their immediate relatives, the dermopterans and the scandentians. If this opinion is correct, then the adapisoriculids might represent the earliest common ancestor of the primates that has been found in the fossil record. Initially, the oldest adapisoriculids, with *Deccanolestes*[34] as their main representative, were found in Late Cretaceous (~67–64 Mya) deposits in India. More recently, *Brasilestes*[35], another adapisoriculid even older than *Deccanolestes* (age between 84 and 72 Mya),

Figure 16. Possible phylogenetic relationships of primates and their immediate relatives (dermopterans and dendromygales) based on vicariance resulting from palaeogeographical rearrangements of Indo-Madagascar and Antarctica (see Figure 15). A) A vicariant topology without resolved branches (i.e. without assigning the branches of the topology to specific taxonomic classes of primates). Identification and matching have been done in panels B and C. B) One possible vicariant phylogenetic tree, in which the dermopterans are placed within the clade of primates. C) Another possible vicariant phylogenetic tree, in which the dermopterans are placed outside the clade of primates. The differences between the two trees (B and C) are limited to the identification of the branches marked in bold.

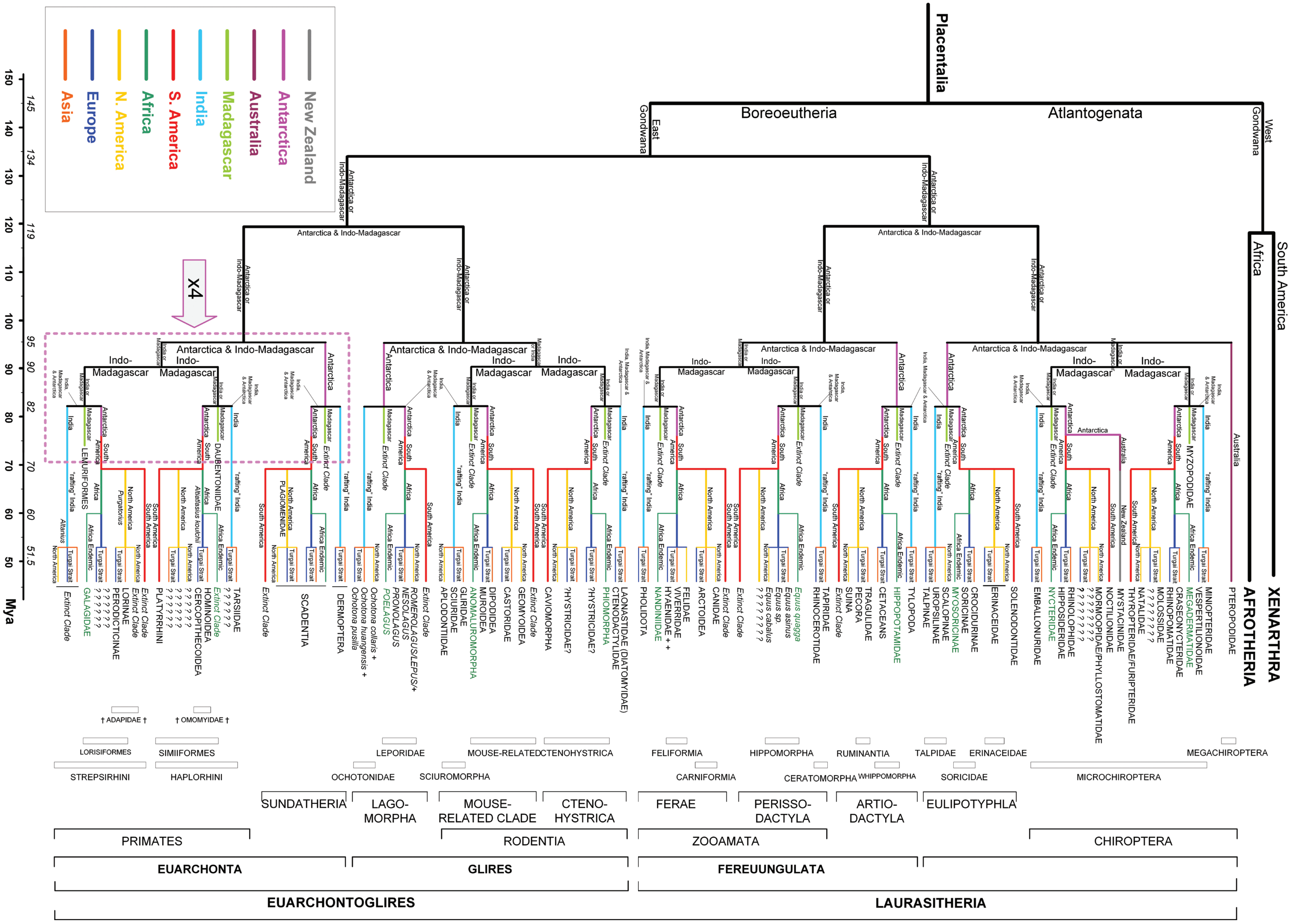


was found in Brazil. Adapisoriculids appeared in Africa and Europe later, during the Early Palaeocene (~66–61.6 Mya)[36]. Their nearly simultaneous appearance in South America, Africa, Europe, and India is surprising in the context of current biogeographical beliefs about the boreoeutherians. This is because India, being geographically isolated from the other continents from 82 Mya until ~55 Mya, when it collided with Asia, was an island that travelled northwards in the ocean. Given the geographic isolation of India throughout its long journey to the Northern Hemisphere, the only reasonable way to explain the presence of adapisoriculids in India during that time is for them to have colonised it when India was still connected to Antarctica. Thus, the presence of adapisoriculids in the Late Cretaceous of South America and India, and in the Early Palaeocene of Africa and Europe, supports the biogeographic scenario described in **Figure 17**.

If early euarchontan lineages such as the adapisoriculids had the southern continents as their cradle and centre of spread, then the same must be true for the rest of the boreoeutherians. In this case, they should have had a dispersal pattern parallel to that of the euarchonta, as described in **Figure 17**. Consequently, in addition to the adapisoriculid *Deccanolestes*, more eutherian lineages representing other early branches of the boreoeutherians should be found in India. The exact number of such lineages is predicted in the phylogenetic tree of **Figure 18** (the lineages marked with blue lines). Indeed, many new fossils were recently discovered in India, including at least three new species of eutherian mammals in addition to *Deccanolestes*[37]. What is remarkable is that the finding of all three new eutherian species in India is incongruous with widely held biogeographical and palaeontological beliefs. It fits perfectly, however, with the biogeographic scenario developed here.

In summary, the biogeographic scenario presented here is the only hypothesis capable of explaining the current diversity and biogeographical evolution of primates and boreoeutherian mammals. It also explains their otherwise inexplicable

Figure 17. A schematic illustration of the routes for the dispersal of primates from the Southern Hemisphere towards the Northern Hemisphere. Yellow boxes mark the most nodal land bridges referred to in the text. While the aye-aye remained confined to Madagascar with the lemurs, the common ancestors of simians and lorisomorphs dispersed into the Northern Hemisphere via Antarctica and South America. Tarsiers and dermopterans (or scandentians) spread to the Northern Hemisphere through India. Note that the ancestors of the remaining taxa of boreoeutherian mammals must have followed the same routes (**Figure 18**). Black circles mark the presence of adapisoriculids on different and distant continents, which can only be explained by the biogeographical scenario developed here.


Asia
Europe
N. America
Africa
S. America
India
Madagascar
Australia
Antarctica
New Zealand
Mya
150
145
140
134
130
120
119
110
100
95
90
82
80
70
60
51.5
50
X4
Placentalia
Boreoeutheria
Atlantogenata
East Gondwana
West Gondwana
Antarctica or Indo-Madagascar
Antarctica & Indo-Madagascar
Indo-Madagascar
Antarctica
India
Madagascar
South America
Africa
Africa
South America
North America
Turgai Strait
Africa Endemic
"rafting" India
Extinct Clade
Australia
New Zealand
Altanius
Purgatorius
Altiatlasius koulchii
PLAGIOMENIDAE
DAUBENTONIIDAE
LEMURIFORMES
MYZOPODIDAE
Extinct Clade
GALAGIDAE
? ? ? ? ?
PERODICTICINAE
LORINAE
Extinct Clade
Extinct Clade
PLATYRRHINI
? ? ? ? ?
CERCOPITHECOIDEA
HOMINOIDEA
Extinct Clade
? ? ? ? ?
TARSIIDAE
Extinct Clade
SCADENTIA
DERMOPTERA
Ochotona pusilla
Ochotona huangensis +
Ochotona collaris +
POELAGUS
PRONOLAGUS
NESOLAGUS
ROMEROLAGUS/LEPUS/+
Extinct Clade
APLODONTIIDAE
SCIURIDAE
GLIRIDAE
ANOMALUROMORPHA
MUROIDEA
DIPODIDEA
CASTORIDAE
GEOMYOIDEA
Extinct Clade
CAVIOMORPHA
?HYSTRICIDAE?
?HYSTRICIDAE?
PHIOMORPHA
CTENODACTYLIDAE
LAONASTIDAE (DIATOMYIDAE)
PHOLIDOTA
NANDINIIDAE
HYAENIDAE + +
VIVERRIDAE
FELIDAE
ARCTOIDEA
CANIDAE
Extinct Clade
Extinct Clade
? ? ? ? ? ?
Equus caballus
Equus asinus
Equus sp.
Equus quagga
RHINOCEROTIDAE
TAPIRIDAE
Extinct Clade
SUINA
PECORA
TRAGULIDAE
CETACEANS
HIPPOPOTAMIDAE
TYLOPODA
TALPINAE
UROPSILINAE
SCALOPINAE
MYOSORICINAE
SORICINAE
CROCIDURINAE
ERINACEIDAE
SOLENODONTIDAE
EMBALLONURIDAE
NYCTERIDAE
HIPPOSIDERIDAE
RHINOLOPHIDAE
? ? ? ? ? ?
MORMOOPIDAE/PHYLLOSTOMATIDAE
NOCTILIONIDAE
MYSTACINIDAE
THYROPTERIDAE/FURIPTERIDAE
NATALIDAE
? ? ? ? ? ?
MOLOSSIDAE
RHINOPOMATIDAE
CRASEONYCTERIDAE
MEGADERMATIDAE
VESPERTILIONIDAE
MINIOPTERIDAE
PTEROPODIDAE
AFROTHERIA
XENARTHRA
† ADAPIDAE †
† OMOMYIDAE †
LORISIFORMES
SIMIIFORMES
STREPSIRHINI
HAPLORHINI
LEPORIDAE
OCHOTONIDAE
MOUSE-RELATED
CTENOHYSTRICA
SCIUROMORPHA
FELIFORMIA
CARNIFORMIA
HIPPOMORPHA
CERATOMORPHA
RUMINANTIA
WHIPPOMORPHA
TALPIDAE
ERINACEIDAE
SORICIDAE
MEGACHIROPTERA
MICROCHIROPTERA
SUNDATHERIA
LAGO-MORPHA
MOUSE-RELATED CLADE
CTENO-HYSTRICA
FERAE
PERISSO-DACTYLA
ARTIO-DACTYLA
EULIPOTYPHLA
PRIMATES
RODENTIA
ZOOAMATA
CHIROPTERA
EUARCHONTA
GLIRES
FEREUUNGULATA
EUARCHONTOGLIRES
LAURASITHERIA

Langhian stage, which led to the re-exposure of the Suez and Mesopotamian seaways (**Figure 27A**). Based on evidence of marine transgression in the northern part of the Suez Seaway, this seaway should have been exposed between 16.5 Mya and 15 Mya (Late MN7 to MN9 foraminiferal zones)[72], separating the Arabian Peninsula from Africa. During the same period (~15.1 Mya), the Mesopotamian Seaway was also re-exposed[61]. At the northwestern end of Balkanatolia, the Transtethyan Trench Corridor, which separated Balkanatolia from western Europe in the area of present-day Slovenia, was delayed in being fully exposed by the marine transgression. More recent data suggest that this was achieved between 14.9 Mya and 14.4 Mya[73].

After the formation of the Transtethyan Trench Corridor, the wider region around Balkanatolia was fragmented into five isolated territories (**Figure 27A**)—Balkanatolia, Africa, Arabia, Asia, and Europe—and at least one insular region in the Carpathian and/or Caucasus region. In this way, the original population of hominines (represented by the tooth found at Engelswies), which had previously dispersed from Africa in all directions when the *Compotherium* land bridge was formed, became separated by vicariance into (at least) six geographically isolated subpopulations. The long-term genetic isolation of these six subpopulations resulted in the phylogenetic divergence of six different lineages (**Figure 28**).

When the sea regressed during the Early Serravallian (14.3 Mya), the land bridges were re-formed (**Figure 27B**), and populations of newly evolved species dispersed into neighbouring areas, taking advantage of new opportunities to exploit food resources. A renewed marine transgression during the Middle Serravallian—more precisely, during the Konkian stage of the eastern Paratethys (~13.4–12.7 Mya)—again fragmented the peri-Balkanatolian area into smaller territories[63]. The only exception was Africa and the Arabian Peninsula, which remained permanently connected through the Suez region from the end of the Langhian transgression until the present day (**Figure 27C**). The new episode of geographic isolation in the Middle Serravallian caused further vicariant speciation, followed by dispersal of the new species in all directions when the sea regressed and terrestrial dispersal corridors re-formed. In this way, through the Langhian and Konkian marine transgressions, the great diversity of Middle Miocene hominines was created (**Figure 28**).

3.5. THE DIVERGENCE OF THE GORILLA LINEAGE

The divergence of the gorilla lineage is widely believed to have occurred at least 10 Mya, given the morphological relationships between modern gorillas and the

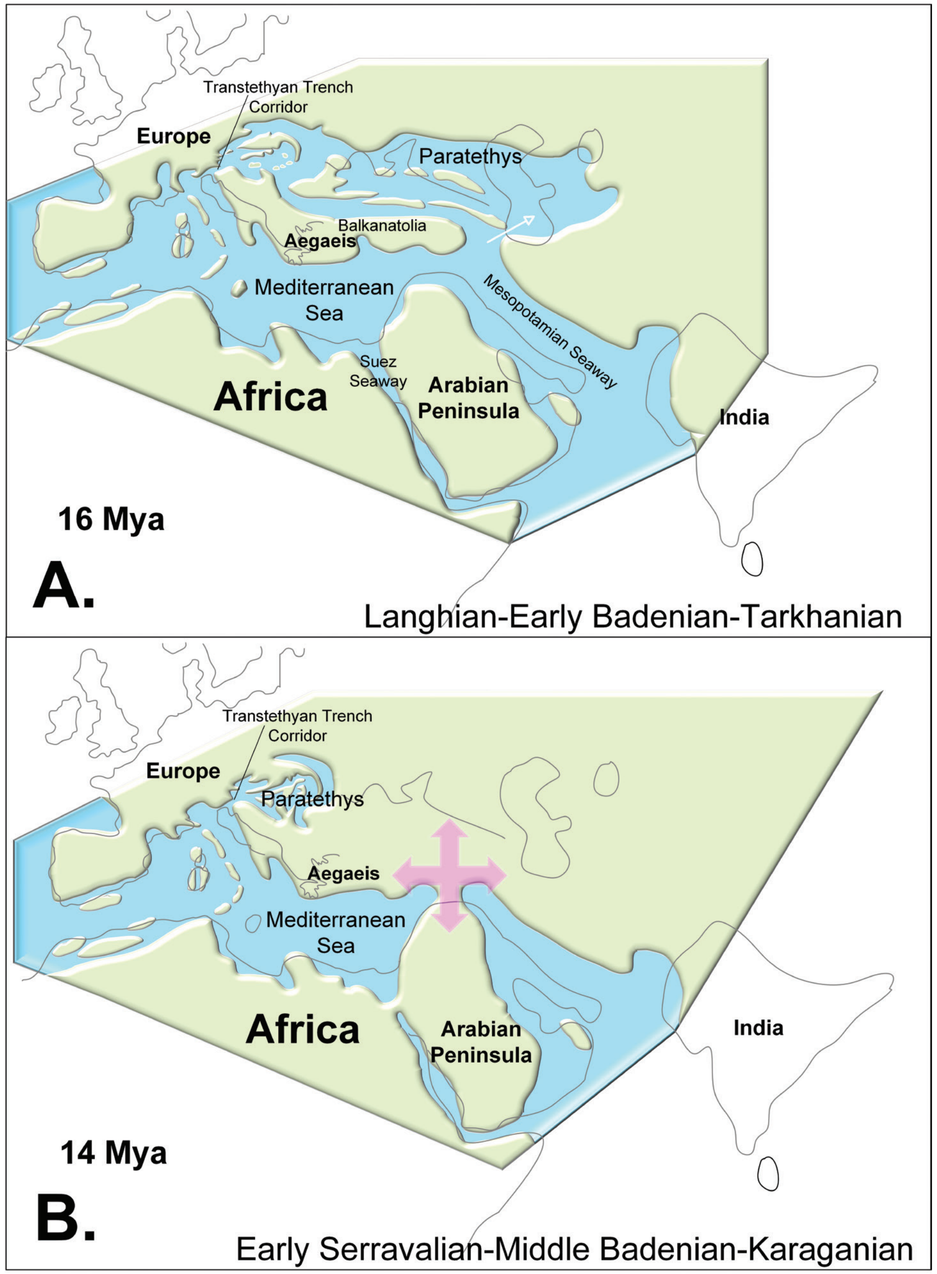
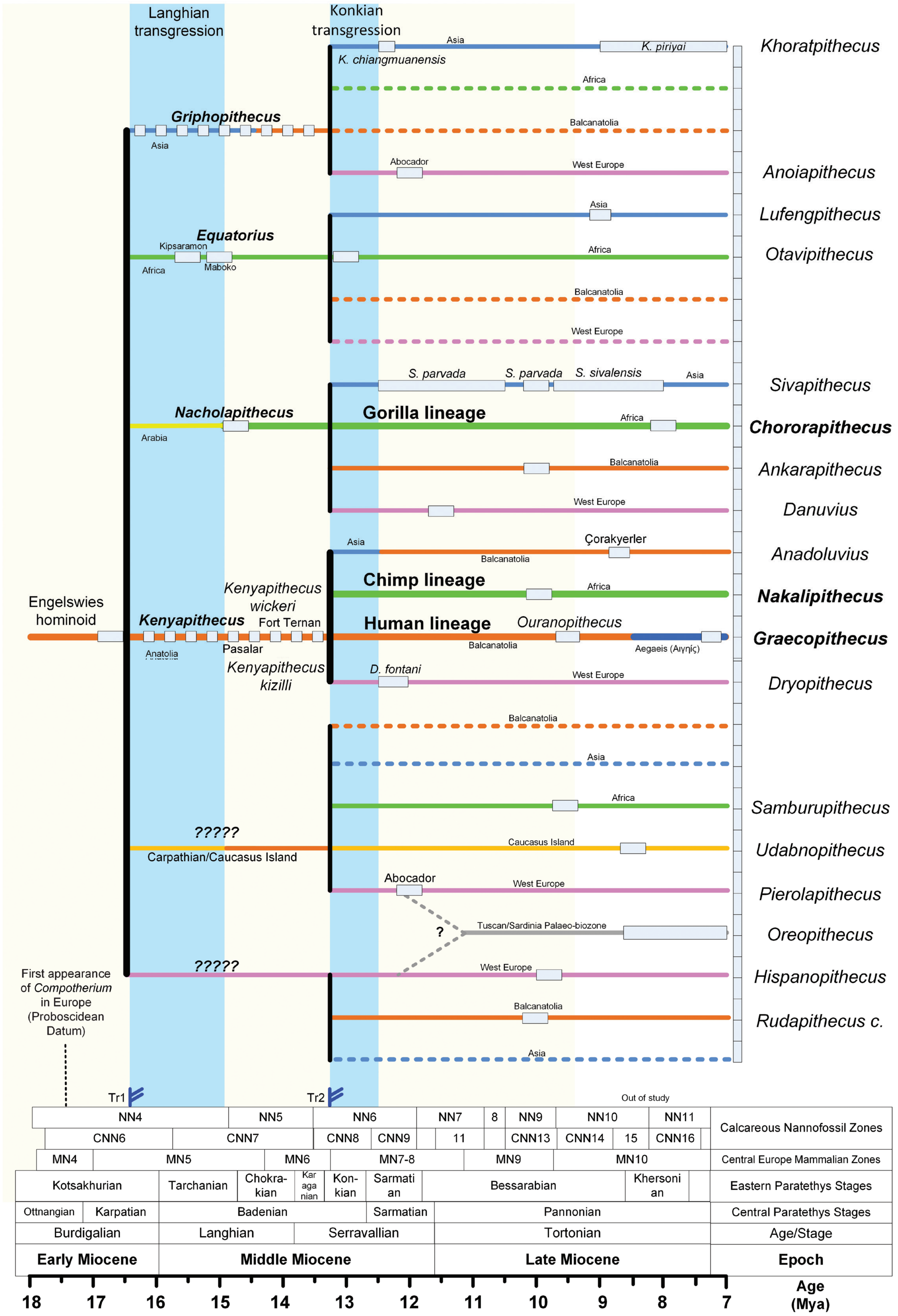


Figure 27. Reconstruction of the rapid palaeogeographical rearrangements that took place in the peri-Balkanatolian region during the Middle Miocene. A) During the Langhian marine transgression ~16 Mya, Balkanatolia essentially became an island surrounded by a multitude of smaller islands. B) At the end of the Langhian stage ~14 Mya, marine regression allowed the re-establishment of terrestrial →

Langhian transgression
Konkian transgression
Khoratpithecus
Asia
K. piriyai
K. chiangmuanensis
Africa
Griphopithecus
Asia
Balcanatolia
Abocador
West Europe
Anoiapithecus
Asia
Lufengpithecus
Equatorius
Kipsaramon
Maboko
Africa
Otavipithecus
Balcanatolia
West Europe
S. parvada
S. parvada
S. sivalensis
Asia
Sivapithecus
Nacholapithecus
Gorilla lineage
Arabia
Africa
Chororapithecus
Balcanatolia
Ankarapithecus
West Europe
Danuvius
Asia
Çorakyerler
Balcanatolia
Anadoluvius
Chimp lineage
Africa
Nakalipithecus
Engelswies hominoid
Kenyapithecus wickeri
Kenyapithecus
Fort Ternan
Human lineage
Ouranopithecus
Pasalar
Anatolia
Balcanatolia
Aegaeis (Αιγηίς)
Graecopithecus
Kenyapithecus kizilli
D. fontani
West Europe
Dryopithecus
Balcanatolia
Asia
Africa
Samburupithecus
?????
Caucasus Island
Carpathian/Caucasus Island
Udabnopithecus
Abocador
West Europe
Pierolapithecus
?
Tuscan/Sardinia Palaeo-biozone
Oreopithecus
?????
West Europe
Hispanopithecus
Balcanatolia
Rudapithecus c.
Asia
First appearance of *Compotherium* in Europe (Proboscidean Datum)
Tr1
Tr2
Out of study
NN4
NN5
NN6
NN7
8
NN9
NN10
NN11
Calcareous Nannofossil Zones
CNN6
CNN7
CNN8
CNN9
11
CNN13
CNN14
15
CNN16
MN4
MN5
MN6
MN7-8
MN9
MN10
Central Europe Mammalian Zones
Kotsakhurian
Tarchanian
Chokra-kian
Kar aga nian
Kon-kian
Sarmati an
Bessarabian
Khersoni an
Eastern Paratethys Stages
Ottnangian
Karpatian
Badenian
Sarmatian
Pannonian
Central Paratethys Stages
Burdigalian
Langhian
Serravallian
Tortonian
Age/Stage
Early Miocene
Middle Miocene
Late Miocene
Epoch
18
17
16
15
14
13
12
11
10
9
8
7
Age (Mya)

morphology of the maxillary canines in male specimens of extant and extinct apes, extinct hominins, and modern humans showed that in the lingual view, the crowns of the teeth are shaped like a distorted triangle in extant and extinct apes, a distorted tetragon in *Ouranopithecus*, and a pentagon or diamond in hominins[83]. Also, the marginal ridge of these teeth is short in extant and extinct apes (being located at the basal crown), whereas it is extended from the cervical region to the apex in *Ouranopithecus*, and extended even farther towards the apex in *Ardipithecus ramidus* and later hominins[83]. Consequently, in terms of these dental features, only *Ouranopithecus* appears to represent an intermediate evolutionary stage between apes and humans.

Because some of the features reported by de Bonis and Koufos are not exclusively shared between *Ouranopithecus* and the australopithecines, their view has not found wide acceptance among palaeoanthropologists[84], who remain faithful to the traditional view that Africa is the most likely centre of origin and evolution of the human species. Apart from the location of its fossils outside of Africa, another reason *Ouranopithecus* is not accepted as a member of the human lineage is its age. Because the divergence of humans and chimpanzees is widely believed to have occurred 5–7 Mya, the older age of *Ouranopithecus* (9.5 Mya) places it outside of human ancestry (see the example in **Figure 12**). But what does the latest molecular evidence say about the age of the human-chimpanzee divergence?

Since Professor Arnason's team[20] first gave an age of 13 Mya for the human-chimpanzee divergence (based on mitochondrial DNA) in 2000, other molecular studies have arrived at similar ages. The main difference between these studies and those that conclude an age of 5–7 Mya is that the molecular clock of the former is calibrated on new and independent evidence rather than on age estimates from the fossil record. From this point of view, their chronological results are unaffected by the incompleteness of the fossil record and thus represent an opportunity to re-evaluate the dating results from fossil-based studies. Molecular dating based on the average generation time of chimpanzees and gorillas living in nature concluded that the age of divergence between humans and chimpanzees should be older than 7–8 Mya, reaching up to 13 Mya[85]. Another approach uses the rate of DNA mutation specifically at cytosine-guanine* (CpG) dinucleotide transition sites, which can give highly reliable results for molecular clock calculations[86]. Using this approach, the human-chimpanzee divergence age was determined to be 12.1 Mya

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* The DNA strand is made up of only four bases: cytosine (C), guanine (G), thymine (T), and adenine (A). CpG transitions refer to the mutation of the C position in a CG dinucleotide to a T.

(compared to the age of 13 Mya determined by both Prof. Arnason's team and the vicariance approach), and the human-gorilla divergence age was determined to be 15 Mya (compared to the ages of 16 Mya determined by Prof. Arnason's team and 16.5 Mya determined by the vicariance approach). The results of other analyses based on *de novo* mutations are even more enlightening.

3.8. THE MOLECULAR CLOCK: THE REVOLUTION OF DE NOVO MUTATIONS

To calculate the age of divergence of two phylogenetic branches using a molecular clock, the DNA sequences of representatives of each branch are compared to determine the genetic differentiation (i.e. the number of nucleotides that differ) between the branches. To convert genetic differentiation into units of time, it is necessary to know the rate of molecular evolution of the lineages (i.e. the average amount of time needed for a single mutation to appear*). This rate was not directly measurable until recently, so molecular clocks took as a reference point an estimated divergence age based on available fossils. For example, based on the palaeontological estimate that the 5.5–6-million-year-old fossils of *Orrorin* and *Ardipithecus* constitute the first representatives of the human lineage, an age of ~6.5 Mya was used as a reference to calculate the mutation rate of the human lineage. The mutation rate estimated in this way is sometimes referred to as the *phylogenetic rate*[87].

Recently, the application of next-generation sequencing to parent-offspring triads has allowed the mutation rate of the human genome to be calculated in a more direct way. These studies rely mainly on non-inherited (*de novo*) mutations and have decidedly shown that the true mutation rate of hominins is 50% lower than that estimated from the study of fossils**[87–88]. As a reduction of the mutation rate by one half corresponds to a doubling of the age of divergence, this means that the divergence of humans and chimpanzees occurred not ~6.5 Mya, but rather 13 Mya.

A study published in the journal *Science* in 2014 confirmed the human-chimpanzee divergence age of 13 Mya on the basis of *de novo* mutation rates calculated for the human genome and the chimpanzee genome[89]. In the same year, a study published in the journal *Nature* confirmed the *de novo* mutation rate calculated for

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* The average mutation rate μ in two diverging lineages is calculated from the relationship $\mu = 2d / t$, where d is the sequence divergence (the number of substitutions per base pair) between the lineages, and t is the time at which the divergence occurred[87].

** The average mutation rate derived from the study of *de novo* mutations is $\sim 0.5 \times 10^{-9}$ bp^{-1} yr^{-1}, whereas that derived from the study of fossils is about 1.0×10^{-9} bp^{-1} yr^{-1} (bp = base pair, yr = year)[87–88].

bipedalism is considered to be the most decisive step in human evolution and is one of the main characteristics of the human lineage.

The age of the fossilised footprints in Crete was estimated to correspond to the normal polarity of Time C3An.1n (which translates to 6.023–6.272 Mya)[100]. This is contemporaneous with the appearance of the earliest potentially bipedal hominin in Africa, *Orrorin tugenensis*, which was found in Kenya[101]. No skeletal remains have yet been found to indicate the locomotor behaviour of the 5.7-million-year-old *Ardipithecus kadabba* from the Afar region of Ethiopia, another African candidate hominin. Furthermore, serious doubts have been expressed regarding the bipedal capacity, and more generally, the inclusion in the human lineage, of the 7-million-year-old *Sahelanthropus tchadensis* from Chad[75,101–102]. Consequently, the earliest known evidence of human bipedalism is 6–6.2 million years old and comes from two sources: the fossilised skeletal remains of *Orrorin*, from Africa, and the fossilised footprints in Trachilos, Crete.

Soon after the Trachilos footprints were discovered and initially associated with a bipedal hominin, some researchers argued that they could actually have been made by an invertebrate (e.g. an octopus), or even something other than a living organism. These arguments were answered in a special publication[103], and in any case, the similarity between the fossilised markings and hominin footprints seems clear (see **Figure 31**). Professor Robin Crompton of the University of Liverpool, who is an expert on fossil footprints and co-founder of the Fossil Footprint Archive, prefaced the initial published evaluation of the Trachilos footprints with an article[104] arguing that the footprints could belong to a human ancestor or an ancestor of the African great apes. Similarly, the palaeoanthropologist David Begun stated that "The footprints are curiously hominin-like, but that doesn't mean they were made by one of our distant ancestors. The tracks lack several really important human characteristics that we find in the oldest known, unambiguous [ancestral] human footprints," which were found in Laetoli, Tanzania.[105] The tracks to which Professor Begun refers are 3.7 million years old and have been attributed to *Australopithecus afarensis*, one of the first undoubted ancestors of humans. Furthermore, Professor Begun opined that the tracks do not show a deep heel impression or a clear impression of the foot arch, both of which would be expected in a hominin that has evolved heel-strike locomotion (as humans walk, the heel first hits the ground, and then the arch of the foot rolls along the ground, leaving a bulge in the middle of the footprint). Consequently, Professor Begun found the fossilised markings in Crete to be inconclusive, noting that they might have been made by a primate with a form of bipedalism different from that of humans.[105]

Figure 30. Footprints of a hominin biped on the beach of Trachilos in northwestern Crete. Photo courtesy of Gerard Gierlinski.

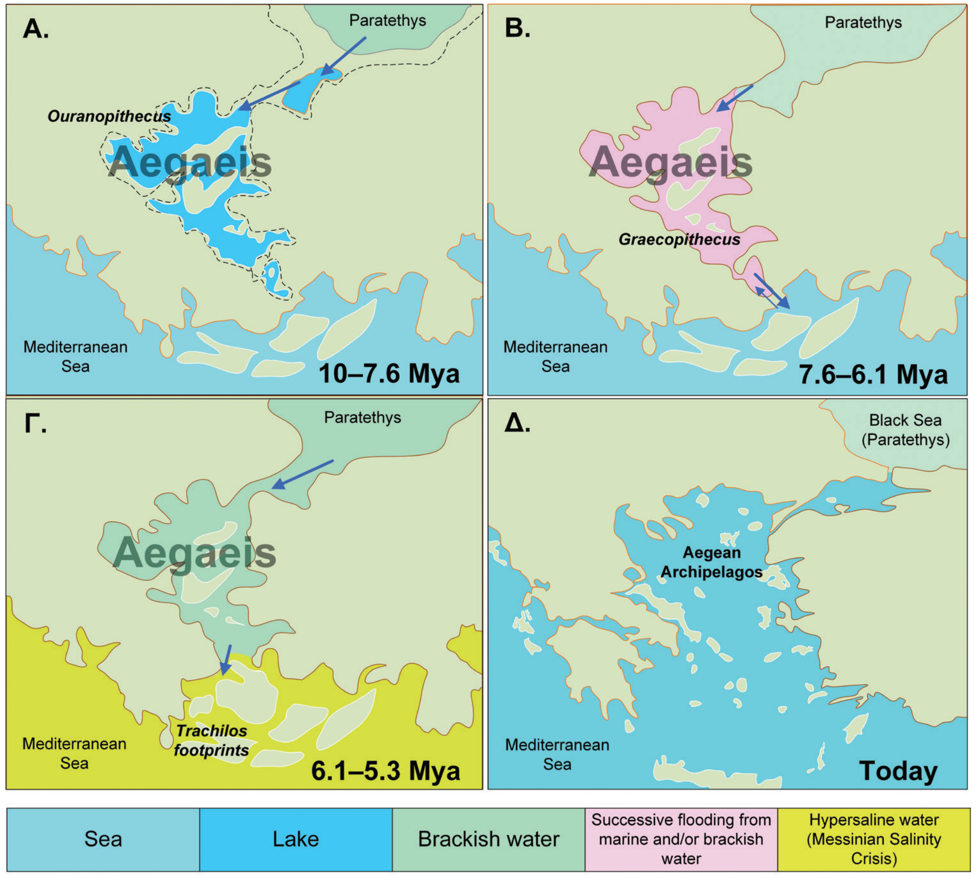

Figure 35. Palaeogeographical evolution of Aegaeis during the period when *Ouranopithecus* evolved into *Graecopithecus*. A) Tortonian, ~10–7.6 Mya, the age of *Ouranopithecus*. Aegaeis is a mostly lowland area, scattered with lakes that are periodically fed by Paratethyan waters during periods of high sea level in the Paratethys. B) Early Messinian, ~7.6–6.1 Mya, the age of *Graecopithecus*. The sea periodically invades central and northern Aegaeis from the southeast through the sea corridor of the Dodecanese. C) Late Messinian, ~6.1–5.3 Mya, the age of the Trachilos footprints. Northern and central Aegaeis is dominated hydrologically by the brackish waters of the Paratethys. D) The Aegean Archipelago today. Palaeogeographical maps are based on reference[129].

During the period from 9.75 Mya to 5.3 Mya, the basins of the northern and central Aegean region were dominated by continuous changes in hydrological level and salinity, as they were constantly alternating between freshwater and brackish lake conditions and marine basin conditions. In this way, central Aegaeis was fragmented into a cluster of islands during periods of high water level, whereas many of these islands were joined by land during periods of low water level. I call this

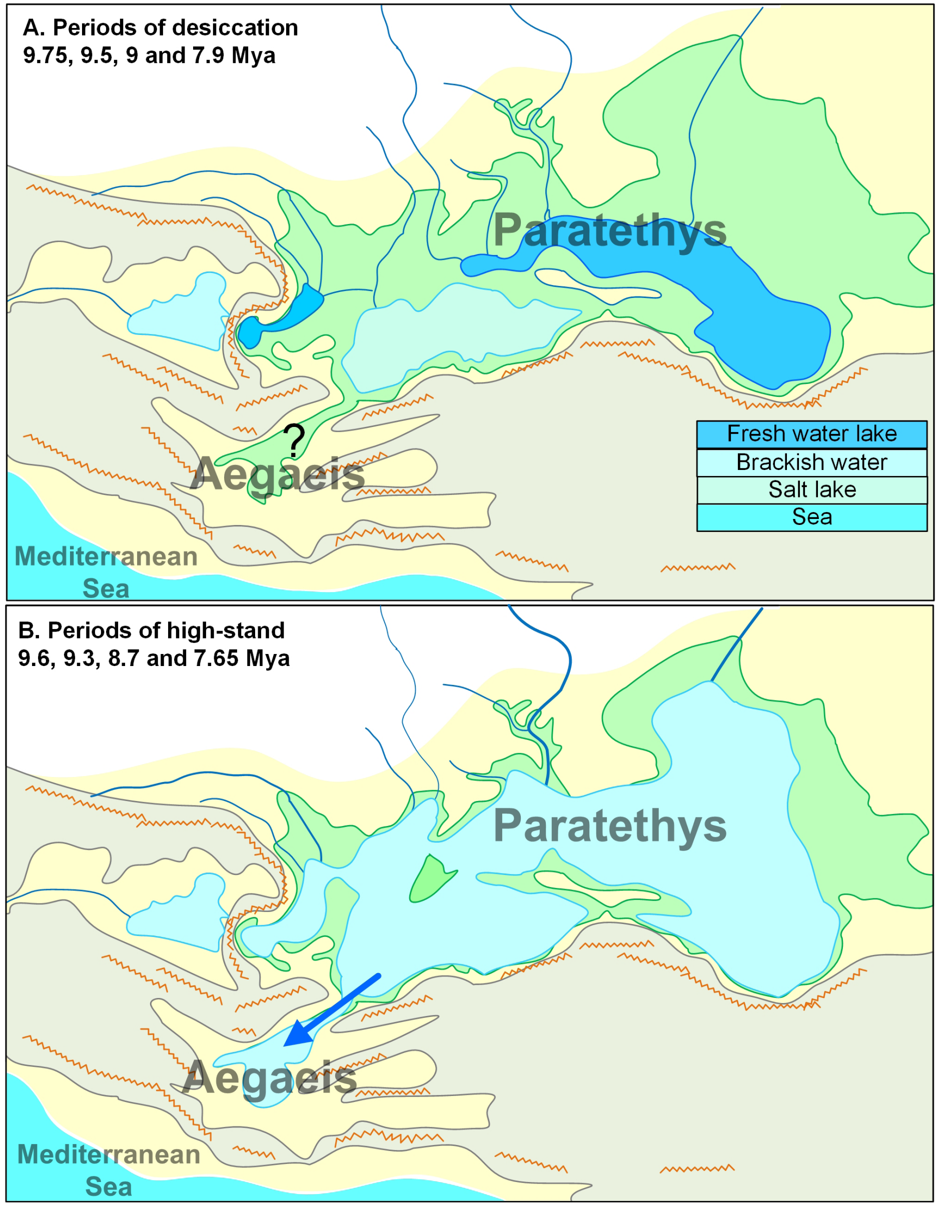

Figure 36. Palaeogeographical reconstruction of the interacting hydrological complexes of Aegaeis and the Paratethys during the Late Miocene. Hydrological interconnection through the straits of the pre-Bosporus and the Dardanelles should have compensated the water levels of the two basins during the intervals when Aegaeis was isolated from the Mediterranean Sea. A) Periods of desiccation (Paratethys partially desiccated). B) Periods of high stand (Paratethys at high water level). Maps and time periods of high and low water levels of the Paratethys are based on reference[131].

Figure 42. Geographic representation of the course of the Nile River and the locations where the fossils of *Orrorin* and *Ardipithecus kadabba* were found on the African continent. *Orrorin* seems to have followed the course of the White Nile, whereas *Ardipithecus kadabba* followed that of the Blue Nile. The two arcs indicate the two possible dispersal routes of *Graecopithecus* from Aegaeis to the mouth of the Nile.

Turkana and Lake Victoria, where the White Nile now originates. *Ardipithecus kadabba*[*] was found in the Afar Valley of Ethiopia, near the origin of the Blue Nile (**Figure 42**). Both *Orrorin* and *Ardipithecus kadabba* were found in deposits that indicated a lacustrine paleoenvironment[149].

The next question is whether the flows of the White Nile and the Blue Nile between 5 Mya and 6 Mya were the same as they are today. Recent geodynamic[150] and sedimentological[151]studies of the palaeo-flow of the Blue Nile have confirmed that the current flow of the Blue Nile from the Ethiopian highlands to the Mediterranean has been the same for at least 30 million years. The origin of the White Nile is closely linked to the development of the western branch of the East African

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[*] There is a second species of *Ardipithecus*, *Ardipithecus ramidus*, which is younger than *Ardipithecus kadabba* by about 1 million years. Because I am referring here only to the older species, *Ardipithecus kadabba*, I use its full scientific name.

Rift system, which is considered to have taken place between 11 Mya and 5 Mya. This event led to both the northward flow of the river, which was previously arranged westward through the drainage valley of the palaeo-Congo River, and the formation of the great lakes (Victoria, Albert, Edward, George, and Kyoga) from which the White Nile originates today. Because the complex geological evolution of the region makes palaeogeographical reconstruction very difficult, the flow of the White Nile is reliably documented only for the last 500,000 years[152]. In any case, the western branch of the East African Rift system is currently thought to have developed 11–5 Mya, and this is compatible with the biogeographic scenario for the dispersal of *Orrorin* via the White Nile.

The Messinian Salinity Crisis, as a palaeogeographical event, can provide more explanations and plausible answers regarding the dispersal/migration of *Orrorin* and *Ardipithecus kadabba* from Aegaeis to eastern Africa. Given that all the evidence available today suggests that during the second phase of the Messinian Salinity Crisis, the Mediterranean Sea was dried up to a large extent, a route following the remaining water basins between southern Crete and the Nile River would be the shorter of the two possible dispersal routes (see the blue straight arrow in **Figure 42**).

The ages at which *Orrorin* and *Ardipithecus kadabba* appeared in eastern Africa show a remarkable chronological coincidence with the occurrence of the Messinian Salinity Crisis. Specifically, in the period between 5.6 Mya and 5.52 Mya, the Mediterranean sea level seems to have fallen by 800–2,000 metres[153]. This fall increased the flow velocity and erosive power of the rivers flowing into the Mediterranean, resulting in the formation of deep gorges, such as the enormous Nile River Gorge, which reaches a depth of 1500 metres below present-day Cairo. The deep gorges of southern Crete were also formed at this time. It is likely that all these rivers shared a common estuary basin, allowing the dispersal of coastal species between Crete and Africa. Indeed, the dispersal of the endemic Cretan date palm (*Phoenix theophrastii*) from northern Africa to Crete (or vice versa) took place precisely at that time. This is evidenced by the molecular clock of the Cretan date palm, which indicates that it diverged from Afro-Asiatic ancestors ~5 Mya[154]. The Cretan date palm lives exclusively in coastal areas, within a few metres of the beach or along the banks of streams. In this respect, its coastal nature is similar to that of the early human ancestors and suggests the same cause and route of dispersal.

So when did *Orrorin* and *Ardipithecus kadabba* live in Africa? The dating of the oldest specimens of *Ardipithecus kadabba* concluded a safe age between 5.54

Figure 31. A fossilised footprint from Trachilos beach in northwest Crete. It is easy to see the similarity to a human footprint. Photo courtesy of Gerard Gierlinski.

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