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A Brief Overview of the Origin of the Land Mammals of Costa Rica

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Abstract: Despite its small size (51.000 km^2), there is approximately 5% of the world's known mammal species (over 260) in Costa Rica alone. This rich biodiversity is due, at least in part, to its geographical position along the bridge that connects North and South America and separates the Atlantic from the Pacific Ocean. To understand whence, when, and how mammals settled in Costa Rica, it is necessary to take into account the geological, climatic, and ecological processes that occurred in Central America during the Cenozoic. The origin of Costa Rica follows from a series of complex geological events ensuing from the interaction of three tectonic plates, a microplate, and several exotic tectonic fragments from different plates. Central American vertebrate fossils mainly are from the late Cenozoic and represent all the major taxonomic groups. However, the history of Central American mammals lacks further direct fossil evidence. Known vertebrate fossils date not only to before and after the closure of the Isthmus of Panama, but they also constitute the direct fossil record documenting what clearly was a dispersal route between North and South America. The mixture began with the exchange that took place over the islands making up the current Central American region, and increased when the Central American isthmus was closed and became dry land, because it allowed a greater traffic of mammals. Within this framework of global and local abiotic patterns of change, the Great American Biotic Interchange (GABI) stands out because it constitutes one of the most significant biogeographical events worldwide. Central American mammal fossils help provide an understanding of the GABI after the closure of the Panamanian isthmus. This work analyzes these facts and summarizes some of the more recent pertinent findings to provide a brief overview of mammalian history in Costa Rica.

Key words: Central America, dispersal routes, faunal interchanges, geological history, Great American Biotic Interchange, marsupials, tectonic.

Introduction

Costa Rica is a small country: with an area of 51,100 km^2 covering only 0.034% of the land surface of the Earth (Mora *et al*., 2021). Despite its small area, the country has a rich biodiversity, due, at least in part, to its geographical position along the bridge that connects North and South America and has allowed for the movement of species from the north to the south and vice versa. In addition, Costa Rica occupies an interoceanic position at the narrow Central American isthmus, which separates the Atlantic from the Pacific Ocean (Alvarado and Cárdenes, 2016). There are over 260 mammal species documented from Costa Rica , that is approximately 5% of the world's known mammal species (SINAC, 2014). This represents almost a 150-fold difference between the proportion of area covered and the proportion of mammalian biodiversity present. Ecological conditions for this high diversity have been discussed widely (Burger, 1981; Gómez, 1986; Pillay *et al*., 2022), and a large amount of information has been generated regarding the history of the origin and arrival of the mammals of Costa Rica. The present work summarizes some of the more recent pertinent findings to provide a brief overview of mammalian history in Costa Rica.

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Major mammalian dispersals occurred at times of low sea levels, resulting in loss of endemism on continents that originally were isolated, such as South America and Africa, along with changes in the composition of the Holarctic fauna (Janis, 1993). Historical invasions have been through exchange routes working as bridges that could become filters: some taxa are able to pass but others are not. The Central American isthmus has been such a corridor for many species of mammals, but also acted as a filter for other species (Alvarado, 1994; Alvarado and Cárdenes, 2016). Deserts, mountains, xeric vegetation, and rainforests, are strong filters for many species of mammals (Simpson, 1977).

To understand whence, when, and how mammals settled in Costa Rica, it is necessary to take into account the geological, climatic, and ecological processes that occurred in Central America during the Cenozoic; the same processes underway in South and North America similarly had important influences. However, the geological history of the Central American region—and that of Costa Rica in particular—is of fundamental importance. "Distant" aspects of these processes had important local biological influences here including the uplift and formation of the Andes Mountain range and the formation of Amazonian forests (Antonelli *et al*., 2009; Hoorn *et al*., 2010; Antoine *et al*., 2016; Pelegrin *et al*., 2018). At the same time, "local" aspects are also critical, such as the formation of open savannah-type habitats associated with the cyclical Quaternary glaciations, the establishment of a terrestrial connection between South and North America and its impact on oceanic and atmospheric currents, and therefore on global climate in general (Bacon *et al*., 2015; Carrillo *et al*., 2015; Montes *et al*., 2015). Within this framework of global abiotic patterns of change, the Great American Biotic Interchange (GABI) stands out because it constitutes one of the most significant biogeographical events worldwide (Webb, 2006; Lucas and Alvarado, 2016; Pelegrin *et al*., 2018). The GABI had an enormous influence on the development of mammal communities in the Americas (Pelegrin *et al*., 2018). This context was the framework for key evolutionary events to understand the establishment of the mammal fauna in Central America and of the fauna in the Neotropics in general and the mammals of Costa Rica in particular (Bacon *et al*., 2015; Carrillo *et al*., 2015; Erkens, 2015; Chávez, 2016).

Geology of Costa Rica

The origin of Costa Rica follows from a series of complex geological events ensuing from the interaction of three tectonic plates: Caribbean, Cocos, and Nazca, as well as the Panama microplate, and several exotic megablocks, tectonic fragments from different plates (Alvarado and Cárdenes, 2016) (Figure 1). The oldest rocks of Costa Rica date to about 200 Ma and developed many km southwest of the actual position (Table 1). The geological history of Costa Rica can be separated into several stages, some of which occurred simultaneously (Table 1). The territory of the country is part of the bridge connecting North and South America and occupying the Central American seaway (Figure 2). The active subduction of the Cocos plate beneath the Caribbean plate, volcanism, and several other tectonic phenomena, are examples of Costa Rican geological history that continues today.

Mammals of the Neotropics

The Americas comprise two zoogeographic regions (Figure 3): The Nearctic includes almost all of North America while the Neotropical begins in northeastern Mexico and includes Central and South America (Cox, 2001). The Neotropical region is considered as the most biodiverse globally, in particular insofar as mammals are concerned, with about 25% (about 1145 spp.) of the global diversity of the group residing in this region (Patterson, 2000; Rull, 2008, Pelegrin *et al*., 2018). The region includes rainforests, temperate forests, deserts, savannahs, paramos, and steppes, associated

Table 1. Principal geological events related to the development of Costa Rica according to the division of the geological time scale (GTS) and its age (Ma = million years ago)

Division GTS	**Ma**	**Events**	**Observations**
Jurassic	200	Oldest rocks in Costa Rica	At Santa Elena, Nicoya Peninsula, others. Formed to the southwest of the current position.
Late Cretaceous	80 – 66	Loma Chumico Formation (Nicoya) Volcano-sedimentary unit	Product of accumulation of organic matter in anoxic and deep environments High global °T No ocean currents
Cretaceous	> 66	No landmasses with terrestrial faunas	There is no record of continental fossil vertebrates in South Central America for the Paleogene, nor prior to the late Oligocene
		Proto-Antilles bridge	Exchange of biota between North and South America Territories moving east – northeast
End of the Cretaceous	66	Shallow seas “nearby” Island Arc	Some biological interchanges
Paleocene – Lower Eocene	66 – 49	Tectonic activity Cerro Turrubares was an active volcano	Cerro Turrubares is part of the Herradura promontory (an island that went from Cerro Turrubares to Jacó)
		“Territory” acquired current position	Current Costa Rican location occupied by islands and promontories Establishment of tectonic features similar to the current ones Developing of carbonate platforms (Basin of Tempisque River)
		Subduction is established in the Mesoamerican Trench	Tectonic activity increases.
Upper Eocene	41 – 34	Regional uplifting	Basins with shallow water marine sedimentation (< 200 m) Promotes sedimentation of carbonate platforms
		Interruption of volcanic activity	
		Formation of the La Candelaria basin begins.	Basin accumulated several km thick sediments. Continued into the Miocene
Oligocene	34 – 24	Decrease of the sea level in the Central American seaway	Separation of basins Local reef development Decreases the depth of sedimentary basins Biota exchange by island hopping and swimming
		Submarine volcanism in back basins of Talamanca (among others).	In the Térraba River area, very thick marine sediments are deposited on the continental slope.
		Northern part of Costa Rica emerges Continuous sedimentation in the southern part.	Northern part of Costa Rica subjected to erosion
	27 – 25	Farallon Plate broke up into the Cocos and Nazca plates High volcanic activity all over Costa Rica	Modern tectonic configuration of Costa Rica begins

Miocene	24 – 5	Shallow marine deposition all over the country Sedimentation in independent basins Growth of Talamanca Intense erosion on both slopes High volcanic activity continues (to 8 Ma)	Biological exchange island hopping or swimming islands in what is now Central America
		Reorganization of tectonic plates Consolidation of volcanic activity	Ignimbrite and other pyroclastic deposits Witnesses: Cordilleras of Aguacate, Tilarán and Cutris – Sarapiquí
		High tectonic activity Uplift associated with the collision of the Cocos Ridge with the Mesoamerican trench (5.4 Ma)	Exhumation of Talamanca characterized by a sudden increase in uplift rates between 5.5 and 3.5 Ma Tectonics and intense seismicity off Quepos and Osa Extinction of volcanism in Talamanca Decrease in the depth of the Mesoamerican trench in the collision zone Existence of underwater landslides Coastal uplift Talamanca uprising accelerates
		Since 8 Ma the inner arc has been parallel to the modern volcanic front,	It progressively retreated towards the northeast of the country
Pliocene	5 – 1.8	High volcanic activity Clogging of sedimentary basins	Closure of the Central America bridge (Isthmus of Panama) Biological exchange (GABI)
		Melting of glaciers and snowcaps of higher mountains	Together with volcanic activity in a tropical environment contributed to generate very thick lahars and alluvial deposits.
Quaternary	1.8 – present	Establishment of current volcanic mountain ranges	Central Valley depression forms This highland basin filled with a thick accumulation (> 1 km) of volcanic products (andesitic to dacitic lavas, pyroclastic rocks, lahar, and debris avalanche deposits)

with a wide latitudinal range and a highly complex topography (Tews et al., 2004). It is the second most diversified region in terms of the number of mammal families (after tropical Africa), with at least fifty-six families (compared to fifty-eight families in Africa; Vaughan *et al*., 2015). However, Africa has twenty endemic families whereas in the Neotropics, twenty-eight are endemic. South America was separated from North America by the Central American Seaway more than 150 million years ago (Dartnell, 2019). The separation of these two continental masses began 190 – 180 Ma with the breakup of Pangea (Figure 4) through the rift that separated Laurasia from Gondwana (Veevers, 2004; Dartnell, 2019). South America and Africa began their separation with the subsequent formation of the South Atlantic Ocean 100 –110 Ma (Ezcurra and Agnolín, 2012). Although linked to other landmasses for several million years after this separation between them, the biota of North and South America evolved independently, with successful radiations and extinctions, and with some exchanges between the continents (Simpson, 1950). There is also evidence that the Neotropical mammalian biodiversity was higher in the past than it is today, partly because many species have gone extinct owing to the effects of climate change, habitat fragmentation, disease, and more recently, human impact (MacFadden, 2005).

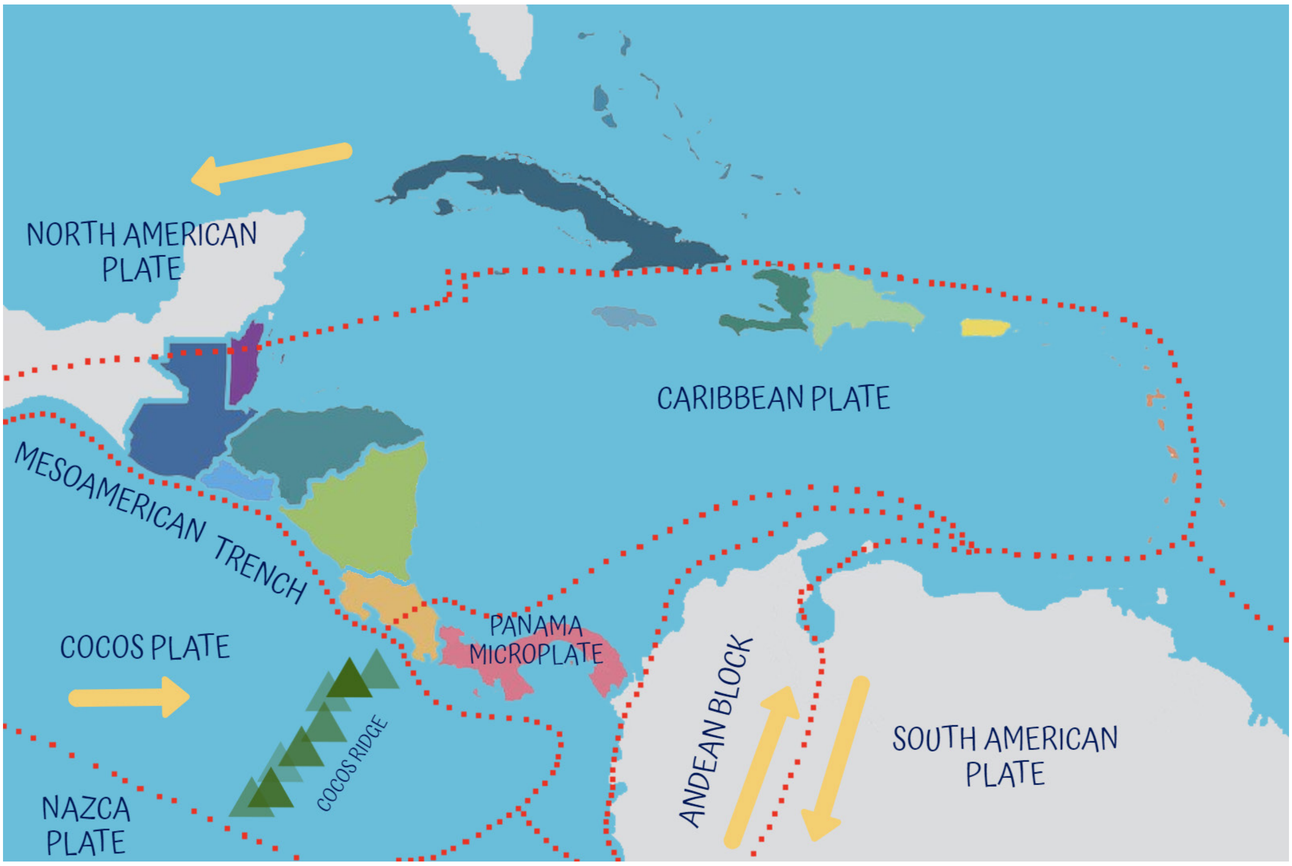

Figure 1. Location and relationship of Central America, including Costa Rica, with the tectonic plates that have determined the geological history of the country. Figure by Lucía I. López.

The magnitude of the faunal exchanges before the land connection between North and South America through the Isthmus of Panama about 3 – 4 Ma is still under debate (MacFadden, 2005; Agnolin *et al*., 2019). A wide variety of tetrapod, including mammals such as camels, peccaries, horses, monkeys, procyonids, mustelids, and ground sloths, among others, are known to have crossed the passage between North and South America long before of the establishment of the bridge (Cione *et al*., 2015; Pelegrin *et al*., 2018; Agnolin *et al*., 2019). Taxa that successfully crossed between continents prior to the establishment (i.e., established themselves) have been designated "herald" taxa (Webb, 1985). Similarly, the age of the connection is still under debate, as some authors argue that it occurred several million years ago, 3 Ma (Coates and Stallard, 2013; Montes *et al*., 2015; Erkens, 2015). In that respect, Iturralde-Vinent and MacPhee (1999) proposed the presence of a precursor steppingstone connection along the Greater Antilles and Aves Ridge landspan, termed GAARlandia, permanently subsiding <32 Ma. Taxa transgressing in either direction prior to 32 Ma (e.g., Dasypodidae, Pampatheriidae, Megalonychidae, Mylodontidae, Caviomorpha, and Platyrrhini) may have taken that sweepstakes route initially, with recent taxa instead using the Panama land bridge or its precursor stepping stone island systems.

In any case, during the time that North and South America were separated, camels and horses, for example, evolved in the former, but later became extinct from this continent (Webb and Stehli, 1995; Honey *et al*., 1998). However, before their extinction they passed from North America to Eurasia. Camelids originated in North America, and some authors consider them indicators of the GABI that began with the closure of the Isthmus of Panama (Webb and Stehli, 1995).

However, there is evidence that camels colonized South America before the existence of the Central American land bridge (Reguero *et al*., 2007), potentially

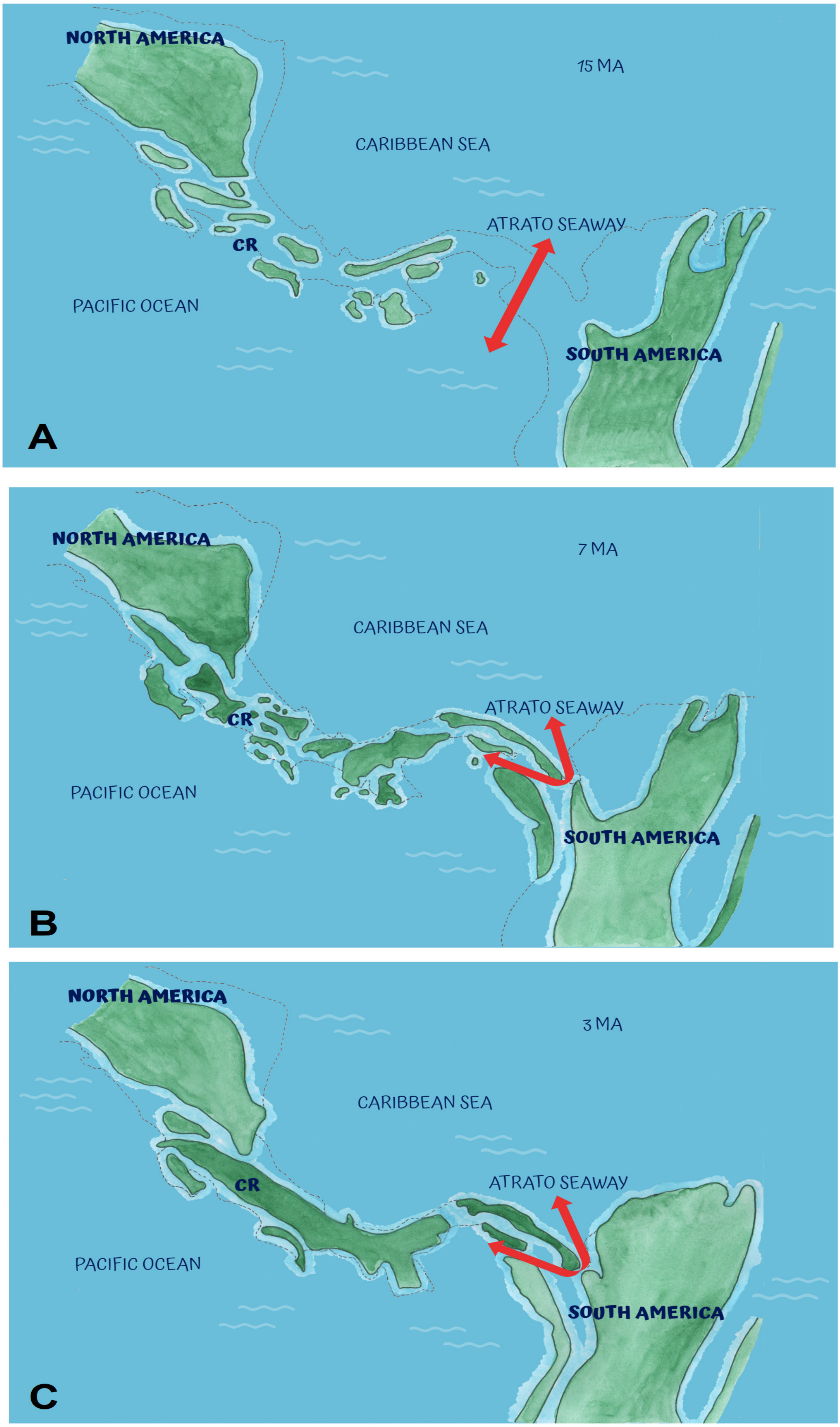

Figure 2. Three phases of the geological history of Costa Rica (CR): A) 15 Ma during the Miocene, B) 7 Ma also during the Miocene, and C) 3 Ma during the Pliocene. Figure by Lucia I. López.

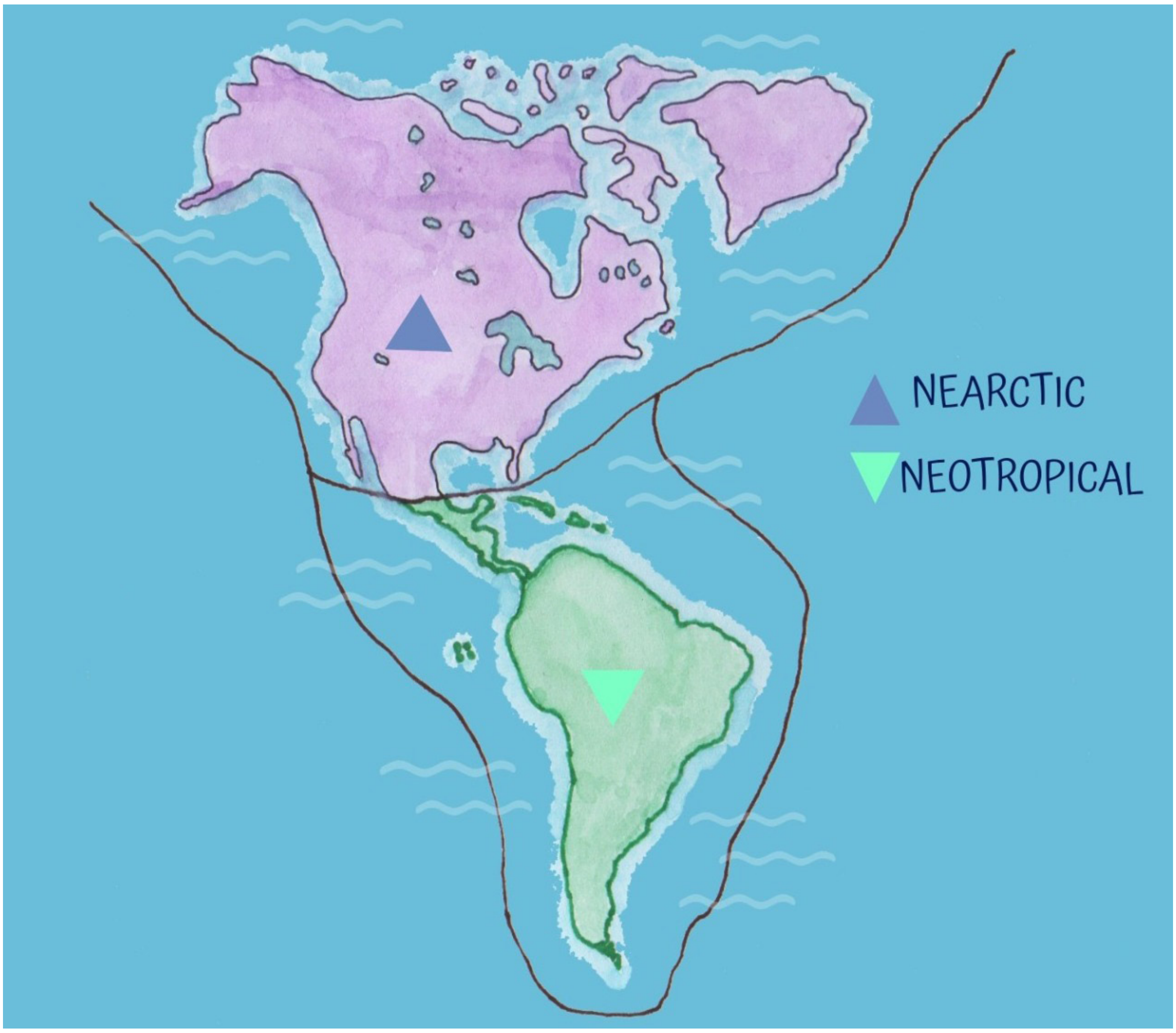

Figure 3. The Neartic and Neotropical zoogeographic regions occupy the territory of the Americas. Figure by Lucía I. López.

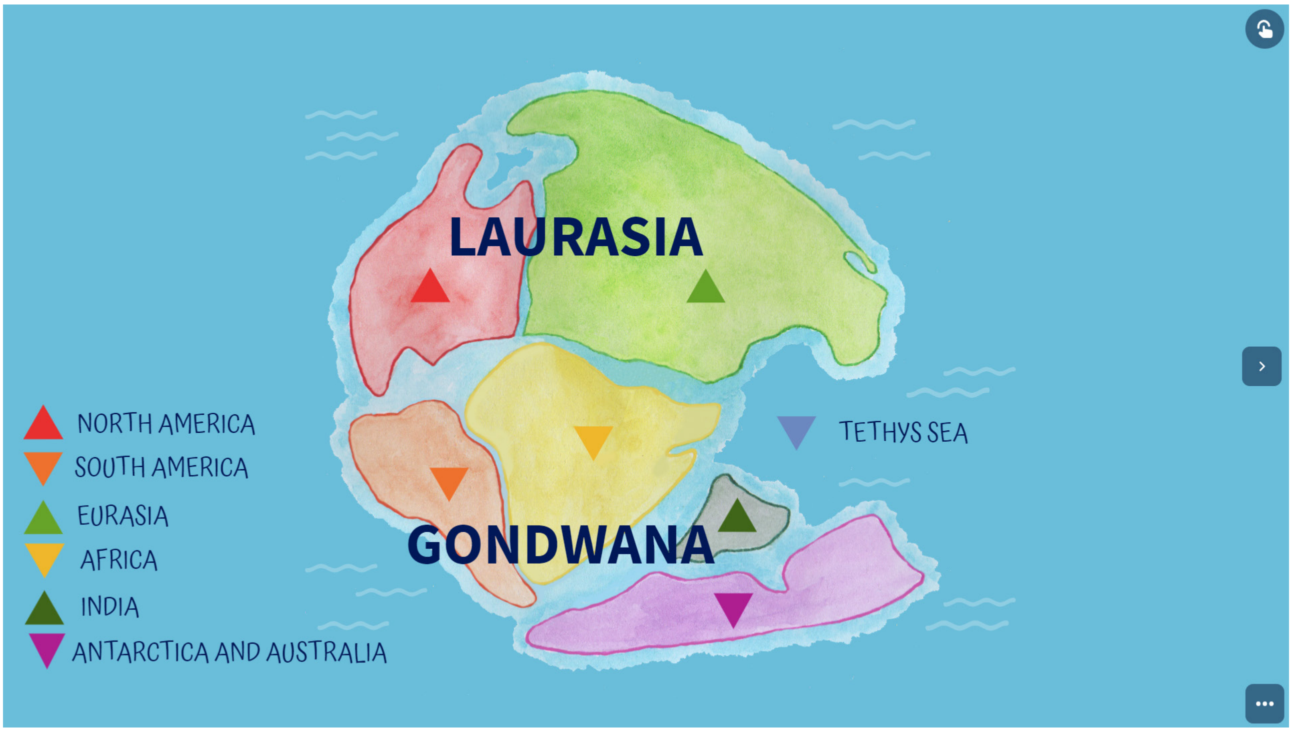

Figure 4. Land masses of the Earth at the end of the Triassic 190 Million years ago. Figure by Lucía I. López.

supporting the GAARlandia hypothesis. In South America, in turn, there was a great radiation of large edentate mammals such as the giant armadillos and the giant ground sloths (Simpson, 1950); similarly, some taxa among which were successful at establishing themselves in North America.

The Neotropics does not constitute all of South America but does include Central America and portions of Mexico (part of North America). However, to contextualize the origin of Costa Rican mammals more fully, it is convenient first to analyze the history of South American mammals separately. At this level, it is key first to review the biogeographical isolation of South America and subsequently the impact and consequences of the GABI, both in North and South America, and in Central America in general and Costa Rica in particular. However, it is clear that the taxa of North American mammals have had a great influence on the species and community composition of the mammal fauna of Central and South America, and therefore, the origin of these mammals is also relevant. With the exception of the southernmost part of the Florida peninsula and Greenland, the Nearctic Biogeographical Region includes nearly all of North America north of the tropical sections of Mexico. The Cenozoic history of North America mammals is examined in detail in Woodburne (2004). It is generally accepted that South America remained isolated from the rest of the continental masses around 80 Ma, until the establishment of the Isthmus of Panama 3 – 4 Ma, which connected it with North America (MacFadden, 2006; Agnolin *et al*., 2019). However, more recent interpretations suggest that South America retained a connection to Antarctica until the Oligocene (30 Ma; McLoughlin, 2001). This connection allowed faunal exchanges between South America and Australia according to recent evidence based on marsupials. This information proposes a dispersal of marsupials from their origin in North America to Australia via South America and Antarctica (Woodburne and Case, 1996; Luo *et al*., 2003; Meredith *et al*., 2008). In addition, it is possible that after the separation of South America from Africa at the end of the Cretaceous (75 Ma), the formation of a volcanic arc of islands began in the Caribbean that allowed faunal exchanges from North America (Horne, 1994; Iturralde-Vinent and MacPhee, 1999). As a result, the splendid isolation of South America was neither as large nor as long as previously thought (Erkens, 2015; Hoorn and Flantua, 2015; Agnolin *et al*., 2019). The isolation of South America varies between 80 Ma, as traditionally assumed, (Simpson, 1980; Flynn and Wyss, 1998) and 50 Ma according to the most recent paleontological evidence (Ezcurra and Agnolín, 2012; Bacon *et al*., 2015). This difference is key when considering the evolution of South American mammals.

The mammals of South America have four components, with marsupials as ancient colonizers being the first to arrive. Marsupials arrived from their area of origin in North America to South America in the Late Cretaceous and diversified into groups such as current didelphids (Wilson *et al*., 2016). The first records of various lineages of placental mammals date back to the Paleocene and Eocene (de Oliveira and Goin, 2011; Herrera *et al*., 2012). Among these groups are xenarthrans and various lineages of ungulates (de Oliveira and Goin, 2011; Herrera *et al*., 2012). Xenarthra is the taxon that is currently hypothesized to contain the orders Pilosa (sloths and anteaters) and Cingulata (armadillos). Although one species of armadillo has invaded North America, as have in the recent past some species of ground sloths, they otherwise are an exclusively South American group (Simpson, 1980; dos Reis *et al*., 2014). Based on fossil data, these mammals appeared in the Upper Paleocene (Riochican of Argentina [Chubut], 55.8 – 57.0 Ma, for Dasypodidae [Simpson, 1935]) and diversified during the Oligocene (Vizcaíno, 2009, see dos Reis *et al*., 2014). For their part, ungulates developed during the Paleocene from North American ancestors and diversified into groups such as litopterns, notoungulates, pyrotherians, xenungulates, and astrapotherians (Billet, 2011; Cione *et al*., 2015). Recent evidence suggests that *Macrauchenia* (litopterns) and *Toxodon* (Notoungulata) constitute a sister group to the extant perissodactyls (Buckley, 2015; Westbury *et al*., 2017). This suggests that the ancestors of these groups came from North America and radiated extensively, resulting in substantial species diversity during the Oligocene and Miocene. Marsupials, xenarthrans, and ungulates make up the first autochthonous faunal component of South America (Pelegrin, 2018); they are the members of the first stratum of Simpson (1950).

The second component is the arrival of the ancestors of South American primates and rodents (de Oliveira *et al*., 2009) that make up the second stratum of Simpson (1950) occurring from the end of the Lower Eocene to the upper one when conditions for dispersal from Africa were present (Springer *et al*., 2011; Ezcurra and Agnolín, 2012). This process could have been possible by physical means such as the formation of potential island arcs between the continents and the directionality of the oceanic currents in the Atlantic, which was just being formed and therefore at a shorter distance between the two continents. These currents may have carried rafts of vegetation from the large river basins of Central and West Africa (Antoine *et al*., 2011; Bond *et al*., 2015).

Some faunal interchanges between North and South America were facilitated by a hypothetical Antillean arc that connected the southeastern USA to Venezuela, the tongue of land called GAARlandia, (Lucas and Alvarado, 1994). This hypothesis explains the brevity of the Caribbean – Mainland exchanges between the Eocene and the Oligocene. The possible existence of GAARlandia has key implications for understanding the early phases of biotic exchange between North and South America before the Pliocene (Agnolin *et al*., 2019). However, there is no geological evidence for this hypothesis. On the contrary, colonization was apparently heavily filtered and assembled in a piecemeal fashion consistent with over-water dispersal (Ali and Hedges, 2021). Recent evidence suggests that Central America played little or no part in these two oldest components: Late Cretaceous/Paleocene and Eocene/Oligocene (Lucas and Alvarado, 2016). During those dispersal times, Central America was either nonexistent (in part), or was isolated as an island arc, so the most likely north–south pathway for land vertebrate would be across GAARlandia (Lucas, 1986; Alvarado, 1994; Lucas and Alvarado, 2016), but see Ali and Hedges (2021).

Current evidence suggests that island chains existed between North and South America during the Paleogene (e.g. Dávalos, 2004; Pindell and Kennan, 2009; Agnolin *et al*., 2019). These islands could be related to the proto-Antilles or to the Panamanian tectonic microplate and the igneous complexes derived from the Galapagos hotspot (Montes *et al*., 2012b). Regardless of origin, the island chains enabled faunal exchange between North and South America at various times. This phase has been called Pre-GABI or Proto-GABI (Wroe *et al*., 2004; Cione *et al*., 2015) and has been supported by the recent increase in fossil finds in North, Central, and South America. At the Oligocene-Miocene boundary, a new phase of exchanges began that preceded the GABI itself (Bacon *et al*., 2015). These exchanges lasted throughout the Neogene until the first stage of the GABI with the formation of the connection between North and South America (Woodbourne, 2010). These were very complex geological processes that have found support in molecular phylogenetic studies. Already during the Neogene, the degree of connection between the two continents increased (Prothero *et al*., 2014; Carrillo *et al*., 2015).

During the ProtoGABI, several mammal taxa participated in the exchanges, based on evidence from molecular data. Also, there is fossil evidence of *Panamacebus* from the Lower Miocene of Panama (Arikareean Ar4 faunal zone, ca. 21 Ma), which is not only the first platyrrhine fossil primate found outside of South America, but also the earliest fossil evidence of mammalian exchange from South America to North America (Bloch *et al*., 2016). Added to this exchange, are the oldest records of sloths in the Greater Antilles from the Oligocene and Early Miocene of Puerto Rico and Cuba (White and MacPhee, 2001; MacPhee, 2005). The Oligocene glaciations could have caused a sea level drop, thus allowing the passage of mammals due to low sea levels, and the connection between northwestern South America and the island arc between Costa Rica and Panama (Coates *et al*., 2004).

Later, continental drift and plate tectonics caused the formation of a bridge mainly by means of the uplift of the earth's crust and volcanism, which created a geological corridor between North and South America (Alvarado, 1994; Laurito and Valerio, 2012b; Alvarado and Cárdenes, 2016). This corridor allowed the passage of fauna from South America to North America and vice versa, including the GABI as a highly relevant biological event. The Mesoamerican bridge has also acted as a filter in both directions, but particularly from South America to North America, because climatic conditions in North America are less favorable for tropical taxa (Alvarado, 1994; Pelegrin *et al*., 2018). During the Miocene (23.8 Ma – 5.3 Ma), climatic regimes generally were less seasonal than those of comparable regions of today, and many forested biomes were replaced with more open-country woodlands or grasslands (MacFadden, 2006).

The mammals of Costa Rica within the context of Central America

The mammals that inhabit Central America derive from four sources: The North Americans, the old South Americans, the young South Americans, and the Mesoamerican unit (Simpson 1950; Rich and Rich, 1983; MacFadden, 2006; Woodbourne, 2010). The North Americans dispersed to the southern limit of nuclear Central America (Nicaragua). During the GABI, they also managed, to some extent, prior to that event, to disperse southward as far as South America (Simpson, 1950). The old South Americans are the American marsupials, the xenarthrans, and some bats. Before the GABI, these taxa arrived in Central America, most likely by drifting over water or, in the case of bats, by flying; most likely wind aided during storms (Simpson, 1950). Young South Americans include primates and rodents (Simpson, 1950). Before the GABI, these mammals arrived in Central America possibly as "waif dispersers" by means of sweepstakes routes through the Central American seaway (Coates *et al*., 2004). The Mesoamerican unit evolved in this region, whence they spread to other areas (Rich and Rich, 1983). This unit is questioned by some on the basis that there is no convincing evidence that this region was the center of origin for mammals before the GABI (Webb, 1985). Following this reasoning, Central America acted as a filter to dispersal during the GABI, as well as a center of mammalian evolution, although there is no evidence of something similar occurring during the Pleistocene (Alvarado, 1994; Alvarado and Cárdenes, 2016).

Central American vertebrate fossils are mainly from the late Cenozoic and represent all the major taxonomic groups of vertebrates (Lucas and Alvarado, 2016). This vertebrate fossil record is concentrated in Miocene and Pleistocene sedimentary strata (Lucas and Alvarado, 2016). However, the history of Central American mammals lacks further direct fossil evidence. There are basically no fossils from the Mesozoic (> 66 Ma) and there are very few fossils prior to the Miocene (beginning 23 Ma; Rich and Rich, 1983). That results in the fact that perhaps only 25% or less of the mammalian history of Central America is known, and virtually all of that known history in each case is documented by few fossils (Rich and Rich, 1983). Several fossil sites have been found in all Central American countries, but with little information (Rich and Rich, 1983; Cisneros, 2005). The most diverse group of mammals known from Central American fossils are armadillos, glyptodonts and several other taxa now in the orders Cingulata and Pilosa;

all are of South American origin (Lucas and Alvarado, 2016). These include giant ground sloths of the families Megalonychidae and Megatheriidae (Lucas and Alvarado, 2016). The group also contain small ground sloths (Mylodontidae), including two taxa endemic to Central America from the Pleistocene of Barranca del Sisimico (El Salvador; Webb and Perrigo, 1985). On the other hand, all fossil carnivore taxa, including cats, sabertoothed cats, dogs, bears, and raccoons are of North American origin (Lucas and Alvarado, 2016). Fossil remains of these latter are from Miocene and Pleistocene faunas generally of low diversity and are uncommon (Webb and Perrigo, 1984; Cisneros, 2005, 2011). The southernmost Pleistocene record of the coyote *Canis latrans* is from Costa Rica (Lucas *et al*., 1997). Most Central America ungulates are of North American origin: proboscideans, perissodactyls, including *Tapirus* sp. cf *terrestris*, and artiodactyls, including a Camelidae (*Palaeolama mirifica*) from lacustrine deposits (Pérez, 2013). The only ungulates of South American origin are the notoungulates, and mostly pertain to a *Mixotoxodon*, apparently endemic to northern South and Central America (Laurito, 1993; Lucas and Alvarado, 2016).

In Costa Rica, fossil mammals are known from more than forty-five Pleistocene localities (Alvarado and Cárdenes, 2016). Most of these are proboscideans such as *Cuvieronius hyodon* (Gomphotheriidae), and the mammoth *Mammuthus columbi* (Mammutidae), the southernmost record of mammoths in Central America (Alvarado and Cárdenes, 2016). These localities contain only one or a few large mammalian taxa, but small mammals have been poorly studied (Alvarado and Cárdenes, 2016). This suggests a likely bias towards the preservation of high energy fluvial, alluvial, ignimbrite, and lahar deposits, as well as a bias towards the collection or preservation of large-sized fossils (Alvarado and Cárdenes, 2016). Rodents are basically absent, excluding capybaras (Hydrochoerinae, Caviidae) that are large; rabbit (Lagomorpha) records are scarce, and only few fossil bats have been reported (Webb and Perrigo, 1984; Czaplewski *et al*., 2003; Lucas and Alvarado, 2016). However, a rodent fossil fauna was described by Laurito (2003) from La Palmera locality at San Carlos county in Alajuela province likely of the Upper Pleistocene age and including four species: *Tylomys watsoni*, *Reithrodontomys mexicanus* (which should be reexamined in light of taxonomic changes), *Sigmodon hispidus* (now *S. hirsutus*), and *Proechimys semispinosus*.

Other documented fossil groups include horses, tapirs, camels, and proboscideans, that represent three distinct orders of North American origin (Lucas and Alvarado, 2010a, b). The proboscidean gomphotheres (*Gomphotherium*) first arrived in Central America about 10 Ma. *Cuvieronius* arrived in Central America about 3 Ma and continued expanding their range to southern South America (Lucas, 2013). Finally, there is record of a Pleistocene arrival in Honduras based on a single record of the American mastodon, *Mammut americanum* (Lucas and Alvarado, 1991; Lucas and Alvarado, 2016). A frequent problem is that many fossiliferous sites have not been reported or adequately safeguarded. They also have not been assessed due to the lack of institutional support for investigations as well as other factors (Lucas and Alvarado, 2016). Due to the sparse knowledge generated and the general lack of mammalian fossil remains in Central America, the faunal exchanges of the Paleogene and Neogene (“Tertiary”, between 66 and 2.5 Ma), remain unclear, a situation aggravated by the fact that the exact positions of some parts of Central America, and even of its mere existence, are also unknown, both in broad strokes as well as in many other details (Rich and Rich, 1983). It is possible that these regions could have contributed to the exchange of mammals, but it is not known how much. For example, the only dinosaur fossil reported from Central America is a femur discovered in 1971, possibly from a hadrosaur (Lucas and Alvarado, 2016). This fossil comes from the Cretaceous of Valle de Angeles

(Honduras), a locality interpreted as part of a possible terrane that was attached—or at least was close to—southwestern Mexico during the Cretaceous (Lucas and Alvarado, 2016), arriving there in a "Viking funeral ship" as defined by McKenna (1973). After the Neogene, about 2.5 Ma, the situation is better known, for example, as noted above for Costa Rica.

The fossil faunas of the Central American Quaternary reflect a mixture of elements from North and South America that began with the terrestrial connection between these two continental masses 5 – 1 Ma, particularly by means of the GABI (Rich and Rich, 1983). North American mammal families from the Pleistocene of Central America include Leporidae, Felidae, Canidae, Gomphotheriidae, Mammutidae, Elephantidae, Tapiridae, Equidae, Tayassuidae, Camelidae, Cervidae, and Bovidae (Alvarado and Cárdenes, 2016). Families of South American origin include: Dasypodidae, Glyptodontidae, Megalonychidae, Megatheriidae, Mylodontidae, Caviidae (Hydrochoerinae) and Toxodontidae (Alvarado and Cárdenes, 2016).

An important case to note across the history of Central American mammals is that of the Guanajuato Fauna, from the Eocene – Oligocene transition (ca. 34 Ma), being one of the oldest in the region (Rich and Rich, 1983). The Guanajuato Fauna includes two genera of rodents and contrasts with previously mentioned sites in two senses, first, practically all the other sites contain fossils of species of medium or large body sizes, and date to later than the Miocene (< 23 Ma; Rich and Rich, 1983). One of these genera, *Guanajuatomys*, is of clear phylogenetic affinity with the caviomorphs of South America (Black and Stephens, 1973). Perhaps the high affinity of Central American mammals with those of North America can be attributed to the fact that the fossils found belong to the largest mammals (Rich and Rich, 1983). The Guanajuato fauna could be the evidence of a second component of the "tertiary" fauna of Mesoamerica, those smaller endemic mammals (Rich and Rich, 1983). Three genera of rodents from Texas (USA) of approximately the same date as the Guanajuato fauna, as well as a didelphid from the middle Miocene, support the previous idea. One of the Texas rodent genera, *Prolapsus*, also has evolutionary affinities with the caviomorphs of South America (Slaughter, 1978; Wood, 1980). These data have led to speculations on the possible evolutionary role of mammals originating in Mesoamerica that could have resulted in the American caviomorph fauna without the need for an exchange across the Atlantic (Rich and Rich, 1983; but see de Oliveira *et al*., 2009).

Molecular evidence suggests a genetic divergence about 43 Ma between the South American caviomorphs (Parvorder: Caviomorpha) and its sister group, the African parvorder Phiomorpha (Antoine *et al*., 2011). The oldest records of caviomorphs date to the Peruvian Middle Eocene (Antoine *et al*., 2011). Subsequently, caviomorph rodents diversified widely during the Oligocene (Bertrand *et al*., 2012; Boivin *et al*., 2016) and created several lineages adapted to different ecological conditions; some of them even acquired considerable sizes, for example *Josephoartigasia monesi* (Dinomyidae) being of around 1000 kg (Pelegrin *et al*., 2018; Rinderknecht and Blanco, 2008). Based on these two aspects, the pacaranas (Dinomyidae), agoutis (Dasyproctidae), pacas (Cuniculidae), maras, capybaras and guinea pigs (Caviidae), tuco-tucos (Ctenomyidae), and spiny rats and hutias (Echimyidae), among others, were consolidated.

The African origin of South American rodents is supported by the arrival of primates also from Africa (de Oliveira, *et al.,* 2009; Defler, 2019). These constituted the origin of the new world primates whose oldest known representative is *Perupithecus* from the Peruvian Eocene (Divisaderan) (Figure 5). This primate has phylogenetic affinity with African taxa such as its approximate contemporary *Talahpithecus parvus* (Bond, *et al.,* 2015; Kay, 2015), which is considered the closest relative of the platyrrhines, the modern 'New World' monkeys. The parvorder Platyrrhini includes marmosets

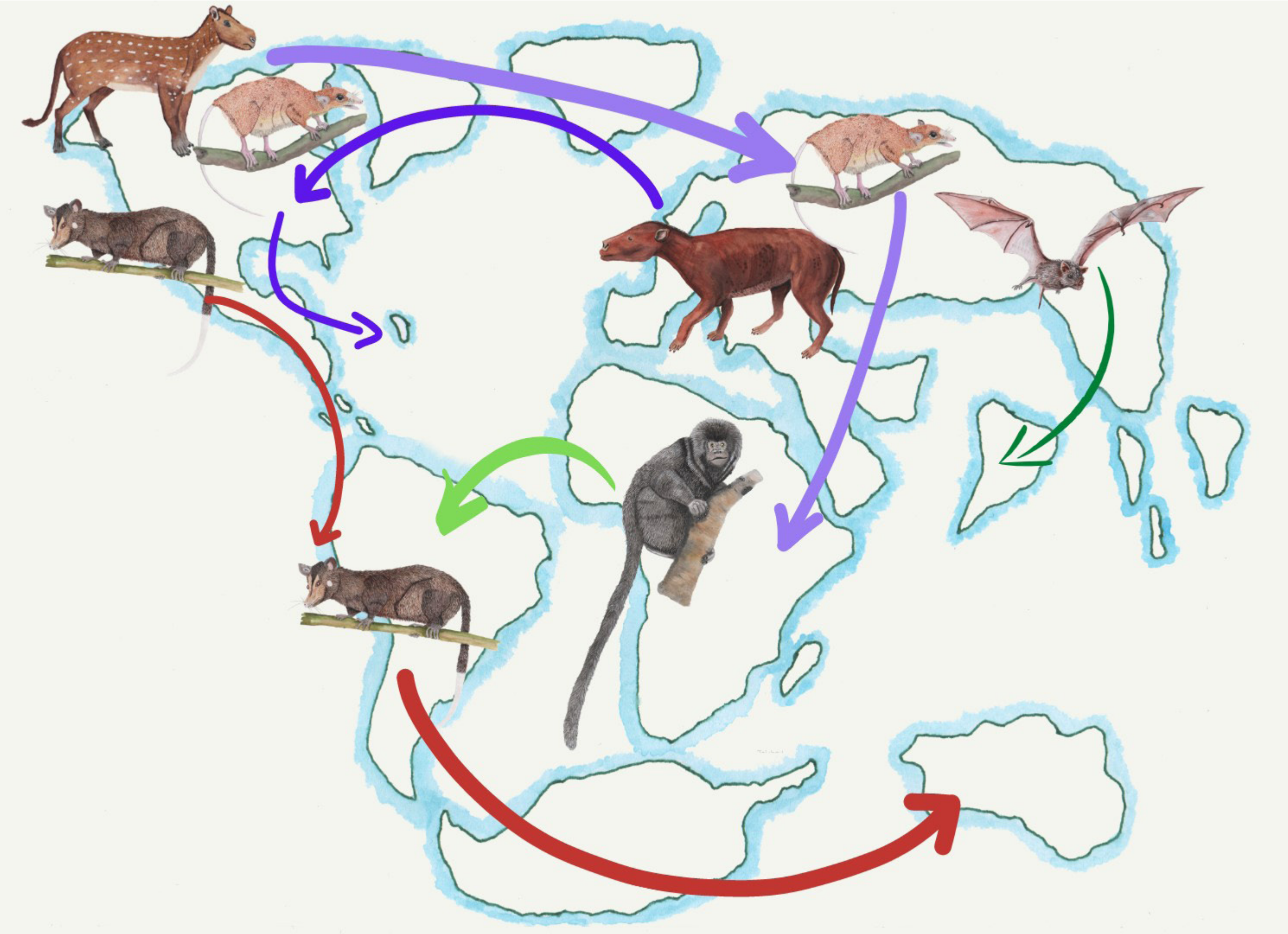

Figure 5. Some examples of mammalian dispersals during the Eocene including the arrival of *Perupithecus* ancestors in South America from Africa (green arrow). Also, the dispersal of marsupials from North to South America and then to Australia via Antarctica (red arrows). Figure by Lucía I. López.

and tamarins (Callitrichidae), capuchins (Cebidae), night monkeys (Aotidae), sakis and uakaris (Pitheciidae), and spider and howler monkeys (Atelidae; Rylands and Mittermeier, 2009). *Branisella* from the Upper Oligocene of Bolivia is the oldest fossil record of the group; it therefore is assumed that they diversified at the beginning shortly prior to that time (Pelegrin *et al*., 2018).

The similarity between hystricomorph rodents from Africa and South America may be attributed to exchanges across the Atlantic Ocean during the late Eocene (Lavocat, 1980). This was possible because the distance between these two continents at the end of the Eocene was smaller, thereby allowing for taxa to raft across the Atlantic in less than fifteen days (Houle, 1999).

Fossils of large mammals such as artiodactyls are relatively well-known from Central American and include anthracotheres, camels, deer, gelocids, oreodonts, peccaries and even bison. These fossils are from generally dispersed localities in the Miocene and Pleistocene (Webb and Perrigo, 1984; Lucas *et al*., 1997, 2008; Cisneros, 2005, 2008; Rincon *et al*., 2013; Lucas, 2014). Perissodactyls are represented by a few records of tapirs and rhinoceroses, as well as many horses. *Aceratherium* rhinoceros are known from the Miocene of Honduras and Panama. The horses include hipparionine records from the Miocene and *Equus* records from the Pleistocene, including some interesting horse assemblages from the late Miocene of Costa Rica (Laurito and Valerio, 2010b). Another example from these times, which is endemic to Central America, is *Pliohippus hondurensis* from Honduras (Lucas and Alvarado, 2016). Fossils and knowledge of marine mammals in the region are scarce. Recently recovered fossils include true whales and other cetaceans and sirenians from the Pliocene and the Miocene of Costa Rica, Nicaragua, and Panama (Lucas *et al*., 2009; Laurito *et al*., 2011; Uhen *et al*., 2011; Lucas and Alvarado, 2016). The locality of San Gerardo de Limoncito is the only one in Costa Rica containing both aquatic and terrestrial mammals (Laurito and Valerio, 2012b). With respect to aquatic mammals, this locality has yielded freshwater cetaceans such as the Iniidae *Goniodelphis* sp., and marine forms such as *Hadrodelphis* sp., *Orycterocetus* sp., and *Eurhinodelphis* sp., jointly denoting paleocaribbean epicontinental affinities with the Florida peninsula, North Atlantic, and the Mediterranean Sea (Valerio and Laurito, 2012; Alvarado and Cárdenes, 2016).

It has been claimed that all the pre-Pleistocene mammalian faunas from Central America to Panama had no affinities with those of South America (Ferrusquia-Villafranca, 2003). Even the Miocene Panama Canal Cucaracha (Gaillard Cut) Fauna (15 Ma) only contained congeners of North American faunas (MacFadden, 2005). The variety of the Cucaracha Fauna is large, including horses, rhinoceros, and artiodactyls, as well as carnivores and even rodents (Rich and Rich, 1983); it is considered as having the oldest vertebrate records in Central America (Laurito and Valerio, 2012b). However, it is surprising that all these fossils are of North American origin despite their proximity to South America, suggesting overland dispersal into southern Central America just west of the Central American seaway (MacFadden, 2005). A Miocene fauna from Colombia, 400 km to the east of the Bolívar Trench, contained only South American genera (Rich and Rich, 1983). In contrast, Late Miocene mammal localities from Honduras, El Salvador, and Mexico produced fossils similar to those found in North America (MacFadden, 2005). These faunas date back to 20 – 8 Ma and include a canid, cat, proboscidean, horse, peccary, camel, and a horned artiodactyl (MacFadden, 2005).

Thus, the general pattern appears to indicate that all Central American "Tertiary" faunas were related to North American faunas, with some rare exceptions. In the last three decades, data have been generated and further illuminated the pre-Pleistocene faunas of Central America, in particular in Costa Rica. For example, the Fauna of San Gerardo de Limoncito in the Coto Brus Valley, dating back to about 8.5 – 6.5 Ma (Miocene), is characterized by a mixture of vertebrates of Palearctic, Nearctic, and Neotropical origins, and contains representatives of the first South Americans mammals that arrived in southern Central America (Laurito and Valerio, 2012b). These investigations have concluded that the arrival of South American mammals to the land connection over the Isthmus of Panama can be attributed to the shortening of the ocean passages among the islands due to normal subduction processes and the rapid uplift that southern Central America experienced because of the tectonic activity in the region (Laurito and Valerio, 2012b). Added to this are the climatic elements prevailing at that time, which favored the predominance of humid and warm basal forests both in northwestern Colombia and in southern Central America (Laurito and Valerio, 2012b). These conditions allowed xenarthrans, which are considered to be good swimmers and island jumpers, to migrate north. In contrast, they seem to have limited the southward migration of North American mammals (Laurito and Valerio, 2012b). The latter managed to cross into South America later, when the climate became drier and after a continuous land corridor was established (Laurito and Valerio, 2012b). Early Pleistocene or Late Pliocene fossil records from Bajo Barrantes (Costa Rica) of *Mixotoxodon larensis* (Notoungulata: Toxodontidae), may predate the arrival in Costa Rica of North American immigrants (Laurito, 1993; Lucas *et al*., 1997).

The first fossil record of megatheriine sloths (Megatheriidae) in Central America was obtained from the Fauna of San Gerardo de Limoncito, which also represents the earliest record of this subfamily outside South America, dating back to 5.8 Ma, i.e., before the closure of the isthmus of Panama (Rincón *et al*., 2020). The first fossil record of

Tayassuidae from the Cenozoic of Costa Rica also was obtained from this fauna, including the first confirmed record for the Northern Hemisphere of two species being distributed sympatrically (Valerio and Laurito, 2020). In addition, the fauna includes the first Costa Rican and Central American record of the camel *Hemiauchenia vera*, a finding that also constitutes the southernmost record of this species in the Northern Hemisphere (Laurito and Valerio, 2016).

In the late Miocene, the exchange of fauna increased by island hopping across the Bolívar Trench (MacFadden, 2006). Fossils of two genera of ground sloths from the Miocene of South America that are also found in North America similarly should have been found in Central America. However, they do not appear in the Gracias Fauna of Honduras, the only Central American paleofauna with temporal correspondence (Rich and Rich, 1983). This highlights the lack of information regarding the fossil history of Central American mammals. It has been postulated that perhaps these two genera passed from South America to North America by island hopping using Caribbean islands. However, had that been the case, these genera would have dispersed rapidly back south (Rich and Rich, 1983). This can be attributed to the fact that the exchange of the Miocene was not one way as evidenced by procyonids which arrived in South America from North America over 7.0 – 7.5 Ma (Patterson and Pascual, 1972) probably via the isthmus of Panama (Laurito and Valerio, 2012b).

Faunal exchanges between both continents increased in the Upper Miocene (Smith and Klicka, 2010; Bacon *et al*., 2015). These exchanges allowed tapirs, peccaries, and ruminants, of North American origin to transgress the Bolívar Trench and be recorded from the Amazon basin about 9.5 Ma (Campbell *et al*., 2010; Prothero *et al*., 2014). Other North American mammals found in South America support these periodic incursions, including gomphotheres in Peru (Campbell *et al*., 2000), the first South American procyonids (*Cyonasua*), about 9 Ma (Forasiepi *et al*., 2014), and sigmodontine rodents, whose first remains have been recorded in South America by the end of the Upper Miocene, about 5.8 Ma (Pelegrin *et al*., 2018). The colonization of mammals from South America in North America includes sloths of the genus *Pliometanastes* (Megalonychidae), recorded in sediments from the Upper Miocene (8.5 – 6.5 Ma) in Costa Rica (Laurito and Valerio, 2012a). The earliest records of peccaries (Tayassuidae) in Costa Rica date back to the Late Miocene (5.8 Ma), from the locality of San Gerardo de Limoncito. This record constitutes the southernmost locality for *Protherohyus brachydontus*, and the only one from Central America (Valerio and Laurito, 2020). Moreover, for the first time for the Northern Hemisphere, this finding confirmed the distribution of this species being sympatric with that of *Prosthennops serus* (Valerio and Laurito, 2020).

The classical view is that the South American mammals' splendid isolation was negatively affected by the invasion of somehow more advanced North American mammals, which resulted in the competitive exclusion of well-established groups such as marsupials and in particular sparassodonts (e.g., Piper, 2009). For example, the arrival into South America of some of the aforementioned groups coincided with the decline of the South American carnivorous Marsupialiformes of the family Borhyaenidae (Wilson *et al*., 2016). The first interpretations of the dichotomy in species diversity resulting from the intercontinental faunal interchange explained the lower diversification of the autochthonous faunas of South America as having resulted from this fauna's lower competitive capacity in relation to the immigrant taxa from North America (e.g., Piper, 2009). However, ecological pressures were derived from the dramatic tectonic, climatic, and biogeographical changes in the region associated with both the formation of the Central American bridge and that of the Andes in addition to the development of the Pleistocene glaciations. Interspecific competition, therefore, was unlikely to have been a highly relevant factor at a macroevolutionary scale (Antonelli *et al*., 2009; Prevosti *et al*., 2013; Bacon *et al*., 2016).

Most of the exchanges included groups that inhabited forests, for which reason the existence of a forested corridor was necessary, and therefore also that of a continuous tongue of land between North and South America. The first candidate for this union is the Baudó land bridge that existed about 10 Ma, which allowed for the connection of northwestern South America with the central area of Panama through the San Blas-Darién and Baudó mountains (Campbell *et al*., 2000). By this means, one closure of the Central American seaway may have occurred around 10 Ma (Montes *et al*., 2012a, 2015). Faunal exchanges would depend on fluctuations in sea level, because when sea levels rose, passage by land was severely limited (Prothero *et al*., 2014).

When the bridge was complete, exchanges became more feasible, but would have depended on the biology of the species involved. For example, the cold climate of the Pleistocene allowed for the exchange of savanna-adapted forms due to the existence of a nearly continuous belt of savanna between North and South America through Central America (e.g., MacFadden, 2006). Mammoths arrived in Central America at the beginning of the Pleistocene and are found throughout most of the region, which demonstrates the presence of savannahs and grasslands in the rain shadow areas of Pleistocene volcanoes and ignimbrite plateaus (Cisneros, 2005; Lucas *et al*., 2008; Lucas and Alvarado 2010a; Lucas and Alvarado, 2016). The savannahs and thorny shrub habitats of the Pliocene and Early Pleistocene (5 – 2 Ma) were fit for the exchange of more xeric adapted fauna and grazing animals, as well as other taxa adapted to the savannah such as glyptodonts, horses, ground sloths, and camels (Rich and Rich, 1983). Fossils from these epochs show that 22 of 31 mammalian genera involved in the exchange between the Americas were adapted to savannah habitats (Rich and Rich, 1983). Grasses—and the corresponding mammalian grazers—evolved in South America (ca. 25 Ma) earlier than they did in North America (ca. 15 Ma) based on fossil evidence (MacFadden, 1997, 2006). From the end of the Pleistocene (ca. 12 Ka) to the present, there was an extension of the tropical humid forest in Central America from South America that cut into the savannah corridor, which led to a decrease in the exchange of grassland taxa through the isthmus. During that time, only the taxa adapted to humid forests and savannahs were able to advance from South America to North America and vice versa. The fauna of the tropical forests of northern South America passed to Central America at a time when the fauna of the isthmus took on its modern Neotropical character (Rich and Rich, 1983).

Costa Rica and the GABI

For the GABI to have taken place, the existence of Costa Rica is essential because its territory is one of the principal components of the geological and terrestrial bridge that connects North America with South America. It is clear that to form the bridge, the closure or consolidation of the Isthmus of Panama has also been essential: a complete land union through the Bolivar Trench to South America (Montes *et al*., 2015). The GABI has been divided into four phases based on analysis of the fossil fauna of South American mammals (Simpson, 1980). The first two phases are not part of the GABI per se (Simpson, 1950), but the third and fourth are. As already noted, during the first stratum of the Cretaceous-Paleocene, the entry of autochthonous components occurred, represented by early migrants from North America. The second stratum is constituted by the transatlantic colonization from Africa in the Eocene by the ancestors of Neotropical rodents and primates (Boivin *et al*., 2016). The third stratum groups all exchanges undertaken during the formation of the Central American land bridge in the Pliocene (Marshall, 1988; Webb, 1991).

It should be emphasized that recent conclusions indicate that the GABI was much more complex and gradual than had been supposed, which is why it has been suggested to abandon the simplistic vision of a singular migratory event (Bacon *et al*., 2015, Winston *et al*., 2016). The GABI had distinct intervals of active exchange (Woodburne, 2010; Table 2).

This implies complex scenarios of exchanges where—as already noted above—the groups of mammals involved experienced strong selective pressures derived from tectonic, climatic, and biogeographical changes in the region. The GABI was a dynamic exchange that included bidirectional migrations, consisting of phases throughout the Pliocene and Pleistocene, with each of the phases including different waves of lineage colonization between the two continents (Table 2). The core of the GABI was composed of a series of large migratory waves that began about 3 Ma and persisted throughout the Pleistocene (Woodburne,

Table 2. Some examples of the main groups of mammals participating in the faunal interchange between North and South America during each of the four events of the GABI* after Woodburne (2010).

* GABI = Great American Biotic Interchange. Table prepared based on data from Woodburne (2010).

Event	Age Ma	From NA	From SA
GABI 1	3 - 2.4	Grisons: *Galictis*-Mustelidae Foxes: "*Dusicyon*"-Canidae Horses: Hippidion, Equidae Gomphotheres: *Stegomastodon* = *Notiomastodon*- Gomphotheridae.	Large herbivorous armadillos: *Holmesina*-Pampateridae Insectivorous armadillos: *Dasypus*-Dasypodidae Giant sloths: *Eremotherium*-Megatheriidae Arboreal porcupines: *Erethizon*-Erethizontidae
GABI-2	1.8	Bears: Arctotherium-Ursidae Cats: *Felis*, *Puma*, *Panthera*, *Smilodon*-Felidae Skunks: *Conepatus*-Mephitidae Otters: *Lontra*-Mustelidae Peccaries: *Catagonus*-Tayassuidae Deer: *Epyuriceros*, *Antifer*-Cervidae Camelids: *Hemiauchenia*-Camelidae Tapirs: *Tapirus*- Tapiridae Gomphotheres: *Cuvieronius*-Gomphotheriidae Horses: *Equus*-Equidae	Anteaters (*Myrmecophaga*)
GABI-3	0.8 - 0.7	Pampas cat: *Leopardus*-Felidae Peccaries: *Tayassu*-Tayassuidae Deer: *Paraceros*, *Hippocamelus*-Cervidae	Opossums (*Didelphis*)
GABI-4	last 0.125	Coati: *Nasua*-Procyonidae Giant otter: *Pteronura*- Mustelidae Dogs: *Canis*-Canidae Cats: *Herpailurus*-Felidae Glyptodont: Glyptothorium-Chlamyphoridae Rabbits: *Sylvilagus*-Leporidae The human species	

2010). This great exchange is explained by the appearance of the Central American bridge and the consequent closure of the isthmus of Panama (Woodburne, 2010). However, there were dispersals—albeit more limited—before that time, of which perhaps the oldest is represented by the sloths *Thinobadites* and *Pliometanastes*, derived from South American mylodontid and megalonychid ancestors respectively (Woodburne, 2010). These faunas are about 8.5 – 9 Ma (Woodburne, 2010).

Today representatives of these groups include the three-tod sloth (*Bradypus variegatus*: Bradypodidae) found in Costa Rica from sea level to highlands (Figure 6). Woodburne (2010) divided the GABI into four events. GABI-1 event lasted from about 3 to 2.4 Ma and included several North American lineages as well as some from South America (Table 2). Procyonids were the first placental carnivores that arrived in South America after the closing of the Central American seaway (Woodburne *et al*., 2006; Soibelzon, 2011). Today representatives of this family in Costa Rica includes the Cacomistle (*Bassariscus sumichrasti*) found at low and middle elevations (Figure 7). South American lineages include Erethizontidae although there is evidence that the arrival of these rodents into North America dates to the Upper Miocene (Upham and Patterson, 2012). The interchange during the GABI-2 event (1.8 Ma) was biased in favor of North American families, with only anteaters (Myrmecophaga) entering North America (Woodburne, 2010; Prevosti *et al*., 2013; Cione *et al*., 2015).

The North American continent included the prominent presence of carnivorous lineages (Table 2). Opossums (*Didelphis*) colonized North America during the GABI-3 event (0.8

Figure 6. A female three-toed sloth (*Bradypus variegatus*), a member of Bradypodidae, a typical South American family. The green color is due to algae growing on the sloth hair. Photo by José M. Mora.

Figure 7. The cacomistle (*Bassariscus sumichrasti*) a member of Procyonidae, a family of North American origin. Photo by José M. Mora.

– 0.7 Ma), a time when a number of North American taxa arrived in South America. The last event, GABI-4 is hypothesized to have taken place in the last 0.125 Ma time, when several North American carnivores and herbivores entered South America (Table 2). This event also includes the arrival of the human species to South America during the Late Pleistocene, probably between 18,000 and at least 15,000 years ago (Pérez *et al*., 2016). This is a key component of the GABI-4 event due to the negative impact that humans had on the environment provoking the extinction of many species during the Pleistocene-Holocene (Goebel *et al*., 2008; Cione *et al*., 2009; Barnosky and Lindsey, 2010).

Fossils of Central American vertebrates date not only to before and after the closure of the Isthmus of Panama, but they also constitute the direct fossil record documenting what clearly was a dispersal route between North and South America. The mixture began with the exchange that took place over the islands making up the current Central American region and increased when the Central American isthmus was closed and became dry land because it allowed for a greater traffic of mammals. About twenty families of mammals that inhabit Costa Rica are of South American origin, but a similar number are of North American origin. Because these interpretations are based entirely on the study of fossils, and because fossils are not common in the region, there remain many limitations regarding a more complete understanding of the chronology of the GABI (Rich and Rich, 1983). There are also still many unknowns regarding the physical conditions and dates of the mammal exchanges between the Americas, and the role of the Caribbean and Central American islands in these exchanges.

Conclusions

Central American mammal fossils are primarily of the late Cenozoic age and help provide an understanding of the GABI after the closure of the Panamanian isthmus (Lucas and Alvarado, 2016). Late Pleistocene mammals have been collected from several localities extending from Panama to Mexico, most of which are similar to those from rain forest habitats, with the addition of the white-tailed deer (*Odocoileus virginianus*) of a North American origin (MacFadden, 2006). However, several taxa occupied more open grassland habitats, such as *Toxodon*, mammoths (*Mammut*), horses (*Equus*), and even pronghorns and the 'Old-World' migrant bison (*Bison*). The region and its mammal fossils record the northern limit of toxodonts and the southern limit of bison and white-tailed deer. This classic interchange fauna combines extant genera with North and South American megafauna that subsequently became extinct during the late Pleistocene (MacFadden, 2006).

The land connection between North and South America provided a way for mammals from both landmasses to move between them. The most important of those exchanges was the so-called GABI. However, it is known now that the GABI was not a singular event, but was divided into different phases that have been dated and documented with greater precision as fossil records have increased (Pelegrin., 2018). The novel concept of a compound GABI was a very complex process with a network of biotic interactions conditioned mainly by changing abiotic factors that occurred during the process of paleoenvironmental configuration of the entire American continent.

Central America is the bridge that allowed both the GABI and other faunal exchanges between North and South America. However, Central America could have been the center of origin for mammals before the Paleocene (> 66 Ma). From this epoch until the Eocene (~55 Ma), there was a shift towards more tropical conditions in North America that could imply a northward shift of the mammalian fauna originating in Central America, as documented by fossils in North America (Rich and Rich, 1983). There is evidence to support this hypothesis based on the finding of fossils of ancestral groups of South American and southern North

American affinities in more northern areas of North America. Because of this, the existence of tropical mammals in Mesoamerica has been postulated during the Paleocene, with extensive documentation only of the faunas of the United States from the beginning of the Eocene, when they already had arrived from the south due to more favorable climatic conditions (Rich and Rich, 1983).

In any case, Central America served as a route of biological exchange between North and South America, but it also could have been an important center of origin for mammals. Likewise, and being of no less importance , is the fact that at the same time, the Isthmus of Panama interrupted the connection between the Atlantic and Pacific oceans, which led to the independent evolution of their biota, and allowed for an increase of marine biodiversity in the region (Haug and Tiedemann, 1998). In addition, this barrier caused changes in ocean currents that impacted the planet's climate, including the drier climate in Africa. This new climate may have influenced changes from forested to more open habitats. This, in turn, has impacted some primates to become terrestrial and bipedal, initiating perhaps the evolutionary process that eventually ended with what came to be *Homo sapiens*.

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