

WHERE DID THEY COME FROM?

THE ORIGINS OF SOUTH AMERICAN FAUNA



Lee E. Harding

Bentham Books

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The Origins of South American Fauna

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FOREWORD

Paleontology is a wonderful discipline for gaining some perspective. It illustrates that things haven't always been like they are today: not only animals and plants, but also biomes, ecosystems, landforms, and even the continents themselves. This is easy to forget because changes in the natural world usually occur at an imperceptible pace, far beyond one's lifetime. But for a paleontologist who studies remains that are thousands, millions, or even billions of years old, such differences between the present and the past are eminently clear. It is also clear that the present day (broadly speaking, the Anthropocene) is an arbitrary interval that is no more "normal" than any other time period. In fact, it is pretty abnormal from many perspectives! The modern world is simply the interval with which we are most familiar. I am of the opinion that no place on Earth highlights this concept more clearly than South America, though I admit that this comes from the biased perspective of a paleontologist who specializes in mammals.

What makes South America stand out compared to other continents? For one, it still boasts an incredible diversity of terrestrial life. That is no longer true of Antarctica, which has been covered by ice for more than 30 million years. Among the remaining continents, South America is the only one that has been in the "Goldilocks Zone" of faunal exchange since the extinction of the dinosaurs 66 million years ago; enough immigration for the continent to be populated with more than a dozen major mammal groups, but not so much that the species in those groups broadly resemble those on other continents. To see this phenomenon, you only need to scratch the surface, literally and figuratively; the Pleistocene megafaunal extinction that took place some 12,000 years ago hit South America harder than any other continent, which means you don't have to go back very far in the geological record to uncover species quite unlike anything alive today. As you dig deeper into geological time, you find fewer familiar mammals and more exotic ones. A mere 20 million years ago, South America's mammal communities were nearly as distinct as those of modern Australia.

This book looks backward from today to trace the origins of South America's mammals and other animals that call the continent home. As you will see, the histories of the major groups of backboned animals (vertebrates) vary in their ecological adaptations, their dispersal abilities, and how long ago their families, orders, and other major groups originated. Reconstructing such histories relies on many different types of information in addition to the fossil record, but the fossils themselves and their geological contexts (including their ages) are the most important clues for documenting when particular groups reached particular areas. Since most mammals are characterized by sturdy bones and durable teeth, they have left a better fossil record than other groups of terrestrial vertebrates. As a consequence, we can provide more details about their history in South America than we can about other groups. Nevertheless, mysteries remain among the mammal fossil record, and the search for answers is what fuels the fieldwork undertaken by me and many other investigators in South America.

One major unanswered question is how South America's native ungulates (SANUs) fit into the Tree of Life. Some molecular data suggest that some of them may be most closely related to horses, rhinos, and tapirs (perissodactyls) among mammals alive today, but even if that is the case, it isn't clear whether this is true of all major SANU groups or just some of them. Moreover, it raises some perplexing biogeographic questions. The oldest SANU fossils are from about 65 million years ago, but current evidence indicates that perissodactyls didn't reach North America (from Asia) until about 55 million years ago. Is there a 10-million-year gap in the perissodactyl record in North America, or did the ancestors of SANUs get to South America by some other route? Perhaps we aren't recognizing some ancient mammal remains

as the ancestors of SANUs that they are. SANUs were cornerstones of South American terrestrial ecosystems for most of the Cenozoic, but there is still much to be learned about their origin and diversification.

When I first visited the Neotropics, the animal I most wanted to see was a sloth. It looks calm, cool, and collected, and there isn't anything else like them. I don't think there is any modern mammal as quintessentially South American as a sloth. It is also characteristic of the continent's fossil record. For some 30 million years, sloths spanning a wide range of shapes and sizes occupied medium to large herbivore ecological niches throughout South America. Despite that, we have no clue about their diversity or ecology prior to the middle of the Cenozoic; the first half of their evolutionary history is a black box. How is that possible? They either left no fossil record, or the fossils they left are in the sites that remain to be discovered. I very much hope the latter is the case and that we uncover something about these early sloths within my lifetime. They are likely the only example of a group of plant-eating mammals that evolved from an ancestor specialized for feeding on social insects such as ants and termites. Tracing the steps in this unlikely journey requires fossils of the earliest members of the group.

The renowned evolutionary biologist George Gaylord Simpson described the late Cenozoic faunal exchange between the Americas as "one of the most extraordinary events in the whole history of life." It occurred when a land connection developed between North and South America - for the first time in nearly 60 million years - making it possible for many North American groups to disperse to South America and vice versa. According to the fossil record, most of this exchange took place during the past 3 million years, but some exchange took place much earlier, as early as 9 million years ago. Explaining this pattern is a topic that has been and will continue to be controversial, partly because of the many types of data involved. In addition to the mammal fossil record, there is the marine record to take into account; for marine animals, the great connection between the Americas created a great schism between the Atlantic and the Pacific. Add to that geological data from this tectonically complex area of the globe, and the result is a mixture of perspectives using different tools to look at different aspects of the same phenomenon. It has been a bit like the parable of a group of blind men trying to describe an elephant based only on the part they are touching. However, it is also clear that we are missing big parts of the puzzle. For example, the oldest records of North American mammal groups in South America are from the southern half of the continent. We are undoubtedly missing much of their early history in tropical latitudes, a deficit that may be possible to resolve only through new fossil discoveries.

So, "Where Did They Come From?" You will find many answers to this question in this book, but I think you will find these and other mysteries that remain as compelling as the answers we have. Hopefully, both will inspire you to visit South America to see some of these animals in the flesh as well as some of the myriad fossils that have helped us document their geographic and evolutionary journeys through the millennia.

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PREFACE

In a 2009 trip to Chile, high in the Altiplano (high plains) region of the Andes, I saw my first vicuñas, guanacos, rheas, and three species of flamingo. Like Charles Darwin and many naturalists and biologists since, I was struck by their close resemblance to camels, ostriches and flamingos, respectively, of Africa and the Middle East. How did they get there? Where did their ancestors come from? What combination of continental drift, climate change and the animals' dispersal ability could have caused such odd, disjunct distributions?

Everyone who has read even a little about South America's biodiversity knows about the collection of very strange, extinct mammals with no relatives anywhere else, whose ancestors were presumably in the part of Gondwana that would become South America when it split from Africa about 110 MYA; and about the Great Biotic Interchange occasioned by the closure of the Isthmus of Panama about 3.5 MYA, allowing a flood of North American species to enter South America, and vice versa. But relatively little has been written about the species that managed to populate the "island" continent during the 100 million years or so that it was not connected to any other land mass.

Considering these questions, more appeared: How did the five species of tapir, all in the same genus, come to be distributed in Southeast Asia and South America and nowhere between? Why do two members of the weasel family—*Galactis*, grison, two species and *Lyncodon*, Patagonian weasel—occur in South America when their closest relatives, zorillas (*Ictonyx*), are only in Africa? Besides flamingos, why do some genera of unrelated birds, such as jacanas, painted snipe, thick-knees and dippers, have only a handful of species worldwide with one or two in South America and the others scattered across Africa, Eurasia and/or Asia?

The temporal scope of this enquiry is the late Cretaceous era starting about 110 MYA through the Cenozoic (starting 66 MYA) to the late Pliocene (3.5 MYA). This is the period that South America was essentially an island continent, isolated from other land masses. However, land bridges or island chains persisted among Australasia, Antarctica and South America for the first half of this period, more or less, depending on the sea levels relative to islands and coastal plains. When Antarctica became glaciated, approximately 30 MYA, these connections were severed by ice for terrestrial biota. Since no story about South America's biodiversity would be complete without at least mention of the Great Biotic Interchange, initiated with the closure of the Isthmus of Panama around 3.5 MYA, I include a brief review of the animals that immigrated subsequently.

Geographically, the scope is South America. Other land areas are mentioned to the extent that they may be sources of South American biota or recipients of lineages that evolved within South America and emigrated.

South America has a fauna that elicits superlatives in every sphere. It has the largest beetle on the planet, the longest snake (Anaconda), the largest rodent (capybara), the smallest and largest species of hummingbirds, the mightiest freshwater fish and the smallest and largest anurans (frogs). It has the Andean condor, the most majestic of flying birds. No other tropical region rivals the magnificence of the diversity in form and colour of the butterflies and birds of the Neotropical rainforest.

Part 1 is about how South America came to be: its separation from Africa and Laurasia (including what would become North America) about 110 MYA, its separation from Antarctica and its subsequent glaciation about 30 MYA, and finally the connection to North

America. Both plate tectonics and volcanism were involved in the final connection to North America, with filter pathways for north-south dispersal in the Caribbean and the Isthmus of Panama. During its long isolation, changing global temperatures and sea levels assisted dispersal across what are now oceans. I comment on mechanisms of trans-oceanic dispersal and conclude Part 1 with a mention of some of the earliest biological explorers. In Part 2, the creation of the main geographic and ecological features of South America is reviewed. Part 3 is about the plants and animals whose ancestors were in South America at the time of its separation from Africa and their lineages that evolved within the isolated continent. In a sense, the modern descendants of these ancient lineages are “native”: neither they nor their ancestors came from somewhere else. Part 4 introduces “exotic” species, or taxonomic groups (“taxa”, for short), whose ancestors managed to reach South America during its long isolation and then evolved and diversified there. Part 5 summarizes the latest wave of new arrivals: those whose ancestors invaded South America from North America as part of the Great Biotic Interchange, after the connection with North America. This wave continues today. In Part 6 we consider research questions for the future.

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Part 1 - Building South America

INTRODUCTION

The Neotropical zone boasts seven of the world's 25 "Biodiversity Hotspots": Mesoamerica, Caribbean, Chocó/Darién/western Ecuador, Tropical Andes, Brazil's Cerrado, Atlantic Forest and Central Chile (Myers *et al.* 2000 cited by Bagley & Johnson, 2014). This distinctiveness results in part from the continent's high level of endemism.

As will be seen in Chapter 1, when Gondwana broke up ~110 million years ago (MYA), for about 56 million years, South America remained connected to a land mass that would later become New Zealand, Australia, Antarctica, and adjacent lands, collectively termed Australasia. This created a single biotic realm where, for another 54 million years, plants and animals evolved separately from former Gondwana lands and separately from the rest of South America.

The vast majority of South America's biota are endemic: they occur nowhere else on Earth. Many lineages of extant plants and animals evolved completely within the continent from ancestors that were within South America or the southern continents when they separated from Africa and began drifting west, the rift creating the Atlantic Ocean. This is vicariance: isolation by physical events such as tectonic plate movement or sea level rise.

Yet other lineages, like New World monkeys, arrived during the vast reach of time from then until about 3.5 million years ago when South America finally connected to North America *via* the Isthmus of Panama. This is dispersal: organisms moving from their place or origin to colonize new lands. These, too, became endemic, evolving into forms unique to the continent. Their source and route have long bedeviled naturalists. Only recently has the DNA revolution, combined with fossil study, revealed their distant ancestors—some in Africa, some in Australasia, and some even in Europe. How did they get there? By what route?

These questions are complicated by the fact—relatively recently realized—that the continent is not now as—or where—it was. The similarity of rocks, minerals, and fossil animals on the coasts of Africa and South America had perplexed geologists

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and biogeographers for centuries, and the dovetailed shape of these continents seemed too perfect for coincidence. Yet no one had any idea of how this could be until Wegener (1912) proposed the idea of continental drift. But it was slow to gain acceptance and, when I entered high school in 1960, continental drift was not mentioned in our geology textbooks. It needed new advances in seismology, global magnetism, bathymetry, and marine geology. Plate tectonics was proposed as the mechanism of drift in a series of papers from 1965, when I started university, to 1968, culminating in a paper by W. Jason Morgan (Morgan, 1968).

This was only the beginning of understanding how South America came to be. Sea levels rose and fell with global climate changes, driving ocean waters alternately inland and back out. Tectonic forces drove the Nazca Plate against the South American plate, crumpling it to form the Andes, the highest mountain range outside of the Himalayas. This changed regional climates as prevailing easterly winds hit the mountains and rose, cooling, and dropped their loads of rain. The high runoff to the east formed the great rivers—the Orinoco, Amazon and Paraná—and these deposited sediments eroded from the mountains into deep layers in lowlands, filling basins and extending coastlines from Venezuela to Patagonia.

This is the backdrop of the creation of South America as we know it today.

REFERENCES

Bagley, J.C., Johnson, J.B. (2014). Phylogeography and biogeography of the lower Central American Neotropics: diversification between two continents and between two seas. *Biol. Rev. Camb. Philos. Soc.*, 89(4), 767-790.

[<http://dx.doi.org/10.1111/brv.12076>] [PMID: 24495219]

Morgan, W.J. (1968). Rises, trenches, great faults, and crustal blocks. *J. Geophys. Res.*, 73(6), 1959-1982.

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CHAPTER 1**Tectonic Plate Movements****INTRODUCTION**

In the 1700s, with specimens of exotic animals and plants flooding into European capitols from their far-flung colonies, natural historians rushed to publish catalogues and pictorial folios. The foundations of natural history were laid down by luminaries including Linnæus, Buffon, Cuvier, Audebert, Lacépède and Daubenton. South America was among the sources of animals sent by early naturalists (see Chapter 5 Biological Explorations). Already, naturalists knew from fossils in earlier and later strata that plants and animals somehow transformed or evolved from older forms into related, newer forms. Theories of evolution were proposed. A related question was how related lineages travelled from one continent to another. In the 1800s, catalogues of fossil plants and animals were published (e.g., Brongniart, 1828; Lydekker, 1885; Pidgeon, 1830). Charles Lyell's *Principles of geology* (1830-1833) brought these questions into focus. Charles Darwin (see Charles Darwin, Chapter 5) took Lyell's volume 1 with him on the Beagle and received volume 2 by mail while moored at Montevideo. Lyell argued against Lamarkian evolution (Lamark, 1809) and inspired Darwin to seek a better explanation. Naturalists began defining biological realms characterized by related forms of life that contrasted with other realms. The two-volume work by Alfred Russell Wallace—who spent four years collecting in the Amazon and co-published with Darwin, the theory of natural selection (Wallace, 1855, 1858)—*The Geographical Distribution of Animals* (Wallace, 1876), which included analysis of fossil distribution in relation to living forms, refined and extended earlier works.

The idea of continental drift was put forward in the 1910s and elaborated in the 1920s, but not widely accepted by geologists until the 1950s; the hypothesis has been replaced by plate tectonics, which explains the drift (reviewed by Briggs, 1987).

Prior to continental drift and plate tectonics, biologists thought that odd, disjunct distributions with related plants and animals in far distant continents and islands must be explained by dispersal: somehow, they flew, swam or drifted across vast expanses of ocean. Now they had a better explanation: vicariance. Vicariant distributions are explained by animals and plants getting on board a continent, or

a piece of one, and riding it across. This surely explains how some ancient lineages came to be in both Africa and South America with last common ancestors diverging around the time that the latter continent broke away from Gondwana in the mid-Cretaceous, about 110 MYA (Fig. 1.1).

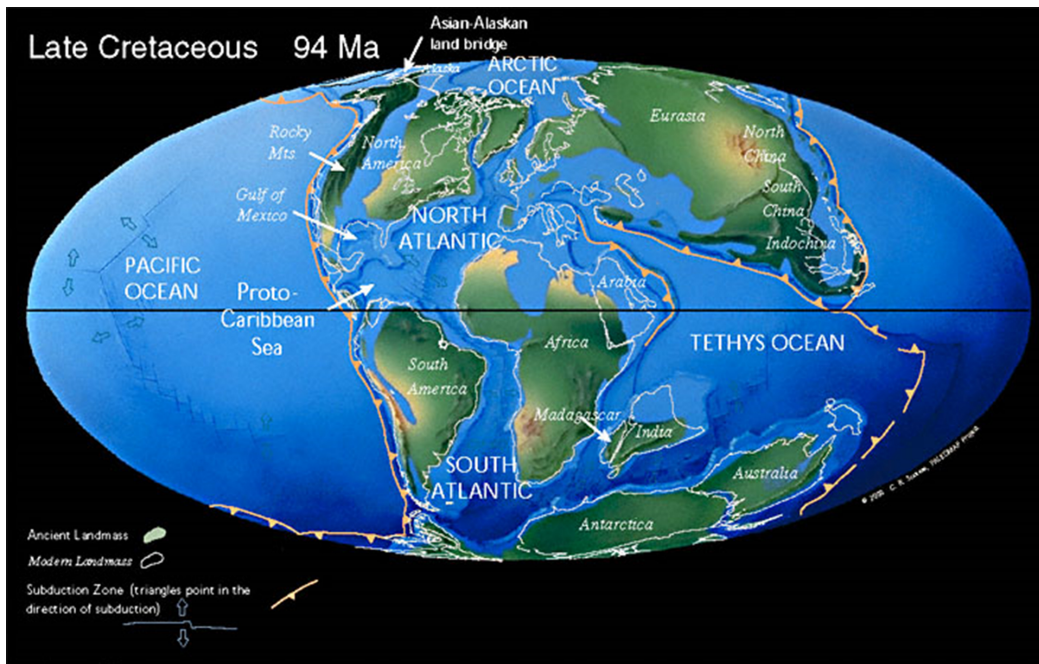


Fig. (1.1). Position of Gondwanan elements 94 MYA. Christofer R. Scotese, Paleomap Project, www.scotese.com, accessed 8 October 2022, used with permission.

As the movements of the plates and their positions at various times since then, as well as ancient climate reconstructions, became refined, vicariance also explained somewhat more recent lineages shared among the southern continents: Australasia, Antarctica and South America. These were connected until around the start of the Eocene, 54 MYA (Fig. 1.2). South America remained connected to Antarctica for another 20 million years after that, part of which time the globe became much warmer than today, giving Antarctica a semi-tropical environment.

When the idea of continental drift or tectonic plates finally became accepted, scientists jumped on it to explain the disjunct distributions of many South American plants and animals: as continents drifted apart, the biota on them became isolated from those left behind and evolved independently (*e.g.*, Croizat, 1962; Croizat *et al.*, 1974). This resulted in “remnants of an ancestral biota that underwent geographical fragmentation followed by allopatric speciation

(vicariance)” (Rosen, 1975). This model of speciation is opposed to natural dispersal: organisms moving (or their seeds being spread, in the case of plants) to new territories, while the land stays in one place. For the last few decades, taxonomists and paleoecologists have debated whether vicariance or dispersal was the dominant model in creating the strange distributions of South American plants and animals, with vicariance gaining more leeway until a recent resurgence of dispersal. The recognition that many taxa could only have achieved their disjunct distributions by trans-oceanic dispersal heralded a “counter-revolution” in biogeography (de Queiroz, 2005) forcing many biogeographers to rethink some long-held hypotheses.

But both processes have been in operation during the last 100 million years of South American biological history. Dispersal is discussed below, following a review of plate tectonics.

SOUTH AMERICA SPLITS FROM AFRICA

During the Jurassic, all the continents were aggregated in one giant land mass, Pangaea. Later, about 130–180 MYA (Cox, 2000), Pangaea began to break up and at first, created two supercontinents, Laurasia (with what would become North America, Europe, and Asia) and Gondwana. These were separated by the Tethys Sea, but there were evidently ways for animals to cross it, because some taxa that originated in Laurasia got to Gondwana (or some of its parts as it splits up) and vice versa. Gondwana had broken up to form South America and Africa sufficiently to prevent most dispersal of 120 MYA (Nishihara *et al.*, 2009). By about 110 MYA, Antarctica, Australia, New Zealand, New Guinea, Madagascar and India had also broken away from Pangaea.

The break-up was not uniform or symmetrical. As the continents pulled apart, the lithosphere (rocks comprising the mantle of the Earth) was stretched, with accompanying volcanism and rift valley formation (Pitman III *et al.*, 1995). The new continents weren’t simply pulled apart, but also rotated with respect to one another. Not until new oceanic lithosphere was created from magma welling up into the rift and spreading out on either side of it were the new continents fully formed.

Nor were these processes steady and continuous through time; the starts and stops left magnetic lineations and fracture zones that help geologists identify the sequence and plot the relative positions of the plates and the continents that ride on them (Pitman III *et al.*, 1995). Africa and South America began rifting at the north and south ends earlier than in the middle, near the equator. By 137–131 MYA, South America was probably completely separate from North America and the South Atlantic was opening between South America and Africa south of the

Changing Sea Levels

AFTER GONDWANA'S BREAKUP

In the Cretaceous (146–66 MYA), before Gondwana's breakup and during the early separation of the southern continents, Antarctica had mixed coniferous and broad-leaf forests, with southern beech (*Nothofagus*, Photo 2.1) becoming more prominent. At the end of the Cretaceous (66 MYA) Antarctica (still connected to Australia) had a tropical to subtropical climate.



Photo (2.1). *Nothofagus* forests, often wet and gloomy from the clouds and rain, comprise an ancient, primitive and diverse ecosystem shared with Australasia (and formerly with Antarctica). Photographed near Valdivia, Chile. LEH © photos.

Global temperatures during the late Palaeocene and Eocene were elevated, variously referred to as the Late Paleocene Thermal Maximum (LPTM, 55.5 MYA) and the Early (or Initial) Eocene Climatic Optimum (EECO or IECO, 55–54 MYA). They created wet, botanically diverse subtropical forests much closer to the poles than in today's climate. Following this was a period of very low sea levels about 49 MYA. These climate features allowed semi-tropical biota to cross between Europe and North America and between Asia and North Ameri-

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ca, which maintained tectonic connections as noted above. This is the period when prosimians proliferated in North America.

ANTARCTICA FREEZES

About 40–30 MYA when Australia-New Guinea separated from Antarctica, sea currents isolated Antarctica from Australia, and global temperatures plunged, ushering in the Oligocene (Fig. 2.1).

Ice accumulated at the poles and in high altitudes and the sea level began dropping. Prosimians (primitive primates) disappeared from North America. Between 41 and 23 MYA (depending on one's source; the paleogeology is uncertain), the opening of Drake Passage¹ between South America and Antarctica allowed the Antarctic Circumpolar Current to circulate around Antarctica (Fig. 2.1). This caused rapid global cooling and led to full glaciation of Antarctica. About 11.6 million years ago, the current intensified, further driving species diversification and redistribution.

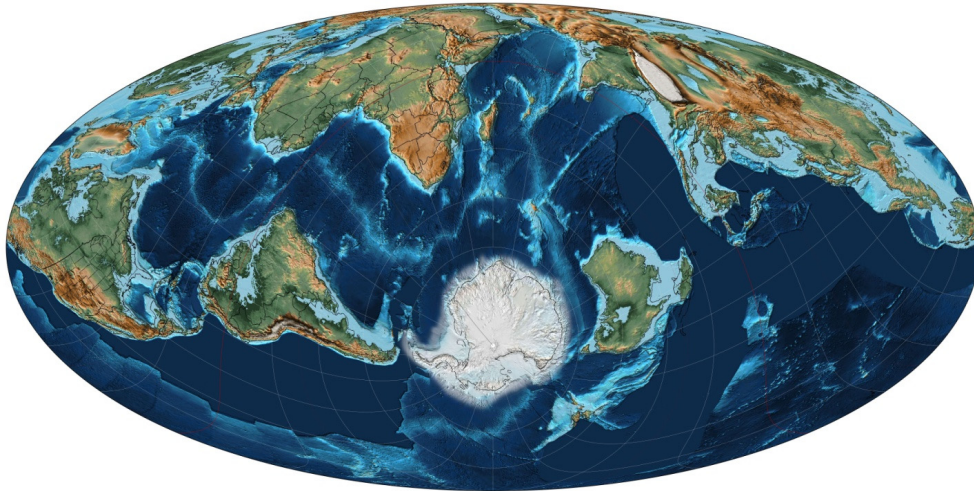


Fig. (2.1). Position of tectonic plates and sea level in the Oligocene between 30 and 23 MYA, after the establishment of the Circumpolar Antarctic current and full glaciation of Antarctica. Map courtesy Christopher R. Scotese, PALEOMAP Project.

For such a seminal event in world biogeography, the date of the opening of Drake Passage is surprisingly uncertain. Neodymium (Nd) isotope ratios in fossil fish teeth show that shallow seawater was flowing between Atlantic and Pacific Oceans by about 41 MYA (Scher & Martin, 2006). However, widespread and

permanent glaciation of Antarctica did not occur before the Eocene-Oligocene boundary at about 34 MYA (Zachos *et al.*, 2001). Evidently, it took some 13 million years for the Antarctic Circumpolar Current to begin to circulate at sufficient speed and volume to affect the global climate enough to bring down temperatures. Also, for Antarctica to freeze, the global atmospheric concentration of CO₂ had to decline enough to eliminate the greenhouse conditions of the Eocene. During this time, Drake Passage—like the Isthmus of Panama—performed as an increasingly fine dispersal filter. When the distance was short, land and sea temperature were warm and temperate ecosystems covered Antarctica, many taxa could float or fly across Drake Passage. As it stretched, fewer could manage the distance; moreover, as ecosystems went from temperate, mainly evergreen forests to tundra and then to polar deserts (Francis *et al.*, 2008), the plant and animal communities living on either side of Drake Passage changed, so that there were fewer land taxa with adequate dispersal capabilities.

Moreover, the Antarctic glaciers did not form all at once. For millions of years, there was at least a periglacial fringe of habitable land between the glaciers and the sea. At last, the separation of these proto-continents and the glaciation of Antarctica essentially closed off any chances of dispersal between Australasia-Antarctica and South America, except for cold-adapted, coastal and marine species, by about 18 MYA.

Zealandia (Chapter 1), the continent surrounding New Zealand, had a diverse flora and fauna including fish, a sphenodontid, a crocodylian, geckos, skinks, bats, at least 24 bird species and a primitive mammal representing an unknown lineage separate from both monotremes and therians that survived to the middle Miocene, about 16 MYA (Worthy *et al.*, 2006); since then, no native, non-volant (non-flying) mammals are known to have inhabited New Zealand.

ZEALANDIA SINKS

Sea level rise in the late Oligocene apparently flooded New Zealand (summarized in Waters & Crow, 2006 citing Campbell and Landis 2003). This landmass was later uplifted by tectonic activity, but not enough to expose the whole of Zealandia. Therefore, flora and fauna whose ancestors only evolved in the Oligocene and later can only have populated it by over-sea dispersal (Waters, 2008; Waters & Crow, 2006).

After the low temperature/low sea level of the Oligocene, both again increased, giving rise to the Mid-Miocene Climatic Optimum, 17–15 MYA (Zachos *et al.*, 2001). Then there was a marked cooling of the global climate near the end of the Middle Miocene associated with global ocean circulation that continued through

CHAPTER 3

Breaching the Isolation

CROSSING THE ATLANTIC OCEAN

In the middle to late Eocene (55–34 MYA), the Atlantic Ocean was about 1,400 km wide (Croft, 2016). Schrago and Russo (2003) stated the problem, with reference to New World primates: “...if an African origin for the South American platyrrhines is admitted, .. how they made the journey remains to be clarified. The problem is that a transatlantic journey from Africa to South America is not an easy feat for primates.” Their comment also indicated how recently the uncertainty of primates’ origin persisted.

As outlined above, however, several factors make this possibility less unlikely than suggested by a glance at the map. Africa and South America were nearer to each other by 40 MYA and ocean currents of that time would have facilitated a crossing from Africa to South America and not from North America (Tarling, 1982; cited in Fleagle, 1988).

Houle (1998) modelled paleocurrents and paleowinds for the Eocene Atlantic Ocean to estimate that floating debris could have crossed this oceanic barrier in ~11 days. This finding is consistent with studies that small-to-medium-sized mammals can survive 10-15 days without water, and suggests that caviomorph and primate ancestors may have originated in temperate regions of Africa with discrete wet-dry seasonality (Houle, 1998; Houle, 1999). The Mid-Eocene Climatic Optimum (MECO), known from deep-sea isotope records in the Southern Atlantic Ocean (and the Indian Ocean)—the same region where trans-Atlantic dispersal is hypothesized— consisted of 4 °C warming in less than one million years. If the intensity of coastal storms in Africa increased from ocean warming, then caviomorph and primate ancestors might have traveled a MECO “conveyor” of sorts, riding coastal debris across the Atlantic to South America (Upham & Patterson, 2015 and references therein).

During the middle Oligocene, as seen in Chapter 2, there was a large drop in sea level that exposed land now submerged and would have allowed rafting for much shorter distances than across the entire Atlantic Ocean (Fleagle, 1988). South Atlantic Ocean ridges such as the Sierra Leone Rise and the Walvis Ridge were exposed as island chains or long ridges, creating pathways that, in conjunction

with favorable water and wind currents, may have enabled faunal migration to isolated South America (Houle, 1999).

CROSSING THE CARIBBEAN

Most biogeographic reconstructions of Central/South American vicariance infer at least two connections: one, probably intermittent in the late Cretaceous-early Tertiary (90–60 MYA), when a series of volcanic arcs presumably permitted island-hopping by organisms able to disperse by this means; and the second with the closing of the Isthmus of Panama that initiated the Great Biotic Interchange (3.5 MYA to present). Earliest arrival (or at least earliest known presence) dates give evidence that various taxa arrived in the Lesser Antilles and other islands about 33 MYA and again in the Pliocene around 7 MYA (see The Caribbean, Chapter 2). At no time, however, was there a continuous land bridge between North and South America until the Great Biotic Interchange.

CROSSING THE SOUTHERN OCEAN

For much of the time after South America split from Africa, there was no Southern Ocean and animals could walk from New Zealand across Antarctica to South America. The complex geologic/tectonic history was described in Chapter 1: while it was never easy, there were times in the late Cretaceous through Eocene to the mid-Oligocene when low sea levels and subtropical to temperate to subpolar climates would have allowed some dispersal to and from Antarctica, which shared flora and fauna with Patagonia. There were also long periods lasting millions of years when biota were isolated in West Antarctica and evolved independently. Before Antarctica became glaciated about 34 MYA, dispersal by this route would have been possible, sometimes even easy. After that, dispersal of terrestrial fauna, except for the most cold-adapted ones, became increasingly difficult, although Part 4 shows that some animals made the trip.

REFERENCES

- Croft, DA (2016) *Horned armadillos and rafting monkeys: the fascinating fossil mammals of South America*. Indiana University Press.
- Fleagle, JG (1988) *Primate adaptation and evolution*. Academic Press, New York.
- Houle, A (1998) Floating islands: A mode of long-distance dispersal for small and medium-sized terrestrial vertebrates. *Divers Distrib*, 4, 201-16.
- Houle, A (1999) The origin of platyrrhines: An evaluation of the Antarctic scenario and the floating island model. *Am J Phys Anthropol*, 109, 541-59.
[[http://dx.doi.org/10.1002/\(SICI\)1096-8644\(199908\)109:4<541::AID-AJPA9>3.0.CO;2-N](http://dx.doi.org/10.1002/(SICI)1096-8644(199908)109:4<541::AID-AJPA9>3.0.CO;2-N)] [PMID: 10423268]
- Schrago, CG & Russo, CAM (2003) Timing the origin of new world monkeys. *Mol Biol Evol*, 20, 1620-5.
[<http://dx.doi.org/10.1093/molbev/msg172>] [PMID: 12832653]

Upham, NS & Patterson, BD (2015) Evolution of the caviomorph rodents: A complete phylogeny and timetree for living genera. *Biology of caviomorph rodents: Diversity and evolution* Buenos Aires, Argentina 63-120.

Mechanisms of Dispersal

INTRODUCTION

How animals crossed seas to colonize new lands has long been a matter of speculation and debate, but the biogeographic record shows that, over geologic history, many did. Fonte *et al.* (2019), in a meta-analysis of 41 studies, recovered at least 90 long-distance dispersals (LDD) of amphibians over water (3 active, 87 passive) involving at least 56 extant species and 38 genera. Most events (73) involved the colonization of islands, with rafting being suggested as the most conceivable means of overwater passive dispersal for amphibians. They showed that LDD events have played an important role in shaping current amphibian biogeographic patterns, especially the occurrence of disjunct distributions and the colonization of islands. They listed many dispersal events between South America and islands in the Caribbean and off Brazil and between South America and Central America and a few between Africa and South America in both directions.

RAFTING

Rafting, or waif-dispersal, means plants or animals caught on floating mats of vegetation drift at sea until they land on a new continent or island, where they found a new colony. The problems for non-volant (non-flying) mammals, reptiles and amphibians are clearly profound. They can't fly and most can't swim for long, especially in seawater. They need food and water. Even if there are food sources such as insects and vegetation on the log or raft when launched, these would soon be consumed or soaked with seawater. Rain might slake their thirst, but how often would it rain on a raft as it drifts from Africa to South America? Even for birds and bats, such a crossing is well-nigh impossible. Because of the obvious difficulties for vertebrates rafting across oceans, dispersal biogeography has been criticized as the study of 'miracles' (Craw, 1979). Nevertheless, overwater dispersal has caused disjunct distributions in many terrestrial and marine taxa throughout the world, especially in the Southern Hemisphere.

Not only terrestrial plants form drifting "islands", but also floating marine algae. Waters (2008) points out that the Southern Ocean has an estimated 70 million bull-kelp rafts at any one time and these rafts may float for vast distances.

Obviously, to found population, plants need to have seeds or the ability to propagate vegetatively and animals need a pair, a female with eggs or a pregnant female. Then, unless many individuals made the voyage, the new colonists would also have the problems of inbreeding or other genetic founder effects. Waif dispersal over long distances of open water is clearly challenging. On the other hand, over millions of years, there is a lot of time for stochastic events to conspire with good luck to make it possible. Luck is why this is often called “sweepstakes” dispersal: many animals find themselves stranded on a raft and most die at sea, but the few that survive to colonize a new land win the sweepstakes.

Colonization by waif dispersal has been documented many times. For example, Waters and Craw (2006 and references therein) reviewed evidence for oceanic dispersal by reptiles including chameleons, *Anolis* lizards, geckos and skinks. Many species of frogs have apparently dispersed across marine barriers between Africa, Madagascar, the Comoros Islands and the Seychelles (Vences *et al.*, 2003). The ancestors of lemurs could only have reached Madagascar by rafting. A hippopotamus colonized Madagascar during the Pleistocene and shrank through island dwarfism before going extinct in the Holocene; the semi-aquatic mammals probably swam there. Both hippopotamuses and elephants of several lineages swam to and colonized the island of Crete, became “pygmies” by island dwarfism and were hunted there by humans (Poulakakis *et al.*, 2006).

In Southeast Asia, many examples of overwater dispersal are known. For example, ancestors of extant *Maxomys*, a genus of spiny rats, crossed deep water barriers from Sundaland or the Philippines to colonize the island of Sulawesi at least 4 times (Achmadi *et al.*, 2013).

Other examples: Mascarene Islands endemic skink *Leiopisma telfarii* and related Mascarene taxa are nested phylogenetically within a clade of Australasian skinks (Waters & Craw, 2006 and references therein). Waters and Craw (2006) suggested that long-distance rafting from Australasia best explains their colonization of the western Indian Ocean. In light of this finding, dispersal by rafting across the Tasman Sea is probably how skinks colonized New Zealand, and the same may be true for other reptile fauna such as *Hoplodactylus*, *Naultinus* and *Oligosoma*. Examples relevant to South America are given in Part 4.

ISLAND-HOPPING

Recognizing the difficulty of crossing such a large expanse of saltwater by drifting on mats of floating vegetation, in the case of terrestrial plants and animals, or of simply floating in the sea in the case of certain plant seeds, theorists proposed the stepping-stone idea. Organisms could have dispersed by rafting from island to island across much shorter distances, if there were islands that formed a

chain linking continents. And there are a few groups of islands in the mid-Atlantic, besides the island chains, ridges and plateaus mentioned above. Birds that could not fly across the Atlantic Ocean could fly or be blown in a storm from island to island across such a chain. Plant seeds could be blown, or could drift in ocean currents for short enough time that the salt water would not kill them. Some mammals could swim if the distances were not so great that they would die of thirst. This idea is problematic, however, for freshwater fish and for amphibians that are intolerant to salt water.

Rafting depends on the presence of rafts of vegetation, and these are common in regions with heavy rainfall and large rivers, where flood waters topple large trees and rip loose chunks of riparian vegetation. I have seen huge rafts on large, tropical rivers such as the Kinabatangan River in Borneo, the Mekong River in Cambodia/Vietnam, and the Yangtze River in China. Small patches of floating vegetation like that in Photo 4.1 can latch onto each other, coalesce, and become large floating islands. River currents take them out into the ocean, where sea currents and wind can disperse them—and any animals entrained on them—long distances. Salt-tolerant plants would obviously have an easier time of it than freshwater ones, but because fresh water is lighter and salt water, the plumes of large rivers extend freshwater far into the oceans; and these fresh water layers would also permit animals to drink scores or even hundreds of kilometers at sea. Rain also creates a temporary freshwater layer, until surface turbulence mixes it. The Congo and other large rivers emptying into the west coast of Africa are doubtless sources of rafts that, carried by wind and currents, could cross the Atlantic Ocean.



Photo (4.1). Floating mats of vegetation in the Mekong Delta, Vietnam. Photo by Jill Harding, used with permission.

CHAPTER 5**Biological Explorations****INTRODUCTION**

The first notices of South American fossils appear in the reports of early Spanish explorers to South America and in the earliest histories of America (*e.g.* Cieza de León 1553, Falkner 1774, cited by Croft, 2016). The first fossil, a giant ground sloth, was named *Megatherium americanum* by Cuvier (1796) “based on the specimen recovered by Fray Manuel Torres in 1787 from Luján in Buenos Aires Province, Argentina” (Fericola *et al.*, 2009).

The early biological explorers of South America did not merely describe many thousands of new species; they developed the theories of evolution that today guide all of biology. By the end of the 18th Century, naturalists knew that, over unimaginably vast periods of time, species went extinct and new species, related to the extinct ones, appeared. They had an understanding of how geological strata were formed from the erosion of mountains, the sediments deposited in lakes or seas with newer layers lying on top of older. They had catalogues of extinct fossil plants and animals, each corresponding to the time periods of the strata where they were discovered. They knew marine from freshwater species that left shells behind. They knew how older fossils were related to newer ones, and could trace their lineages that changed over time. They just did not know how, or what biological mechanisms were involved. Lamarck’s (1809) theory of transmutation was prominent, and just as prominently attacked by the leading evolutionary theorists of the day. The following are just a few of the more prominent early biological explorers of South America.

FÉLIX DE AZARA

Félix de Azara (1746–1821) was a Spanish military officer, naturalist, and engineer. He was sent to negotiate the boundary between the Portuguese and Spanish colonies; however, the Portuguese delegation never arrived, and Azara ended up remaining in the region during 1781–1801. He described 381 currently recognized bird species, 178 of which are the types upon which the scientific names are based; and 78 quadruped species including 43 new to science. Many bear his name, for example, Azara's night monkey *Aotus azarae*, Azara's agouti *Dasyprocta azarae*, Azara's grass mouse *Akodon azarae* and Azara's spinetail

Synallaxis azarae. Dorsum Azara, a geographic feature on the Moon, is also named after him. Before leaving South America, he sent his brother José Nicolás de Azara (then Spanish Ambassador at Paris) his zoological notes and observations, which Moreau de Saint-Méry published at Paris in 1801 under the title of “*Essai sur l’histoire naturelle des quadrupèdes du Paraguay*”.

ALEXANDER VON HUMBOLDT

Alexander von Humboldt (1769–1859), a botanist and geographer, travelled extensively in South America. He explored the Orinoco River to Venezuela’s border with Brazil during 1799–1804. His description of the 2,776 km (1,725 miles) journey was published in an enormous set of volumes over 21 years. After a brief expedition to Cuba, where he continued botanical collections, he explored in Colombia and Ecuador. He lived and wrote up data and ideas in Mexico and the United States, and later explored in Russia. Von Humboldt was one of the first people to propose that the lands bordering the Atlantic Ocean were once joined (South America and Africa in particular). He made many biological discoveries, including electric eels, and was the first to scientifically describe the oilbird, *Steatornis caripensis*. He was interested in native Americans and described peoples and their cultures in all of his travels. Perhaps von Humboldt’s most important contribution to science was in “the unity of nature” uniting physical and biological sciences using quantitative physical and environmental data to define where specific plants grew, and where they could grow if transplanted elsewhere.

JUAN IGNAZIO MOLÍNA

Juan Ignazio Molína (1740–1829) was a Jesuit priest born and educated in Chile who made major contributions to ornithology, botany and other phases of natural history, as well as geology and history. He was forced to leave South America when the Jesuits were expelled from the Spanish Empire in 1768. He settled in Bologna, Italy; hence the Italian version of his name, Giovanni Ignazio Molína, in scientific publications. His *Saggio sulla Storia Naturale del Chili* [*The Geographical, Natural and Civil History of Chile*] (1782), the first account of the natural history of that country, described many species for the first time.

SPIX AND MARTIUS

During 1817–1820, Johann Baptist von Spix (1781–1826), together with Carl Friedrich Philipp von Martius, collected plants, insects, mammals, birds, amphibians and fish throughout Brazil. They constitute an important basis for today’s National Zoological Collection in Munich. After Spix’s death in 1826, possibly of a tropical disease, von Martius continued their work on the 3-volume publication of their expedition, describing some 600 species. Many animals were

named for Spix: Spix's guan, Spix's macaw, Spix's disc-winged bat, Spix's yellow-toothed cavy, and so on. Martius went on to publish many finely illustrated volumes on plants of Brazil, including *Historia naturalis palmarum* (1823–1850) in three large folio volumes, in which he described and illustrated all known genera of the palm family.

After Spix's, or little blue macaw (*Cyanopsitta spixii*), among the rarest birds in the world, was declared extinct in the wild in 2010, conservationists began a captive breeding program. In June 2022, they released eight into Brazil's caatinga (see Chapter 7). Another 12 are ready for release in December 2022 from a captive population of about 250.

ALCIDE D'ORBIGNY

Alcide Charles Victor Marie Dessalines d'Orbigny (1802–1857) was a French naturalist who made major contributions to South American zoology (and other fields). On a mission for the Muséum National d'Histoire Naturelle, Paris, during 1826–1833, D'Orbigny travelled through Brazil, Argentina, Paraguay, Chile, Bolivia, Peru, Ecuador and Colombia. He returned to France with a collection of more than 10,000 specimens; many of these he described in a series of papers, *La Relation du Voyage dans l'Amérique Méridionale pendant les années 1826 à 1833*, published between 1833 and 1847, while others were described by other zoologists at the Museum. A score of fossil and living animals (e.g., d'Orbigny's chat-tyrant, *Ochthoeca oenanthoides*; a subspecies of rusty flower-piercer, *Diglossa sittoides dorbignyi* and d'Orbigny's pond slider, *Trachemys dorbigni*, (Photo 9.4) and plants and a meteorite were named after him.

In Argentina, D'Orbigny made his base at what is now the Estancia San Juan Poriahú, a cattle ranch in the Iberá wetland complex, Corrientes province, established in 1670 by the Jesuit Mission. Generations of owners of the estancia, many of them naturalists themselves, have maintained D'Orbigny's study as a sort of museum (Photo 5.1).

CHARLES DARWIN

Several misconceptions pervade the popular imagination about Charles Darwin. Although he is known for the “theory of evolution,” natural history scholars knew that evolution had occurred, and were developing theories as to how, long before Darwin set sail on HMS Beagle. He shared with Alfred Russel Wallace (see below) the credit for the theory of natural selection: their papers on it were published simultaneously in the Journal of the Proceedings of the Linnean Society (Darwin & Wallace, 1958). He is identified popularly with the Galapagos Islands off Ecuador, but spent only a few weeks there, gained no momentous

Part 2 - Ecosystem Diversity

INTRODUCTION

After the continents were more or less in place as they are today, South America continued to evolve. Sea levels rose and fell, alternately flooding and drying interior basins. The Andes Mountains rose, creating barriers to dispersal between the west coast and the rest of the continent. The Andes also blocked moisture-laden atmospheric currents from the east, forcing clouds to rise, cool, and drop their loads. The great rivers—Orinoco, Amazon, Paraná—were born, but not yet configured as they are today.

Beyond the Andes, the land also rose and fell (uplifted and subsided) with tectonic movements and in response to glaciations: sagging under the weight of glaciers or rising with the release of the weight. On top of this, fluvial outwash from the rising Andes deposited immense quantities of sediment on the plains. In Argentina, as Charles Darwin had seen (Chapter 5), fluvial sediments in some places alternate with marine sediments, revealing the interaction between fluvial sedimentation and marine deposition over time to create the landforms that we see today.

Along with changing landforms, changes in the global climate created new environments in which new ecosystems could evolve. Physical changes such as the opening of the Drake Passage, which allowed Antarctica to freeze and Patagonia to cool, also drove the evolution of new ecosystems.

The last major change that drove the development of ecosystems was the evolution of plants. Many of the Gondwanan ancestors of plants that ended up evolving and diversifying within Australasia and/or its neighbours Antarctica and South America were mosses, lichens, and so on. Many lichen and bryophyte (mosses and relatives) genera have species in New Zealand/Australia and South America (Briggs, 1987 and references therein).

Angiosperms (flowering plants) only evolved in the mid-Cretaceous. However, some 27 orders of angiosperms, including at least 80 primitive families, dispersed throughout Gondwana before the continents separated; in many cases, subfamilies, tribes or even a few ancient genera were present when the continents separated

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(Goldblatt, 1995). Until about 80 MYA, the flora of southern Africa, South America, Australia and Antarctic were so similar they constituted one botanical province. After that, when they were finally separate, plant species began to evolve independently on the four southern continents, with those in South America showing increasing endemism (Coetzee, 1995). By the end of the Cretaceous (66 MYA), South American angiosperms were differentiated at the family level, with new genera emerging in the Ulmaceae, Moraceae, Stereuliaceae, Leguminosae, Protaceae, Gunneraceae, Myrtaceae, Onagraceae, Aquifoliaceae, Humeraeae and Sapindaceae (Romero, 1995).

The Asteraceae (the family of composite flowers that are now so ubiquitous worldwide) probably originated in South America (Bremer, 1995).

Angiosperms may have originated in Asia before the breakup of Gondwana and spread to South America *via* Australasia and Antarctica (Briggs, 1987 and references therein). Those with ancient lineages in Australia include Araucariaceae (including *Agathis*, Kauri pine, and the monkey puzzle tree), Podocarpaceae (a conifer family), Epacridaceae and Winteraceae. This last, Winteraceae, a “southern counterpart to the Magnoliaceae” (Briggs, 1987:49), although centred in Australia, has four species in South America. In the cedar family Cupressaceae, related genera are found in New Zealand, New Caledonia or New Guinea and Chile. The close floral connections between New Zealand and Chile, in particular, “are shown by a sharing of 40% of the genera of ferns and 43% of the genera of seed plants” (Briggs, 1987:64).

A major innovation was the evolution of photosynthesis from C3 (starches with three carbon atoms) to C4 (those with four carbon atoms). C3 plants—their modern descendants include soybean, cowpea, cassava, rice, wheat, and potato—comprise the majority of plant species on Earth. In C3 photosynthesis, the first carbon compound they produce (through the Calvin-Benson cycle) contains three carbon atoms. However, toxic two-carbon compounds are also produced, with which the plants must deal. Also, the conversion of carbon into sugar only works when stomata are open, allowing the plant to draw in carbon dioxide (CO₂), which in turn allows water loss by respiration through open stomata. This is not much of a problem for plants in moist environments, but deadly in deserts and other dry environments.

The photosynthesis of C4 plants such as maize, sorghum, and sugarcane, uses oxygen (O₂) more efficiently and can continue when the stomata are closed, reducing water loss. C4 plants have approximately 50% higher photosynthesis

efficiency than C3 plants. C4 plants also decompose more efficiently, producing organic matter more quickly and abundantly. This develops soil structure and nourishes animals as well as other plants.

C4 carbon fixation evolved independently in at least 19 plant families, all about 30 million years ago (Christin *et al.*, 2011), making it a prime example of convergent evolution. In arid environments such as the llanos, pampas, and dry mountains, the development of C4 photosynthesis was a major driver of the ecosystem development (Sage, 2004).

These forces, together, created the biomes—deserts, grasslands, forests, wetlands—and the varied ecosystems within them that give South America a unique character and sustained its evolving animal communities.

REFERENCES

- Bremer, K. (1995). Intercontinental relationships of African and South American Asteraceae: a cladistic biogeographic analysis. *Biological Relationships Between Africa and South America*, New York: American Geographical Society of New York. 105-135.
- Briggs, J.C. (1987). *Biogeography and plate tectonics*. Amsterdam, The Netherlands: Elsevier.
- Christin, P. A., Osborne, C. P., Sage, R. F., Arakaki, M., Edwards, E. J. (2011). C4 eudicots are not younger than C4 monocots *Journal of Experimental Botany*, 62, 3171-3181.
- Coetsee, J.A. (1995). African flora since the terminal Jurassic. *Biological Relationships Between Africa and South America*, New York: American Geographical Society of New York. 37-61.
- Goldblatt, P. (1995). *Biological Relationships Between Africa and South America*.
- Romero, E.J. (1995). South American paleofloras. *Biological Relationships Between Africa and South America*, New York: American Geographical Society of New York. 62-85.
- Sage, R.F. (2004). The evolution of C₄ photosynthesis. *New Phytol*, 161(2), 341-370.
[<http://dx.doi.org/10.1111/j.1469-8137.2004.00974.x>] [PMID: 33873498]

CHAPTER 6

Creating the Landforms

CHANGING SHAPE OF SOUTH AMERICA

South America is rooted by two pre-Cambrian shields, or cratons, made of crustal rock dating from before the Cambrian: hence, pre-Cambrian. Cratons are old and stable parts of the continental lithosphere that have survived cycles of merging and rifting of continents (Wikipedia); they contrast with newer geologic regions made up of igneous (from volcanos) and sedimentary rocks, and metamorphic rocks formed from the igneous and sedimentary rock under high heat and pressure. Cratons in South America were part of the same geological features in Africa, before Gondwana's breakup.

The changing shapes of South America through the epochs of the Cenozoic were shown in Fig. (1.2), Chapter 1. Fig. (6.1) shows a detail of the map for 52 MYA in the early Eocene. Sea levels were up to 120 m higher than now and the continent was about half underwater. Ocean transgressions (flooding in lowlands due to sea level rise or land subsidence) essentially isolated south-eastern Brazil, the Guyanian Shield, and the Guyanian-Suriname highlands from the Andes. The Andes range was already there, though much lower than now, and was the source of sedimentary layers that, along with marine sediments, filled the basins of what would become the Orinoco, Amazon and Paraná Rivers. The Paraná and Amazon River basins today are the two largest in the world.

Hoorn *et al.* (1995:237) summarized the development of the Amazon and Orinoco basins:

“During the late Oligocene to early middle Miocene, the Central Cordillera was drained by a fluvial system that had an eastern transport direction..., and the Eastern Cordillera was embryonic. In northwest Amazonia, fluvial systems drained the Guyana shield and had northwest transport directions; they probably formed tributaries of the ancient Orinoco river system, which had a northward course, toward a delta in the present Lake Maracaibo. The Central Cordillera was drained by fluvial systems that had an eastward direction and also formed tributaries to the Orinoco. The Mérida Andes was a more prominent mountain range that had developed already in the late Oligocene and early Miocene and supplied sediment to the northern foredeep and the Barinas-Apure basin. Periods of global high sea level (Burdigalian) caused marine incursions connecting the present Lake Maracaibo, Llanos region, and northwest Amazonia.”

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Fig. (6.1). Detail from Figure 1.2 showing marine intrusions and landforms at 52 MYA. Courtesy Christopher R. Scotese, used with permission.

“During the late middle Miocene..., the first effects of the rise of the Eastern Cordillera were noticeable in northwest Amazonia with the development of the Amazon River. At the time, however, no connection existed with the Atlantic. The paleo-Amazon River formed a fluvio-lacustrine system with an estuarine character that was still partly connected to the paleo-Orinoco. The area of the present upper and middle Magdalena Valley, previously connected to the Llanos and Amazonian lowlands, became an isolated area, and a new west-directed fluvial system developed, originating in the Garzón massif. The Mérida Andes were uplifted more, and fluvial systems provided large amounts of clastic sediments to the northern foredeep, Barinas-Apure basin, and Táchira area. During periods of high sea level ..., Maracaibo, the Llanos, and Amazonia were still connected.”

“Between the late Miocene and the Holocene, the Andes attained their present configuration.... The late Miocene marked the start of a paroxysm in the uplift of the northeastern Andes and represents the most dynamic episode during the entire Miocene. During this time, the Eastern Cordillera, the Santander massif, and the Mérida Andes were all uplifted further. In the foredeeps, molasse sediments were deposited by alluvial fans and braided fluvial systems. The Amazon River evolved as a transcontinental drainage system and covered the carbonate platforms of the Atlantic shelf. At the same time, the Orinoco changed to its present course and abandoned the area of Lake Maracaibo. In the upper Magdalena Valley, the Magdalena River started its development as a braided river, with the Central Cordillera and the newly formed Eastern Cordillera as source areas. The Amazonian-Caribbean connection was closed by late Miocene tectonic events and a relatively low global sea level.”

Further south, the Paraná Sea filled what is now the Paraná River basin in northeastern Argentina at various times in the Eocene (55–34 MYA), Oligocene (34–28 MYA) and Miocene (28–5 MYA). Its warm waters probably created a moderate, moist climate. Its estuarine, brackish or shallow marine waters—probably all of the above at various times and places—provided the conditions for the evolution and speciation of marine animals. The sea likely also partially isolated peninsulas extending northeast from Patagonia and southwest from coastal Brazil on the Atlantic coast, creating more conditions for the speciation of terrestrial taxa (Croft, 2016).

Since these transgressions lasted for millions of years and were repeated in other epochs, one can understand how unique faunas developed in places like the Atlantic Forest, Caatinga, Cerrado, and the Guinean Shield, as described in Chapter 7.

REFERENCES

Croft, DA (2016) *Horned armadillos and rafting monkeys: The fascinating fossil mammals of South America*. Indiana University Press.

Horn, C, Guerrero, J, Sarmiento, GA & Lorente, MA (1995) Andean tectonics as a cause for changing drainage patterns in miocene northern South America. *Geology*, 23, 237-40. [[http://dx.doi.org/10.1130/0091-7613\(1995\)023<0237:ATAACF>2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1995)023<0237:ATAACF>2.3.CO;2)]

Biomes and Ecoregions

INTRODUCTION

Besides geological events such as mountain-building and flooding of inland basins to form seas, biological evolution of plants was obviously a major factor in creating modern ecosystems. Flowering plants, for example, evolved about 160 MYA and diversified greatly during the late Cretaceous and Palaeocene (65–55 MYA), in South America as elsewhere. In forest ecosystems, these angiosperms replaced conifers as the dominant trees. Many extant plant families evolved during the Palaeocene-Eocene (65–24 MYA); some were endemic to South America but many were not.

Recent molecular phylogenies identify many immigrant tree lineages that arrived in South America during its period of oceanic separation from Africa. According to Pennington and Dick (2004), long-distance sweepstakes dispersal across oceans played an important and possibly predominant role. They show that stepping-stone migration from Africa and North America through hypothesized Late Cretaceous and Tertiary island chains (Chapter 1) may have facilitated immigration for about 20% of the species of an Amazon tree community in Ecuador. They also present data on the community-level similarity between South American and palaeotropical (*i.e.*, African/Asian) rainforests, and suggest that most taxonomic similarity derives from trans-oceanic dispersal, rather than a shared Gondwanan history.

On the other hand, long after South America and Africa had split, South America remained connected to Australia and New Zealand *via* Antarctica, and for much of that time during the Eocene, the Earth was much warmer than the Oligocene and it was not glaciated until after about 34 MYA when the opening of Drake Passage allowed the formation of the Arctic Circumpolar Current; thus, a cool, moist temperate forest covered the Patagonia-Antarctica-Australia-New Zealand land mass, creating a single, connected biome with a shared and still closely-related flora.

As mentioned in the Introduction of Part 2, the large-scale replacement of C3 by C4 grasses in non-forested habitats near the end of the Miocene (~7 MYA) had a major impact on mammal and other vertebrate communities (Croft, 2016). Since

this coincided with the first influx of mammal migrants prior to the actual Great Biotic Interchange (see Part 4), it was another factor fostering large-scale turnover of species.

About 3.3 MYA, a meteorite impact spread escorias (impact glasses) across south-central Argentina. “This impact seems to have caused an abrupt change in the species living in central Argentina, an event that has been called the mid-Pliocene faunal turnover” (Croft, 2016:203). This was also in the early stages of the Great Biotic Interchange, with sites such as Chapadmalal on the Buenos Aires coast of Argentina revealing the earliest sigmodontine rodents (see Part 5).

BIOMES

Geologic features are also overlain with climate to produce South America’s modern ecosystems. The continent has some of the driest and wettest habitats on Earth. Fig. (7.1) shows South America’s biomes: a high-level ecological classification above ecoregions and below ecozones. This classification scheme was developed by the World Wildlife Fund (Olson *et al.*, 2001).

ECOREGIONS

But these large-scale biomes hardly capture the biodiversity of the continent. A smaller-scale system of ecoregions, also based on the World Wildlife Fund’s mapping (Olson *et al.*, 2001), is nested within the biome classification, but is too finely divided to be shown in a single map. In the following sections, South American ecoregions are discussed in the northwestern, Amazon, Atlantic (eastern) and southern parts of the continent.

NORTHWESTERN SOUTH AMERICA

Looking over the northern third or so of the continent with its astonishing number of defined ecosystems (Fig. 7.2), it is not hard to see why the diversity of plants, bird, mammals, reptiles, amphibians and other taxa is so high. Colombia alone, with Pacific and Caribbean coastlines and landforms ranging from Andes Mountains to Llanos grasslands, is second (after Brazil) among world’s 17 most biodiverse countries, and the most densely biodiverse of these per square kilometer (Potes, 2002).

The Andes curl around the western edge, separating the Amazon and Orinoco river systems from the Pacific coastal environments. The Andes capture moisture in the prevailing winds from the Atlantic Ocean, creating a high-runoff environment. So much water falls that innumerable rivers flow northeast and east, already wide and full before they leave sight of the mountains. Other mountain

ranges intervene, further isolating biota. Where they flood out to the Caribbean and Atlantic oceans, they create coastal forest ecosystems. The moist forests of the Guianan Highlands rise above the Orinoco lowlands to the north and the Amazon River valley to the south; from the highlands rise the tepuis, steep-side blocks of ancient rock that are so high, each creates its own climate and ecosystems, many with endemic plants and animals. In the west, the Andes is not a single range, but a much-divided block of mountains and valleys. The evolutionary history has created so many areas of isolation, and so many of these remain at least partially isolated, that ecological differences are enough to define distinct ecosystems. Fish, because they can't easily travel between river systems, are especially diverse.



Fig. (7.1). Biomes of South America (World Wildlife Fund ArcMap files distributed by ESRI based on Olson, 2001).

Part 3 - Endemic Vertebrates

INTRODUCTION

The usual meaning of endemic is a species (or a genus, family, order, *etc.*) that lives in one place and nowhere else, and I have used it in that sense in these pages. Woodburne (2010), for example, and others, have used “endemic” to mean “a taxon that either phyletically originates in, or is introduced to, but in any case, subsequently remains restricted to, the area indicated.” In Part 3, however, I use “endemic” to categorize the lineages of animals whose ancestors were either in South America when it split from Gondwana about 110 MYA, or in Antarctica/Australasia when it was connected to, and formed a biotic realm with, Patagonia. They are deep lineages with ancient ancestors (in some cases unknown) on other continents that were in South America at its creation; vicariance usually explains their distribution. They evolved there, in Simpson’s (1980) phrase, in “splendid isolation.” These are contrasted in Part 4 with “exotic” biota: those that colonized the island continent when it was completely isolated from other land masses, i.e., the second half of Woodburne’s definition quoted above. These are not the usual meanings of “endemic” and “exotic”; no one would say, for example, that New World monkeys are not endemic to South America, even though their ancestors arrived there some 60 MYA after the continent split from Africa.

Taxa that evolved continuously within South America after its separation from Gondwana, or in the “southern continents”—Australia, New Zealand, New Guinea, Antarctica, and South America—are the subject of this section.

“Exotic” lineages that evolved elsewhere and immigrated to South America during its long isolation will be discussed in Part 4, but I ask the reader to be aware that whether taxa arrived by vicariance or natural dispersal is often a gray area, given the uncertainties about ancient shorelines, sea currents, sea levels and other physical features that could have either helped or hindered dispersal, as well as the biological uncertainties about where and when certain lineages arose.

REFERENCES

Simpson, G.G. (1980). *Splendid isolation: the curious history of South American mammals*. New Haven, Connecticut: Yale University Press.

Woodburne, M.O. (2010). The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *J. Mamm. Evol*, 17(4), 245-264.

[<http://dx.doi.org/10.1007/s10914-010-9144-8>] [PMID: 21125025]

Endemic Amphibians

AN ANCIENT LINEAGE

The living amphibians are one of the most diverse groups of terrestrial vertebrates, numbering > 6,800 species. Taxonomy is evolving rapidly, with about 2,700 species having been described in the 26 years up to 2011, according to Pyron and Wiens (2011), who produced a new, major phylogeny after sequencing genes of 2871 species from 432 of the ~ 500 currently recognized, extant genera.

Amphibians are such an ancient group that it is no surprise that vicariance explains disjunct distributions of the deeper lineages. South America is especially diverse in amphibians. Anurans (frogs and toads) are classed into two clades (Hoegg *et al.*, 2004), Archaeobatrachia (archaic frog lineages, but the clade is not monophyletic) and Neobatrachia (advanced frogs). The latter evolved in the early Cretaceous, before the breakup of Gondwana.

Neobatrachia contain two well supported clades that correspond to the superfamilies Ranoidea (Hyperoliidae, Mantellidae, Microhylidae, Ranidae, and Rhacophoridae) and Hyloidea (Bufonidae, Hylidae, Leptodactylidae, and Pseudidae). Two other families (Heleophrynidae and Sooglossidae, of Africa and Seychelles-India, respectively) occupy basal positions and probably represent ancient relicts within the Neobatrachia (Hoegg *et al.*, 2004).

Neobatrachia families native to the Americas, with centers of diversity and abundance in the neotropics (Central and South America), include (from Wikipedia, accessed 27 April 2023):

- Amphignathodontidae, marsupial frogs, which some include with Hemiphractidae.
- Hemiphractidae (formerly a subfamily in Hylidae).
- Aromobatidae, colorful forest frogs that are sometimes poisonous, but not as deadly as those in Dentrobatidae, to which they are a sister clade.

- Dendrobatidae, poison-dart frogs. Perhaps the best-known South American frogs outside of that continent, their combinations of chemical defenses coupled with warning coloration evolved at least four times (Roland *et al.*, 2017).
- Brachycephalidae, endemic to cloud forests of southern Brazil.
- Calyptocephalellidae, helmeted frogs (see below), sometimes included in Bufonidae: two genera are endemic to Chile (all species are threatened except for two that are critically imperiled).
- Centrolenidae, glass frogs: originated in South America and dispersed multiple times into Central America and Mexico, with a disjunct range in Uruguay and Argentina.
- Ceratophryidae, horned frogs. The fossil, giant *Beelzebufo* of Madagascar may belong to this family (Evans *et al.*, 2008); if so, it would imply a Gondwanan distribution or a later trans-oceanic dispersal. But its inclusion is not widely accepted (c.f. Ruane *et al.*, 2010).
- Hylodidae, are hylid-like frogs of uncertain affinities native to Brazil and northern Argentina.
- Leptodactylidae occurs in South America (three subfamilies), Australia (two subfamilies) and southern Africa (one subfamily).
- Psuedidae is a proposed family of “swimming frogs”, not yet widely accepted: the genus *Psuedis* is currently within the Hylidae (see below). They range mainly east of the Andes.
- Rhinodermatidae, Darwin's frogs: monotypic genus of the SW coast of South America has two species, one of which (Chilean Darwin's frog, *Rhinoderma rufa*), may be extinct.
- Strabomantidae, endemic to South America, have no larval stages and hatch directly into “froglets”.
- Craugastoridae, direct-developing frogs (*i.e.*, no tadpole stage), a large family (~746 species) native to the Americas. The membership of genera in the family is in flux.
- Eleutherodactylidae, direct-developing frogs native to the Americas.

Several of the above families have Gondwanan ancestry, while others dispersed within the South America-Australasia realm, presumably prior to the glaciation of

Antarctica. Those with populations in North America probably dispersed there from South America, the origin of many families.

An Eocene fossil of a relative of Chile's helmeted frogs, formerly with extinct relatives in Argentine patagonia, was recently discovered on Seymour Island in Antarctica and assigned to the Calyptocephalellidae, in the anuran clade Australobatrachia (Mörs *et al.*, 2020). It is further evidence of the temperate climate of Antarctica 40 million years ago, and of a common Australasian biotic realm.

Besides the above, many Neobatrachia families that are nearly globally distributed include South American clades, some of which are endemic:

- Bufonidae, toads, have nearly a global distribution except Polar Regions and Australasia. There are many taxa in South America. An example is Tepui toads, genus *Oreophrynella* (Bufonidae), which are most closely related to toads in Africa, suggesting trans-Atlantic dispersal after the evolution of the family. Each species has an extremely limited range, occurring only on tops of tepuis in Venezuela and Guyana.
- Hylidae, tree-frogs, Americas, Eurasia, Africa and Australasia. Hylidae genera in Australia and South America are closely allied, those of each continent representing different subfamilies.
- Microhylidae, narrow-mouthed frogs with 584 species in 61 genera in the Neotropics, Africa and Asia. The initial radiation estimate of 66 MYA implies a Pangaean origin and Australasian-Antarctica-South America dispersal.
- Ranidae: true frogs, probably comprising at least seven families.

The family-genus level phylogenies continue in a state of flux, as many genera and even families were of uncertain affinities in Pyron's and Wiens' (2011) phylogeny, and herpetologists continue to describe new species.

REFERENCES

- Evans, SE, Jones, MEH & Krause, DW (2008) A giant frog with south american affinities from the late cretaceous of madagascar. *Proc Natl Acad Sci*, 105, 2951-6. [<http://dx.doi.org/10.1073/pnas.0707599105>] [PMID: 18287076]
- Goldblatt, P (1995). *Biological relationships between Africa and South America*. Yale University Press.
- Hoegg, S, Vences, M, Brinkmann, H & Meyer, A (2004) Phylogeny and comparative substitution rates of frogs inferred from sequences of three nuclear genes. *Mol Biol Evol*, 21, 1188-200. [<http://dx.doi.org/10.1093/molbev/msh081>] [PMID: 14963093]
- Mörs, T, Reguero, M & Vasilyan, D (2020) First fossil frog from antarctica: Implications for eocene high latitude climate conditions and gondwanan cosmopolitanism of australobatrachia. *Sci Rep*, 10, 5051.

Endemic Reptiles

INTRODUCTION

South America's herpetofauna (amphibians and reptiles) is more closely related to Australia and New Zealand than to Africa or North America, reflecting shared Gondwana ancestries. As with other taxa, however, some are shared with New Zealand but not Australia and some with Australia but not New Zealand.

Several lineages, including primitive snakes, crocodylians, dinosaurs and lizards, crossed from Central to South America or vice-versa during the late Cretaceous-early Tertiary (90–60 MYA), when a series of volcanic arcs presumably permitted dispersal by island-hopping. Some evidently also came to South America across the sea from Africa, and from Australasia *via* Antarctica.

DINOSAURS

The similarity of many fossil dinosaurs and other reptile species found in South America, Africa, India, and Antarctica was one of the first proofs that these continents were once connected. Of all the Gondwana land masses, South America has the richest collection, with most dinosaur fossils being from Argentina and Brazil. Lamanna (2013:13) notes that:

“Early Late Cretaceous (Cenomanian–Turonian) South American dinosaurs include abelisauroid, spinosaurid, allosauroid, and coelurosaurian theropods, rebbachisaurid and titanosauriform sauropods, and basal ornithopods. Coniacian–Maastrichtian dinosaurs include abelisauroids and titanosauriforms (principally titanosaurs), with allosauroids, coelurosaurs, ankylosaurs, and ornithopods also present but less common. Hadrosaurs colonized South America during the Campanian and rapidly became a significant component of that continent's biota. .. The hadrosaur, a South American immigrant, demonstrates the existence of a latest Cretaceous land route between that continent and Antarctica.”

Fossils of more than 194 genera of dinosaurs have been discovered in South America, mostly from the Cretaceous, but many from the Jurassic and Triassic (https://en.wikipedia.org/wiki/List_of_South_American_dinosaurs, accessed 12 October 2022).

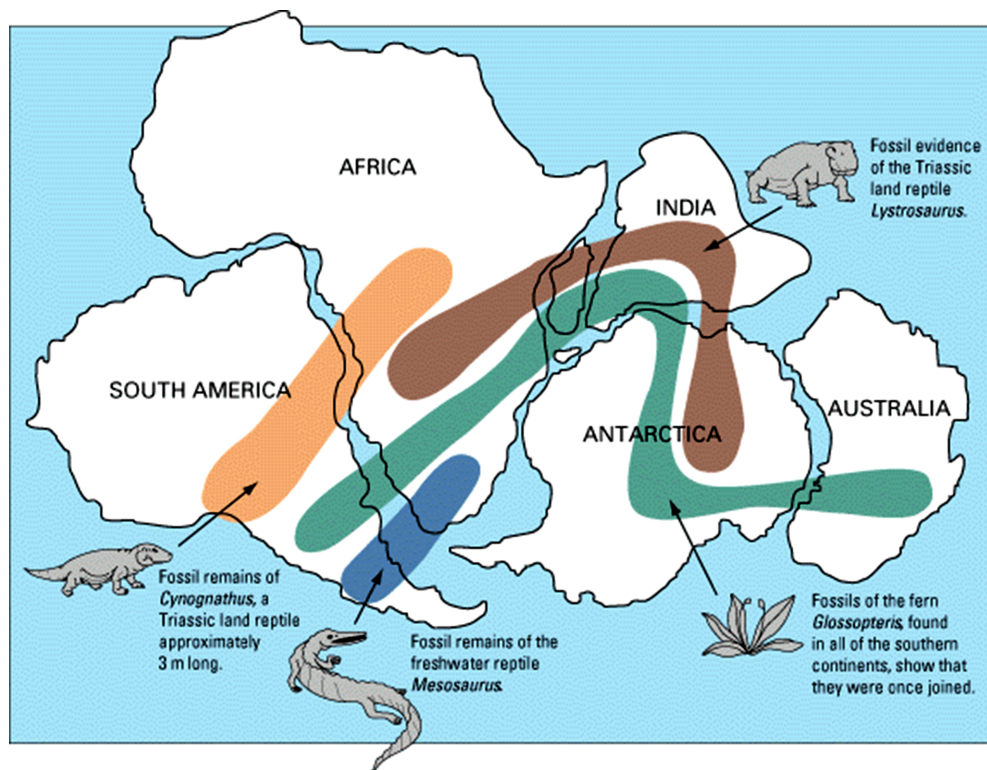


Fig. (9.1). Reptile and fern genera of the Triassic age spanning Gondwana land areas. Created by Osvaldocangaspadilla, original file name: Snider-Pellegrini Wegener fossil map.gif (Wikipedia Commons).

SAUROPODS

Before the rise of the giant sauropods, before the tectonic split from Africa, *Leoneosaurus taquetensis* lived in the Late Triassic–Early Jurassic of Gondwana, in what would become central Patagonia (Pol *et al.*, 2011). Although not large, its vertebrae and sacrum show it to be a sauropodomorph dinosaur, a sister group to the sauropods. Its sauropod-type of sacrum predated the marked increase in body size that characterizes the origins of sauropods (Fig. 9.1).

Titanosaurs (Titanosauria) were a diverse group of huge sauropods with massive bodies, long necks and tails, and small heads. These herbivores were widespread in Pangea before the break-up of continents ~110 MYA. More than 40 species are known worldwide showing a huge diversity of forms, ranging from about a tonne to perhaps 50 tons, making them among the largest animals that ever lived. Eight species have been described from Brazil, with species from north-eastern Brazil representing lineages related to African species and those from south-western Brazil showing affinities to those of southern landmasses (Santucci, 2013).

Argentine scientists have discovered several species in Patagonia, other regions of Argentina and Antarctica, including *Argentinosaurus*, 96–94 MYA (Photo 9.1), Nequén formation in Rio Negro province; *Saltasaurus*, 70 MYA from Salta province and Uruguay; *Andesaurus*, late Cretaceous from Nequén formation in Rio Negro province of Patagonia, Argentina; *Epachthosaurus* (late Cretaceous, from several locations in Patagonia); and *Puertasaurus*, 69–66 MYA from Patagonia.

A new titanosaur, *Sarmientosaurus musacchioi*, from the Upper Cretaceous (Cenomanian—Turonian) of the Bajo Barreal Formation of southern Chubut Province in central Patagonia, Argentina, was described in 2016; its unique skull morphologies suggest that “multiple titanosaurian species with dissimilar cranial structures coexisted in the early Late Cretaceous of southern South America” (Martínez *et al.*, 2016). As yet unidentified titanosaurs have been found at Agua del Padrillo and La Invernada, both in Argentina (González Riga *et al.*, 2016).

Atacamatitan, a late Cretaceous titanosaur was found in the Antofagasta region of Chile. *Bonitasaura* and *Tapuiasaurus* fossils were recovered from the late Cretaceous in Minas Gerais State, Brazil.

Recent discoveries include *Dreadnoughtus*, 84-66 MYA from Salta province; *Futalognkosaurus*, late Cretaceous, Nequén; *Mendozasaurus*, late Cretaceous, Mendoza; Argentina; and *Aeolosaurus*, São Paulo State, Brazil (Santucci, 2013). A new species, *Notocolossus gonzalezparejasi* from Mendoza province, Argentina, was described in 2016 (González Riga *et al.*, 2016).

Another new titanosaur was discovered in 2014 in Argentine Patagonia, by researchers from Argentina’s Museo Paleontológico Egidio Feruglio. Fossils of at least six individuals were found. It was about 37 m long and 20 m tall, with an estimated weight of 77 tonnes, making it among the largest land animals in Earth’s history (Carballido *et al.*, 2017). In 2016 a cast of a full skeleton was unveiled in the American Museum of Natural History, New York. It was named *Patagotitan mayorum* in 2017 (Photo 9.2). Analysis of *P. mayorum* and comparison with other titanosaurs shows (Carballido *et al.*, 2017) that an

“endemic clade of giant titanosaurs inhabited Patagonia between the Albian [113–100 MYA] and the Santonian [86–84 MYA] Ages. This clade includes most of the giant species of titanosaurs and represents the major increase in body mass in the history of Titanosauria.”

CHAPTER 10

Endemic Fish

INTRODUCTION

Freshwater fish fauna with connections between Africa, Australasia, and South America have been discussed since before the continental drift was accepted; they include lungfishes, osteoglossomorphs, characins, catfishes, cichlids, nandids, cyprinodonts, polypterids, galaxiids and synbranchids (reviewed by Lundberg, 1993). These are Gondwanan groups with vicariance explaining most, but not all, of their disjunct distributions.

Some orders of fish evolved within South America. The knife fishes (Gymnotiformes), for example, are entirely Neotropical.

Among the Characiformes—an order with 18 families and >2,000 species including piranhas and tetras—there appear to have been at least three splits among African and South American lineages, the last two being too recent to be explained by the continental drift/vicariance model; some, such as the Hepsetidae, must have dispersed across the sea eastwards, back to Africa (reviewed by Lundberg, 1993).

Marine dispersal of some groups that may have had euryhaline capabilities has been invoked for some taxa, such as the Phareodontinae subfamily of osteoglossids and aplocheiloids (killifishes, a suborder of the order Cyprinodontiformes with two families, one New World and one Old World) (Briggs, 2003). These are “secondary freshwater fishes” that adapted to freshwater from an ancestor that had marine or euryhaline abilities and could survive in brackish or even ocean water; they contrast with “primary freshwater fishes” that evolved within freshwater and can not cross saltwater barriers. Since the greatest diversity of cyprinodont fishes is in the New World (28 genera, compared to 11 in Africa, four in the Near East, and one in southeast Asia), their origin was probably in the New World with migration to the east by skipping across Gondwana remnants or by crossing the Atlantic Ocean in the late Cretaceous, with subsequent dispersal to Asia and to islands in the Indian Ocean (Briggs, 2003).

Fig. (10.1) shows cladograms of two groups, killifishes (Cyprinodontidae: Cyprinodontiformes) and cichlids (Cichlidae: Perciformes) that have members

both in Africa and South America. These disjunct distributions have long led to speculation that trans-Atlantic dispersal was involved in their biogeography.

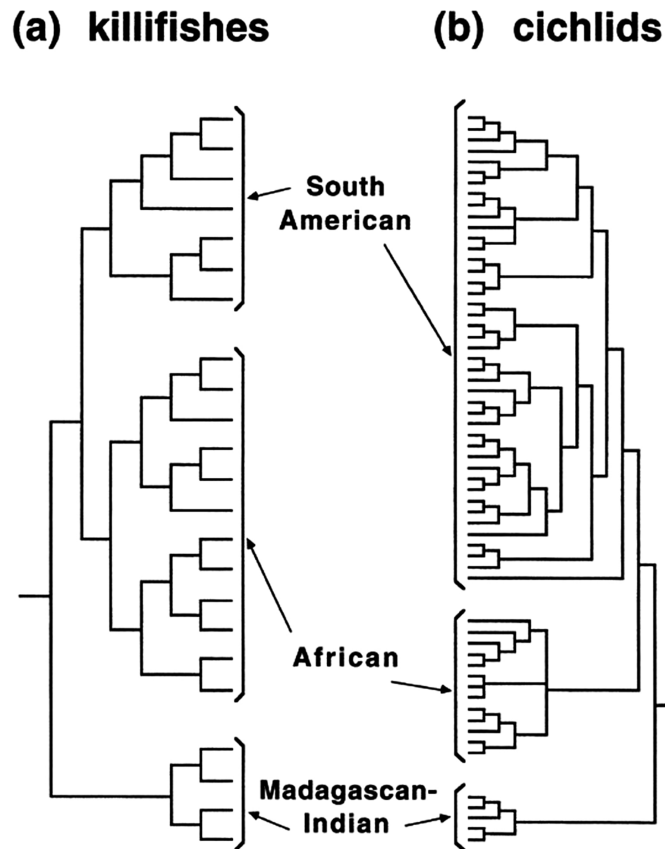


Fig. (10.1). Cladograms of killifishes, left, and cichlids, right (from Biggs 2003).

By using fossil-calibrated mitogenomic analysis, however, Azuma *et al.* (2008) calculated the divergence time between Malagasy and Indo/Sri Lankan cichlid clades at about 87 MYA, very close to the time of separation between Madagascar and India; and between African and Neotropical clades at about 89 MYA, close to the time of separation between Africa and South America. They conclude that, “Taken together, these results are consistent with the vicariant divergence of continental cichlid groups during Cretaceous times and argue against their Cenozoic dispersal” (Azuma *et al.*, 2008).

Within the nascent Neotropics, vicariance also dominated the origination of cichlid distributions, although other means of dispersal may have been involved

for certain clades. Using mitogenomic analysis to unravel Neotropic cichlid biogeography, Řičan *et al.* (2013) proposed that cichlid fishes colonized the Greater Antilles and Middle America simultaneously through the GAARlandia land bridge (Part 1) during the Oligocene. Central America (including eastern Panama) was colonized from northern Middle America in the Early–Middle Miocene; Central America was later (late Miocene) repeatedly fragmented, leading to the formation of the present ichthyological provinces prior to the final closure of the Panama Isthmus (Řičan *et al.*, 2013).

REFERENCES

- Azuma, Y, Kumazawa, Y, Miya, M, Mabuchi, K & Nishida, M (2008) Mitogenomic evaluation of the historical biogeography of cichlids toward reliable dating of teleostean divergences. *BMC Evol Biol*, 8, 215. [<http://dx.doi.org/10.1186/1471-2148-8-215>] [PMID: 18651942]
- Briggs, JC (2003) Fishes and birds: Gondwana life rafts reconsidered. *Syst Biol*, 52, 548-53. [<http://dx.doi.org/10.1080/10635150309318>] [PMID: 12857645]
- Lundberg, JG (1993) African-south american freshwater fish clades and continental drift: Problems with a paradigm. In: Goldblatt, P., (Ed.), *Biological relationships between Africa and South America* Yale University Press, New Haven, London 156-99. [<http://dx.doi.org/10.2307/j.ctt22726mc.12>]
- Řičan, O, Piálek, L, Zardoya, R, Doadrio, I & Zrzavý, J (2013) Biogeography of the mesoamerican cichlidae (teleostei: Heroini): Colonization through the GAARlandia land bridge and early diversification. *J Biogeogr*, 40, 579-93. [<http://dx.doi.org/10.1111/jbi.12023>]

Endemic Mammals

INTRODUCTION

“Endemic” is used in the sense of mammals whose ancestors were in South America at the time of Gondwana’s breakup, vicariance explaining their occurrence there, for the most part.

Mammaliform and mammal fossils from the Middle to Late Jurassic have been found in Chubut and Santa Cruz, “all of which predate the seafloor spreading between Africa and SAM” (Reguero & Goin, 2021 and references therein).

Monotremes split from Theria about 220 million years ago (Madsen, 2009). In the Late Cretaceous, non-therian mammals, mostly comprised of gondwanatheres, dryolestoids, and monotremes, were present in the Antarctic Peninsula-Patagonia, Río Negro and Chubut provinces in southern Argentina and the Magallanes Region of southern Chile (Reguero & Goin, 2021). Vicariance—the breakup of Gondwana and partial isolation of its parts—explains their presence.

Within Theria, Metatheria (marsupials and extinct relatives) split from Eutheria (placentals and extinct relatives) perhaps as early as 161 MYA (Luo *et al.*, 2011). Vicariance also accounts for marsupials in South America and their split from Australian marsupials.

Paleontologists agree that all known Cretaceous eutherians were small (<500 g) insectivores or omnivores, and that the earliest accepted crown members are found on the northern continents (Phillips, 2016). A consequence is that their fossils, even of lineages that would later evolve huge differences, look similar and many may be misclassified (Foote *et al.*, 1999; O’Leary *et al.*, 2013).

The deepest split of Eutheria was when a clade of Xenarthra+Afrotheria split from Boreoeutheria, a clade uniting superorder Laurasiatheria (Cetartiodactyla, Carnivora, pangolins, bats and hedgehogs) and Euarchontoglires (rodents, rabbits, primates, Dermoptera and Scandentia) (Kriegs *et al.*, 2006). The origin of Boreoeutheria was in Laurasia (Murphy *et al.*, 2007). Molecular analyses also tie Xenarthra either to Afrotheria (Hallström *et al.*, 2007; Meredith *et al.*, 2011) or Boreoeutheria (Romiguier *et al.*, 2013). The former would mean that Xenarthra, at

least, evolved within South America from primitive therians already there and that South America's split from Africa or Australasia likely drove a vicariant split.

However, combining phenomenal 4541 phenomic characters of 86 fossil and living species with molecular sequences for the latter suggests that Placentalia originated not long before the Cretaceous ended, with crown-clade Placentalia originating after 66 MYA (O'Leary *et al.*, 2013). Westbury *et al.* (2017) also showed, *via* mtDNA, that Litoptera split from Perissodactyla about 66 MYA (56.64–77.83). O'Leary *et al.* (2013) also placed the origin of Afrotheria in either North or South America, after which they dispersed to South or North America and to Africa. This timing precludes a vicariant explanation for the origin of all placental orders except Xenarthra.

Boreoeutheria diversified 79–88 MYA, after Gondwana began breaking up, when South America was isolated, with some moving north to Laurasia to become the presumptive basal group (Murphy *et al.*, 2007), while the ancestors of the South American orders remained there, or arrived by some other route. They might have returned to South America *via* Africa, or dispersed from North America around the Cretaceous-Tertiary boundary (66 MYA), when there was apparently a relatively brief filter connection across the proto-Caribbean Sea.

The above only refers to living taxa for which molecular estimates are available; but other research has proposed that at least some of the extinct eutherian mammalian orders unique to South America were related to the Perissodactyla (see below). If true, the ancestors of these orders must have been among the early Boreoeutheria that originated in South America while it was connected to Africa, or else found their way east while it was not too far away. Perhaps they crossed an island chain or ridge connecting Africa with South America, across the young Atlantic Ocean, when it was little more than a rift valley filled with water. Maybe they swam and swam again to reach Laurasia.

MONOTREMES

The report of a single molar fossil in a mammal-bearing deposit from the early Paleocene (64 MYA) of Punta Peligro, Golfo San Jorge, Chubut Province, Patagonia, Argentina in 1992 caused quite a stir among paleontologists. This was because *Monotrematum sudamericanum* was a platypus. It is the only monotreme known, fossil or living, outside of Australasia (Pascual *et al.*, 2002). Since then, other specimens have been found in Patagonia (Forasiepi & Martinelli, 2003). Its close relatives in the genus *Obdurodon*, an extinct platypus, have been found only in Australia—further confirmation of a biotic realm with dispersal among the southern continents. Dental analysis of monotremes and the dryolestids (see below) suggest a sister relationship, rather than monotremes being the

descendants of dryolestids (Pascual *et al.*, 2002); but the exact relationship remains uncertain.

Monotremes are egg-laying mammals (order Monotremata; formerly sub-class Prototheria, which may yet prove a useful distinction from Theria) that are today represented only in Australasia by the spiny anteaters (echidnas, family Tachyglossidae: four species in two genera) and the platypus. They retain some primitive, reptile-like features. Their ancestors apparently diverged from a common ancestor with therians (metatherians [marsupials] and eutherians [placental mammals]), before the divergence of marsupials from placental mammals, about 220 MYA, within the Gondwanan land mass that would become the southern continents. How they dispersed among South America, Antarctica, and Australasia, or whether they were there at Gondwana's breakup, is unknown; Pascual *et al.* (1992) assumed that they dispersed from Australia *via* Antarctica to South America. They never reached any other realm (Madsen, 2009).

ARCHAIC MAMMALS

Current understanding of the origins of endemic South American mammals indicates three sources (Woodburne & Case, 1996; Woodburne *et al.*, 2014):

- Some archaic non-therian lineages must have been in South America—many also would have been in what would become Australasia and Antarctica—in the Cretaceous when they split from Africa. They were mostly “pre-tribosphenic” taxa¹ derived from lineages known from the Jurassic and diversified in the Cretaceous as Gondwana was breaking up; they were already diverse in the Alaman SALMA, 84–66 MYA, to which their earliest fossils are dated. Their distributions result presumably from vicariance. A single multituberculate (see below) was found, possibly indicating an early dispersal from North America.
- In the earliest Palaeocene, the Tiupampan SALMA (64–63 MYA), a diversity of metatherians (marsupials and their stem relatives) and the oldest placental mammals (eutherians including “condylarths”, pantodonts, and a notoungulate) appear in the fossil record. These suggest dispersal from North America (metatherians a little earlier: late Cretaceous) where similar taxa are found at roughly the same ages. This dispersal route vanished and few if any North American taxa entered South America for most of the Neogene (all of the epochs after the Cretaceous period). All of the mammal taxa found during and after the Tiupampan age are unrelated to earlier taxa, suggesting a high evolutionary turnover. The last Gondwanan archaic mammals (dryolestids, gondwanatheres and the monotreme) died out by the Peligrean SALMA (62–60 MYA), although some persisted in Antarctica until the middle Eocene.

Endemic Birds

INTRODUCTION

“Endemic” as used here means taxa whose lineages were in what would become South America at the breakup of Gondwana, or at least by its separation from Antarctica and Laurasia. However, I use the term a bit loosely, and include some lineages that are very old, but probably not as old as the Paleocene. Since birds can fly, there cannot be a strict separation between dispersal by connected land, and by air over seas.

Molecular studies are producing evidence that species-level diversity is substantially underestimated. New species are described every year and many avian taxa comprise large complexes of subspecies that often represent several or many species.

Because of their obvious dispersal ability, many bird orders are globally distributed: Passerines, parrots, hawks, owls, grebes, trogons, and ducks and geese are examples. But even within globally distributed orders, some members arrived in South America early and evolved into new families. In other cases—New World vultures, for example—Old World representatives went extinct, leaving the lineage only in South America, from where they later migrated back to North America. This chapter gives examples of uniquely Latin American bird families—and in some cases whole orders—that evolved entirely with South America. That is, their lineages cannot be traced to other continents. These “endemic” birds must include those of the Patagonia-Antarctica-Australasia biotic realm before Antarctica froze about 34 MYA.

EVOLUTION OF BIRDS

Since bird-like reptiles originated in the Mesozoic, they were in the part of Gondwana that became South America. Birdlike reptiles, closely related to the stem lineages leading to modern birds, were in the South America-Antarctic-Australasia realm after it split from Africa, presumably descended from Gondwanan ancestors. They include Dromaeosauridae fossils from South America and Patagonia, and Maniraptoriforms from Patagonia (Wikipedia, 13 December 2018). No reptiles that were definitely the ancestors of modern birds

are known from the continent, however; evidently, these lineages died out, leaving no descendants. Bird ancestors living in South America at the time of the breakup did, however, persist in one modern bird: Rheas, as discussed below. The rest, as far as is known, came from somewhere else.

Prum *et al.* (2015), using the latest DNA sequencing techniques, analysed > 390,000 bases from each of 198 species of living birds to produce a phylogeny with the following sequence: The earliest true birds, just a little this side of *Archaeopteryx*, evolved from dinosaurs deep in the Cretaceous, around the time of the first flowering plants. The oldest living bird lineage is the Palaeognathae—ostriches and their cousins—(Haddrath & Baker, 2001; Harshman *et al.*, 2008; Prum *et al.*, 2015). Their ancestors split from other birds in the mid-Cretaceous 110–70 MYA (Haddrath & Baker, 2001); about 50 MYA this clade then split into the line leading to ostriches of Africa and the rheas of South America.

This brings us to a time when the sizeable Atlantic Ocean separated Africa from South America, which was still quasi-connected with islands to Antarctica. How the ostrich's ancestors reached Africa—or the rheas' ancestors reached South America—is unknown, but 50 MYA was at the end of the Eocene warm period and the beginning of a cool period when sea levels were dropping, exposing ridges and islands across the Atlantic Ocean. This is discussed below.

Meanwhile, the Neognathae (all birds other than Palaeognathae) split into Galloanseres (Galliformes: landfowl + Anseriformes: waterfowl) and Neoaves (all other birds) about 87 MYA. For most of the Late Cretaceous, until around 66 MYA, there were close though not complete connections among India, Africa, Madagascar, Antarctica/Australia and South America. Then three things happened to greatly accelerate the evolution of birds (and other taxa): (1) a comet or meteor crashed into the Caribbean/Mexico shoreline, creating atmospheric havoc that destroyed the dinosaurs, (2) the southern continents drifted further apart, isolating nascent avian lineages, and (3) the global temperature rise during the late Paleocene/early Eocene ~55 MYA made these southern continents almost tropical.

Between the end of the Cretaceous, when dinosaurs went extinct at 66 MYA, and about 50 MYA, most of the modern orders within the Neoaves had evolved in radiation of ten major clades: seven comprised multiple orders (“the magnificent seven”) and three “orphan orders”. The seven are shown with Roman numerals and colour-coded in Figs. (12.1 and 12.2).

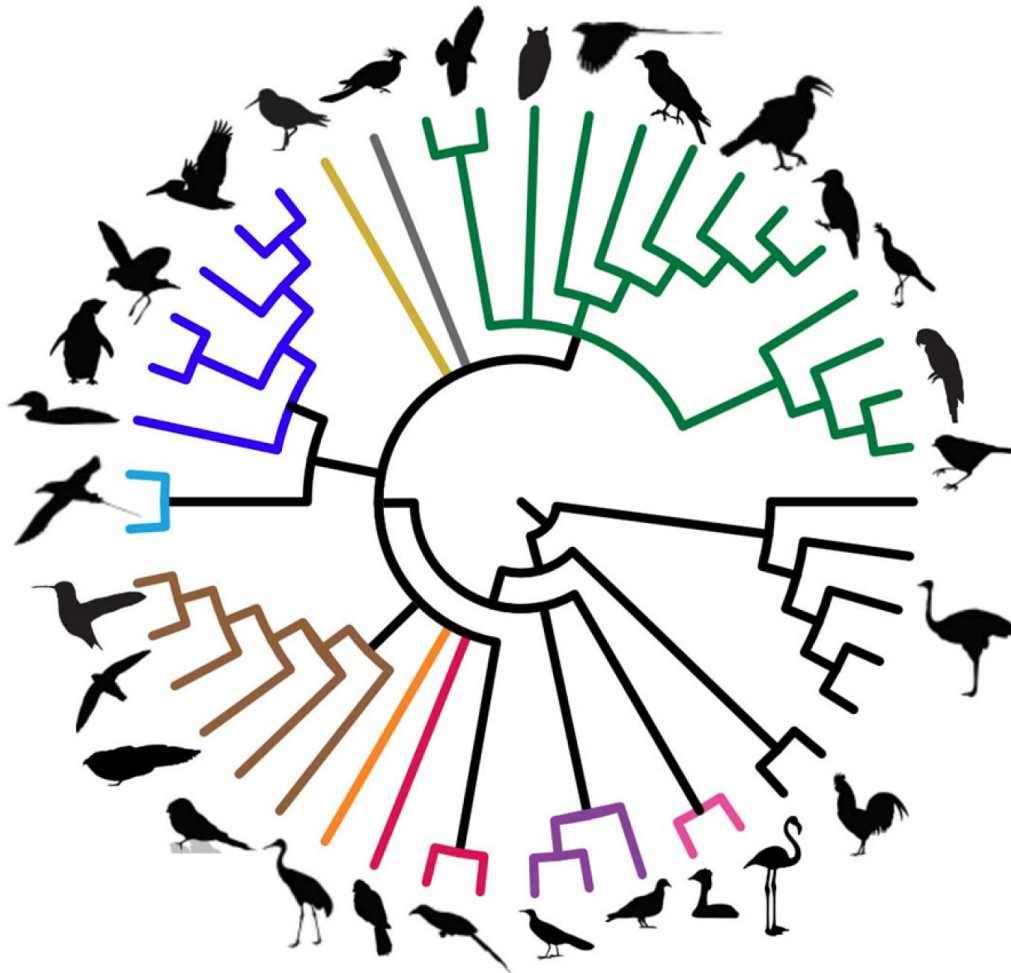


Fig. (12.1). Greater Rhea, subspecies *Rhea Americana intermedia* that Darwin saw in Uruguay in 1832. Summary of bird radiation (Braun and Kimball 2021). Colours correlate with Fig. (2.1): I green “core landbirds” or Telluraves; II blue, “core waterbirds” or Aequornithes; III light blue, Phaethontimorphae; IV red, Otidimprhae; V brown, Stricores; VI purple, Columbimorphae and VII pink, Mirandornithes. Creative Commons Attribution License.

The Ratites: Rheas and Tinamous

In July, 1832, Charles Darwin (1839) rode inland from Maldonado, Uruguay:

“On the fine plains of turf we saw many ostriches (*Struthio rhea*). Some of the flocks contained as many as twenty or thirty birds. These, when standing on any little eminence, and seen against the clear sky, presented a very noble appearance... it was easy to gallop up within a short distance of them; but then, expanding their wings, they made all sail right before the wind, and soon left the horse astern.”

Part 4 - Exotic Vertebrates

INTRODUCTION

“Exotic” as used here has a different meaning from the usual. Exotic groups are those that evolved somewhere else, some members of which immigrated to South America during the time that it was an isolated, “island” continent. They founded new lineages and their descendants are what we know today as “native” or “endemic” South American fauna.

Mostly these are higher-order taxonomic divisions such as orders or families that came during the Eocene or Miocene because the genera that lived then have, for the most part, gone extinct and the ones that live there now had not yet evolved.

This period essentially—because it is a geologically and logically grey area—begins with the final separation of South America by the opening of Drake Passage, causing Antarctica to freeze and foreclosing dispersal from Australia or elsewhere by that route. It ends with the closing of the Bolivar Strait and the continent’s connection to Central America that ushered in the Great Biotic Interchange about 3.5 million years ago.

An area of uncertainty is whether there were “filter” connections between North America and the Caribbean, and between the Caribbean and South America. Strings of islands not far from each other could, for example, have allowed some efficient dispersers to transit those seas. Some animals made this transit—such as deer and elephants immigrating from North America and giant sloths and glyptodonts emigrating to North America—in the Eocene, suggesting that something like this occurred; the great majority of taxa that did not so disperse precludes any kind of solid passage.

Lee E. Harding

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CHAPTER 13**Exotic Reptiles****INTRODUCTION**

I continue using “exotic” to mean species whose lineages immigrated to South America during its isolation, having arisen somewhere else.

DINOSAURS

As noted above in Part 3, at least one dinosaur immigrated to South America after it had split from Africa, but when it was still connected to Antarctica: a hadrosaur immigrated at the latest Cretaceous, demonstrating the existence of a land route between South America and Antarctica at that time (Lamanna, 2013). After immigrating, the lineage diversified locally into at least two genera of hadrosaur: *Willinakaqe salitralensis* described in 2010, and a previously known, closely related *Secernosaurus koernerii*.

This was part of a pattern that saw dinosaur families emigrating from Europe to South America and Australia until the end of the Cretaceous, even though, by then, these continents were separated by oceans (Dunhill *et al.*, 2016). In an interview (Science Daily, www.sciencedaily.com, 25 April 2016), the lead author, Dr. Alex Dunhill from the University of Leeds, said:

“We presume that temporary land bridges formed due to changes in sea levels, temporarily reconnecting the continents. Such massive structures—spanning, for example, from Indo-Madagascar to Australia—may be hard to imagine. But over the timescales that we are talking about, which is in the order of tens of millions of years, it is perfectly feasible that plate tectonic activity gave rise to the right conditions for such land bridges to form.”

LIZARDS

After a 2004 revision, five families of Geckos, formerly family Gekkonidae, are recognized: Eublepharidae, Gekkonidae, Pygopodidae, Diplodactylidae, and Carphodactylidae, collectively called the gekkotan families; the higher-order sphaerodactyls require more analysis to determine their taxonomic status (Han *et al.*, 2004). In Part 3, I mentioned the ancient lineages that were in South America at the time of the breakup of Gondwana, and that dispersed vicariously. The

Sphaerodactylini, a tribe of Sphaerodactylid gekkos, for example, was associated with the split of Eastern Gondwanaland from Western Gondwanaland (Gamble *et al.*, 2007; Han *et al.*, 2004).

But gekkos are famously dispersal-friendly: a suite of characteristics, including hard-shelled eggs that resist desiccation, eggs that tolerate immersion in salt water, and a digital adhesive mechanism that lets them hold tightly to surfaces of flotsam, allowing them to survive sea-water crossings (Gamble *et al.*, 2008). New phylogenetic and biogeographic analysis with fossil dating of divergence nodes shows that gekkotan taxa crossed the Atlantic Ocean no fewer than six times; another four clades achieved their disjunct distributions *via* the Beringian land bridge, or anthropogenic dispersal (Gamble *et al.*, 2011; Han *et al.*, 2004). Fig. (13.1) shows the cladogram of Gamble *et al.* (2011) with gray shading indicating South American clades of otherwise Old World groups.

SNAKES

Pit vipers (Viperidae) probably diverged from other vipers in Eurasia in the early Tertiary (or Paleogene, 66–24 MYA) and invaded North America *via* Beringia no later than the Miocene (Zamudio & Greene, 1997). The four species of bushmasters, for example, arose probably in Central America in the Miocene and split 17–6 MYA into Central and South American clades; both lineages then split into two species each during the Pliocene and Pleistocene (Zamudio & Greene, 1997). This implies a sea crossing of the Bolivar Strait.

TURTLES

The Neotropical wood turtles (*Rhinoclemmys*: Geoemydidae), with several Asian relatives but no links to Africa, is a post-Gondwanan arrival in South America probably *via* across the Bering Strait during the early Eocene; however, the clade invaded South America at least four times and one of the species (*R. nasuta*) reached South America in the early Miocene, before the emergence of the Isthmus of Panama (Le & McCord, 2008). Likewise, the South American testudinid tortoises such as *Geochelone* and *Chelonioidis* species arrived as waif dispersals during the Miocene (26–27 MYA), probably from Africa (Bauer, 1995). Their ability to cross ocean barriers is well established because they have close relatives in the Galapagos, Madagascar, the Seychelles and, formerly, the Mascarene islands, which are east of Madagascar (Bauer, 1995).

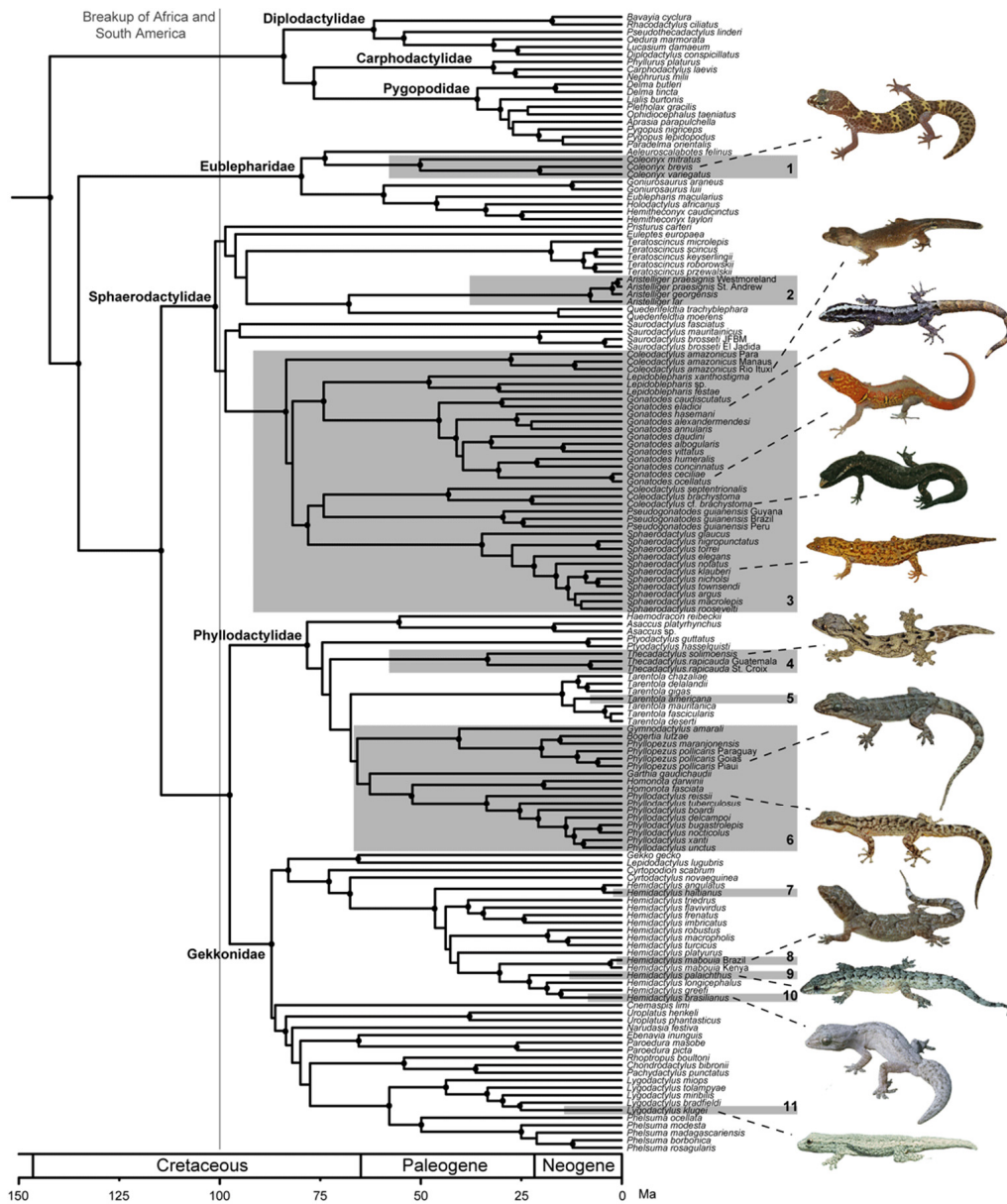


Fig. (13.1). Gekkonid cladogram showing 11 independent cross-Atlantic dispersals between Africa and the New World. Grey boxes are New World taxa. Fig. (1) from Gamble *et al* 2011. Used with permission from authors.

Exotic Birds

INTRODUCTION

In Part 3, we looked at a few birds whose lineages are so ancient that their ancestors were present at the breakup of Gondwana, or shortly after, when they could walk to South America from Australasia or Laurasia. They were mostly order-level lineages. The birds of Part 4 are “exotic” in the sense that their lineage dispersed into South America from elsewhere, even though many millions of years ago, during the time that it was isolated and before the Great Biotic Interchange, the subject of Part 5. The orders having originated elsewhere, these are mostly family-level or lower clades.

HOATZINS

No other bird is like the hoatzin (Photo 14.1). Its size is of a large pheasant and rather ugly. It is a ruminant and, like cows, its bacterial fermentation chamber is in its foregut. *Opisthocomus hoatzin* has its own order, Opisthocomiformes. There are no other members. It does not live anywhere else on the planet. Its phylogenetic position in the evolution of birds is unresolved: some morphological and genetic studies have placed it close to turacos (a medium-sized, colourful African bird group related to cuckoos) and others with Columbidae (doves and pigeons). Livezey and Zusi (2007), in an extensive phylogenetic reconstruction of higher-order modern birds by comparative anatomy, remarked that,

“Opisthocomus is ambiguous at best: most studies place the genus as closely related to the Cuculiformes (Hughes & Baker, 1999; present study), whereas a few analyses suggest a more distant relationship.”

The latest genetic analysis, using targeted next-generation sequencing, places hoatzin neither with cuckoos nor with pigeons. It is at the base of Neoaves, a land bird clade, as a sister group (of one species) to all other land birds (Prum *et al.*, 2015), from which it diverged at the time when the dinosaurs went extinct. In an arrangement provided by Prum *et al.*, the land birds (Telluraves—Jarvis *et al.*, 2014) include Accipitriformes (hawks, New and Old World vultures, secretarybird, ospreys), owls, Coraciimorphae (trogons, hoopoe, kingfishers, motmots, mousebirds, toucans, barbets), and Australaves (a clade containing Caracara, falcons, terror birds and parrots plus the Passeriformes).



Photo (14.1). A trio of hoatzins, *Opisthocomus hoatzin*. Rio de Dios, Amazon basin, Peru. LEH © photo.

Hoatzin ancestors have been in South America for at least the last 38 MYA, based on fossils from the Middle Miocene (13.5–11.8 MYA) in Colombia, the Oligo-Miocene (24–22 MYA) in Brazil, and the lower Eocene (38 MYA) of Argentina (summarized by Mayr *et al.*, 2011). For many years, they were thought to have been of purely South American origin, albeit with uncertain affinities.

To the surprise of paleontologists, hoatzin relatives have recently been found in Early Miocene deposits in Namibia (Mayr *et al.*, 2011), from the Late Eocene, 34 MYA, in France (Mayr & De Pietri, 2014) and from the Early Miocene in Kenya (Mayr, 2014).

By 38 MYA, South America had been isolated from Africa for some 60 million years, with the wide Atlantic Ocean in between. How did they get from Africa to South America? Hoatzins today are tropical birds; unless their ancestors were very different, they could not have dispersed *via* Antarctica, which was cooling in the late Eocene/early Oligocene. It is too big and clumsy for sustained flight. As Mayr and De Pietri (2014) note, “...although recognition of hoatzins in Europe may challenge their presumed transatlantic dispersal, there are still no North American fossils in support of an alternative, Northern Hemispheric, dispersal route.”

HUMMINGBIRDS

The first time I saw giant hummingbirds, by the sea coast in southern Chile, it took me a few minutes to even realize that's what they were. They acted like hummingbirds, hovering by big, red flowers and probing for nectar with long beaks; but they were the size of sparrows and their wings were too big and slow to hum or buzz: they flapped. I've since seen them in the high Andes of Argentina (Photo 14.2) feeding on cactus flowers and they never cease to amaze.



Photo (14.2). Giant Hummingbird, *Patagona gigas*. LEH © photo.

Hummingbirds (Family Trochilidae) are exclusively Neotropical today, but their ancient lineage originated in Eurasia, or possibly Laurasia. They are another taxon that made the sea crossing journey to South America, but by what route is unknown. Their ancestors split from insectivorous ancestors of swifts and treeswifts (treeswifts only live in Southeast Asia today) about 42 MYA (McGuire *et al.*, 2014). A 50,000 years old fossil in Wyoming was a predecessor to both hummingbirds and swifts before the groups diverged. A proto-hummingbird fossil dated to 30 MYA has been found in Germany and other fossil stem hummingbirds from Europe have been dated to 28–32 MYA (reviewed by McGuire *et al.*, 2014). Between that time and 22 MYA, to which the first true hummingbird fossils are dated, their ancestors had arrived in South America, where they diversified immensely. Today there are about 360 species (Wikipedia, accessed October 13, 2021) with nine main clades (McGuire *et al.*, 2014) from Chile to Canada.

Exotic Mammals

INTRODUCTION

“Exotic” here means that the lineage evolved somewhere else and dispersed into South America *via* land or sea crossings, before the Great American Biotic Interchange.

AFROTHERIA

Elephants

One of the major triumphs of the DNA revolution has been the uniting of animals of such disparate shapes and sizes as elephant shrews, hyraxes, aardvarks, sirenians (manatees and dugongs; see below) and elephants into a new clade, or superorder, Afrotheria. This idea, first seriously proposed in the late 1990s, has been robustly supported by many DNA studies (*e.g.*, Kuntner *et al.*, 2010).

Afrotheria originated about 105 MYA when Gondwana was braking up and is a sister clade to Xenarthra (sloths, anteaters and armadillos): their common ancestor lived in Gondwana and Xenarthra entirely in South America, while there is no evidence of terrestrial Afrotherian (that is, except manatees and dugongs) lineages originating outside of Africa. Gondwana’s breakup no doubt drove the divergence.

The earliest proboscidean fossils are from the Palaeocene and they diversified across Eurasia and North America (*via* Beringia) into at least seven families in the Eocene and Oligocene. Several proboscideans (elephants and their relatives) in the family Gomphotheriidae entered South America as part of the Great Biotic Interchange (see Part 5). One, however, *Amahuacatherium antiquum*, collected along the Río Madre de Dios in southeastern Peru, is dated back to about 9 MYA (Croft, 2016). Its identification as a genus separate from *Notiomastodon* is controversial (reviewed by Alberdi & Prado, 2022), but not its stratigraphic date. It or its ancestor must have swum from North America.

Manatees and Dugongs

Of the living Afrotherians, only the Sirena (dugong and manatees) dispersed very far outside of Africa, obviously because of their mobile marine capabilities.

The order Sirenia is thought, based on fossil distribution, to have evolved from terrestrial ancestors in the Tethys Sea between the eastern Gondwana fragments and Laurasia, in the Eocene, about 60 MYA. The dugong's ancestors went southeast from there and now populate coastlines around the Indian Ocean and the Southwest Pacific Ocean. Meanwhile, the manatees' ancestors went southwest. Three extant species and numerous fossil species are known: one (*Tricheuchus senegalensis*) in coastal and inland western Africa, a marine/estuarine species (*T. manatus*) in the Caribbean and estuaries around the northern coast of South America, and a completely freshwater species (*T. inunguis*) in the Amazon Basin (Vianna *et al.*, 2006). Interestingly, the Amazonian manatee is more closely related to the West African manatee than to its neighbour, the Caribbean manatee (Kuntner *et al.*, 2010; Vianna *et al.*, 2006). Divergence-time estimates place the origin of the genus in the Pliocene and the divergence of the American species about 4.0 MYA (Cabtabgede *et al.*, 2005), implying an ocean crossing about that time. It is possible that strong selection pressures drove speciation (and subspeciation, in the case of the Caribbean manatee) after the initial founding population arrived from Africa.

DEER AND THEIR RELATIVES

Palaeomerycidae is an extinct family of even-toed ungulates related to deer and giraffes. The family evolved in, and is endemic to, North America, except for one species. *Surameryx acrensis* fossils were found at Acre, Brazil, on the Madre de Diós River, dated back to about 10 MYA (<https://en.wikipedia.org/wiki/Surameryx>). It, like the gomphothere mentioned above, must have swum from Central America before formation of the Isthmus of Panama.

Peccaries, or Javelinas, are generally thought to have entered South America as part of the Great Biotic Interchange, but a fossil of extinct *Cynorca occidentale*, from Panama, dated back to about 19 MYA (early-middle Miocene) is a primitive member of the clade that includes all three (known) extant tayassuids (MacFadden *et al.*, 2010). Two genera from fossil sites in western Brazil and eastern Peru have been dated to the late Miocene, 9 MYA (Frailey & Campbell, 2016). One was related to the modern genus *Tayassu*, while the other is closer to *Pecari*. These both indicate arrivals before the Isthmus of Panama closed and a more complex dispersal and evolutionary history than previously thought. The dates of these and other purported late Miocene fossils are controversial, however, and this affects the proposed taxonomy (D. Croft, in lit., 22 June 2017). Javalenas are discussed further in Part 5.

CAVIOMORPH RODENTS

Caviomorph rodents have long been one of the central enigmas of South American biogeography. How did they get there?

Rodents comprise nearly half of the mammal species in Central and South America, but only the caviomorph rodents are truly native to the continent, since they evolved here and do not live anywhere else. The infraorder Caviomorpha is within the suborder Hystricognathi (order Hystriomorpha), which also contains Hystricidae (Old World porcupines) and African Phiomorpha (cane rats, dassie rats, and blesmols). An African origin of Hystricognathi was long assumed, with colonization of South America by waif dispersal across the Atlantic Ocean. New evidence, however, points to an Asian origin. Huchon and Douzery (2001) suggest, based on a genetic phylogeny, that they may have originated in Asia and reached South America *via* Australia and Antarctica, leaving no fossils or surviving lineages along the way. Jenkins *et al.* (2004) support this with their discovery of a hystricognath rodent family in Laos that may be evidence for an Asian origin of caviomorphs. Notwithstanding this intriguing possibility, scientists for now concur that hystricognath rodents first arrived in South America from Africa *via* trans-oceanic dispersal. They suddenly appear in the fossil record 41 MYA in the Middle-Late Pleistocene. Upham and Patterson (2015) date the Hystricognathi crown to the Middle Eocene, 44.9 MYA, the phiomorph-caviomorph split to 42.0 MYA (coinciding with the Mid-Eocene Climatic Optimum), divergence of crown caviomorphs 35.7 MYA, and splits of Cavoidea-Erethizontoidea and Chinchilloidea-Octodontoidea 32.4 MYA and 32.8 MYA, respectively (Fig. 15.1).

There were at last count (December 2016) 246 living species, arranged in four superfamilies, 13 families, and 56 genera.

Upham and Patterson (2012) propose that,

“the absence of beavers, tree squirrels, ground squirrels, gophers, voles, muskrats, and rats and mice from South America prior to the Great American Biotic Interchange may well have contributed to the explosive ecological and morphological diversification of caviomorphs.”

Because of the temporal proximity of the arrival of the caviomorph rodents and platyrrhine primates in South America, scientists have long wondered whether their arrivals were synchronous, presumably by the same mechanism, rafting. The latest fossil-calibrated genetic analysis supports this (Upham & Patterson, 2015).

Part 5 - Recent Arrivals

INTRODUCTION

It is sort of a play on words: The Subcommittee on Quaternary Stratigraphy (of the International Commission on Stratigraphy) declared that the “Recent” (capitalized) era is an obsolete synonym for the Holocene and that, further, it is not an era but an epoch. But really, “Recent Arrivals” means those that immigrated to South America recently: from the end of the Pliocene to the Holocene. I include Humans, but not anthropogenic introductions.

Recent arrivals invaded South America from North America during the Great Biotic Interchange after the Isthmus of Panama closed, about 3.5 MYA. Evidence for and against an earlier closure is mentioned in Part 1. In any case, it is clear that for many millennia, the volcanic islands and tectonic blocks, at times more exposed by lowered sea levels, functioned as biological filters: a few species managed to fly, swim or drift one way or the other to found new populations before the isthmus finally closed and the trickle became a flood.

For the most part, new immigrants were existing genera that further diversified into new species once in South America. When they arrived is not always certain and depends on fossil evidence, but the absence of evidence is not the evidence of absence. In some cases, it is hard to know from fossil evidence if they reached South America before or after the species split. As a general rule, the region with the highest diversity, especially at the higher levels (genus < family < order) is likely the origin of the taxon. But the neotropics’ high habitat diversity and geomorphic history often resulted in high species diversity, even in taxa that originated elsewhere. Reconstructing phylogenies from DNA analysis often tells when lineages diverged, but not where. For example, many taxa evolved into current forms in Central America, but investigators can’t be sure whether they flew, swam, or rafted across the Bolivar Strait before the Isthmus closed, or walked across after.

A fundamental feature of the Great Biotic Interchange was the extinction of many native South American taxa. The cause of the late Pleistocene-Holocene extinctions of South American mammals, especially the “megafauna”, has long been debated. Was it the influx of North American mammals during the Great Biotic Interchange,

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as immigrant herbivores outcompeted the native ones and the new carnivores were more efficient predators than the ones that had been there for many millions of years? Did early humans (see below) hunt them to extinction? New research based on fossil DNA and radiocarbon dates (Metcalf *et al.*, 2016) identifies:

*"A narrow megafaunal extinction phase 12,280 ± 110 years ago, some 1 to 3 thousand years **after** initial human presence in the area. Although humans arrived immediately prior to a cold phase, the Antarctic Cold Reversal stadial, megafaunal extinctions did not occur until the stadial finished and the subsequent warming phase commenced some 1 to 3 thousand years later.. megafaunal extinctions did not occur until human presence and climate warming coincided. Overall, metapopulation processes involving subpopulation connectivity on a continental scale appear to have been critical for megafaunal species survival of both climate change and human impacts. (emphasis added)"*

The authors propose that climate change altered and fragmented habitats, at least in southern South America, isolating subpopulations and leaving them susceptible to natural population threats, as well as humans.

The Great Biotic Interchange was first discussed by Alfred Russel Wallace (Wallace, 1876), who had spent four years in the Amazon from 1848 to 1852, mostly with Henry Walter Bates (Bates, 1863), who stayed on another six years. The event is also called the Great American Interchange and the Great American Biotic Interchange (GABI).

The Great Biotic Interchange is too well studied and accounts too widely published to merit a comprehensive treatment here, but the DNA revolution has added clarity to certain issues that are worth mentioning.

Only mammals are covered in this section. Many reptiles have immigrated to South America since the Great Biotic Interchange, and many more have been brought by humans in modern times. An example of the latter is *Hemidactylus mabouia*, the tropical house gecko of Africa, which has become established in South America, the Caribbean, Mexico and subtropical parts of the United States (reviewed by Vecchi & Harding, 2016).

Too many birds have flown, walked or swam into South America during or since the Great Biotic Interchange to mention here. They include, for example, most of the oscines that occur in South America, since they evolved essentially outside of the continent and many migratory species are only there in winter; similarly for

migratory shorebirds and other taxa. And of course, many, such as house sparrows (*Passer domesticus*), California quail (*Callipepla californica*, introduced for hunting) and domestic pigeons (*Columba livia*) were introduced by people in historic times.

REFERENCES

- Bates H.W. The naturalist on the river Amazons.. Vol. 1 and 2. London: Murray; 1863.
- Metcalf, J.L., Turney, C., Barnett, R., Martin, F., Bray, S.C., Vilstrup, J.T., Orlando, L., Salas-Gismondi, R., Loponte, D., Medina, M., De Nigris, M., Civalero, T., Fernández, P.M., Gasco, A., Duran, V., Seymour, K.L., Otaola, C., Gil, A., Paunero, R., Prevosti, F.J., Bradshaw, C.J.A., Wheeler, J.C., Borrero, L., Austin, J.J., Cooper, A. (2016). Synergistic roles of climate warming and human occupation in Patagonian megafaunal extinctions during the Last Deglaciation. *Sci. Adv*, 2(6), e1501682. [<http://dx.doi.org/10.1126/sciadv.1501682>] [PMID: 27386563]
- Vecchi, M.B., Harding, J.M. (2016). Hemidactylus mabouia (tropical house gecko) predation. *Herpetol. Rev*, 47(1), 136-137.
- Wallace A.R. The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface (Vol. One and Two). London: Macmillan; 1876.

Rodents and Rabbits

INTRODUCTION

As mentioned in Part 4, one subfamily, the Sigmodontinae, including cotton rats, rice rats, and their relatives, invaded from North America in at least two dispersals across the Caribbean or the Atrato Seaway, the first possibly as early as the middle Miocene (~15 MYA). Sigmodontines, having had an earlier start, rapidly diversified, now with around 400 species (depending on the taxonomy used) in 69 genera in South America (Patton *et al.*, 2015).

Three rodent families crossed the dry Isthmus of Panama or Caribbean islands during the Great Biotic Interchange: Sciuridae, squirrels; Cricetidae, New World rats and mice; and Heteromyidae, pocket mice. A few lagomorphs did also: cottontail rabbits. I did not intend to discuss anthropomorphic dispersals (that is, by human agency) but could not refrain from mentioning a few.

RODENTS

Squirrels

Seven sciurid genera are known from South America.

Pocket gophers

Geomyadae (in the Geomyoidea) have dispersed to Central America, but not to South America.

Cricetid Rodents

Cricetidae includes true hamsters, voles, lemmings, and New World rats and mice—more than 600 species total. Cricetid rodents arose in the Old World during the Miocene and spread to North America and Asia when these continents were connected in the north. Neotominae (2 genera) and Tylominae (one genus) came later and found most niches filled. They diversified, but not to the extent of the Sigmodontinae, which had an earlier start (Marshall, 1988).

Pocket Mice

Heteromyidae, the mainly North American pocket mice, are represented in South America by one genus with three species. They have external, fur-lined cheekpouches, a feature not found in other South American rodents.

Anthropogenic Dispersals

Muridae are Old World rats and mice, three of which have become globally distributed by humans: brown or Norway rats (*Rattus norvegicus*), black or roof (because they climb well and often nest in attics) rats (*Rattus rattus*), and house mice (*Mus musculus*).

The muskrat, (*Ondatra zibethicus*: Cricetidae) has been introduced to South America in historic times.

New Discoveries

Rodent species are still being discovered. For example, in 2015, mammalogists at the Universidad Austral de Chile described a new species in Sigmodontinae, *Abrothrix manni* (D'Elía *et al.*, 2015; González-Isla, 2015). It lives on Chiloé Island, the mainland in the Chilean regions of Los Lagos and Los Ríos and at a single locality in the Argentinean province of Neuquén. More recently, Peçanha *et al.* (2019) described a new species of *Oxymycterus* from the transitional ecotone between the Cerrado and the Atlantic Forest in Brazil.

RABBITS AND HARES

Several species of cottontail rabbits (*Sylvilagus sp.*) are “native” to South America, having dispersed across the Isthmus of Panama long ago. A recent taxonomic revision of Brazilian cottontail, *Sylvilagus brasiliensis*, has resulted in adding at least 3 new species to the complex: *S. andinus*, *S. apollinaris*, and *S. fulvescens* (Ruedas *et al.*, 2019).

Lagomorphs introduced early in the last century include the European hare (*Lepus europaeus*) and European rabbit (*Oryctolagus cuniculus*); both have invaded southern South America and Oceania, where they do not have ecological equivalents and are interfering in the ecology of native herbivores (Barbar *et al.*, 2016; Buenavista & Palomares, 2018).

REFERENCES

Barbar, F, Hiraldo, F & Lambertucci, SA (2016) Medium-sized exotic prey create novel food webs: The case of predators and scavengers consuming lagomorphs. *PeerJ*, 4, e2273. [<http://dx.doi.org/10.7717/peerj.2273>] [PMID: 27547575]

Buenavista, S & Palomares, F (2018) the role of exotic mammals in the diet of native carnivores from south america. *Mammal Rev*, 48, 37-47.

[<http://dx.doi.org/10.1111/mam.12111>]

D'Elía, G, Teta, P, Upham, NS, Pardiñas, UFJ & Patterson, BD (2015) Description of a new soft-haired mouse, genus *Abrothrix* (Sigmodontinae), from the temperate valdivian rainforest. *J Mammal*, 96, 839-53.

[<http://dx.doi.org/10.1093/jmammal/gyv103>]

González-Isla, C (2015) They discover a new species in the Valdivian Forest. *Trends*.

Marshall, LG (1988) Geochronology and land-mammal biochronology of the transamerican faunal interchange. In: Stehli, F., Webb, S., (Eds.), *The Great American Biotic Interchange* Plenum Press, New York, N.Y. 49-85.

Rodents Chicago, Illinois, and London Mammals of South America Patton, JL, Pardiñas, UFJ, D'Elía, G (2015). University of Chicago Press, U.K..

Peçanha, WT, Quintela, FM, Jorge Ribas, LE, Althoff, SL, Maestri, R, Gonçalves, GL & De Freitas, TRO (2019) A new species of oxymycterus (rodentia: Cricetidae: Sigmodontinae) from a transitional area of cerrado – atlantic forest in southeastern brazil. *J Mammal*, 100, 578-98.

[<http://dx.doi.org/10.1093/jmammal/gyz060>]

Ruedas, LA, Silva, SM, French, JH, Platt, RN, II, Salazar-Bravo, J, Mora, JM & Thompson, CW (2019) Taxonomy of the sylvilagus brasiliensis complex in central and South America (lagomorpha: Leporidae). *J Mammal*, 100, 1599-630.

[<http://dx.doi.org/10.1093/jmammal/gyz126>]

CHAPTER 17

Elephants

INTRODUCTION

As noted in Part 4, the gomphothere *Amahuacatherium antiquum*, collected along the Río Madre de Dios in southeastern Peru, is dated to about 9 MYA (Croft, 2016). Its identification as a separate genus from *Notiomastodon* is controversial, but not its stratigraphic date (Alberdi & Prado, 2022).

Other than that, as far as is known, gomphotheres (order Proboscidea, family Gomphotheriidae) entered South America from the north only after the closure of the Isthmus of Panama. Pleistocene (*i.e.*, post-Great Biotic Interchange).

These were two species of gomphothere, *Cuvieronius hyodon* of the Andes from Colombia to central Chile and *Notiomastodon platensis* (which now includes South American specimens formerly identified as *Stegomastodon*). The latter was widely distributed with > 140 localities in the eastern lowlands and pampas (Croft, 2016; López M. *et al.*, 2008). *Cuvieronius* had a more restricted distribution in the Andes and west coast south to central Chile (Alberdi & Prado, 2022; López M. *et al.*, 2008). All of the above went extinct in the late Pleistocene or early in the Holocene, after the arrival of humans, except for some *Notiomastodon* that survived at least 6,000 years ago in Colombia (Wikipedia, accessed 30 November 2016).

Two other proboscidian families—Elephantidae (mammoth [genus *Mammathus*] and modern elephants) and true mastodons (genus *Mammut*, family Mammutidae), occupied Central America in the Pliocene, but have not (yet) been found in South America. Since they were grazers, whereas *Notiomastodon* and *Cuvieronius* were browsers, the available habitat in northern South America probably explains why mammoths and mastodons did not reach it (Alberdi & Prado, 2022).

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REFERENCES

Alberdi, MT & Prado, JL (2022) Diversity of the fossil gomphotheres from south america. *Hist Biol*, 34, 1685-91.
[<http://dx.doi.org/10.1080/08912963.2022.2067754>]

Croft, DA (2016) *Horned armadillos and rafting monkeys: The fascinating fossil mammals of south america*. Indiana University Press.

López, MP, Cartajena, FI, García, PC, Vega, LJ & Arévalo, NI (2008) Mastodons and paleocamelids from mid-latitude chile: archaeological, paleontological and paleoenvironmental implications from aguas de ramón 1 site (metropolitan region). In: Goebel, T., (Ed.), *Current research in the pleistocene paleoenvironments: Vertebrates and invertebrates* 182-4.

CHAPTER 18**Deer, Pigs and Camels****INTRODUCTION**

Artiodactyla (even-toed, or cloven-hoofed ungulates) have been merged with whales, Cetacea, into a new order, Cetartiodactyla, after much research showed them to share a common ancestor. However, for convenience, many taxonomists retain the old order names.

JAVELINAS

Peccaries, or javelinas, are in the pig family, Suidae. It is a testament to the immensity and diversity of South America that no one knows how many species of Peccary there are. Traditionally, the family Tayassuidae held two living species: collared peccary (*Pecari tajacu*) (Photo **18.1**) and white-lipped peccary (*Tayassu pecari*). In 1974 a third genus, the Chacoan peccary (*Catagonus wagneri*), which had been described from fossils in 1930, was discovered as a living component of Amazonia's biodiversity (Wetzel *et al.*, 1975). These are the three commonly accepted today. But Gongora *et al.* (2006) found that genetic distances within *P. tajacu* clades from Central America and northern South America were high enough to split it into two new species, and that those in Colombia are paraphyletic—meaning that there could be a fifth species. In 2006, a new species, the giant peccary, *Pecari maximus*, was described in the Rio Aripuaná basin, Brazil (van Roosmalen *et al.*, 2006); it supposedly was longer-legged and taller than *P. tajacu*, but more slender, and had behavioural differences. However, further examination suggested that the specimen described clustered genetically and morphologically within Brazilian *P. tajacu* (Gongora *et al.*, 2011). Groves and Grubb (2011) revised the genus, retaining *P. tajacu* as the “southern type” (with two subspecies in South America) and described two new species: *P. angulatus*, the “northern type” of northern Mexico/southern United States; and *P. crassus* of the humid rainforests of southern Mexico, Central America, northwestern Colombia and Ecuador west of the Andes. Groves and Grubb (2011) reserved judgement on *P. maximus*, citing the need for more specimens, but mentioned that three other specimens that they examined—two from Paraguay and one from Brazil—belong to “unnamed taxa.”



Photo (18.1). Collared peccaries, *P. tacaju*, on Cozumel Island, Mexico. LEH © photo.

The family, Tayassuidae, split from its common ancestor with pigs (Suidae) about 40 MYA (Adega *et al.*, 2008); many fossils are known from North America. A primitive fossil from Thailand suggests Southeast Asia as the origin of the lineage, which dispersed (presumably *via* Beringia) to North America (Ducrocq, 1994), after which those in Asia went extinct.

As noted in Part 4, two genera of Peccary fossils have been found in Peru dating to 9 MYA (Frailey & Campbell, 2016). *Pecari* split from *Tayassu* + *Catagonus* 3.4–7.4 MYA, and the latter two diverged in the late Pliocene, “perhaps concomitant with the invasion of South America by tayassuids, supporting the hypothesis that these two clades diverged in North America before either clade colonized South America” (Theimer & Keim, 1998). This is an example of a possibly false assumption driving biogeographical conclusions. If the Isthmus of Panama formed much earlier than 3.5 MYA as some information suggests (see Part 1)—or if a tayassuid ancestor swam across the strait in the Pliocene—the two clades may have diverged within South America and then re-entered Central and North America. In fact, a fossil extinct *Cynorca occidentale*, from Panama, dated to about 19 MYA (early-middle Miocene) is a primitive member of the clade that includes all three (known) extant tayassuids (MacFadden *et al.*, 2010). Given its

proximity to South America and the fact that other mammals and reptiles are known to have emigrated from South America before 3.5 MYA, it is at least plausible that *Cynorca* or its descendants did, too. At any rate, most fossil extinct tayassuids are from Bolivia and Brazil and most dating to about 3 MYA (Gasparini *et al.*, 2009; Gasparini *et al.*, 2010; Marshall & Cifelli, 1990), suggesting continued dispersal *via* the Isthmus of Panama.

CAMELS

When Charles Darwin first saw guanacos and later vicuñas (and of course their domesticated descendants, the llama and alpaca, respectively) he recognized them immediately as “the South American representative of the camel” (Darwin, 1839). What biological or geological forces of nature, he wondered, caused camelids to occur in South America, Asia (Bactrian camel) and Arabia (dromedary) and nowhere in between?

Fossil distribution shows that camelids evolved during the Eocene (25 MYA), in North America. Mitochondrial DNA (mtDNA) analysis showed that they had split into two tribes, Camelini and Lamini, by the Miocene, earlier than had been suggested by the fossil record (Cui *et al.*, 2007). The ancestors of the Bactrian camel and dromedary may have diverged before representatives of both lineages emigrated west across the Beringia land bridge to northeast Asia, the latter eventually populating the Middle East and North Africa. In the late Tertiary (the Pliocene epoch), the ancestors of guanacos and vicuñas migrated to South America (Cui *et al.*, 2007). This was before the Isthmus of Panama was formed, meaning that they evidently swam, possibly from island to island.

A few million years later, during the Pleistocene, all the camels in North America went extinct, leaving guanacos and vicuñas in South America, disjunct from Bactrian camels in Asia and dromedaries in North Africa and Arabia. Two species of vicuña (Photo 18.2) have been proposed: northern vicuña, *Lama mensalis*, and southern vicuña, *L. vicugna* (Groves & Grubb, 2011), but this is not widely accepted.

Llamas are domesticated guanacos (Kadwell *et al.*, 2001). For this reason, and following international zoological nomenclature rule that domesticates should retain the Latin name of their wild ancestors, the llama has been changed from *Lama guanicoe* to *L. glama*, the prior name of domesticated llamas. Alpacas, smaller and bred for their fine wool, are also domesticated guanacos, but with some vicuña genes (Kadwell *et al.*, 2001). Alpacas are still sometimes referred to as *Vicugna pacos* or *Lama pacos*, obsolete names in view of the modern understanding of its domestic development.

Horses and Tapirs

INTRODUCTION

The Perissodactyla, or odd-toed ungulates, include horses and tapirs, both of which evolved in North America and immigrated to South America as part of the Great Biotic Interchange.

HORSES

At least five fossil species of *Equus* (subgenus *Amerhippus*) and three of *Hippidion* (Photo **19.1**) are known from the middle-late Pleistocene in Argentina, Brazil, Ecuador, Colombia, and Bolivia. The two genera have “different ecological adaptations that are evident in the cranial morphology, the robustness of the limbs and body size” (Prado & Alberdi, 1994; Prado *et al.*, 2011). Another extinct genus, *Onhippidium*, was less common than *Hippidion* (although the genus is controversial and some synonymize it with *Hippidion*). These horses were rather different from *Equus*: skull structure “suggests that hippidiform horses had a well-developed prehensile upper lip like modern black rhinoceros (*Diceros bicornis*) for feeding on the leaves of trees and shrubs” (Croft, 2016). Horses later went extinct throughout the Western Hemisphere, until modern horses and burros were re-introduced by the Spanish in the 16th Century. Feral modern horses have established stable, viable populations in Argentina, the United States of America, and Canada.

TAPIRS

Tapirs are among the few surviving South American megafauna that survived extinction (*e.g.*, Ferreguetti *et al.*, 2017), and remain the largest native mammal.

Tapirs first appear in the fossil record in North America in the Eocene and were distributed across Eurasia by the Oligocene. Asian and American tapirs diverged around 20 to 30 MYA, but became extinct in most of the Northern Hemisphere about 10,000 years ago. Tapirs persisted in southern parts of their North American range and migrated to South America, it was long thought, around 3 MYA, as part of the Great Biotic Interchange (Ashley *et al.*, 1996).



Photo (19.1). The horse, *Hippodion saldiasi*, lived in Patagonia 12,000 to 10,000 years ago. LEH © photo at Museo Egido Feruglio, Trelew.

There are currently four or five species of tapir, one of which (Malayan, *Tapirus indicus*) lives in southeast Asia with the others endemic to Central and South America. They are lowland or South American tapir (*T. terrestris*) (Photo 19.2), mountain tapir (Andes of Colombia and Mexico: *T. pinchaque*) (Photo 19.3), and Baird's tapir (Mexico, Central and northern South America: *T. bairdii*) (Photo 19.4). A fourth South American species was described in the *Journal of Mammalogy* in 2013 as the "Kabomani tapir" (Cozzuol *et al.*, 2013), but a 2014 paper in the same journal showed that the scant evidence does not justify naming a new species (Voss *et al.*, 2014) and Ruiz-García *et al.* (2016) concurred; the issue remains controversial (Cozzuol *et al.*, 2014). The lowland tapir (Photo 19.2) can exceed 320 kg, Baird's tapir 400 kg and mountain tapir 250 kg. The putative Kabomani tapir, if it exists, only reaches about 110 kg.



Photo (19.2). (2 photos) Lowland tapirs, *Tapirus terrestris*: left, Complejo Ecologico Municipal, Presidencia Roque Sáenz Peña, Chaco, Argentina; right, the Buenos Aires Zoo. LEH © photo.



Photo (19.3). Mountain tapir, *Tapirus pinchaque*, near Putumayo in Colombia. JMH © photo.

Experts have long agreed that tapirs (superfamily Tapiroidea) arose in the Holarctic (oldest fossils are in Europe) in the Eocene (~55 MYA) before spreading to North America and then to South America during the Great Biotic Interchange. Fossil *T. webbi* was the North American species whose descendants are thought to have formed the South American clade. Recent morphological data

CHAPTER 20**Carnivores****INTRODUCTION**

Except for the coati and skunk families discussed in Part 4, there were no carnivores in South America—that is, no members of the order Carnivora (there was plenty of bird and marsupial meat eaters)—until the Great Biotic Interchange in the late Pliocene-Pleistocene. Then, carnivores from North America invaded South America across the Isthmus of Panama and lived there long enough to form uniquely South American endemic forms. Only six terrestrial families of Carnivora ever reached South America: procyonids (raccoons and coatis) arrived during the late Miocene > 7 MYA and mephitids (skunks) in the Pliocene, while canids (dogs), mustelids (weasels), ursids (bears) and felids (cats), including the iconic Jaguar, only in the last 3.5 million years or so. Eizirik (2012) illustrated the genetic branching pattern of South American Carnivora and the timing of their presumed immigration from the north (Fig. 20.1).

RACCOONS

The superfamily Musteloidea evolved in Asia about 31 MYA, where it diverged into four major families: skunks, raccoons, the red pandas (Ailuridae: two species¹), and the Mustelidae. Members of these families entered North America at various times, probably over the Beringia land bridge.

Procyonidae, the raccoon family, entered South America in two waves: during the Pliocene as discussed in Part 4, and during the Great Biotic Interchange. *Cyonasua*, which entered South America in the late Miocene, 8–7 MYA, and its descendants, are thought to have gone extinct before the second wave of procyonids immigrated in the late Pliocene, 3–2 MYA—after the Isthmus of Panama closed. In this second wave there were the ancestors of most extant South American procyonids, but possibly not all of them. The Kinkajou's (Poto's) ancestors, for example, may have entered South America contemporaneously with *Cyonasua*'s ancestors (Shostell & Ruiz-Garcia, 2012; Soibelzon & Prevosti, 2012).

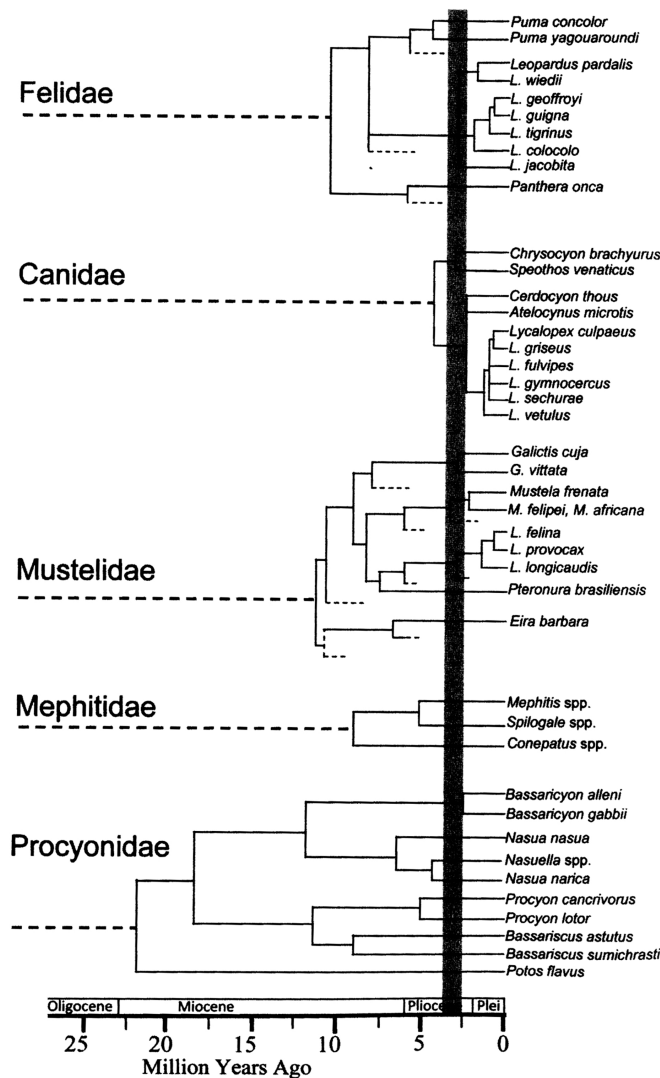


Fig. (20.1). Cladogram and timing of Carnivora radiation and entry into South America. Eizirik 2012. New World weasels and mink are shown as genus “M.” for their former name, *Mustela*. Used with permission.

MUSTELIDS

The Mustelidae include weasels, martens, badgers, ferret-badgers, otters, sea otters, mink and others. Marten and weasel ancestors entered North America from Asia at different times in the Middle-Late Miocene (15–10 MYA) (Sato *et al.*, 2012) and only entered South America as an advance guard in the Great Biotic Exchange. South America has 11 “native” (*i.e.*, arrived after the Isthmus of Panama closed) mustelids but before modern times, plus the introduced American

mink, *Neogale* [formerly *Mustela and Neovison*] *vison*. Of the native species, six (54%) are ranked in IUCN risk categories as Least Concern (lesser grison *G. cuja*, greater grison *G. vittata*, Patagonian weasel *Lyncodon patagonicus*, tayra *Eira barbara*, Amazon weasel *N. africana*, and long-tailed weasel *N. frenata*); one (9%) as Near Threatened (Neotropical otter *L. longicaudis*); and one (9%) as Vulnerable (*N. felipei*). The remaining three (28%) are Endangered (giant otter *P. brasiliensis*, marine otter *L. felina*, and southern river otter *L. provocax*). Most have suffered range declines in the last 30 years (Schiaffini, 2022).

Tyra

The tyra, *Eira barbara* (Photo 20.1), is a member of the subfamily Guloninae (martens, wolverine, fisher and tayra). Its closest relatives are the American badger and the African honey-badger (Sato *et al.*, 2012); and fossils of its close relative, *Eirictis pachygnatha*, dated to the Pliocene between 4.5 and 5.3 MYA, were found in Asia (Li *et al.*, 2014). The timing of tayra's split from wolverine and martens, about 7.5 MYA (Derežanin *et al.*, 2022) suggests the possible arrival in South America before the Great Biotic Interchange, although mustelids are generally thought to have arrived after the closure of the Bolivar Strait.



Photo (20.1). Tayra, *Eira Barbara*, a relative of the North American and Eurasian wolverine and martens. LEH © photo.

CHAPTER 21

Humans

INTRODUCTION

The last Primate family to arrive, well after the Great American Biotic Interchange, Humans (Hominidae) have had an amazing history in the Neotropics. Even before Jesus was born, they built the vast city of Teotihuacán in Mexico (Photo 21.1). With its temples, broad boulevards, massive pyramids and multi-level housing for an estimated 125,000 inhabitants, at the time it was the sixth-largest city in the world.



Photo (21.1). Mexican city of Teotihuacán, built around the time of Christ. LEH © photo 1980

AMERICAN CIVILIZATIONS

Teotihuacanos traded, competed and may have fought with other advanced cultures, such as the Zapotecs, who founded their capital city, Monte Albán (Photo 21.2), about 500 BCE. Zapotecas dominated the Oaxacan highlands and interacted with other Mesoamerican regional states, such as the Maya (Photo 21.4), who began building cities about 750 BCE. But these were new civi-

zations, succeeding the Olmecs, whose culture had emerged about 1,600–1,500 BCE, in coastal Veracruz, Mexico.



Photo (21.2). Monte Albán in 100 BCE–CE 200 had a population of about 17,200, making it one of the largest Mesoamerican cities at the time. LEH © photo, 2005.

Teotihuacán was so ancient that the Aztecs, living in the gilded temples of Tenochtitlán when the Spanish arrived, did not know who built it. The Wari, Tiwanacu, Incas and others in south-western South America were contemporary, but they were far in the future when the Chiripa culture built a city and made beautiful ceramics during 1,400–850 BCE at Lake Titicaca. They, too, were far in the future when ancient Peruvians were building irrigation canals at least 5,400 years ago.

Americans domesticated innumerable varieties of beans, squashes, peppers (and pepper, capsicum), avocado corn, tomatos, chocolate, vanilla, pinapples, papaya, sunflower seeds, cassava, tobacco, quinoa and potatos that today are used as staple foods throughout the world. They domesticated cotton (Photo 21.3), turkeys, llamas, alpacas, guinea pigs and chinchillas. They densely settled the Amazon Basin by learning to amend the soil for agriculture over generations. Some of their civilizations led the world in astronomy and all made later people amazed at their art, architecture and writing systems (Photo 21.5). Outside of cities, they learned the technologies needed to survive and prosper in tropical jungles, savannahs, and high mountains (Photo 21.9, Photo 21.10).



Photo (21.3). Cotton, *Gossypium hirsutum*, grown by local people of Maya descent on Cozumel Island, Mexico, to make textiles. Photo by LEH, 1980.



Photo (21.4). The main temple complex at Toniná, a Mayan city in Chiapas highlands that flourished from about AD 200 to AD 909. It has the last known Long Count date on any Maya monument, marking the end of the Classic Maya period in AD 909. LEH © photo, 2005.

Part 6 – Conclusion

From my first forays into South America in 2005, when I saw New World monkeys and caviomorph rodents for the first time, I was wondering: where did all these species come from? And the reverse question: why are there sloths, anteaters, armadillos and hoatzins here with no relatives anywhere on Earth? My wonderment only deepened the following year when I was fortunate to have a project in Chile that went on for some years, and I took the opportunity to do some bird-watching and mammal-watching in remote corners of the country. As a naturalist, I was thrilled to see hundreds of species representing deep lineages completely unrelated to anything familiar to me from North America: sigmodontine rodents, armadillos, two kinds of camelids, tinamous, rheas, flamingos, and on and on. Many had relatives in Africa, North America or Australia, but having a rudimentary knowledge of plate tectonics, the mystery of all these disjunct distributions only deepened.

There was another sort of disjunct distribution that caught my attention. There are a few genera of birds, mammals and reptiles, each with only a handful of species, that are scattered all over the globe with seemingly no rhyme or reason. Painted snipes are an example: three species in their own family with one species each in Africa-Asia, Australia and South America. Jacanas, another waterbird, has just eight species, again in their own family, but deeper divisions: two genera in Africa/Madagascar, three in South-/Southeast Asia and one (with two species) in Central/South America. And there was yet a third odd distribution, repeated just often enough to postulate a pattern: two genera of otherwise South American endemic partridges occur in Africa: they are formally classified in the family of New World quail and are the only members of this family outside of the Western Hemisphere. Similarly for two genera of parrots in Africa that are members of an otherwise endemic Neotropical subfamily. Finally, there is a quail dove in Cuba whose only relatives are quail partridges in Australia. All of these evolved too recently to have used an Antarctic-Australasian or a Beringian dispersal route, besides which there are no fossils or scattering of related species connecting these disparate distributions. How did they get there?

I naïvely thought that I could just look them up. Surely, the scientists that study these things would know. Sure enough, some were already known: I merely had to

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read about them. For example, the camelids' and tapirs' histories were well-known to specialists: both evolved in North America before diverging lineages spread to South America and Asia, thence to Africa, followed by extinction in North America.

I began thinking about these mysteries about the same time as the DNA revolution exploded in a plethora of publications clarifying lineage relationships that have been intractable for centuries. Genetic methods to estimate divergence time, calibrated with old and new fossils, refined dates of when many taxa split, enabling inference of origins. Results are highlighted throughout this book.

How species, especially non-volant (non-flying) ones, could have spread from continent to continent has been informed—no, enlightened is a better word—by these advances in scientific enquiry. We are now in a position to answer questions first posed by Charles Darwin that have bedevilled scientists and natural historians for a century and a half: where did their ancestors come from? How did they get there?

For South America, with the most diverse and unique biota of all continents, these questions are both pressing and profound: pressing because conservation often depends on understanding the uniqueness and evolutionary relationships; profound because such questions cannot fail to demand our curiosity and inspire scientific discovery.

The ancestors of some uniquely South American animals were in South America when it split from Africa: marsupials, xenarthrans, and at least three of the five (or more) orders of “South American ungulates.” Two of these (notoungulates and litopterns) appear to share a distant lineage with horses and tapirs whose ancestors crossed the Caribbean around 66 MYA. Others originated in the post-Gondwana Australasia-New Zealand-Antarctica-South America land mass way back in the Eocene and stayed in South America after the Drake Passage opened and later when Antarctica finally froze. Yet others originated in Australasia later, in the Oligocene, and immigrated as Antarctica was cooling but had not yet frozen.

The most astonishing immigrations were across the Atlantic Ocean from Africa to South America: Everyone knows that ancestors of caviomorph rodents and New World monkeys made this crossing, but one has to delve deep to discover the variety of other animals that also did. Some birds and lizards and turtles came way back in the Eocene (Table 1). Islands and lowlands exposed by lowered sea levels, volcanism, and tectonic movements no doubt helped these taxa cross the Atlantic,

which was nearer then. But many animals, especially birds, lizards and tortoises made this crossing during the Oligocene and Miocene when sea levels were higher, temperatures cooler and only a few small islands remained above water in the vast stretch of the Atlantic Ocean. Likewise, some birds and a marsupial came from Australia or other parts of Australasia, after it had split from Antarctica, which was then covered by ice.

Table 1. Taxa of "exotic" vertebrates that immigrated *via* transatlantic crossing and estimated dates of their arrival or split from African taxa.

Taxon	Origin	Now Endemic	When? (MYA)*	Chapter-page
Primates	Africa	South America	36	15-343
Caviomorph rodents	Africa	South America	41	15-325
Patagonian weasel and Grison (Lyncodontini: Mustelidae)¹	Africa	South America	2.8	20-394
Amazonian manatee	Africa	South America	4	15-324
Hoatzin	Africa	South America	38	14-268
Trogon	Africa	South America	32	14-273
Potoos and oilbird lineage	Europe	South America	40	14-225
2 genera of Neotropical parrots (Arini)	South America	Africa	49	14-276
Flamingo (2 genera)	South America	Africa	1-4	14-292
2 genera of partridge	South America	Africa	37	14-283
Turkeys¹	Africa	North America	27	14-284

(Table 1) cont....

<i>Donacobius</i>	Africa?	South America	?	14-295
Hummingbirds	Europe?	South America	22	14-270
Mimid (thrashers & mockingbirds) ancestor	Europe or Africa	Caribbean	34	14-294
Toucans and Barbets	Africa	South America	13	14-280
Taxon	Origin	Now endemic	When? (MYA)*	Chapter-page
Thecadactylus gekkos (Phyllodactylidae)	Africa	South America	67	3-225
Aristeliger gekkos (Sphaerodactylidae)	Africa	South America	40	3-225
Thecadactylus gekkos (Phyllodactylidae)	Africa	South America	72	3-225
Tarentola gekkos (Phyllodactylidae)	Africa	South America	12	3-225
2 species of Hemidactylus gekkos (Gekkonidae)	Africa	South America	15	3-225
Mabuya maculata, a skink	Africa	South America	15	9-141
Geochelone and Cheloniodis tortoises	Africa?	South America	26	13-228
Puentemys mushaisaensis, a bothremydid turtle	Europe?	South America	66	9-135
Pitcairnia feliciano, a pebble toad	South America	Africa	12	7-64, 8-124

(Table 1) cont....

Dyrosaurid crocodiles	South America	Africa	66	
Ancestor of all 4 New World Crocodylus species	Africa	South America	4	9-137

* Mid-range of estimates.

MYSTERIES REMAIN

Yet many mysteries remain, among them:

- Did the ostrich and rhea split in South America and the ostrich crossed the Atlantic to Africa, or *vice versa*?
- How did the elephant bird, a “ratite” like the ostrich and a relative of the kiwis of New Zealand, get to Madagascar, off the coast of Africa?
- Where did the Cracidae—guans, curassows and chachalacas—originate? The family is endemic to South America. Their earliest known fossils are in North America, but its sister relationship with Megapodidae of Australasia belies the inference that the family originated in North America. If they originated in Australasia, how did they get to North America other than *via* South America?
- Studies of ancient, fossilized proteins and DNA suggested that two of the unique orders of endemic “ungulates,” Notoungulata and Macrauchenia, may be related to Perissodactyla (horses and allies) but a later study based on morphological analysis of most Eutheria showed notoungulates forming a monophyletic clade with Pyrotheria, Astrapotheria and xenungulata. More is yet to be written.
- Besides the “ungulates”, the origins of several other ancient lineages of mammals are unknown: scholars theorize, with scant evidence, that they may have come from Laurasia (probably meaning a sea crossing) or Australasia or Africa, but no one knows.

The Patagonian weasel *Lyncodon* and the grison, *Galictis*, members of a mustelid tribe (Lyncodontini), split from Old World (mostly African) relatives in the tribe Ictonychini, with no living species in between. How did they get there?

That fact that so many unique animals excite our interest in South American biodiversity should not mitigate our sadness that many have gone extinct. After the Great Biotic Interchange, during the Pleistocene and early Holocene—perhaps because of it—many taxa went extinct. Lessa and Fariña (1996:657) showed that:

“22% of genera present in the Early Pleistocene (*i.e.*, the Marplatan Land Mammal Age) are not found in the Ensenadan, the following Land Mammal Age, and 7% of the Ensenadan genera are not found in the Lujanian. The percentage of the extinct Lujanian genera is 40%, which qualifies for a mass extinction”.

Many authors writing about this assumed that the extinctions were caused by competitive displacement, competition or predation by the incoming North American taxa but this notion was overturned by more recent analyses. Sparassodont carnivores, for example, went extinct in the Pliocene, well before the Great Biotic Interchange (Goin *et al.*, 2007; Prevosti *et al.*, 2013). The probability of extinction was correlated with body size, but not with lineage or niche specialization (Lessa & Fariña, 1996), suggesting that other factors were involved.

There were major oscillations in climate during the Pleistocene. Humans arrived at the end of that epoch to begin the Holocene and are known to have hunted some of the megafauna (*e.g.*, López M. *et al.*, 2008), but that was too late to explain many of the extinctions.

DIVERSITY CONTINUES TO INCREASE

The good news is that, more so than any other place on Earth, new species are still being discovered. In the five years prior to 2006, astonishing 465 new freshwater fish species were described, a rate of a new species every four days (Abell *et al.*, 2008). During 2016, new rodent and marsupial species were described. Many deer, camelid, primate and bird species and even genera have been split to increase known biodiversity of South America. Besides solving the remaining mysteries, we can look forward to the new fossil discoveries and the scientific tools of analysis to reveal yet more of South America's fascinating biological diversity.

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REFERENCES

- Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J.V., Heibel, T.J., Wikramanayake, E., Olson, D., López, H.L., Reis, R.E., Lundberg, J.G., Sabaj Pérez, M.H., Petry, P. (2008). Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *Bioscience*, 58(5), 403-414.
[<http://dx.doi.org/10.1641/B580507>]
- Goin, F., Abello, A., Bellosi, E. (2007). Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno Temprano, Edad-mamífero Colhuehuapense). Parte I: Introducción, Didelphimorphia y Sparassodonta. *Ameghiniana*, 44(1), 29-71. [in Spanish; English abstract].
- Lessa, E.P., Fariña, R.A. (1996). Reassessment of extinction patterns among the late Pleistocene mammals of South America. *Palaentology*, 39(3), 651-662.
- López M.P., Cartajena F.I., García P.C., Vega L.J., Arévalo N.I. Paleoenvironments: Vertebrates and Invertebrates. College Station, Texas: Center for the Study of the First Americans. Current Research in the Pleistocene. Goebel T., editor. 25. 2008. pp. 182.-184..
- Prevosti, F.J., Forasiepi, A., Zimicz, N. (2013). The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? *J. Mamm. Evol*, 20(1), 3-21. [<http://dx.doi.org/10.1007/s10914-011-9175-9>]

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