

Topics in Geobiology 42

Thomas Defler

History of Terrestrial Mammals in South America

How South American Mammalian Fauna Changed from the Mesozoic to Recent Times

 Springer

Topics in Geobiology

Volume 42

Series Editors

Neil H. Landman

American Museum of Natural History, New York, NY, USA

Peter J. Harries

North Carolina State University, Raleigh, NC, USA

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Neil H. Landman Department of Paleontology American Museum of Natural History New York, USA E-mail: landman@amnh.org Peter J. Harries Department of Marine, Earth and Atmospheric Sciences North Carolina State University Raleigh, USA E-mail: pjharrie@ncsu.edu

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How South American Mammalian Fauna
Changed from the Mesozoic to Recent Times



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Thomas Defler
Department of Biology
National University of Colombia, Bogota
Bogota, Colombia

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I dedicate this book to all students of neotropical mammals.

Preface

I wrote this book during a 10–15-year period of teaching a course in the evolution of South American tetrapod mammals at the Universidad Nacional de Colombia in Bogotá. While the book is primarily intended for the lay reader and the student of South American mammals, I hope that it might also be of service to many professional zoologists and paleontologists, who have been unable to keep abreast of the flood of new discoveries and yet wish to learn something of the more significant published results. How far I have succeeded in a most difficult task must be left to the judgment of such readers. I am not a paleontologist but rather a vertebrate zoologist who has specialized in modern neotropical primates. Since I have rather broad interests in vertebrate zoology and primatology, I elected to teach a course on the evolution of mammals after transferring from another campus to the Bogotá Campus, and frankly, I wanted to learn something more about this field of South American mammals. The course was well-attended throughout the years, and I dedicated myself continuously to study the literature. There is now a lot of literature! For a generalist like myself, I have acquired a broad education on the evolution of terrestrial mammals in South America, but I cannot claim to have dominated the hundreds of technical articles now available. Nevertheless, I have learned to appreciate the vast story that has resulted in the mammalian fauna of today, and I am surely an aficionado on the outline of the story of diversity that has gone before.

Who cannot be fascinated by the evolution of the multitude of species that filled South America during earlier epochs of the Cenozoic, such as the specialized carnivorous Sparassodonta metatherians and the hundreds of species of ungulates that we can now associate with the evolution of perissodactyl and artiodactyl ungulates from the northern continents? What primatologist does not thrill to the evolutionary history of the platyrrhine primates and their last African origins, lost in the veil of time and their improbable rafting from Africa to South America? As well, the rafting of tiny rodents from Africa and their evolution into giant 1000 kg semiaquatic mammals provide us with so much evolutionary color that we pine for more detail and we dream of being able to see these fascinating beasts. I thrilled when I discovered the South American platypus in the literature and the narrow peninsula that connected South America to a warmer Antarctic, all of which provided a highway for South American marsupials to Australia.

Since we can no longer see these animals, we have to rely on reconstructions. When I read GG Simpson's 1980 book on the evolution of South American mammals, I was somewhat disappointed by the poverty of illustrations in that book. At the time there were fewer artists who try to recreate prehistoric fauna, and I guess that the great paleontologist himself illustrated the book, although not too successfully, even though people like the paleoartist Charles Knight were well-known. Reading about lost, extinct fauna is one thing, but an effort to visualize the fauna is an effort that anybody wanting to learn about these animals tends to make, and my wish was to be able to illustrate these animals as richly as possible, just as the dinosaurs have been brought to life by illustrators. I was lucky to discover the Ukrainian artist Roman Uchytel on the Internet, who has specialized in using computer art to depict how these animals might have looked. Computer art fools the eye into thinking that we are viewing a photograph of the animal, and if it is well-done, we are drawn into a prehistoric world that lets us imagine how this world might have been, satisfying the basic urge of all of us to be a witness to such lost worlds. This book, then, publishes many images of Roman that illustrate the animals discussed here, although images of a few other artists also supplement the story that I tell.

Roman Uchytel was born in Ukraine of the Soviet Union and grew up near a zoo, and he spent most of his time there dreaming of becoming a zoologist and sketching animals. Eventually he graduated from art school and university with a love for nature and training as an artist. His knowledge of anatomy helps him to depict all manner of birds and beasts; although he rarely draws a dinosaur, he specializes in rarely depicted ancient mammals and birds, and with computer art he is able to place them in a natural setting that suggests a photograph of an ancient world. Roman, like myself, continues to be fascinated by animals and is dedicated to depicting the ancient ones in now lost worlds. He has considerably enriched this book. You can see more of Roman's work at his Internet site (<https://prehistoric-fauna.com>).

Bogota, Colombia

Thomas Defler

Acknowledgments

I am particularly grateful for the time and space provided to me by the Universidad Nacional de Colombia to continuously teach a course by this name and to continue preparing to manage this great and voluminous theme. I could not have managed the library research necessary without the help of Dr. Scott Raymond and the University of Calgary library services in Canada. Thank you, Scott, for being there when I needed your help and with no thought of recompense. I am very grateful to the many neotropical paleontologists and aficionados of ancient mammals who positively answered my questions and to some who made very helpful suggestions. There were many (aficionados and professionals) who, like myself, are anxious to illustrate to the best of their abilities, the prehistoric mammalian life that lived on this continent, and I thank those who allowed me to reproduce their images in this book. I hope you are satisfied with the result. I am also grateful to the many Colombian students who listened to me over the years and, as a result, learned something about our mammalian history. I am especially grateful to the careful reading of the text and the many spelling corrections made to this book by Claudia Moreno and Enrique Forrero. They have improved the text in a manner that is very important to me and to all who read it.

About the Book

During the last 10 years, as I taught a course at the Universidad Nacional de Colombia with the same title as this book, it came home to me that the information for this fascinating subject was spread out in many journals and that the only attempt to address a history of South American mammals had been G. G. Simpson's 1980 book *Splendid Isolation*, now thoroughly out of date and almost bereft of images. My Internet research had taught me that there now were many images attempting to illustrate the prehistoric fauna of South America, but nobody had attempted to use them to tell the complete story as it is known up till the present. There were hundreds of published articles available, but they were not organized into the great story that is emerging about how South American mammals became what they are today and what history had gone before, though many understand that there was a strange and beautiful mammalian fauna before the two Americas became connected and the invasion of northern fauna occurred that changed everything. What was the fauna like before the American interchange? What were the origins of the several fantastic groups that became extinct when northerners arrived and out-competed the southerners? How did the modern mammalian fauna come into being with such disparate elements as two great rodent groups with two different origins, primates (where none had lived before), strange armadillos, sloths and anteaters with little understanding of their origin, and other mammals such as felines, canines, and deer that clearly had evolutionary connections to the north?

So I set out to write the history of these South American mammals that I was dedicated to studying, hoping that others would be interested in this story as well. I have attempted to write the story on a level that might be interesting to university students and professionals working with mammals and their paleontology. Perhaps those more broadly interested in South American fauna will also want to read this book. This is not a technical book, though some basic biology and paleontology are assumed. Very important are the many illustrations used that will hopefully indicate how these animals might have looked. The major artist used is the Ukrainian Roman Uchytel, who is an expert at illustrating prehistoric mammals (www.prehistoric-fauna.com) and has made many species come alive. I attempt to tell this history in 15 chapters.

More Detailed Description

Based on my university course “Historia de los Mamíferos Terrestres de Sudamérica” and the series of lectures that I developed for this course, I have written a book outlining the evolutionary changes in the fauna of South America, beginning in the Mesozoic and ending at the present time. I have summarized a very large and disparate literature for this evolutionary history. Knowing that 35 years (after the publication of Simpson’s book) of paleontological studies in South America are found in many technical journals and books, I have organized much of this literature into a history that tells the story of the changes that South American mammals have gone through since their beginning around 165 million years of so ago.

Besides an introductory chapter and a chapter discussing the ancient pre-Cenozoic fauna, the most detailed story, of course, took place during the Cenozoic or “Age of Mammals” of the last 65 million years, since the amount of information in terms of fossils begins to accumulate. So the majority of the chapters deal with this period from Chap. 3, starting with the first mammals of the Paleocene. Then I change focus, highlighting in each chapter the major mammalian groups that have made up the South American mammals: the marsupials, the ungulates, the xenarthrans, the caviomorph rodents, and the platyrrhine primates (Chaps. 3, 4, 5, 6, 7, and 8).

Once again, I change focus to highlight some specific assemblages that illustrate certain points. The La Meseta fossils (Chap. 9) illustrate an Eocene Antarctic group of mammals, and they underline the strong connection that Antarctica had with South America, at least until the two continents became disconnected around 30 million years ago. The La Venta fauna (Chap. 10) illustrates an ecological community of a geologically short period of time ago from about 13 to 12 million years and is the richest description that we have of an ancient ecology. I include a complete chapter on the neotropical mammals that invaded the Caribbean Islands (Chap. 11). The story of the formation of the Amazon River (Chap. 12) is important, inasmuch as it was obviously the center of evolution for so many mammals, although we do not as yet have the richness of information that exists from Patagonia (Chaps. 9, 10, and 11).

Concluding the history, I describe the inter-American interchange of mammalian fauna and how South America changed due to the mammalian invasions from the north. Now we appreciate that these invasions did not occur only during three to four million years after a final land connection of the Americas became complete but in fact the invasions began as early as 9 or 10 million years ago when the first gomphotheres, tapirs, camels, peccaries, and raccoons managed to arrive, probably swimming, to South America. The story gets very interesting, since the real dispersal abilities of mammals come to the fore as well as a new understanding about the formation of the Central American gap.

A penultimate chapter describes the Pleistocene fauna and the megafauna that populated South America briefly before it became extinct. Within this context of course is included a consideration of what role newly arrived human beings might have played in this great “dying off.” The book ends with a brief consideration of the modern mammalian neotropical fauna.

Chapter Outline

The book, as written, comprises 15 chapters of which titles follow below with short chapter descriptions.

Chapter 1: Introduction

Chapter 1 includes brief descriptions of the roles played by various early collectors and describers of ancient bones. It also briefly describes the tools that are necessary to interpret the evolutionary history of South American mammals including the problem of calculating geological time, stratification, radiometric dating, paleomagnetism, the establishment of SALMAs (South American Land Mammal Ages), the geological time scale (and table), plate tectonics and the distribution of fauna, the role of Alfred Wegener, continental drift, and molecular phylogenetic research.

Chapter 2: Ancient Mammals of Gondwanan South America

Chapter 2 includes a description of what is known of South American mammals from the Mesozoic Era, which begins (according to present information) in late Jurassic around 168–161 million years ago and comprises australosphenid mammals (relatives of the platypus) and also the now extinct triconodont mammals. The description then moves through the early Cretaceous with increasing numbers of fossils available. This fauna was dominated in South America by dryolestid mammals, which were closely related to modern placental mammals. During these times, there are a couple spectacular fossils known, like *Vincelestes neuquenianus* and *Cronopio dentiacutus*, both of which are illustrated.

Chapter 3: Early Cenozoic Mammals in South America

Chapter 3 includes a description of the earliest (Paleocene) mammalian assemblages known for the South American Cenozoic. These include complete discussions of the Tiupampan, Peligran, Itaboraian, and Riochican South American Land Mammal Age (SALMA), and the Riochican overlapping into the Eocene. These assemblages are very instructive, as they contain the most ancient groups, the marsupials, and native ungulates. These apparently arrived in South America from North America, perhaps in the latter part of the Cretaceous before the beginning of the Cenozoic. These faunas also contain other elements from North America and from the ancient Mesozoic mammalian fauna, which then become

extinct in South America. Several subgroups of marsupials and ungulates make their first appearance, as well as the first xenarthrans. A South American platypus demonstrates the ancient connection of South America to Australia, via Antarctica.

Chapter 4: Marsupials and Other Metatheres of South America

Marsupials and other metatherians apparently arrived in South America before the beginning of the Paleogene, at the end of the Cretaceous. The earliest relatives of Australian marsupials, the Microbiotheria, appear in the earliest assemblage. The carnivorous Sparassodonta evolve and produce the largest marsupial predator known, the 600 kg *Proborhyaena gigantea*, as well as the jaguar-sized saber-toothed marsupial *Thylacosmilus*. Many of these poorly known marsupial predators are well-illustrated by Roman Uchytel.

Chapter 5: The Native Ungulates of South America

The ancient, native ungulates were another fascinating group, which sadly has become totally extinct, but which we now understand were related to the northern Perissodactyla or odd-toed ungulates. These animals apparently evolved from northern condylarths (primitive ungulates) that somehow made it to South America. Evolution produced five orders of quite bizarre ungulates, some more like rodents than like ungulates, but others, toward the end of the Neogene in the Pleistocene, had become large, rhinoceros-like *Toxodon* and camel-like *Macrauchenia*. Although there is much to learn about the many species of South American meridiungulates (native ungulates), many forms are known. Some of the latest forms are known to have been hunted by early humans, who finally arrived in South America. This chapter is well-illustrated especially by images of Roman Uchytel.

Chapter 6: The Xenarthrans: Armadillos, Glyptodonts, Anteaters, and Sloths

From the time that the first xenarthrans appeared as early armadillos in the late Paleocene Itaborai, the group diversified into strange and wonderful forms. Besides the Dasypodidae, a group called the Glyptodontidae arose and diversified; some were the size (and shape) of a Volkswagen bug and were harmless grazers and were very common on the grassy savannas of South America. Also, the sloth lineage appeared with the last species reaching the greatest size of any southern mammal. *Megatherium americanum* one of the largest mammals known, equivalent to an

elephant. Finally a short history of the little-known anteaters is given. A discussion of the possible origins of the Xenarthra is suggested, and the group is presented as one of the most ancient lineages of modern mammals.

Chapter 7: The Caviomorphs: First South American Rodents

The first rodents did not arrive in South America until the mid-Eocene, at about 41 million years ago. This recent discovery makes the history of the caviomorphs extremely interesting, since the earliest known rodents are now known to be from tropical forest and not from dry, savanna-like habitats as previously believed. The group is ancient and is clearly related to the African phiomorph rodents. In this chapter and in Chap. 8, I enjoy describing the probable mode of dispersion of caviomorphs and primates from Africa to South America, since so many have difficulties accepting rafting over the Atlantic Ocean. The history of caviomorphs in South America also includes giant species that appeared during the latter part of the Neogene, culminating in the 1000 kg *Josephoartigasia* of the Río de la Plata (River Plate). This chapter also has some original illustrations by Roman Uchytel and by others.

Chapter 8: The Platyrrhine Monkeys

This chapter presents the partial evolutionary history known of the platyrrhine primates through their known fossils. Recently new evidence for the earliest known primates comes to us from Peru, so that we now have tropical evidence of *Perupithecus* and others, superceding the many higher latitude primates known from the southern cone. The previous earliest known primates (*Branisella*, *Szalatavus*) are known also from a totally different habitat and 20 million years later. Here again new evidence proves the important role of tropical forest in the evolution of South American primates. Additionally the newly discovered Eocene primates have similarities to early African fossils. Again, in this chapter, I describe how primates might have (and probably did) arrived in South America and just what the conditions would have had to be for the success of such a precarious voyage.

Chapter 9: An Antarctic Eocene Mammalian Community

This short chapter describes an Antarctic mammalian community and illustrates the faunal connection that existed between Antarctic and South America, since all of these ancient Eocene Antarctic mammals had living relatives in South America. The

community existed during the early-middle to late Eocene when the earth was very warm, the warmest of the entire Cenozoic. But since marsupials dispersed from South America to Australia in the early Paleocene, it is obvious that Antarctica was covered by forest until the arrival of global plunging temperatures at the end of the Eocene and early Oligocene. Many plants that have been identified from the Antarctic Peninsula are commonly seen on the southern tip of South America even today.

Chapter 10: La Venta: A Miocene Colombian Mammalian Community

The chapter describes the well-known Colombian La Venta fauna. This is the most detailed tropical faunal assemblage known for South America. Although it is located on the upper Magdalena River, at the time that it existed, it was peripheral to the great Amazonian wetlands to the east: unlike today, there was no Eastern Cordillera barrier. This fauna is represented by about 72 species of mammals from the richest deposits (the Monkey Beds) dated from about 11.8 to 13.5 million years ago, so it really represents a tropical community from a very narrow time window. The La Venta habitat was an open riparian-savanna with gallery forests, so mammals from several different conditions illustrate forest and savanna mammals. Compared to previous chapters, this is a fairly modern fauna, yet no elements of the north are yet to be found, and the mix is rather different than that found in the high latitudes further south. It is notable that many species and genera of mammals from La Venta have also been found in tropical central Peru, suggesting that a band of similar habitat west of the Amazonian wetlands was continuous from northern Colombia to southern Peru for that period.

Chapter 11: Mammalian Invasion of the Caribbean Islands

Chapter 11 describes the South American fauna that populated the Caribbean Islands and how this fauna might have arrived. Fossils tell us a story that, because of recent extinctions, probably was at least in part caused by human arrival. Particularly interesting to me are the data about primates that lived on the Caribbean Islands, several species of which lasted until the last few hundred years. All of these primates seem to have descended from one group of South America which arrived as far north as Cuba.

Chapter 12: The Genesis of the Modern Amazon River Basin and Its Role in Mammalian Evolution

This chapter discusses the origin of the Amazon basin and its role in mammalian evolution. Information is still sparse, due to taphonomic difficulties in a moist tropical, acid environment, but lately especially new finds of earliest rodent and primate fossils have added to our knowledge of how the tropical regions have played a large role in South American mammalian evolution. The process by which the great river was originally established is also a theme discussed, and what the conditions must have been to allow invading mammals from the north to arrive to the southernmost parts of the continent is considered.

Chapter 13: The Great American Biotic Interchange

This is the story of the revolutionary changes to South American mammals that occurred when it became possible for mammals from North America to pass to South America. This probably began as early as 8–10 million years ago when a proboscoid, camelid, tayasuid, tapirid, and procyonid arrived in South America. Later at about three million years ago, the invasion became a flood when (apparently) the terrestrial connection between the two continents became complete. Of course some South American fauna went north, as well, including the terrestrial sloths and the glyptodonts, but they became extinct after modest success. Other southern elements persist yet in Central America, including primates and caviomorph rodents.

Chapter 14: Pleistocene Mammal Communities and Their Extinction

During the Pleistocene, the diversity of mammals in South America became extremely elevated. It seems that hyperdiversity reached the highest-known in the world, and there has been nowhere else where the 37 megamammals (weighing up to 1000 kg) were to be found until they all became extinct, the last just 8000–9000 years ago. Of course ecological factors played a huge role in leveling this out-of-balance fauna, but the intriguing question has always been about the role that human beings had to help these mammals to extinction.

Chapter 15: The Modern Mammals of South America

This short chapter discusses the modern mammalian fauna in South America and shows the comparative balance of mammal orders. The rodents make up well over half of the entire terrestrial mammalian biota (without counting the bats). The total terrestrial mammalian fauna numbers about 1500 species, and South America is the most diverse continent in the world. Despite the extensive Pleistocene extinctions, the fauna is amazing in its diversity. Many illustrations are provided for each group.

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