Early Miocene Paleobiology in Patagonia. High-Latitude Paleocommunities of the Santa Cruz Formation

Sergio F. Vizcaino, Richard F. Kay, and M. Susana Bargo (eds.)

Cambridge, UK: Cambridge University Press, 2012, 370 pp. (hardback), $155.00.
ISBN-13: 9780521194617.

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This edited volume deals with new fossil flora and fauna from the Atlantic Coast of Patagonia, South America, dating to 18–16 mya. Two of the editors are affiliated with the Museo de la Plata, Argentina, and a plethora of Argentine colleagues contribute chapters and reviewed preliminary drafts. The volume thus has a spectacularly international authorship. Abstracts of each chapter appear in both English and Spanish.

In contrast to the cold and dismal climate of modern Patagonia, Patagonia 18–16 mya was much warmer and humid, with mixed forests and grasslands. The Andes Mountains were much lower in elevation, which allowed an eastward expansion of habitats now found today on the lower slopes of the Andes. Because South America was an island continent for most of the Tertiary, a unique array of animals are found here—representatives of extinct mammal orders that independently evolve horse-like, tapir-like, sheep, cattle, and rabbit-like specializations. Caviomorph rodents as large as rhinos, giant ground sloths, glyptodonts, and flightless terror birds roamed the land. The mammalian carnivores were all marsupials, independently evolving cat-like and saber tooth specializations. Monkeys that are now found only in the rainforests of Amazonia are found here, as well. The Santa Cruz Formation of coastal Patagonia has been renowned for its wealth of fossils since the end of the nineteenth century. During his *Beagle* voyage in the 1830s, Darwin himself became aware of fossil mammal bones from this area when a gaucho led him to the remains of monsters "created by the devil." Darwin was able to note the anatomical similarity of giant ground sloths and giant armadillo-like glyptodonts to living edentates. By collecting and handling these bones, Darwin therefore intimately understood that strange extinct species could have morphological connections to living species—a fundamental insight about the existence of evolution. He also wondered what these giant animals were eating, given that the modern vegetation of Patagonia is so sparse, and thus he came to appreciate the reality of major environmental change through time.

This book reports on over 1,600 new fossils collected during the summer field seasons of 2003–2012. Many represent new species and genera described here for the first time. However, fossil material collected from the late nineteenth and throughout the twentieth centuries also was examined. Many chapters end in appendices that list all of the fossil specimens that were inspected during the writing of these chapters. These appendices list museum catalog numbers, along with collection area and short descriptions. This volume therefore is a crucial resource for researchers studying mammal evolution, especially for those studying processes like convergent evolution. New black-and-white illustrations reconstruct details of life on the ancient landscapes.

The collection of the fossils is an epic in itself. Because fossils were embedded in sandstone beach rock in the intertidal zone, retrieval of these specimens often entailed hastily using both geological hammers and jack hammers to remove blocks of sediment before the tide turned, and cold Atlantic seawater again swept over the collecting area. Figures 1.7 and 3.3A present an array of photographs documenting the joys of fossil collection at low tide. Teams averaging eight individuals ranged along a 50km stretch of the Atlantic Coast, collecting all identifiable specimens in an unbiased fashion, regardless of their size or taxonomic affiliation. In spite of these conditions, many skulls and articulated skeletons were found, and the area yields the richest abundance of mammal fossils in all South America. The cover illustration shows a color photograph of a long expanse of the fossil-bearing sediments exposed at low tide.

The editors begin with a chapter detailing the history of paleontological work in coastal Patagonia. This includes an analysis of climate change since the Early Miocene and the age of the Santa Cruz fauna. The editors give a summary of fossil localities known since the nineteenth century, along with provisos that strong ocean erosion makes it difficult to guarantee that specimens found 100 years ago come from the same beach rocks sampled today. Fossil trackways observed over 100 years ago have been obliterated, but new vertebrate footprints have again been discovered. An appendix of Santa Cruz localities mentioned in the volume, along with their geographic coordinates, ends the chapter.

The following two chapters summarize the geochronology of the Santa Cruz and Pinturas Formations, using new radiometric dates and tephrostratigraphy to establish the absolute and relative dates of the fossil localities. While the Santa Cruz Formation dates to 18–16 mya along the Atlantic coastal plain, it extends between 19–14 mya in the foothills of the Andes. The lower part of the Santa Cruz Formation overlaps the Pinturas Formation. A chapter on sedimentology and paleoenvironment is next, followed by chapters on oysters, trace fossils in distal over bank deposits, fossil plants, amphibians, lizards, and snakes, and birds. Despite

  ISSN 1545-0031
doi:10.4207/PA.2013.REV138

their high latitude, these Patagonian localities were warm and humid during the Early Miocene. The warm and seasonal climate began to cool, and became increasingly more arid in the Middle Miocene. Trace fossils allow paleosols to be reconstructed, and these paleosols document a general shift from humid to drier conditions. Plant fossils range from phytoliths to carbonized wood and leaf impressions. These show a mosaic of open, temperate, semiarid forests and warm, temperate, humid forests. Seasonally restricted rainfall limited plant growth. Flightless, cursorial giant terror birds (phorusrhacids) were among the top predators, along with marsupial carnivores.

Non-carnivorous marsupials have a wide range of body sizes and diets. The smallest species were insectivores, medium-sized species were insectivore/frugivores, and the largest species were frugivores. These included a myriad of microbiotherians, relatives of the endemic "monito del monte" ("little mountain monkey" [*Dromiciops gliroides*]) with only a single living species, and paucituberculates, relatives of the living caenolestids or shrew opossums. Living species in these two orders are very small arboreal insectivores. Fossil taxa in these two orders are often much larger in body mass than their living representatives. The largest of the extinct taxa were frugivorous, and all of these marsupials inhabited warm, forested habitats with pronounced seasonal rainfall.

The orders Microbiotheria and Paucituberculata have an importance far beyond their current relict status. Microbiotherians were the marsupials that originally colonized Australia, traveling from South America via Antarctica, which was then fixed to South America and formed a land corridor into Australia. These arboreal marsupials also occupy niches and exploit resources that would otherwise be tapped by small South American monkeys (cf. "monito del monte"). Competition with primates would be magnified in the Miocene, when larger arboreal marsupials overlapped the size range of marmosets and tamarins and entered the size range of owl, titi, and squirrel monkeys. The living "monito del monte" engages in deep torpor or hibernation during the temperate zone winter, and is the only living South American marsupial to exhibit this behavior. This might illuminate how small bodied mammals in high-latitude Patagonia were able to survive pronounced seasonality—just as living fat-tailed lemurs also hibernate during the Malagasy dry season. The climate of late Early Miocene Patagonia becomes increasingly drier through the Santa Cruz Formation, so that both seasonal darkness and drought would have been problems for contemporary mammals.

The diverse marsupial carnivores are reviewed in a separate chapter. They evolve in island South America from the Paleocene through the Middle Pliocene, but reach their apogee during the Santacrucian Land Mammal Age. Eleven species are described here. They range in size from 1kg to over 50kg. All are hyper-carnivorous, and demonstrate a variety of locomotor modes. Some were agile arboreal climbers, and some were cursorial and terrestrial. Geometric morphometrics were used to reconstruct locomotion. The larger marsupial carnivores, which weighed over 100kg, are missing, as are the saber-toothed carnivores, but bone-crushing scavengers are present. Note that the arboreal carnivores are occupying niches that would be filled by felids, mustelids, or viverrids elsewhere in the world. These marsupials would also be potential predators for sympatric primate species.

Two chapters separately target the paleobiology of fossil armadillos and glyptodonts and sloths and anteaters. These diverse species, which later crossed the Central American Land Bridge into North America, are endemic to South America. Abundant arboreal sloths might have competed with folivorous primates, such as howler monkeys. Arboreal anteaters exploited social insects, and therefore were not in competition with insectivorous primates, such as squirrel or owl monkeys. Social insects would need to have been available throughout the year, and this indicates that subtropical and warm temperate environments existed in Patagonia during Santacrucian times. The diversity of armadillos and glyptodonts could only be supported by the presence of bushland or dry forests. Seven families of Santacrucian ungulates that are members of endemic groups (Orders Notoungulata, Litopterna, and Astrapotheria) are discussed in a long chapter that attempts to elucidate diet and locomotion. This chapter reveals a startling degree of convergent evolution to artiodactyls and perissodactyls found on other continents. Relatively complete dentitions, skulls, articulated specimens, and limb indices demonstrate that tapir-like, camel-like, and horse-like morphotypes existed. Examination of both new and old material allows intensive study of body size differences. Figure 14.17 contrasts body mass and shape in these fossil species with living ungulates. A broad array of body sizes existed in the Santacrucian mammals, ranging from 1.5kg to 1,300kg. This is an entirely novel Lost World, with unique species evolving ungulate specializations. Caviomorph rodents, such as the modern porcupines, agoutis, guinea pigs, and capybaras, experience a great radiation in South America, beginning in the Oligocene. A chapter on caviomorph rodents deals with diet and locomotion, as revealed by functional morphology. Many of these species are large and highly terrestrial.

Readers of this journal will probably be most interested in the chapter on platyrrhine primates, which have been collected from this area for over 120 years. All of the fossils come from the genus *Homunculus*. As indicated by the genus name ("little human"), the famous Argentine paleontologist Florentino Ameghino argued in 1891 that this genus was the first hominin. He thought that *Homunculus* was Eocene in age, and not only indicated that hominins had first evolved in Argentina, but also that hominins had diverged at an early date from all other primates, and thereafter followed a separate evolutionary trajectory. This effectively removes other hominoids from human ancestry, and derives genus *Homo* from small, arboreal, small-jawed, large-eyed "little humans" of the Eocene. The Eocene was considered the first epoch of the Cenozoic, since the Paleocene was not then recognized as a geological unit.

Ameghino's idea about human evolution now appears very strange. However, it dates to a time when hypotheses could battle on an equal footing with poor fossil evidence, and when the Americas seemed a wonderfully likely area to search for human ancestors. Note that Ameghino made these arguments at the same time that Eugène Dubois was discovering the first fossil evidence of *Homo erectus* in Java. The possibility of human ancestors being found outside of Africa was very real at this time.

The fossil record of New World primates is very poor, which accounts for many efforts to reconstruct platyrrhine evolutionary history through molecular and DNA analysis utilizing the "molecular clock." Three of the Miocene taxa are known only from a single distorted or fragmentary cranial specimen. These are *Chilicebus carrascoensis*, *Tremacebus harringtoni*, and *Dolichocebus gaimanensis*. *Homunculus* is the best known of the Miocene fossil platyrrhines. Crania, mandibles, dentition, and postcranial elements are present. This allows the paleobiology of this genus to be reconstructed in comparatively great detail. Three species occur in the Santa Cruz Formation.

Homunculus is now known to be a basal platyrrhine. It is an outlier in terms of platyrrhine phylogeny, and has no close evolutionary relatedness to living platyrrhine groups. Kay et al. reconstruct a splendid picture of the paleobiology of this genus. It epitomizes the fine detail that can sometimes be extracted from the primate fossil record. Using three crania, Kay et al. describe features of the cranial anatomy of *H. patagonicus* from high resolution CT scans and composite scans (Figures 16.2 and 16.4). Figure 16.8 presents a mid-sagittal section through the cranium and a reconstructed endocast. The brain to body size ratio is very low, far below that of living higher primates. Sensory capacities (vision, olfaction, tactile information from facial vibrissae, and auditory sensitivity) are assessed. Visual acuity, olfaction, tactile sensitivity of the snout, and hearing were comparable to living diurnal platyrrhines. Relative orbital size also indicates that *Homunculus* was diurnal. Locomotion is studied from the semicircular canals of the inner ear, as well as from the postcranial skeleton. This primate was arboreal, and traits of the postcranium indicate that leaping was important. The semicircular canals indicate that *Homunculus* was agile, with quick movements comparable to that of the living sifaka, which is a highly specialized leaper. Leaves and fruit were eaten. *Homunculus* did not engage in insectivory or bark-gouging to elicit sap or resin flow. Body size was between 2–3.5kgs, comparable to that found in the living sakis or uakaris, and sexual dimorphism was moderate.

The editors conclude the book with an extensive discussion of the paleoenvironment and paleoecology of the Santa Cruz Formation. The preponderance of all lines of evidence indicates that the Early Miocene environment of Patagonia was temperate, with humid to semi-arid forests. Ponds and marshlands existed. Rainfall was very seasonal, with wet, cool winters and dry summers. Volcanism produced airborne tuffs. These yield detailed tephrostratigraphy, and might also account for pronounced mammal tooth wear as grit was incorporated into food.

In conclusion, this volume will long remain an essential reference work for researchers studying the evolution of life in South America when it was an island continent. Because the chapters not only describe new material, but also compare fossils collected over 120 years ago, future students of South American paleobiology will absolutely need to consult this book. I commend the editors for their superb work in corralling and guiding appropriate researchers, as well as for supplying meaningful chapters that synthesize diverse lines of evidence.