

peccari, opossum, anteater, sloth, and armadillo. . . . North America, on the other hand, is characterized by its numerous rodents, and by four genera of solid horned ruminants, of which section the southern half does not possess a single species.

This distinction of the two zoological provinces does not appear always to have existed. At the present day the order of Edentata is much more strongly developed in South America, than in any other part of the world: and concluding from the fossil remains, which were discovered [by Darwin himself] at Bahia Blanca, such must have been the case during the former epoch. In America, north of Mexico, not one of this order is now found: yet, as is well known, the gigantic [extinct] megalonyx . . . has been found only in that country. . . .

Of the Pachydermata four or five species are now found in America; but, as in the case of the Edentata, none are peculiar to the continent north of Mexico; and one alone seems to exist there as a wanderer. Yet the account of the multitude of bones of the mastodon and elephant, which have been discovered in the salt-licks of North America, is familiar to every one. . . . In [the vicinity of Quito] three species of mastodon have been discovered. . . .

It is interesting thus to discover an epoch anterior to the division, as far at least as two important orders among the mammalia are concerned, of the continent into two separate zoological provinces. [Darwin 1839, pp. 152-154]

When Darwin wrote, most of the known fossil mammals from both South and North America had lived relatively late in earth history and in mammalian faunal history: all but a few in the Pleistocene or most recent Ice Age, which ended only some 10,000 years ago. Darwin's discovery that the Pleistocene mammals of North and South America were in some respects more alike than are the now living mammals was a vital clue to an extraordinary event. Now, almost a century and a half after Darwin's discoveries, that event is known as the Great American Interchange and is still the subject of lively, occasionally even almost acrimonious, discussion. It will provide a dramatic climax in the present work.

Among the fossil localities found by Darwin was one then already and now still called Monte Hermoso, "handsome hill." Fifty-four years later, it was visited by Florentino Ameghino, a thirty-three-year-old Argentinian who had become in his own way a devoted follower of Darwin. Florentino and his younger brother Carlos, sons of Italian immigrants, grew up in Luján, a town on the pampa not far from Buenos Aires. Prehistoric mammals had already long been known from that vicinity. Those bones so fascinated the Ameghino boys that they determined to spend their lives probing such marvels and mysteries. So on the fourth of March 1887 Florentino sat on Monte Hermoso and wrote (in Spanish):

Monte Hermoso! On the whole all that is handsome about it is its name. It is a series of semimobile dunes, some thirty-odd meters high, on the highest of which is a lighthouse intended to prevent as far as possible the wrecks that so often happen along that coast. It is an arid and solitary place, scorched by the sun and swept by the winds which lash the face with the burning sand, without water and without pasturage, or, if there is some, hard and prickly as upholsterers' needles. . . .

But this place, isolated from any center of civilization, stuck away in a region all but uninhabitable, is for the naturalist, if not a handsome hill, a golden hill, a hill of life unknown until now, dead, if you like, but coming alive before our eyes under the blows of a pick against the hillside.

Monte Hermoso some day will have its monograph, but it would be selfish if in the meantime I were to keep to myself alone the summing up of the discoveries that I have made there and of the considerations so strongly brought to my mind both by the remains dug up there and by the sight of the strata in which they were buried. . . .

It seems that almost all of the fossil mammals of Monte Hermoso are species and even frequently genera hitherto unknown, very distinct from those we know as coming from the Pampean formation. . . . They form a real transitional fauna whose types, although different, resemble on one hand

those from the lower Pampean of Buenos Aires and La Plata, and on the other hand those from the much older deposit . . . of the Paraná. . . . [Ameghino 1916, pp. 331-333]

Although the ages of these faunas in modern terms had not yet been established, Florentino Ameghino's remarks here take us back of Darwin's and into a different part of an extraordinary history. Darwin had noted the marked distinction of the recent faunas of North and South America and their partial mingling in a previous epoch, the Pleistocene represented by the Pampean in Argentina. Now Ameghino was starting to push the story farther back, into an earlier stage, into pre-Pleistocene ages when the faunas of the northern and southern continents were even more distinct than they are today.

It had also been known since Darwin's visit to Argentina that fossil mammals occurred in the bleak southern reaches of that country called Patagonia, but before 1887 there had been little serious investigation of them. Now in the same year as Florentino's trip to Monte Hermoso his brother Carlos went off alone to Patagonia in search of fossil mammals. He worked there with astonishing success almost steadily until 1903, sixteen years of hard, slogging, lonely work in what was then one of the most desolate regions on earth.

Florentino had done little collecting himself before 1887 and thereafter he did almost none. In the brothers' busiest years he worked hard for the barest support of them both, for most of that time in the city of La Plata. There he also labored day and night studying, describing, and interpreting the collections that poured in, almost all from Carlos, who was an experienced collector even before he went to Patagonia.

There was a certain provinciality in Florentino's outlook and work, and some critics have assumed that he was a rather naive, poorly educated, self-taught researcher, an *autodidáctico* in the rather pejorative Argentine term. His formal schooling indeed was not impressive, but like all really successful scientists he never stopped learning and his horizons were far wider than the pampas. While still in his twenties but already the author of a number of

scientific studies, he spent three years in France. There he met many prominent scientists and worked especially with Paul Gervais, one of the greatest nineteenth-century paleontologists. He married a French girl, née Léontine Poirier, and thereafter with her help he published some of his most important work in polished French, which had a wider world audience than Spanish. He kept in touch by correspondence with most of the leading paleontologists of the late 1800s and early 1900s and honored many of them with names of fossil mammals such as *Edvardocopeia*, *Guilielmoscottia*, *Henricosbornia*, and *Othnielmarshia* for North American paleontologists; *Asmithwoodwardia*, *Guilielmofloweria*, *Oldfieldthomasia*, *Ricardolydekkeria*, *Ricardowenia*, and *Thomashuxleya* for some in Great Britain; *Albertogaudrya*, *Amilnedwardsia*, *Edvardotrouessartia*, *Henricofilholia*, and *Paulogervaisia*, French; *Carolozettelia*, *Ernestokokenia*, and *Maxschlosseria*, German.

There are several reasons for introducing that list of odd and rather difficult names at this point. One reason is that they are a roster of great contemporaries of the Ameghinos, who were familiar with their work: Cope (1840–1897), Scott (1858–1947), Osborn (1857–1930), Marsh (1831–1899), Smith Woodward (1864–1944), Flower (1831–1899), Thomas (1858–1929), Lydekker (1849–1915), Owen (1804–1892), Huxley (1825–1895), Gaudry (1827–1908), Milne-Edwards (1835–1900), Trouessart (1842–1927), Filhol (1843–1902), Gervais (1816–1879), Zittel (1839–1904), Koken (1860–1912), and Schlosser (1854–1932) are all revered in the history of science. Florentino also named a genus for his collaborating brother: *Caroloameghinia*. Carlos's dates were 1865–1936. There is a slight question about the date of Florentino's birth, but it was probably 1854. He died in 1911.

A second reason for this list is that all the animals to which these names were given lived in what are now called the Casamayoran, Mustersan, or Descadan land mammal ages. Those were, at the time of the Ameghinos, the three oldest mammalian faunas known from South America, and only one older (the Riochican, about which more later) has been found since then. (There are a few even older scraps now known, but they do not as yet merit desig-

nation as a fauna.) Carlos Ameghino discovered the first two faunas and was the first to characterize the third and to collect a real sample of its fauna. Those discoveries carried the history of South American mammals back tens of millions of years earlier than the previously known Montehermosan and Pampean. It was also Carlos in the field and Florentino in the study who filled in most of the vast time span between the Deseadan and the Montehermosan.

Thus one can say in retrospect that by the time of Florentino Ameghino's death in 1911 much of the essential framework for a history of South American mammals had been attained. Some readjustment, much filling in of detail, and a nearly complete change in faunal nomenclature were still necessary and are not yet completed, but the basic groundwork for the sequence of faunas had been put well in hand. Nevertheless, some essential broad readjustments of Florentino's conclusions had to be made before there was an overall groundwork on which later conceptions of the faunal history could be soundly based.

One of the readjustments had to do with the time scale. With minor exceptions and toward the end of their work, the Ameghinos had the sequence of the faunas then known correct, but not the correlation or comparison of relative times with those on other continents. In every case the Ameghinos' final judgment made the relative ages of their faunas older than they are now known to be. For example, they considered the first three faunas definitely established by them, those now known as Casamayoran, Mustersan, and Deseadan, to be Cretaceous in age. It is now clear that they are all some millions of years younger, Eocene to Oligocene. (The significance of the terms involved will be discussed later.) Really precise relative dating and dating in terms of years before present have been a long, hard problem, work on which is still going forward, but it is clear that the Ameghinos' dates were all much too early.

The second major readjustment has to do with the relationships of the Ameghinos' fossil mammals. Here, too, some of the details are still in question, but it is clear that in many cases Florentino was radically mistaken about the affinities and the lines of descent

illustrated by the fossils brought to him by Carlos. In that respect Florentino was neither stupid nor ignorant. He was caught in what may in retrospect be seen as a sort of then almost unavoidable booby trap: the phenomenon of evolutionary convergence, which still is a source of disquiet and precaution to paleontologists and other biologists. When different lineages of animals are evolving separately but in similar environments and in adaptation to similar ways of life they commonly also become similar in the structure of the functional part involved. That is especially likely to occur when the groups involved are in different geographic regions separated by barriers to expansion and migration. If the lineages involved had different ancestries and were not closely related, this phenomenon of convergence certainly rarely, probably never, resulted in fully detailed similarity, but the resemblance is often close enough to deceive the unwary. Florentino Ameghino had little reason to be wary, and that was particularly unfortunate because it finally turned out that various South American mammals through the ages had been convergent toward, rather than specially related to, those of other continents in unusually numerous instances and sometimes to extraordinary degrees.

In the following pages we will find many examples of convergence, but one may be briefly particularized here as evidence of how insidious was the trap into which Ameghino fell. He had numerous fossils of mammals that were plainly predaceous, dog-like carnivores. He concluded that they were closely related, some of them indeed ancestral, to living members of the dog family, Canidae, and other widespread living carnivores. In fact those animals, which we call Borhyaenidae, one of the names given to them by Ameghino, were only convergent toward the Canidae and had no ancestral or other special relationship to the latter. Ameghino also saw resemblances between the Borhyaenidae and American opossums, and he concluded that the ancestors of the Borhyaenidae were early, primitive opossums. All students of these matters now agree that in this respect Ameghino was essentially correct. Thus in this case, and in many others, Ameghino, faced by real resemblances of a group of his fossils to two other groups of mammals, interpreted these resemblances as represent-

ing special relationship to both of the latter groups and was radically mistaken as to one relationship but essentially right as to the other.

Ameghino's belief that so many of his fossil groups were ancestral to others to which they were in fact only convergent was combined by him with his overestimates of the ages of his fossils to produce a stunning conclusion: that practically all the known fossil and now living groups of mammals (including mankind) originated in Argentina and that their descendants subsequently occupied the rest of the world.

The reorientation, or perhaps one should more fairly say continued orientation, necessary as a basis for the history of South American mammals was the work of many hands and was only gradually achieved. Indeed it is still under way, but now not at such broadly basic levels. One of the early steps must be credited to another Argentinian, one of Swiss origin: Santiago Roth. He also grossly overestimated the ages of early mammalian faunas, and much of his exchange of polemics with Ameghino did little credit to either side, but he made one great step forward. In a paper published in 1903, while the Ameghinos were still fully engaged with such matters, he held that the great majority of extinct South American hoofed mammals, ungulates, belonged to a group confined as far as then known to that continent and, contrary to Ameghino's opinion, were not ancestral to any ungulates known on any other continent. That is still considered essentially correct, and the group, which will occupy much of this book, is still known by the name that Roth gave it: Notoungulata, "southern ungulates."

The next major step forward in the basic reorientation was marked by the beginning of direct collaboration between South and North American paleontologists, a friendly association that came to include many from both continents and that continues at the present time. In the 1890s William Berryman Scott, then already a leading student of North American fossil mammals (he was born in 1858), became interested in what the Ameghinos were finding. With the support of a wealthy New Yorker, he arranged for Princeton University, where he spent virtually all of

his long adult life, to send an expedition to collect fossils in Patagonia. That expedition was led by John Bell Hatcher, an able North American fossil collector, and worked seasonally from 1896 to 1899. The rich collections were described, illustrated, and discussed from 1905 to 1932 in a series of sumptuous publications, those on the fossil mammals by Scott and his colleague at Princeton, William John Sinclair.

Scott did not himself visit Patagonia or collect any South American fossils, but in 1900 he visited La Plata and Buenos Aires, where he studied and photographed many of the Ameghinos' fossils. He also won and treasured the friendship of Florentino, about whom he wrote many years later in his autobiography:

The only medium of communication that I had with [Florentino] Ameghino was bad French, which he spoke very fluently, but pronounced as though it were Spanish. Gradually, however, we reached a basis of mutual understanding, and could communicate with each other readily. Every afternoon, at half-past four or five, he would appear with a tray for making tea [surely so-called Paraguay tea, *yerba mate*, not "tea" in the English sense]; I could not bear to dull his enthusiasm by telling him how greatly I disliked that beverage and solemnly imbibed two large cups. During the tea-drinking we discussed the problems of paleontology and squabbled with the most perfect amiability, for we never agreed about anything and yet we never lost our tempers and always kept the discussion on a purely objective plane. . . .

I went to La Plata decidedly prejudiced against [Florentino Ameghino] but a brief acquaintance removed that prejudice entirely. Not only did his heroic devotion compel respect, but I came to value his work as I had not done before. [Scott 1939, p. 251]

The year after Scott's visit, Ameghino named one of his beloved fossils *Guilielmoscottia*.

Most of the fossil mammals collected by Hatcher and his associates belonged to the fauna now called Santacrucian. On these

Scott reported to the Sixth International Congress of Zoology in 1904 (published in 1905): "On looking over a series of representative Santa-Cruz mammals, we are immediately struck by the strangeness of the assemblage; not a single genus of these mammals occurs in any part of the northern hemisphere and, what is more surprising, the difference from the northern faunas is not only one of families and genera, but of orders."

Those words by his friend were a death knell for Ameghino's theory of the Argentine origin of so many groups of mammals in the rest of the world. Ameghino did not abandon his theory in the few years of life remaining to him, but other paleontologists found that the extraordinary, unique nature of so many South American mammals made them, and Ameghino's own work on them, still more valuable and interesting.

Hatcher and his associates also made a large collection of fossil invertebrates, mostly shells, from marine strata lying below the Santa Cruz beds from which their fossil mammals came. Those marine fossils provided another deathblow to the Ameghinian system, for they provided conclusive evidence of the fact, previously suspected, that Ameghino's claimed dates for his faunas were indeed much too old. When studied by Arnold Edward Ortmann, a German paleontologist then temporarily at Princeton, these marine fossils indicated a probable early Miocene age, and in any case certainly tens of millions of years later than the early Eocene age ascribed to them by Ameghino. As the Santa Cruz mammals were later than those marine animals, they, too, could not possibly be of Eocene age.

It may here be explained why the relative dating of South American fossil mammalian faunas has been such a difficult problem. The time-honored and still useful method of relative dating of rocks from one region or continent to another has been by resemblance or difference of fossil faunas. For example, when fossil mammals from certain strata in the Bighorn Basin of Wyoming are compared with those of some strata in the London and Paris basins of Europe, it is found that a number of those from the two continents are closely related, in some cases almost identical.

As mammalian faunas on those continents changed rather rapidly in time, it is evident that the strata here in question are of nearly if not quite the same age. But that method would not work for South American mammalian faunas for the reason that Scott emphasized: many of them had practically no true affinity with those of other continents. However, as Ortmann found, the method did work, not precisely but nearly enough to be useful, for at least one South American marine fauna which resembled those of other continents closely enough to indicate an approximate age. That provided a maximum approximate age for the great Santacrucian mammalian fauna, and from that datum point some extrapolation could be made to other mammalian faunas without so crucial a relationship to marine beds. Now other methods of dating have been devised and are being applied in South America in conjunction with faunal comparisons. More will be said about that later.

Here it appears that the most fundamental requisites for study of the history of South American mammals had been acquired with one exception: a reasonable explanation for the evident peculiarity of so many of the faunas involved. The general explanation in broadest outline now seems obvious. It was implicit in early work by Scott and some others, but it was not clearly stated by Scott, at least, for some time, and then only with some cautious qualifications and restrictions. The final contribution at this level of basic foundation laying may be credited to a great French paleontologist who, like Scott, never collected a South American mammal and indeed, unlike Scott, never even visited that continent. He was (Jean) Albert Gaudry, who during the later years of his life became fascinated by the discoveries made by the Ameghinos. He asked a young friend, André Tournouër, who had been working in Argentina, to go to Patagonia and collect fossils for "the honor of French science." Tournouër replied, "I will go to Patagonia; the Paris Museum shall have fossils," and it did. Tournouër became a good friend of both Ameghinos, and starting in 1898 he made five expeditions to Patagonia, collecting at localities indicated to him by Carlos. Besides several shorter notes from around 1902, Gaudry based five memoirs, 1904-1909, on the

fossils collected by Tournouër. He planned to continue, "If God lends me life," but God did not—Gaudry died in 1908 at the age of eighty-one.

It is worthwhile to interpolate here that, although the Ameghinos reacted adversely to some undue antagonism, they were cordial and helpful to anyone who, like Scott and Tournouër, approached them with friendly courtesy even when in disagreement with them. Thus the Ameghinos themselves made indirect but real contributions to the correction of what in retrospect we see as errors in some of their interpretations.

Although Gaudry wrote two later papers in his series on Patagonian fossils, his most important summing up was published in 1906 as "A Study of Part of the Antarctic World." He then wrote, in French, "We do not have any animal from the Descadan or the Santacrucean that we might consider as coming from the Northern Hemisphere." Gaudry named the Casamayor and Deseado as geological formations; we now use the terms in the form Casamayoran and Deseadan for geological ages and for the mammalian faunas that lived in South America during these ages. The term Santacrucean, variously spelled, now similarly used, had already been applied by the Ameghinos and was adopted by Gaudry.

Farther along in the same publication Gaudry wrote that "There was a lowering [of the land] in Central America which lasted until the beginning of the Pliocene epoch; then [in the Pliocene] Central America formed a bridge between North and South America, which for a long time had been [separate] continents. But this bridge did not exist in the Santacrucean epoch."

Those statements are clear enough as far as they go, and they did indicate the basis that has been clarified and extended in later studies. It would not be expected, and it did not occur, that Gaudry or anyone else in 1906 could all at once understand all the implications that hindsight can now draw from Gaudry's statement. It was at its date the clearest indication that South America was long an island continent. That was the last of the necessary basic elements for study of the history of South American mammals.

Gaudry believed that the Casamayoran fauna, the oldest then known from South America, was similar to faunas now classified as Paleocene in North America and that there was some connection between the two continents at that time. It now seems clear that there was no such land connection then. Yet the placental mammals as a whole had then diverged less from their considerably more remote common ancestry. It was true that the distinctions between South and North American mammals were not yet quite so obvious or nearly so extreme as they later became.

Gaudry also wrote that "Certain remarks make one think of communication between Patagonia and Australia, without our knowing in what epoch they took place." The particular "remarks" to which Gaudry was referring do not seem to support his suggestion, but as will be discussed here on later pages, the history of marsupials does indicate that there was at a remote time some kind of limited "communication" between South America and Australia. Gaudry further suggested that South America and Australia had at some time been parts of a vast Antarctic continent. The evidence for this thought to be available in 1906 was inadequate or indeed erroneous, but more recent studies do suggest that both South America and Australia had once been if not parts of at least more nearly associated with Antarctica.

Gaudry noted that (placental) rodents first appeared in South America in the Deseadan (still true of known appearances), and after commenting on the differences between the Deseadan fauna and any in the Northern Hemisphere he added in a footnote, "I leave aside the rodents because I don't know where they came from." That remark now seems both wise and amusing because (as will later be discussed) there are now a number of paleontologists who profess to know where the rodents came from but who ardently disagree as to where that was.

Here brief reference may again be made to W. B. Scott. In 1932 he finally completed the great series of studies on Santacrucian mammals with some general remarks on the history of South American faunas. He emphasized their peculiar nature and ascribed this, as everyone does now, to the long isolation of the continent. However, he held that South America had at some time

been connected to Africa and to Australia, the latter by way of Antarctica, and had also "almost certainly" had a land connection with North America in the late Cretaceous and "perhaps" also in the Paleocene. There was then, as he noted, no direct mammalian evidence for the latter times. As will be made clear in due course, Scott's final views now seem largely correct, partly prophetic of results of later discoveries and studies, and partly but not egregiously wrong.

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