Roots

There is an aphorism, sometimes known as "Simpson's Third Law," that no matter what the problem is there is never enough information to solve it definitively. To historians of life that means that there are never enough fossils to answer once and for all the questions that such historians put to them. That is particularly true of questions, to many of us the most interesting ones, that involve origins or what are in a now popular sense the roots of histories. In the present case the first question is, "How did the South American mammalian fauna get started?" A really complete answer might have to begin with the origin of the earth itself, but here we do not need to dig into roots that far back even if we could do so. It would be interesting to start with the origin of mammals as such, and indeed there is much to say on that topic. However, what can now be said about that does not really help with the more specific question of the origins of the South American mammalian faunas and therefore is not included here.

There is still incomplete but reasonably good information about the composition of South American mammalian faunas early in the Cenozoic, Age of Mammals, provided by the Riochican, Casamayoran, and Mustersan faunas, earliest known for the South American Cenozoic. As will be shown, they are very peculiar in some respects, and the reasons for those peculiarities are still in considerable part mysterious. We are at least better off than if we were considering Australia, where there is no direct information at all about early Cenozoic faunas, or Africa, where there is only a little. Here in South America before the Cenozoic we have just a

handful of scraps from the late Cretaceous. They do help, but they do not solve the major mysteries.

It was this sort of paucity of information, increasing as one delves farther into time, that led Scott to write faunal history backward (as mentioned in chapter 1), starting with the present fauna, which is known best of all, and then going back through the earlier ones until times are reached for which the faunas are known little, if at all. When Scott originally wrote his history of South American mammals, the Cretaceous scraps and the Riochican fauna were still completely unknown and the Casamayoran and Mustersan faunas were much less well known than they are now. Here the start will be made as near the beginning as there are any really known facts, recognizing that this requires putting up with doubts and mysteries. As the history proceeds some of the uncertainties will disappear, but some will continue right down to the present. It is another aphorism that no one knows everything about anything. That need not dull the pleasure and fascination of the fact that a great deal is known about some things.

So the present positive knowledge of this history starts with that scanty handful of fragments of mammals from late Cretaceous strata. These were found in 1965 and 1967 by a French expedition on the tremendous high Andean plateau of Peru not far from Lake Titicaca and near the small Laguna Umayo. The first specimen found was a fragment of a lower jaw with the posterior half of the first molar and the anterior half of the second molar. Later a small fragment of an upper molar apparently of the same species was found. This animal was with high probability a primitive hoofed mammal, a condylarth rather like the Didolodontidae, the condylarth family known from later faunas. It is not much like anything known from the late Cretaceous of North America but does somewhat resemble some later (Paleocene and Eocene) North American, European, and Asiatic condylarths. The French paleontologist Louis Thaler named it *Perutherium altiplanense.*

The other specimens in this collection are parts of eleven tiny teeth, all more or less broken and incomplete, and two jaw fragments with remains of roots but not crowns of teeth. All of these, as far as identifiable at all, represent primitive opossums, members

of the family Didelphidae of the classification in chapter 4. They closely resemble some of the numerous opossums known from the late Cretaceous of North America, to such an extent that their describer, Bernard Sigé of Montpellier, France, has referred the most characteristic fragments to a genus, *Alphadon,* better known from the North American Cretaceous. Another interesting fact about this exiguous sample of so old a fauna is that these small tooth fragments show that there was at least one other fairly distinct opossum present. Thus some differentiation of the Didelphidae, later and still today varied and characteristic in South America, was already under way.

Surely some other kinds of mammals were already there in South America in Cretaceous times, but that is all we really know at present: a very primitive hoofed mammal, ungulate, that could be in or near the ancestry of the many and varied later South American ungulates, and some very primitive opossums, marsupials, that could be in or near the ancestry of the many and varied later South American marsupials. From what we do know of later faunas, it would have been expected that mammals like these would occur in the Cretaceous of South America, and the confirmation is welcome as far as it goes.

The next oldest mammals are those of Riochican age, more or less late Paleocene, perhaps some 55 to 60 million years ago. The first scraps of Riochican mammals were found long ago by Santiago Roth, the paleontologist mentioned in chapter 2 as having recognized and named the great group Notoungulata. Neither he nor at the time anyone else recognized the significance of what we now know were the first Riochican mammals to be found. In 1930 two petroleum geologists, A. Piatnitzky and J. Brandmayer, working for the Argentine government, found a few fragments of Riochican mammals at a locality some distance south of Roth's in Patagonia. They also misunderstood the discovery at first, but it was followed up by Coleman Williams and me, working for the American Museum of Natural History. We found fossils of this age at several localities in the general vicinity of the Rio Chico in central Patagonia, and study of those enabled me to characterize the fauna and to name it Riochican.

Much the richest Riochican local fauna so far discovered comes from a remarkable deposit at São José de Itaborai in the state of Rio de Janeiro, Brazil, across the bay from the city of Rio de Janeiro. At that locality there is an isolated basin filled with limestone—or was, for the limestone has almost all been quarried out to make cement. There are (were) solution channels in the limestone, and these were early filled with marl and debris. In 1943 L. I. Price and others from the Brazilian equivalent of a national geological survey (Divisão de Geologia e Mineralogia) found some remains of mammals in the fissure fillings. For many years starting in 1945 large collections were made, and the mammals were studied by the Brazilian paleontologist Carlos de Paula Couto. He soon recognized that the fauna was at least approximately contemporaneous with the Riochican in Argentina, and he referred it to that age.

These earliest known South American Cenozoic mammalian faunas, those of Riochican age, are remarkable both for the extent and, in a different way, for the limitation of the diversification of the mammals in them. They already include five orders and fourteen families: Marsupialia (three families), Xenarthra (one family), Condylarthra (one family), Litopterna (two families), Notoungulata (five families), Trigonostylopoidea (one family), and Xenungulata (one family). Obviously a great deal of evolutionary divergence and expansion had already occurred among these mammals. It is probable that most of it and possible but less probable that all of it had occurred in South America itself.

It is, however, the limitation of the number of basic stocks and of ecological specialists that is most peculiar in the Riochican. All the mammals known from this age represent divergent lines of just three basic stocks, and the same is still true of the following Casamayoran and Mustersan faunas. There were marsupials, all of which could have been and probably were derived from primitive Cretaceous opossums, Didelphidae in a broad sense. There were Xenarthra (pronounced zee-nar′-thruh) represented in these three earliest known South American Cenozoic faunas mostly by armadillos, which constitute the family Dasypodidae. Their origin is quite uncertain and will be further discussed. And there were

relatively abundant herbivores, ungulates in a broad sense, all of which could have been and probably were derived from primitive, relatively generalized ungulates classified as Condylarthra.

The collections from these faunas are now so extensive that it can be asserted with considerable confidence that in Riochican, Casamayoran, and Mustersan times all the South American land mammals belonged to those three basic groups and to no others. Such a mix is not only peculiar; it is absolutely unique. No other continent, present or past, is definitely known ever to have had a fauna consisting of just those three basic stocks, and it is quite unlikely that any ever did. It is clear that North America and Europe and highly probable but with less complete evidence that Asia and Africa in the early Cenozoic had mammals from considerably more than three such basic stocks. For Australia there is virtually no direct evidence, but by reasonable extrapolation backward from later faunas it is highly probable that the origins of the Cenozoic mammals of that continent were even more limited than those of South America, with only two basic stocks. One of those was originally the same as one in South America, deriving from opossumlike marsupials, but the other, represented by the still surviving egg-laying monotremes, the platypus and the several so-called spiny anteaters or echidnas, was quite unlike any of the South American basic stocks.

In North America, for example, at times approximately equivalent to the span of Riochican–Mustersan in South America, there were also marsupials and ungulates as basic stocks. But the marsupials there, all opossums, Didelphidae, were not nearly as abundant or as diversified as those of South America. The ungulates were about equally abundant and diversified on the two continents, but apart from survivors of the most primitive, originally ancestral group, the Condylarthra, the ungulates had already evolved in quite different ways on the two continents with just one peculiar exception that will require further discussion. The greatest contrast, however, is that in North America there were at least eight orders of land mammals not derived either from ancestral marsupials or from ancestral ungulates. As will appear on further analysis, one of the eight may or may not have had some

relationship to the third South American basic stock, that of the Xenarthra, but the other seven early North American orders definitely had no South American relatives. Thus North America had a much more varied, more balanced, more ecologically complete early Cenozoic fauna than South America. That was probably true of all the rest of the world with the exception of Australia and probably of Antarctica, which has no native land mammals now but could well have had some in the early Cenozoic. No fossil land mammals have yet been discovered there.

South America was already surely an island continent in Riochican time and must have been so for an indefinite but geologically long time before that. This is clear from the fact that each of the three original stocks had become sharply diversified in ways unique to South America and demonstrating evolution in isolation. That is not so evident for the Xenarthra in Riochican time, when the positive evidence includes only armadillos, but in the Mustersan there are known specimens, still rare, of at least two and perhaps three other families of xenarthrans. Their absence in the present Riochican and Casamayoran collections is probably due not to their later origin but to chances of preservation and collection or to geographic and ecological factors.

The general characteristics of successive faunas and the histories of the separate orders and families of mammals will be discussed in later chapters. Just here concern is with the origin of such a peculiar mix and of each basic stock in the earliest known faunas. The next step is to consider possible connections of members of the basic stocks with mammals living elsewhere.

First consider the marsupials. It has already been noted that extremely primitive and closely similar marsupials are known from the Cretaceous in both South and North America. No Cretaceous or earliest Cenozoic mammals are yet known from Australia, but ancestral marsupials must have been early present on that continent, almost surely in the late Cretaceous. Those three continents have not been parts of a single land mass since mammals evolved, and therefore marsupials cannot have arisen on such a mass and then have become separated when the mass split into three (or more) separate continents. Early marsupials must somehow have

spread among the three continents after their earliest forms evolved. Marsupials also spread to Europe in their primitive form as didelphids, but that is rather beside the point. The spread may have occurred at any time from late Cretaceous through early Eocene, when what are now North America and Europe were parts of the same continent. When they split apart, around the end of the early Eocene, the marsupials were in a dead end in Europe and became extinct there, as they did also for a time in North America.

Cretaceous marsupials certainly spread directly between South and North America. The available evidence does not indicate in which direction they spread, and although some authorities insist that it was from North to South America others are equally confident that it was in the opposite direction, and no one really knows. The problem of spread to or from Australia involves further difficulties.

It is reasonably certain that Australia has never been directly connected to either South or North America. It has long been known that, whenever they may have originated, marsupials were abundant in North America in the late Cretaceous. There has also long been some, now increased, evidence of some early faunal connection between North America and Asia. It used to be believed that Australia had formerly been directly connected to Asia, and even when that idea was given up by almost all students of the subject, it still was evident that for some undetermined time there had been stepping-stone islands between Asia and Australia and that some animals had spread from one continent to another along those stepping-stones. One that basis until fairly recently the favored hypothesis was that marsupials spread from North America to Australia by way of Asia. (It apparently did not occur to anyone that it could have been Australia to North America by way of Asia.)

More recent research has made that hypothesis so nearly impossible that it can hardly be supported at present. For one thing, the late Cretaceous and early Cenozoic mammalian faunas of some parts of Asia have become fairly well known, and there are no definitely identifiable marsupials in them. That is suggestive, but, as often is true of negative evidence, it is not conclusive. Asiatic

marsupials might just have been missed in collecting so far, or they may have been living in regions where fossil mammals of appropriate age are not yet known. However, there is another recent development that makes the Asia–Australia hypothesis seem really impossible. Marsupials probably got to Australia in the Cretaceous and if not then certainly quite early in the Cenozoic. If they spread *from* rather than *to* Australia, that was certainly in the Cretaceous because of our positive knowledge that they were then in both Americas. But there is now rather extensive and widely accepted evidence that at those times Australia was nowhere near Asia and that stepping-stones between those two continents did not yet exist. Australia was then fairly close to East Antarctica, possibly even a part of that land mass. Then in the early Cenozoic Australia started to drift north, and it probably reached approximately its present position and relationship to Asia sometime in the Miocene, tens of millions of years too late for the initial intercontinental spread of marsupials.

The evidence is still not quite complete enough to call this a settled theory in the strict scientific sense of the word "theory," but at present the most probable hypothesis is that marsupials spread between South America and Australia in one direction or the other by way of Antarctica. It is, however, quite unlikely that a continuous and practicable land connection was involved. The dispersal of mammals over such a land connection is rarely or never in one direction only. Thus, if there had been such a route between these two continents some of the many different early South American mammals other than marsupials would probably have reached Australia. On present evidence it cannot be absolutely ruled out that some did so, but that seems highly improbable. As with other mysteries that will be met in this history, a complete solution still evades us, but progress toward one has been made and more can be expected.

It is reasonable to suppose that marsupials did not originate on a hypothetical and improbable land mass including two, three, or all of the continents now North America, South America, Antarctica, and Australia, but probably on only one of them at first. There is some evidence in favor of North America as the area of origin, and

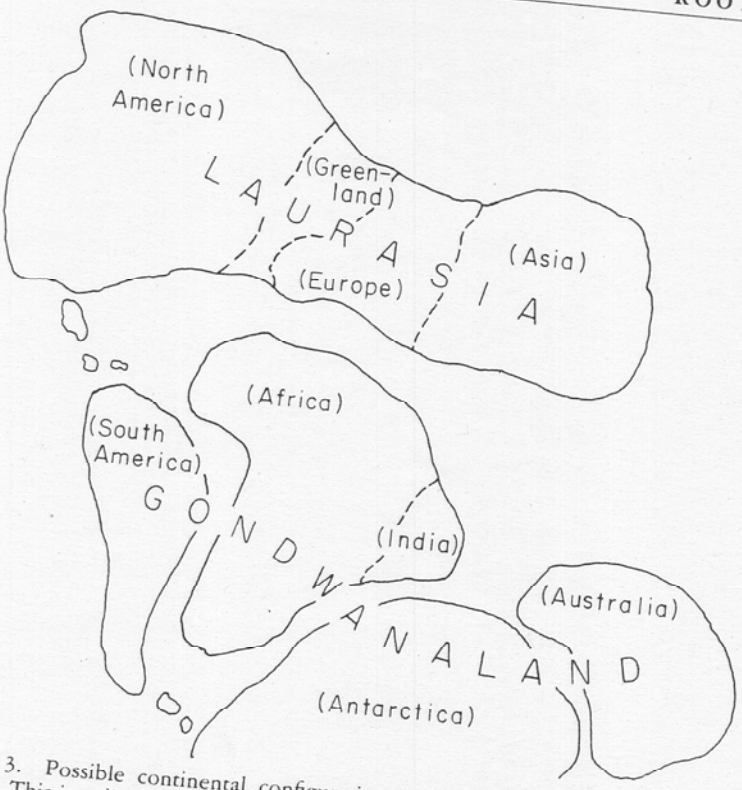

Fig. 3. Possible continental configuration in approximately mid-Cretaceous time. This is a diagram, showing topological relationships of land masses, rather than a map, showing their shapes. Two main masses, Laurasia in the north and Gondwanaland in the south, are indicated. By the end of the Cretaceous, and probably well before that, Gondwanaland had begun to break up. Shallow seas on the continental masses (epicontinental seas) not shown in this diagram complicated the geography. The names in parentheses show in a summary way where the present continents came from, including the North American island of Greenland and the Asiatic subcontinent of India.

that is perhaps the consensus of those concerned with such matters. However, the possible evidence for the other continents is not merely negative: at present it is completely lacking either one way or the other. It would seem to be wisest and fairest just to say that marsupials probably did first evolve in a region now in one of these four continents but that we simply do not know which. The

true directions of early spread of course depend on where the origin occurred.

To a certain point the mysteries about the Xenarthra have been partly cleared up. This group, evidently comprising mostly armadillos, glyptodonts, sloths (tree and ground), and anteaters, may have acquired its definitive characteristics in South America (but see added note, p. 47–49). Practically the whole of its complex later evolution did occur on that continent. Only toward the end of the Cenozoic did members of the order Xenarthra spread, clearly from South America, partly by island hopping or overseas dispersal and partly over an eventually continuous land connection from South to Central America. Thus, members of the order reached North America and also islands in the Greater Antilles. In those lately occupied areas the xenarthrans, especially the now extinct ground sloths, underwent some but limited further evolution. Outside of South America xenarthrans now survive only in Central America and as a single species of armadillo onward into the southern United States.

Although the Xenarthra certainly evolved mainly in South America they must have had ancestors there or somewhere else. Even after they became distinct from the ancestors of most other mammals, such prexenarthran ancestors might have given rise to xenarthran relatives on other land masses. That is the xenarthran mystery not yet solved to general satisfaction. There is a group of now fairly well-known mammals in the North American Paleocene, Eocene, and Oligocene that was named Palaeanodonta by the great North American paleontologist W. D. Matthew (1871–1930). Some of those creatures resembled armadillos, although they did not have bony plates in the skin as all armadillos do, and also resembled pangolins now living in Africa and southern Asia. The pangolins are often called scaly anteaters, although they are quite different from the South American xenarthran anteaters and are now usually called Pholidota to distinguish them from the Xenarthra. The groups now called Pholidota and Xenarthra had been put together as early as the eighteenth century in a larger unit of classification called Edentata, "toothless."

(Most "edentates" in that broad sense do have teeth, but the South American anteaters and the pangolins do not.)

Matthew believed that his Palaeanodonta were also Edentata in the old, broad sense and that they represented a third offshoot of the edentate ancestry, diverging from both the Xenarthra and the Pholidota. Thus both the marsupials and the xenarthrans would have some sort of early connection with early ancestral, probably Cretaceous, groups that also reached or arose in North America. That was generally accepted by students of mammals until 1970 when R. J. Emry maintained that one family of Palaeanodonta (the Metacheiromyidae of previous authors) not only resembled pangolins but were in fact members of the same family (Manidae) and had nothing to do with the Xenarthra. Emry did not go into the fact that another branch of the Palaeanodonta (the family Epoicotheriidae) does not resemble pangolins. Two leading students of fossil mammals, especially those of South America, R. Pascual and B. Patterson, have since (in 1972) maintained that the Palaeanodonta were derived from the same ancestry as the Xenarthra and that the resemblance of some of them to pangolins is convergent.

Quite recently, in late 1978, the discovery of an unquestionable pangolin (manid) in the middle Eocene of Germany has been announced. Although it has not yet been fully described, it is clearly more advanced, shares more specialized or derived characters with the Recent pangolins, than the middle Eocene palaeanodont *Metacheiromys* of North America. This makes it unlikely that Emry was right in considering *Metacheiromys* directly ancestral to the living *Manis* and weakens but does not in itself disprove his view that the palaeanodonts were Manidae and not just convergent toward the latter.

Since this chapter was written and sent to the publisher, the problem of the origin and affinities of the Xenarthra has been further complicated by notice of a discovery in the People's Republic of China. I am indebted to Minchen Chow and Su-yin Ding, both of the Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, Beijing (Peking), for a preliminary

publication, notes, and photographs recently (May 1979) received. The specimen in question is a nearly complete skeleton from the late Paleocene Nonshan formation in Nanxiong, Guangdong, southern China. It has been named *Ernanodon antelios* by Ding, who classifies it as a "primitive form of xenarthran."

If this is indeed a xenarthran, it is the earliest known from outside of South America. That poses difficult questions as to where the Xenarthra originated and how they came to be distributed in South America and south China, areas extremely remote from each other and not directly connected, certainly since long before the Xenarthra originated and probably never. The possibility that *Ernanodon* is a xenarthran must be taken seriously on the authority of Ding and of Chow, who in personal communication supports Ding's views, but it may not yet be entirely established. *Ernanodon* has some primitive features, not clearly xenarthran and apparently casting little light on relationships. Definite and no longer similarly primitive xenarthrans were present in South America at the same time, and *Ernanodon* cannot be in the xenarthran ancestry. Among its derived or specialized characters only a few have been definitely stated to be Xenarthra-like. Notable among them are the "incipient development of a xenarthran type of articulation on the posterior thoracic vertebrae" and the presence of two spines on the scapula. In South America at this time xenarthran articulation was not incipient but fully developed. The two-spined scapula, while suggestive, is not conclusive. Some xenarthrans do not have two distinct spines and some nonxenarthrans, including some insectivores, do.

Ernanodon also has derived, specialized, or advanced characters, for example in the humerus, that seem to be adaptively convergent to those of edentates in the broad sense. The details are not so close to those of xenarthrans, or of other xenarthrans. Some of the derived characters of *Ernanodon* differ even more markedly from any South American Xenarthra and also from both families of North American Palaeanodonta: Metacheiromyidae and Epoicotheriidae. Thus, pending further study, two hypotheses in addition to possible reference to the Xenarthra may not yet be fully excluded: (1) that *Ernanodon* belongs to a distinct branch

from a general edentate or preedentate stock, or (2) that it has only convergent resemblances to the Xenarthra, Palaeanodonta, and Pholidota and is of quite separate ancestry.

As to the biogeographic problem, Ding suggests several alternatives: that edentates in general (and presumably xenarthrans) originated on Gondwanaland, that they originated on the northern continents with *Ernanodon* in China as evidence in support of that, or "that it may not be entirely improbable that *Ernanodon* is a relic of earlier immigrants from (or to) the South via a route other than the one from the north, or by other means or route" (Ding 1979, pp. 63–64). There is some implication of the involvement of continental drift. Such points will need further discussion when the characters and affinities of *Ernanodon* have been more fully studied.

At present it seems necessary, or at least prudent, to say that we do not know where the Xenarthra originated or what their ancestry was. We do know that xenarthrans were present in South America in the late Paleocene or earlier and that almost all of their later evolution occurred on that continent.

As for the ungulates, it has been noted that all probably arose from members of the relatively primitive order called Condylarthra. Condylarths are known from late Cretaceous rocks in both South and North America and they also occur in the early Cenozoic of South and North America, Europe, and Asia. Some of those from South America are so like some from the northern continents that their placing in different families may exaggerate the moderate differences. Condylarths are not now definitely known from Africa, but the Paleocene and early Eocene mammals of that continent are practically unknown. The somewhat later complexity of indigenous African ungulates suggests that early condylarths had been there and had undergone a progressive radiation within that continent. It is, however, quite unlikely that condylarths, or any other placental ungulates, ever occurred in Australia.

From those facts and reasonable inferences it is easy to form a hypothesis. Perhaps condylarths originated on the likewise partly hypothetical continent called Laurasia, which in pre-Cenozoic

times included all the lands now distinguished as North America, Europe, and Asia. Perhaps then the incipient ungulates spread, or island-hopped, from western Laurasia, now but not then distinct as North America, to South America and also to Africa from central Laurasia, now Europe and during part of the Cenozoic but not at some earlier times and not now separated by sea from what is now called Asia. Thereafter the many other families and orders of ungulates evolved at times separately on each of what are now North America, Europe, Asia, and Africa, but with some interaction by faunal interchange from time to time between North America and Eurasia and between Eurasia and Africa. In contrast, during most of the Cenozoic the ungulates evolved in complete isolation in South America.

That hypothesis becomes less purely hypothetical as it goes along, but the earlier part could almost as well be called imaginary history. It is a reasonable possibility, but it is not the only possibility. It is even possible that Ameghino was right, for the wrong reasons, on this point and that ungulates did first evolve in South America. On that point, and some others that have been suggested in connection with this history, we may well repeat a remark often quoted by W. B. Scott, who was introduced in chapter 2. Scott derived the quotation from Jack Robinson, an old frontiersman whom he met in 1877 at Fort Bridger, Wyoming. When anyone told "Uncle Jack" anything he would say, "Well, mebbe it is, but I don't believe it."

There is a most peculiar circumstance that becomes relevant here. Throughout most of the Cenozoic the great majority of South American ungulates belonged to the order Notoungulata. No other group seems more typical of South America or more surely to have evolved there. But a few specimens of apparent notoungulates have been found in the United States, Mongolia, and China. The rocks in which they occur are of approximately the same age in North America and in Asia and may be considered as latest Paleocene or earliest Eocene, depending on just where the artificial line is drawn between those two epochs. Calling these fossils "apparent notoungulates" may be excessive caution, for their dentitions do have distinctive characters otherwise known

only in early and still relatively primitive or unspecialized South American notoungulates. A modicum of caution is in order because the dentitions are distinct enough to warrant classifying them in a family not known in South America, named Arctostylopidae by the W. D. Matthew previously mentioned, and because the structure of their ears is not yet known. The ear structure of South American notoungulates is well known, highly complex, and unlike that known in any non–South American mammals.

If, as is after all reasonably sure, the Arctostylopidae really are notoungulates, there seem to be only two possible explanations. Either the Notoungulata started their evolution outside South America, perhaps in southern North America for example, and the Arctostylopidae are late survivors of that basal stock, or some still primitive South American notoungulate lineage left the island continent of South America and reached North America by waif or sweepstakes dispersal across the sea barrier and before long, geologically speaking, also passed from North America to Asia. The authorities Pascual and Patterson, previously cited in other connections, lean toward the former alternative, but I find the latter alternative somewhat more probable. Discovery of early mammals, preferably Cretaceous or Paleocene at latest, in Central America may eventually settle the matter. In any event it is highly probable that most or all of the known families of South American ungulates originated on that continent.

All that has been discussed so far in this chapter does not solve the mystery of why the South American Cenozoic mammalian fauna started with just the three basic stocks of marsupials, xenarthrans, and ungulates, but some light has been cast on that mystery. In general terms, the paucity and imbalance of basic stocks seem most probably to result from South America's already having become an island continent not long after marsupials and placentals had become differentiated and when the placentals were just beginning to radiate into what later became numerous orders in terms of classification. Then South America had or received as waifs from across the sea barriers only a scanty representation of such mammalian diversity as was developing in the great land

masses, periodically joined and separated, that are now North America, Eurasia, and Africa.

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First Phase: The Old-Timers Alone

During almost certainly all of the Paleocene and much but probably not quite all of the Eocene, it has been shown, the known South American mammalian faunas consisted of just three major groups: marsupials, xenarthrans, and ungulates. Each group had already become diversified and somewhat specialized by evolution on a continent completely isolated. These are the real old-timers, the oldest faunal stratum of the Age of Mammals on this continent. Their communities, their environments, in general their ecology while they monopolized this spendid isolation, are now to be considered. Those are the topics for this chapter dealing with the three land mammal ages Riochican, Casamayoran, and Mustersan. What eventually happened to these old-timers will be told in later chapters.

It is necessary to bear in mind that our positive information, especially in the early phases, usually comes from small parts of a large continent. Inference yields generalities that are probably valid for the continent as a whole, but the details are likely to be local. In particular localities and areas many different situations occurred and events happened for which there may be no direct information. The force of that remark is at once revealed by the fact that although they have similarities that indicate approximate contemporaneity the Riochican faunas of Argentina (several localities in Patagonia) and Brazil (only Itaborai) are markedly different in some respects. Undoubtedly the environments and general ecology of the two were dissimilar in some ways.

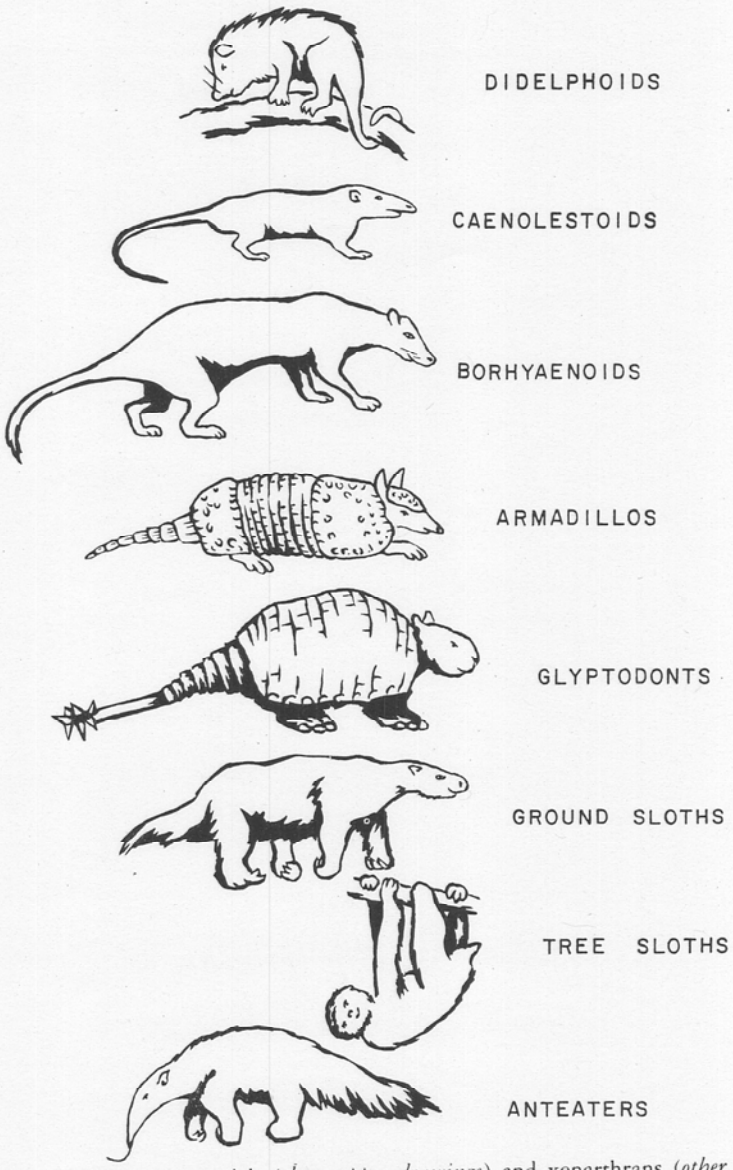


Fig. 4. Some marsupials (*three upper drawings*) and xenarthrans (*other drawings*) descended from old-timers of the first faunal stratum. The didelphoid (opossum), caenolestoid, armadillo, tree sloth, and anteater shown are still living. The others are restorations of mid-Cenozoic representatives of their groups.

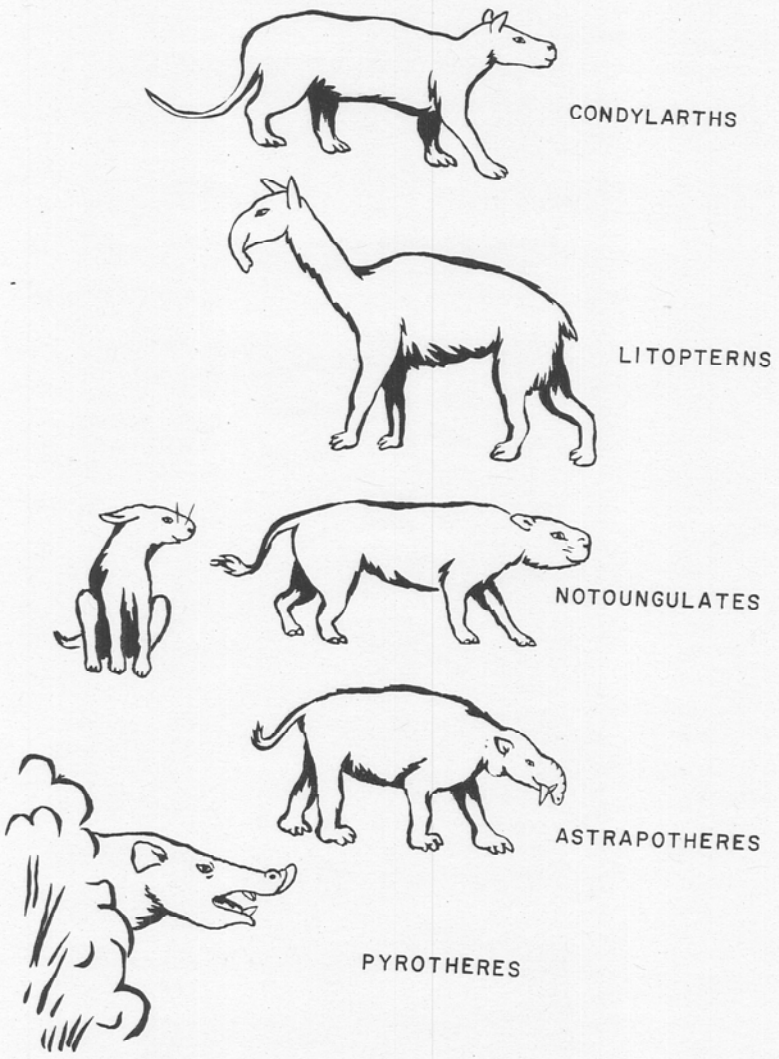


Fig. 5. Some ungulates descended from old-timers of the first faunal stratum. The condylarth restoration is based on a North American specimen, because the skeleton is not known in any South American condylarth, but the more primitive forms must have looked very much alike on the two continents. The litoptern shown is the Pleistocene *Macrauchenia*. The highly varied notoungulates are represented by a hegetothere and a rather generalized early form (isotemnid). Astrapotheres and pyrotheres are represented by their type genera. The body of *Pyrotherium* is inadequately known and so is not included in the restoration.

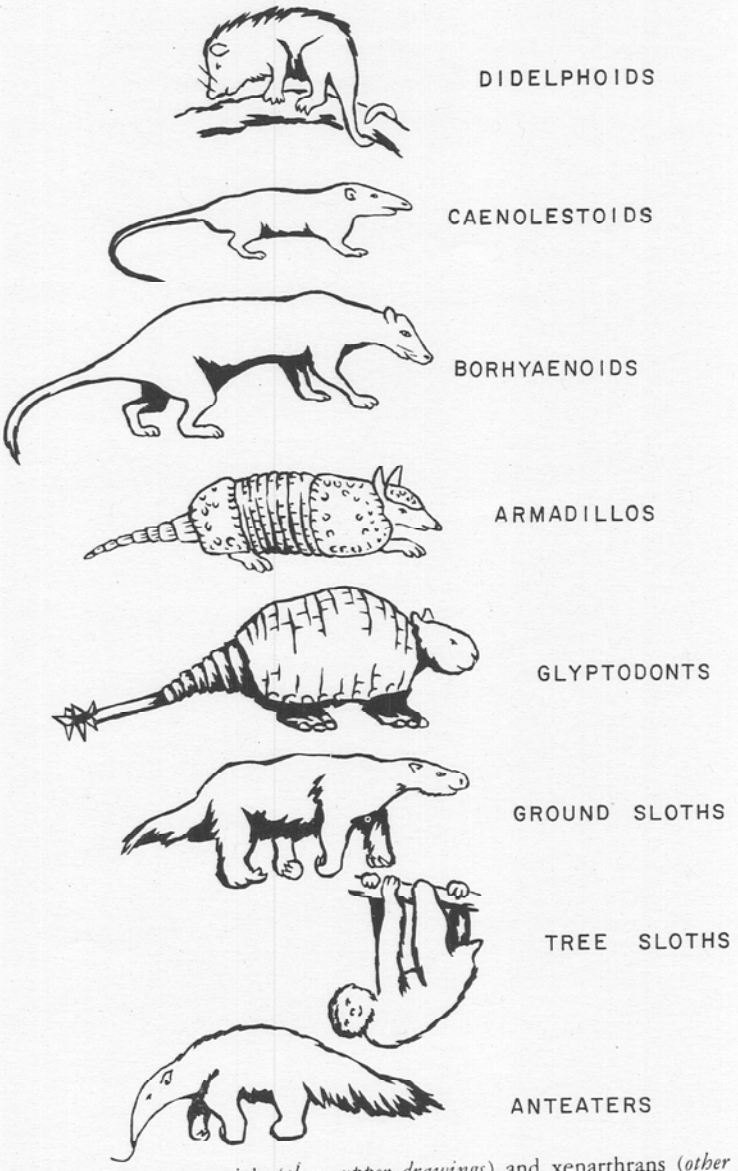
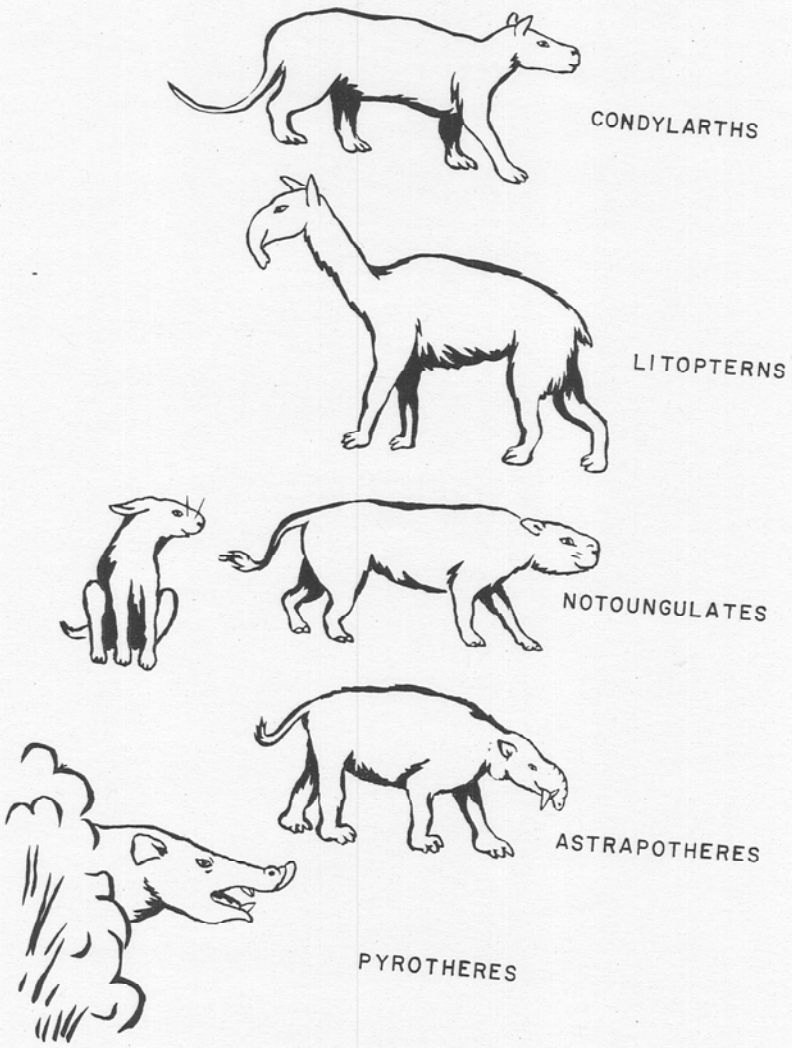


Fig. 4. Some marsupials (*three upper drawings*) and xenarthrans (*other drawings*) descended from old-timers of the first faunal stratum. The didelphoid (opossum), caenolestoid, armadillo, tree sloth, and anteater shown are still living. The others are restorations of mid-Cenozoic representatives of their groups.



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In Patagonia the Riochican sediments are predominantly water-laid sands deposited on a low floodplain by streams flowing from hills somewhere to the west. There were trees, in clumps or forests, and doubtless also much low, shrubby vegetation. There were alligatorlike crocodilians in the streams and doubtless also fishes, although the latter are not known for this age. The climate was at least warm temperate and perhaps subtropical, in either case very different from the cold present climate of the now treeless Patagonian plains and mesetas.

The Patagonian Riochican fauna is dominated by ungulates, all but one of those known being small, primitive, browsing animals. Four litoptern species of two families (Macraucheniidae and Proterotheriidae) have been found, the two families then being less clearly distinct and much less specialized than their later descendants. As usual in early South American faunas the notoungulates are most abundant and most varied: ten known species in four or five still not very different families (Henricosborniidae, ?Notostylopidae, Oldfieldthomasiidae, Interatheriidae, Isotemnidae). One large ungulate, the xenungulate *Carodnia,* already had specialized, sharply crested teeth also evidently adapted to browsing, probably on small trees or on higher bushes than those eaten by the much more numerous smaller browsers. Two perhaps omnivorous condylarths, the most primitive ungulates, are known. Armadillos were present but very rare, and there are no other known xenarthrans. The only marsupials definitely known are four species of the peculiar family Polydolopidae. Those animals had enlarged piercing or nipping lower incisors followed (in most genera) by a crested, shearing cheek tooth and then by crushing and chewing molars. As will be more fully considered when discussing the history of marsupials, the ecological position of the polydolopids is uncertain. They may have been eaters of seed and small fruit, but probably also ate some animal food.

As the Itaborai fossils occurred in fissures and caves, nothing very definite can be inferred about their environment from the rocks. The animals whose bones are found in them certainly did not live in the fissures and caves. The fossils themselves indicate a well-watered region with a warm climate, as in Patagonia, but the fauna was different in ways difficult to interpret ecologically.

Only two species of notoungulates have been described from Itaborai, but one of these is fairly abundant there. There is also an abundant trigonostylopid, member of a group of browsing ungulates not known from the Patagonian Riochican but common in the immediately following Casamayoran. *Carodnia,* first found in Patagonia, is common at Itaborai. There are some condylarths and litopterns not markedly different from those known from Patagonia. There is also a relatively primitive polydolopid. The most remarkable feature of the Brazilian Riochican fauna is the abundance and variety of opossums, Didelphidae in a broad sense; thirteen different genera have been described. This family is not known at all from the Patagonian Riochican or Mustersan and is rare in the intervening Casamayoran.

So many and such diverse genera of opossums are not known from any other one locality at any one time, including the present. As to the specific, presumably ecological, reason for their occurrence just here and just at this time, I have no suggestions. The occurrence warrants the general inference that a remarkable South American radiation occurred in the family Didelphidae in early Cenozoic times and that most of its lineages became extinct thereafter.

Three small predaceous marsupial carnivores, borhyaenids, are known from Itaborai, none from the Patagonian Riochican, although a primitive genus, *Patene,* occurs in both the Itaborai Riochican and the Patagonian Casamayoran. A characteristic of the known Riochican faunas is that there seems to be a poor balance between mammalian carnivores and herbivores. In what may be considered well-balanced faunas elsewhere or in South America at later times, mammalian carnivores are fewer than herbivores but nevertheless constitute an appreciable and varied part of a mammalian community.

The apparent imbalance of the low carnivore-herbivore ratio in the Riochican and also in the Casamayoran and Mustersan can be at least partly explained by the fact that not all carnivores are mammalian and that reptilian carnivores were present during those ages. There were crocodilians in variety, some of them crocodiles in a limited sense, some more alligatorlike, and some (the genus *Sebecus,* found in both Riochican and Casamayoran)

with high, narrow snouts and large, daggerlike teeth—impressive predators. In the Casamayoran, at least, and possibly also in the other faunas here in question there were also large, predatory, boa- or pythonlike snakes. Thus the abundant crop of herbivorous mammals did not lack predators.

The rocks of Casamayoran age that immediately overlie those of the Riochican at some localities in Patagonia are extraordinarily different from the Riochican rocks. They are almost entirely of volcanic origin, mostly volcanic ash, some, at least, of which was transported by running water after it fell. Much was also altered by groundwater or by weathering that converted it into an odd kind of rock that swells greatly and becomes soggy when wet. That is bentonite, named after Fort Benton, Montana, and its principal component is a clay mineral called montmorillonite, named for a locality in France. Throughout Casamayoran time and, as will later be recounted, for millions of years thereafter there was a series of tremendous volcanic explosions that covered thousands of square kilometers under deep deposits of ash.

In spite of that sensational volcanic activity, the region now known as Patagonia was habitable and was inhabited by great numbers of mammals and other animals. There is some, but scant, evidence of trees, but there must have been abundant vegetation as evidenced by the presence of great herds of many species of herbivores. The ash containing their remains accumulated on a vast plain, not far above sea level and with some streams and small lakes in which there were fishes, frogs, and crocodilians, including the formidable *Sebecus* that has been mentioned as already present in Riochican time. The climate in this part of southern South America must have been humid and warm, perhaps even more so than during the Riochican.

The known Casamayoran fauna has the same mammalian orders as the Riochican except for the Xenungulata, known from the Riochican only, and the Casamayoran and later Astrapotheria and Pyrotheria, not yet found in the Riochican although they must have existed then. The families, too, are largely the same. Apart from families of the unshared orders, only two families of notoungulates first appear in the known record for Casamayoran

time: Archaeopithecidae and Archaeohyracidae. The Archaeopithecidae were still quite primitive as notoungulates went and not markedly unlike some Riochican forms which nevertheless seem nearer to the ancestry of what eventually evolved into a quite distinctive family (Interatheriidae). The Archaeohyracidae, however, were more advanced than anything known in the Riochican. The crowns of their molar teeth were beginning to be higher than in earlier or than in other contemporaneous notoungulates. That represents an incipient change of herbivorous diet from browsing on relatively soft vegetation to grazing on grass or other harsh vegetation.

The predaceous carnivores were still all marsupials, as they would continue to be throughout most of the Cenozoic, and the mammalian carnivore-herbivore ratio was still low, but less so than in the known Riochican. There was also one big, already rather specialized marsupial carnivore, a borhyaenid, convergent toward doglike placental carnivores. This doubtless fierce creature, *Arminiheringia auceta* Ameghino, was at least as large as a robust Recent timber wolf. Convergent evolution had already made up for the imbalance of the absence of any placental carnivores in ancient South America. Among other marsupials, opossums are very rare in the Patagonian Casamayoran but must still have been present in some numbers elsewhere in South America. The strange polydolopids were at their height. They barely survived into the Deseadan and became extinct thereafter.

The Condylarthra were also at their height as far as the known record shows. They survived into the Friasian (middle Miocene), when they were already extinct elsewhere in the world, and they then became extinct as such also in South America—various of their early offshoots survive to the Recent as other ungulates and as the odd African aardvark. Litopterns were numerous but still quite primitive. Notoungulates dominated the fauna, with 7 families and 23 genera described from the Casamayoran by 1967. Others may occur in collections made since that date but not yet described in print. In the Casamayoran they were all relatively primitive and had not yet acquired characteristic divergent specializations that became prominent in later faunas. As previ-

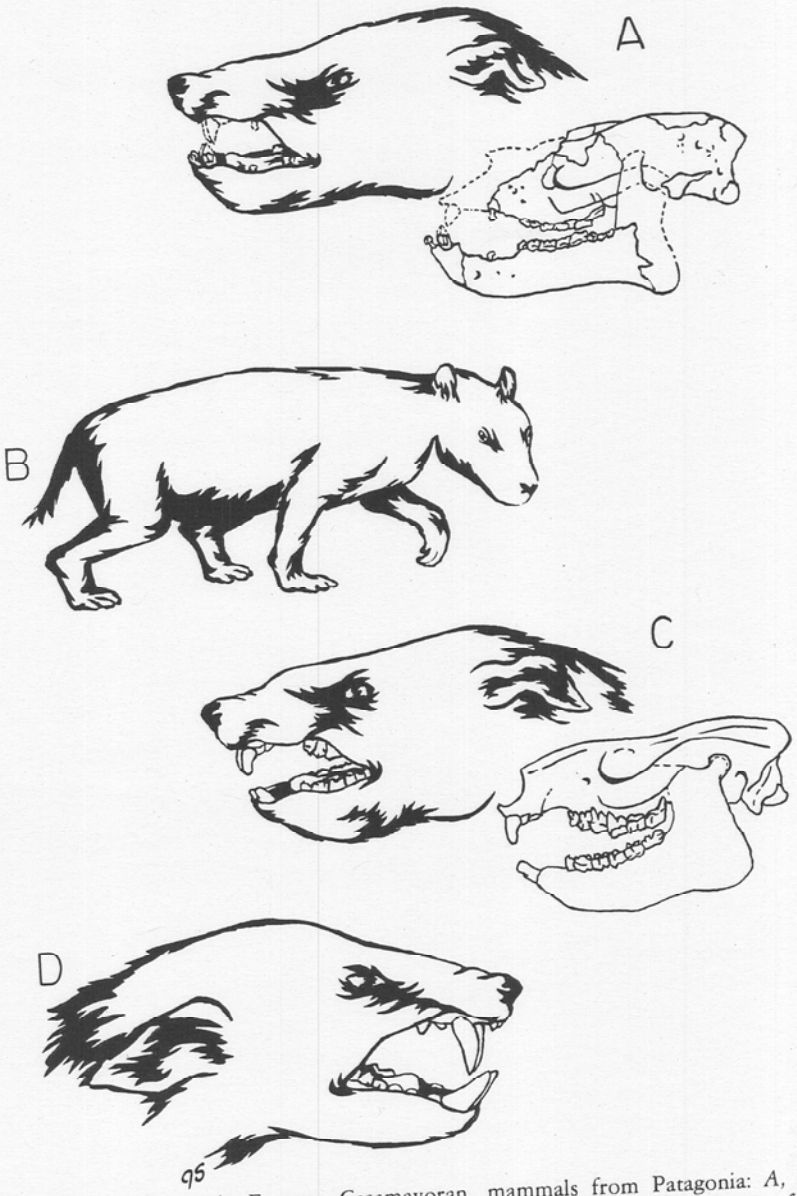

Fig. 6. Some early Eocene, Casamayoran, mammals from Patagonia: *A*, a trigonostylopid, *Trigonostylops*, skull and restoration of head; *B*, restoration of a primitive notoungulate, an isotemnid, *Thomashuxleya*; *C*, a slightly specialized notoungulate, a notostylopid, *Notostylops*, skull and restoration of head; *D*, a large, predaceous marsupial borhyaenid, *Arminiheringia*, restoration of head.

ously noted, the Casamayoran Archaeohyracidae do provide a partial exception to that generalization.

Among the Xenarthra, armadillos seem to be abundant in the Casamayoran. They are usually represented by isolated bony plates, which are so many on one individual that their abundance in collections doubtless gives an exaggerated impression of the abundance of the animals in the fauna. Nevertheless, a considerable part of the skeleton of one was found, and among other interesting things it revealed that this armadillo had enamel on its teeth. Enamel is totally absent on the teeth of all known later armadillos.

Volcanic activity similar to that of the Casamayoran continued through the Mustersan age, but there was some uplift of the Patagonian plains that led to post-Casamayoran erosion. The deposits with Mustersan fossils are consequently more patchy and local in Patagonia than those of the Casamayoran. The Mustersan fauna is somewhat less well known, but there are some recent collections not yet described. The lack of such warm-climate animals as crocodilians and boalike snakes and the relative scarcity of marsupials in the published collections have been taken to indicate that the climate had become somewhat cooler in central Patagonia latitudes, but that may be a chance effect of the smaller collections.

What we do know about the Mustersan shows us a mammalian fauna in transition. A now archaic polydolopid marsupial does occur here. The predaceous borhyaenids are present but rare, probably by luck of sampling. No condylarths are known in the Mustersan or thereafter in Argentina, but we know that they survived into the Miocene in tropical South America.

Among the still dominant notoungulates the primitive Henricosborniidae and Archaeopithecidae are not known after the Casamayoran and the also rather primitive Notostylopidae, Oldfieldthomasiidae, and Isotemnidae have become less common in the Mustersan. Among those, only the Isotemnidae, and they somewhat questionably, are reported in post-Mustersan faunas. The most striking change is that in two families of notoungulates, the Archaeohyracidae and the Notohippidae, the molar teeth have

become high-crowned. There is a definite trend toward teeth more of grazing type, a trend that later appeared also independently in some other notoungulates. At around this time there was perhaps an expansion of grasses and of grasslands in South America, but that is hypothetical. Certainly some of the old native ungulates were adapting to a coarser diet, one that wore down their grinding teeth more rapidly.

Among the Xenarthra, sloths and glyptodonts are first known from the Mustersan. They then already had their peculiar special characteristics and must have been evolving for some time. The most probable explanation for their apparent absence in the Riochican and Casamayoran and rarity in the Mustersan is that they were restricted to or most common in more tropical parts of the continent from which we have as yet few or no fossils of these ages. They eventually became abundant in Patagonia as well.

Here for the time being we will leave the faunal succession. In the next few chapters the histories of the South American old-timers, those whose ancestors formed the first faunal stratum, will be followed. Then in chapter 11 the faunal succession will be resumed with the introduction of the members of a second faunal stratum.

Added note: After this chapter was written but before it was in type the discovery of a rich sequence of late Paleocene and early Eocene mammalian faunas in the northern Argentinian provinces of Jujuy and Salta was announced. Descriptions of these faunas had not been published when the present book went to press.

References

The comments on the mammal-bearing strata are based mostly on my unpublished field notes and observations. Most of what is known about the three faunas here under consideration is given in the following two-volume memoir, which also gives citations to the numerous short papers on the Itaborai Riochican by Paula Couto.

Simpson, G. G. 1948, 1967. The beginning of the Age of Mammals in South America. *Bulletin of the American Museum of Natural History*, 91: 1–232, and 137: 1–260.

CHAPTER 7

Marsupials

Australia has long been known as the Land of Marsupials, but South America has also been a land of marsupials. The reason why the marsupials became especially numerous and varied on just these two continents is the same for both of them. In Australia there were, in all probability, no placental mammals in the early Cenozoic. The marsupials underwent an adaptive radiation that took them into many of the ecological niches or ways of life that were occupied by placentals on most other continents. Well along in the Cenozoic, placental rodents of the rat family, Muridae, did reach there. That may have inhibited convergent rodentlike evolution among the Australian marsupials, where only the wombats, not really ratlike, did become adaptively similar to some larger rodents elsewhere. The only native land placental other than the murids in Australia is the dingo, and it is almost certainly a feral form of semidomesticated dogs introduced by the aborigines. It was no coincidence that the so-called Tasmanian wolf, more distinctively called the thylacine, which is the most doglike marsupial in appearance and habits, became extinct on the continent of Australia when dingos became common there. A few thylacines did survive on the island of Tasmania and may still do so although none has been seen lately.

In South America, as has been noted, the early marsupials were accompanied by placentals, but the latter were limited to the strange xenarthrans and to numerous ungulates. Notably there were no placental insectivores, rodents, or carnivores, which were abundant in North America, Eurasia, and Africa. Thus, the marsupials here, too, had an adaptive radiation that led into many ways